Journal of Ethology
https://doi.org/10.1007/s10164-020-00650-6

VIDEO ARTICLE

Qualitative description of the submission and agonistic behavior of the Spix's Macaw (*Cyanopsitta spixii*, Spix 1824), with special reference to the displacement displays

Vladislav Marcuk[1] · Cromwell Purchase[1] · Donovan de Boer[1] · Marcellus Bürkle[2] · Katrin Scholtyssek[1]

Received: 20 September 2019 / Accepted: 23 April 2020

Abstract
The Spix's Macaw (*Cyanopsitta spixii*) represents one of the four avian taxa, in which its global population is entirely captively managed. The species was declared "extinct in the wild" after several attempts failed to rediscover any remaining individuals in the wild since 2000. As an integral part of the ongoing ex situ conservation efforts, a long-term ethological study was conducted at the ACTP facility to investigate the behavioral repertoire of the largest subpopulation of this species in captivity. In this paper we provide an illustrated comprehensive ethogram with detailed description of the submission, displacement and agonistic behavior. The agonistic behavior is categorized in two subcategories, where qualitative aspects for distinct behavior elements for the intimidatory and conflict behavior are given. In addition, displacement displays are described in detail for the first time for a species of the genera. In total, 35 distinct behavior elements of the agonistic, displacement and submission behavioral repertoire are covered. Digital video images related to the article are available at http://www.momo-p.com/index-e.html, movieid:momo200417sm05a, momo200416sm01a, momo200417sm06a, momo200416sm06a, momo200416sm04a, momo200417sm03a, momo200417sm02a, momo200416sm05a, momo200417sm04a, momo200416sm02a, momo200416sm03a, and momo200417sm01a.

Keywords Agonistic behavior · Ethogram · Displacement display · Spix's macaw · Submission behavior · Extinct in the wild

Introduction

The Spix's macaw (*Cyanopsitta spixii*) was named after Johann Baptista von Spix, who collected the first specimen in Bahia state, north-eastern Brazil in 1819. The Spix's Macaw (*Cyanopsitta spixii*) is one of the world's rarest psittacines, whose entire known population is captively managed since repeated attempts failed to relocate the last remaining wild individual in 2000; the Spix's macaw is, therefore, classified as extinct in the wild (Butchart et al. 2018; Birdlife International 2020).

Many parrot species face an increased risk of extinction—threatened by anthropogenic and natural impacts, like the ongoing degradation of native habitats, rapid deforestation, invasive predators, devastating natural catastrophes and excessive pet trade (Berkunsky et al. 2017; Birdlife International 2020). Coordinated in situ and ex situ conservation measures became an essential part of the long-term conservation strategy for certain species. The Spix's macaw is a flagship project for these coordinated captive conservation measures. This species had to cope with many obstacles to get to the point where a release is possible. Captive breeding was slow and fertility low (Purchase 2018). Many new avenues needed to be researched and implemented to secure a viable breeding population.

Factors like microscopic egg development analysis, reproductive and stress hormone research, artificial insemination (Fischer et al. 2014) where unrepresented birds could have their genetics incorporated into the population, the management of diseases like PDD (Proventricular dilatation disease) in the population and genome sequencing,

✉ Vladislav Marcuk
vladislav.marcuk@googlemail.com

[1] Association for the Conservation of Threatened Parrots e. V., Hindenburgstraße 37, Hannover, Germany

[2] Tierarztpraxis Dr. Bürkle, Eisenbahnstraße 32, 77855 Achern, Germany

Published online: 03 June 2020

that fundamentally improved the genetic compatibility in pairings, and contributed to a steady increase of the captive population from a former world population of 53 individuals in 2000 to a current population of 168 individuals (Fischer et al. 2014; Purchase 2018; unpublished data). Historically pairing options were often difficult with birds held at facilities around the world.

With the importation of the former Al Wabra Wildlife Preservation (AWWP) population from Qatar in 2018 to the Association of the Conservation of Threatened Parrots (ACTP) in Germany, the majority of all existing individuals are now managed in Germany, making it easier to match up pairs with differing genetics. In addition, the remaining individuals are kept for exhibition or for ex situ breeding in Pairi Daiza (Belgium), Jurong Birdpark (Singapore) and Fazenda Cachoeira (Brazil) (Purchase 2018). Furthermore, in 2019, further steps were made towards the reintroduction of this species in its former habitat, in the Caatinga, north-eastern Brazil by the construction of a state-of-the-art facility and the shipment of 52 individuals by March 2020 to Brazil (ACTP 2020), including the establishment of conservation measures and plans for the reintroduction of the species by 2021 (ACTP 2020). These steps compliment the in situ habitat restoration and community involvement techniques of the past 20 years.

For the post reintroduction period, knowledge of ethology, breeding biology and social communication could be essentially helpful to ensure adequate monitoring of the species and assist the establishment of the birds in their native range. However, information about the behavior of this species is limited and the single behavioral elements of the social, sexual, agonistic, submissive and displacement behavior are virtually unknown. Herewith, we provide as a part of the ethology study the first comprehensive description of the single behavioral elements associated with the aggression and territorial behavior (agonistic, submission and displacement) behavior repertoire.

Study site

This study was conducted at the breeding center of the Association for the Conservation of Threatened Parrots (ACTP e. V.) in Brandenburg, Germany. The facility is partitioned in different sectors, where all individuals of the subpopulation are organized either in flocks or formed breeding pairs. Pairs are maintained in several breeding complexes. The breeding complex has up to 14 equal-sized aviaries. Each aviary consists of a heated, indoor enclosure (5 × 2 × 2 m; LBH) that includes two from the indoor floor accessible feeding tables, an individual constellation of perches and an inverse L-form shaped nest box. Visual barriers are attached to the feeding stations to minimize the inter-pair distraction. The outdoor enclosure (16 × 2 × 3 m; LBH) has a selection of natural vegetation, elements of environmental enrichment and several vertical/horizontal perches. The main perches are arranged only at the beginning and end of each outside enclosure to ensure the availability of the maximum flight area.

The flocking aviaries are assembled in smaller clusters and the size of the aviaries differs accordingly to the size of the flock. The two largest study groups are kept in two large, free-flight aviaries. The indoor enclosure of the free-flight aviary is partly divided into four compartments, where each compartment contains a separate feeding station to minimize the likelihood of food competition. The outside free-flight enclosure is connected to all indoor compartments and have a size of 20 × 10 × 4 m. In addition, this aviary includes a variety of plants, perch sites and modulated environment. The smaller flocks are kept in post-weaning or free-mate choice aviaries, which are double in size of a breeding aviary. Each smaller flock consists up to six birds. An artificial raining system is implemented in all outside enclosures and is operated opportunistic.

Materials and methods

To prevent additional disturbance to the study groups, which could result in overtly aberrant behavior, non-invasive observations were conducted using camera systems (Vicon V988D-W311MIR Dome Camera) implemented in every indoor enclosure. The cameras allowed the monitoring of behavior patterns, for a period of several consecutive days without interruptions. Archive recordings were stored on an external server for a period of at least 28 days. In addition, anecdotal observations were made during different maintenance and husbandry activities (feeding, cage cleaning, implementation of enrichment). Archived recordings were analyzed with the DVR System video player (v. 1.21) or iPIMS (v. 1.5.4.28). Specific behavior sequences were extracted and saved in AVI or MP4 format for a more detailed time-frame analysis. For the time-frame analysis, Avidemux (v. 2.7.4) was used.

In total, 108 individuals were included in the study period, including four study groups and 29 breeding pairs. The two larger study groups were organized into two mixed flocks of 18 and 21 individuals, respectively. Birds in these two study groups were between one and five years old. The two smaller study groups consist of five and six immature (age < 1 year) individuals. The observation period lasted from 6:00 am (shortly after visible activity was detected) to 7:00 pm (until last activities were recorded). Each breeding pair were observed for a total period of 4 weeks during the pre-egg laying period. Flocking birds were observed for prolonged periods over the year to collect data of agonistic interactions. In total, $n = 411$ socio-negative interactions

were documented during the study period to record the frequencies of single agonistic and submissive behavior elements. All four study groups were observed for a minimum period of 2 months. For anecdotal observation, most individuals ($n = 148$) regardless of age or demography were considered for the ethogram. All observed behavior elements are listed in the Table 1, including a description of the observed ethological pattern.

Statistical analysis

Whenever applicable, a duration was recorded for assorted behavior elements and is provided in form of the mean size ± standard derivation, range (represented by the abbreviation *r*) and documented sample size (*n*). For the total number of socio-negative interactions, the absolute number of observations and the observed frequency (*f*) is given.

For specific behavior patterns, a comparative analysis was performed to investigate the possible presence of differences between genders. For gender-related differences, a Mann–Whitney U test was conducted (*z*-score as the statistical variable; $p < 0.01$). The descriptive statistics and statistical analyses were performed using R (version 3.6.2).

Results

Agonistic behavior

This species shows a considerable diversity in their agonistic intra- and interspecific behavior. Aggression between members of a flock are exceptionally rare and often associated with conflicts established near feeding sites (e. g., food competition) and favorite perch sites or random socio-negative interaction; like communal congregation at the roosting site (e.g., unexpected approach and spatial competition). Socio-negative intraspecific interactions are usually short in duration; with an average duration of 4.33 ± 3.91 s ($r = 0.88$–25.46; $n = 70$), and rarely have a visible attack intention.

Hereinafter, the agonistic behavior repertoire is divided in two subcategories. Whereas, the first subcategory (intimidatory behavior) aims to:

1. Warn or imitate an outgoing risk from a physical encounter using audio-visual displays
2. Enforce a quick retreat of the opponent to prevent the necessity of a physical conflict

Behavior elements of this subcategory often show a decreased attack motivation and are given in response to low-intensity or mild aggression.

The second category (conflict or defense behavior) describes all forms of agonistic behavior that are involved during direct socio-negative, physical interactions. This subcategory presupposes a higher aggression potential. Most behavior elements from this subcategory show a visible attack intention and increased likelihood of follow-up aggression.

Intimidatory behavior (subcategory I)

1.11 Neck and head feather raise Most common intimidatory display (397 of 411 observed socio-negative interactions; $f = 0.966$), presented as an optical signal towards the opponent to insinuate a larger body volume and outgoing risk of possible physical confrontation.

1.12 Foot lift (Fig. 1c, as shown in video Fig. 3a http://www.momo-p.com/showdetail-e.php?movieid=momo200417sm05a*)* Usually, a low-intense socio-negative interaction which is also used often (168 of 411 observed socio-negative interactions; $f = 0.408$) as defense posture for aggression avoidance (short in duration, approximately 1–2 s).

*1.13 Bill gape (*Fig. 1a*, as shown in video* Fig. 3a http://www.momo-p.com/showdetail-e.php?movieid=momo200417sm05a*)* Frequent observed auto-defense behavioral element (observed in 327 of 411 documented conflicts; $f = 0.796$). If aggressor moves towards opponent, it increases the likelihood that opponent will retreat. If opponent responds vice versa or with more intense aggression, aggressions of higher intensity are likely to follow.

1.14 Wing-raise display (Fig. 2a–c, as shown in video Fig. 3b http://www.momo-p.com/showdetail-e.php?movieid=momo200416sm01a*)* Rare form of intimidatory display, used in both, intra- and interspecific territorial displays (latter more common; 14 vs. 83 observations). Display can be subdivided into three distinct escalation stages. The first stage (Fig. 2a) is less intense and characterized by a degraded form of this display, where the performing bird slowly slides toward the opponent with carpal joints held away from body and wings are partly unfolded. If intruder refuses to retreat, territory affiliated bird initiates the second stage (Fig. 2b) by holding out fully extended wings, with neck and head feathers raised and the bill wide opened pointed, while quickly moving in its direction. The third escalation category (Fig. 2c) combines the above-described elements, which are accompanied by eye-blazing and territorial calls. Wings are unfolded and folded in quick succession. The third stage is associated with an increased risk of a physical confrontation. Display was more frequently observed during the breeding season.

1.15 Lunge (Fig. 1b) Thrusts or lunges usually with closed bill towards opponents' head, leg or upper body parts with a clearly visible mock bite display (in 144 of 411 observed conflicts; $f = 0.35$). Opponent responds equally or

Table 1 List of all observed behavior elements of the agonistic, displacement and submission behavioral repertoire of the Spix's Macaw (*Cyanopsitta spixii*)

Behavior elements	Description of the observed behavioral intention
Intimidatory behavior	
1.1.1 Neck and head feather raise	Feathers of the head, neck, wings and back are raised
1.1.2 Foot lift	A slow, usually sideward directed presentation of one leg, with front toe pointed out towards the opponent, in wave-like motion
1.1.3 Bill gape	Wide opened bill presented towards the opponent or aggressor, usually with an evident mock bite display
1.1.4 Wing-raise display	Bilateral wing-unfolding either partly or fully with opened bill, facing the opponent
1.1.5 Lunge	Thrusts or lunges usually with closed bill towards opponents' head, leg or upper body parts with a clearly visible mock bite display
Conflict behavior	
1.2.1 Bite	Aggressor directs bill wide opened toward the head, leg or upper body regions of the opponent or targets the nearest body point
1.2.2 Bill fence	Reciprocal bill thrusting, where aggressor lunges or thrusts towards opponent's head and opponent responds vice versa
1.2.3 Claw	Physical socio-negative interaction involving the claw, where either the aggressor pushes one leg against opponents' upper body or reciprocal clawing occurs
1.2.4 Rush	Aggressor walks rapidly, with wide open bill, in the direction of the opponent
1.2.5 Flying approach	Aggressor lands directly on or a few centimeters away from opponent
1.2.6 Flight attack	Aggressor attacks subordinate in flight with wide open bill and both claws directed usually to opponent's head
1.2.7 Fight	Physical encounter with high-intensity aggression involving two opponents with majority of the above-described forms of physical socio-negative interactions
1.2.8 Redirected aggression	Redirection of mild- to high-intensity aggression from dominant partner to subordinate mate, when the potential intruder is unreachable
Displacement behavior	
2.1 Displacement preen	Exaggerated preening movement with a noticeable overexcitement in the form of alternating head shakes that intersperse the preening act
2.2 Displacement food intake	Forcefully executed, partial intake of a randomly chosen food item in front of an intruder
2.3 Displacement rub	Pretended beak rubbing demonstrated as a part of a territorial display, performed in an exaggerated way, with beak rubbed on a solid surface in all available directions
2.4 Displacement head scratch	Rapid, alternating movement of the upper claws that in common form intents to remove foreign matter from head and neck region
2.5 Displacement hold bite	Redirected vigorous bite on a perch or other solid surface used for distraction during territorial encounter
2.6 Displacement head-down shake	Degraded or partly executed head shake, usually performed to one side
2.7 Displacement yawn	Identical to the common form; an extension of upper and lower beak under maximal contraction of the mandibular muscles; with head slightly withdrawn back
2.8 Displacement allo-preen	Pseudo socio-positive interaction where one individual starts to allo-preen another individual during territorial encounter
2.9 Displacement mutual feed	Pseudo mutual feeding initiated without evident passing pre-digested food from donor to acceptor
2.10 Irritated body shake	Exalted version of the ordinary body shake, execution accelerated and accomplished by combined eye-blazing and jerking
2.11 Bill clasp	Short convergent interlock of the beaks of two individuals
Submission behavior	
3.1 Turn away	Aggression avoidance by turning away from aggressor without a body disposition
3.2 Slide away	Recede from aggressor by moving or flying away with active body disposition
3.3 Alert-and-fear reaction	Body axis arranged nearly vertically along the perch, the individual remains motionless with eyes wide open and plumage sleeked
3.4 Apparent death display	Auto-defence display used by chicks during the post-natal period as an anti-predatory strategy that feigns muscular rigidity and post-mortal motionless
3.5 Bob	Cyclic repetition of head downward jerk, following a jerk in opposite direction
3.6 Head-tilt solidarity display	Head moved to one side, slowly withdrawn and tilted backwards, following an oscillation to the other side in wave-like motion

Table 1 (continued)

Behavior elements	Description of the observed behavioral intention
3.7 Crouch-quiver solidarity display; after Serpell (1979)	Subordinate assume in a hunched posture accompanied by alternating wing quiver, interspersed eventually with head shakes and submissive calls
3.8 Upside-down lift solidarity display	Performing individual climb on the roof of an aviary or in the canopy of a small tree or bush, lifts body axis hanging either with one leg or both legs on the mesh or on a twig. Legs are moved under the wing over the head
3.9 Peer	Mutual convergent head downward jerk, with one head side directed towards source of disturbance
3.10 Unison jerk	Polyfunctional, highly synchronized display given in unison by a pair or social unit with an initial vertical extension of the body axis, habitually accomplished by a partly wing unfold and high-pitched call in unison
3.11 Singleton jerk	Identical to 3.10, thus performed only by a single bird

Table 2 Comparison of quantitative characteristics of displacement displays and submission postures of this study and the study conducted on the *Trichoglossus* genus (Serpell 1979)

Behavior elements	This study	*Trichoglossus* spp. (Serpell 1979)
Displacement rub	2–3 Strikes to one side. Single strike duration c. 0.3–0.4 s	1–2 Strikes to one side. Duration of single strike c. 0.5 s
Displacement head scratch	In av. 0.51 s ($r=0.19$–0.75; $n=25$)	0.2–0.7 s
Bob	In av. 1.22 s ($r=0.81$–1.92; $n=72$)	In av. 1.5 s
Crouch-quiver solidarity display	Frequency male in av. 0.59 s/quiver ($r=0.37$–0.88; $n=90$) Frequency female in av. 0.59 s/beat ($r=0.38$–0.92; $n=120$)	No quantitative records
Head-tilt solidarity display	In av. 0.94 s ($r=0.7$–1.25; $n=60$)	In av. 2 s[a]

[a]Head tilt was compared with the crane-peering due to visual similarities

retreats by turning or moving away from aggressor. Conflict potential is considerably low, clawing or bill fencing likely follows if aggression persists.

Conflict behavior (subcategory II)

1.2.1 Bite Describes a middle-intensity form of aggression, where an attack readiness is apparent (in 69 of 411 observed conflicts; $f=0.167$). If opponent does not retreat, follow-up aggression in the form of bill fencing or clawing is likely. In rare occasions, the aggressor starts flight-chasing the opponent.

1.2.2 Bill fence Usually interspersed with mild- to middle-intensity aggression between two opponents, like bill thrusting, biting or foot lifting. If receipt is unwilling to retreat, aggressor starts to thrust the beak rapidly, predominately toward opponents' bill or head. If upper body parts are closer, it will bite those parts. Recipient is required to respond vice versa. Bill fencing between pairs are short in duration, with quick de-escalation after c. 1.5–4 s.

1.2.3 Claw (Fig. 4a) Middle-intensity aggression between two birds, which are perched in close proximity to each other. Aggressor usually turns toward opponent and pushes one leg against opponent's upper body parts, preferably wing, in wave-like motion with claws pointed out on it. If opponent responds vice versa, likelihood increases that conflict intensifies (with legs of opponent and aggressor engaging, with biting or bill fencing to follow). Often observed in redirected aggression. If opponent loses balance, it will fly away to land nearby; usually assuming a submissive posture.

1.2.4 Rush Middle-intensity form of aggression, where aggressor walks in direction of the opponent, who will usually immediately retreat or abandon the perch site. Rarely observed in flocks of immature birds, and uncommon in intra-pair conflicts (in 38 of 411 observed conflicts; $f=0.09$).

1.2.5 Flight-approach (Fig. 4b) Defined as high-intensity aggression, where the aggressor intends to enforce an immediate retreat of the opponent by landing directly on or in close proximity to it. If aggressor directly approaches, opponents always retreat, by flying away or falling from the perch. Aggressor will likely continue aggressions and attack the fleeing opponent, which will assume a submissive posture. Supplantation by flight is the highest intensity aggression observed in immature flocks (56 of 411; $f=0.13$).

1.2.6 Flight attack (Fig. 4c) High-intensity aggression that precedes biting, lunging or bill fencing. However, this conflict behavior is extraordinary rare and was observed only five times during the study period involving paired individuals ($n=411$; $f=0.012$) and required immediate intervention as a preventable measurement to eliminate the risk of injuries. Birds were required to be temporarily or permanently

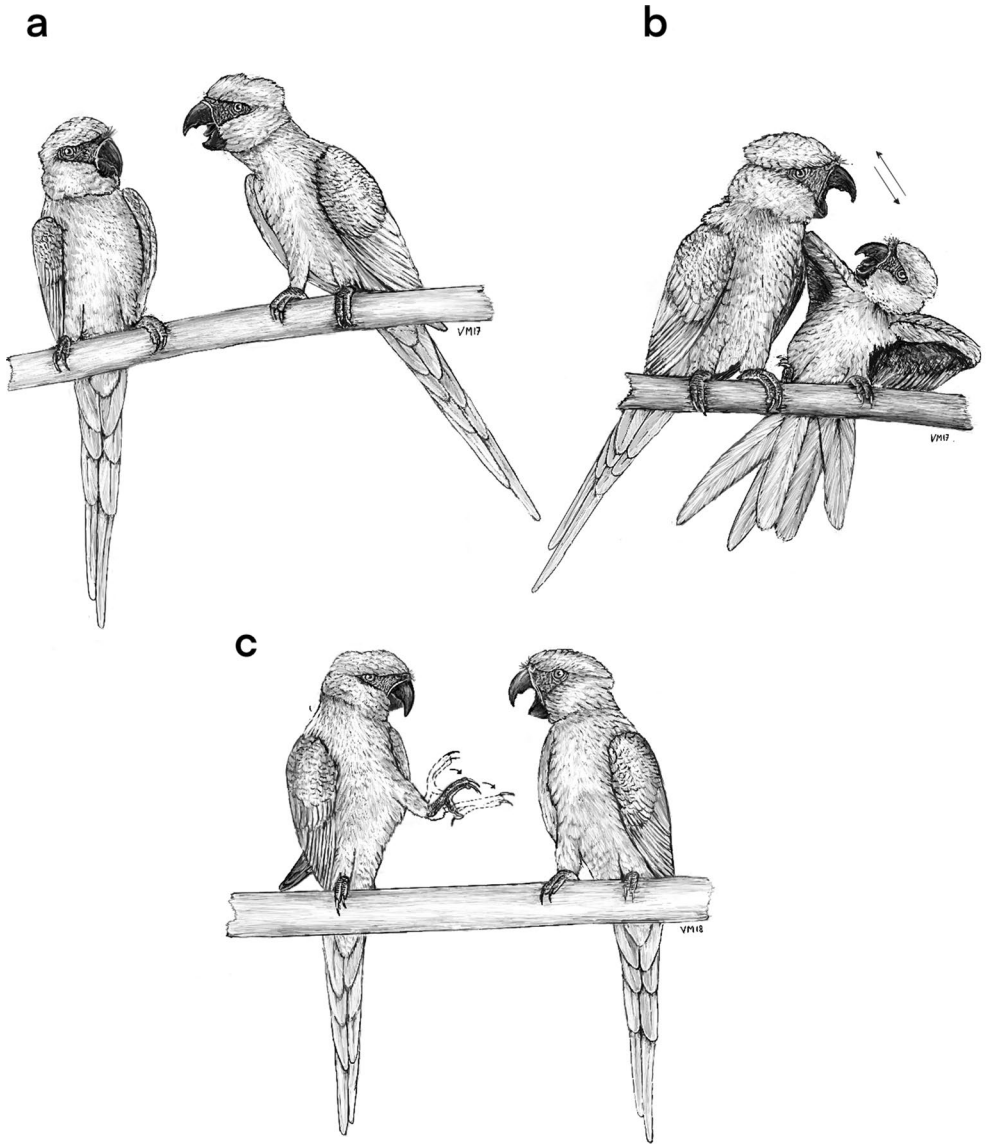

Fig. 1 **a** Bill gape, **b** lunge, **c** foot lift. All illustrations by Vladislav Marcuk

separated. If the aggressor attacks the opponent in flight with pointed out claws and gaped bill directed toward opponent's head, the opponent will assume a defense posture or in the event of a physical confrontation will fall from the perch. If aggressor is unsuccessful, there will usually be a repeated attempt. If opponent should fall, aggressor will continue attacking the opponent on the ground. Antecedent of a fight (see 1.2.7).

1.2.7 Fight (Fig. 4d) Most intense form of interspecific aggression where both combatants are engaged in a vigorous physical fight which involves most of the above-described behavior elements of the conflict behavior. During fight, the aggressor will use flying attack, bite, claw and other high-intensity forms of aggression, usually directed to the opponent's head. The outcome of a fight usually results in a life-threating injury if subordinate is unable to retreat. High mortality rates are recorded due to combined, multiple injuries of the head, beak and toes. Mate trauma is extremely rare (observed only three times during study period; $f = 0.007$). Weak or birds with progressive health issues are more likely to be a victim of high-intensity socio-negative interactions.

1.2.8 Redirected aggression Observed in bonded pairs only. When the dominant bird is unable to reach a potential intruder (for example, avian keeper), it redirects aggression towards mate. Escalation in redirected aggression is often unpredictable and not limited to low-intensity aggression but can escalate to serious physical encounters. Confrontations are usually short, as subordinate bird immediately retreats.

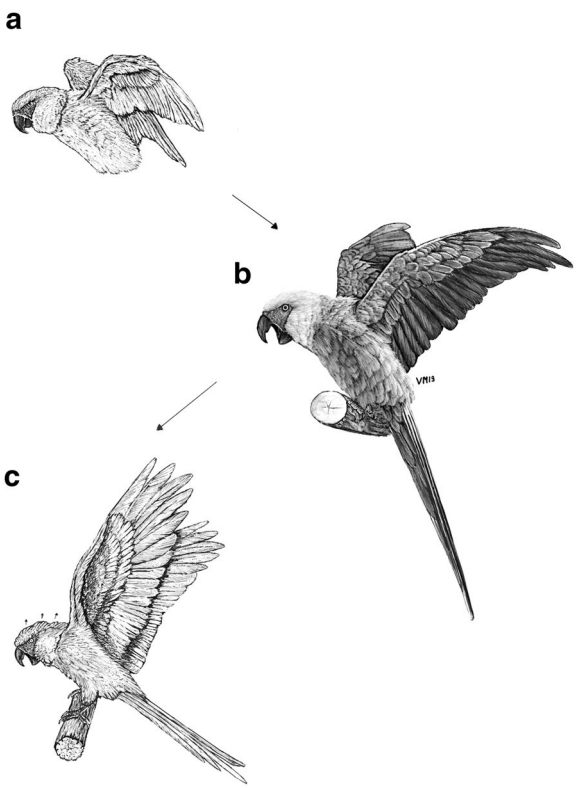

Fig. 2 Illustration of the different escalation stages of the wing-raise display **a** escalation stage I, **b** escalation stage II, **c** escalation stage III

Displacement displays

Spix's macaws evolved a broad spectrum of different displacement displays that can be consistent in structural form and execution to behavior elements of other, non-agonistic behavior categories.

2.1 Displacement preen (Fig. 5a, as shown in video Fig. 7c http://www.momo-p.com/showdetail-e.php?movieid=momo200416sm04a*)* Performed in situations of mild disturbance or as a part of a territorial display, usually observed when new birds are added to a flocking aviary or during a forced-mating attempt. It is always accompanied with high-pitched calls and eye-blazing. Four subtypes of displacement preening were documented: displacement bell preening, displacement wing, touch foot and back preening. The displacement bell preening was the most common type (see Fig. 5a; 43 of 84 total observations; 51.12%;), following the displacement back preening (22.61%), displacement touch foot (15.47%) and displacement wing preening (10.71%). Associated and preceded sometimes by other displacement displays, like irritated body shake or displacement rub, or submissive behavior elements (e.g. jerking).

2.2 Displacement food intake (Fig. 5b, as shown in Fig. 7a http://www.momo-p.com/showdetail-e.php?movieid=momo200417sm06a*)* Observed most common during interspecific territorial defense. Performing bird will usually vigorously bite on a randomly chosen food item with raised neck and head feathers. In extreme cases, it is accompanied

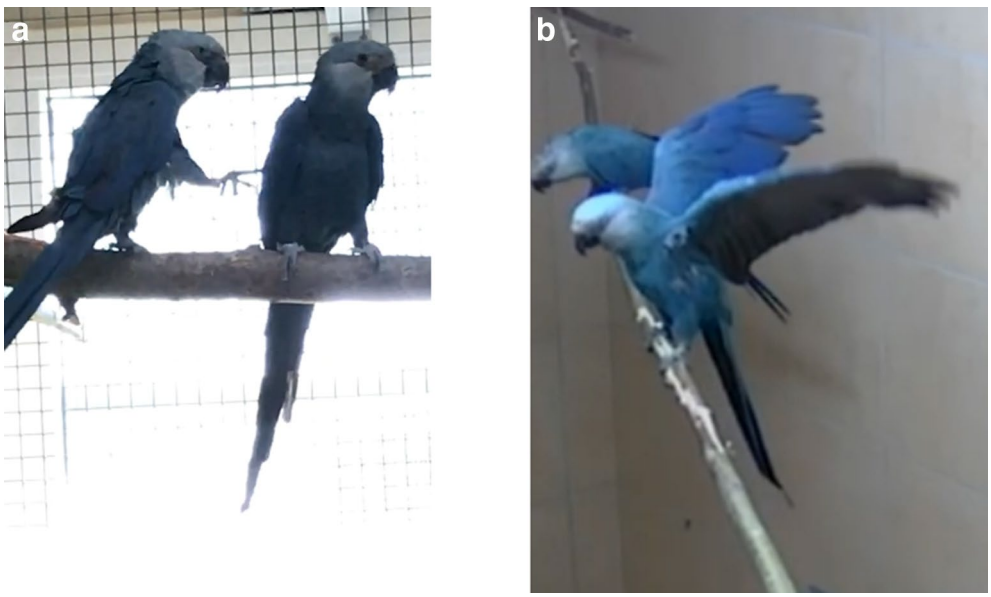

Fig. 3 **a** Video sequence of socio-negative interacting involving bill gape and foot lift in a flock http://www.momo-p.com/showdetail-e.php?movieid=momo200417sm05a. **b** Male performing the wing-raise display http://www.momo-p.com/showdetail-e.php?movieid=momo200416sm01a

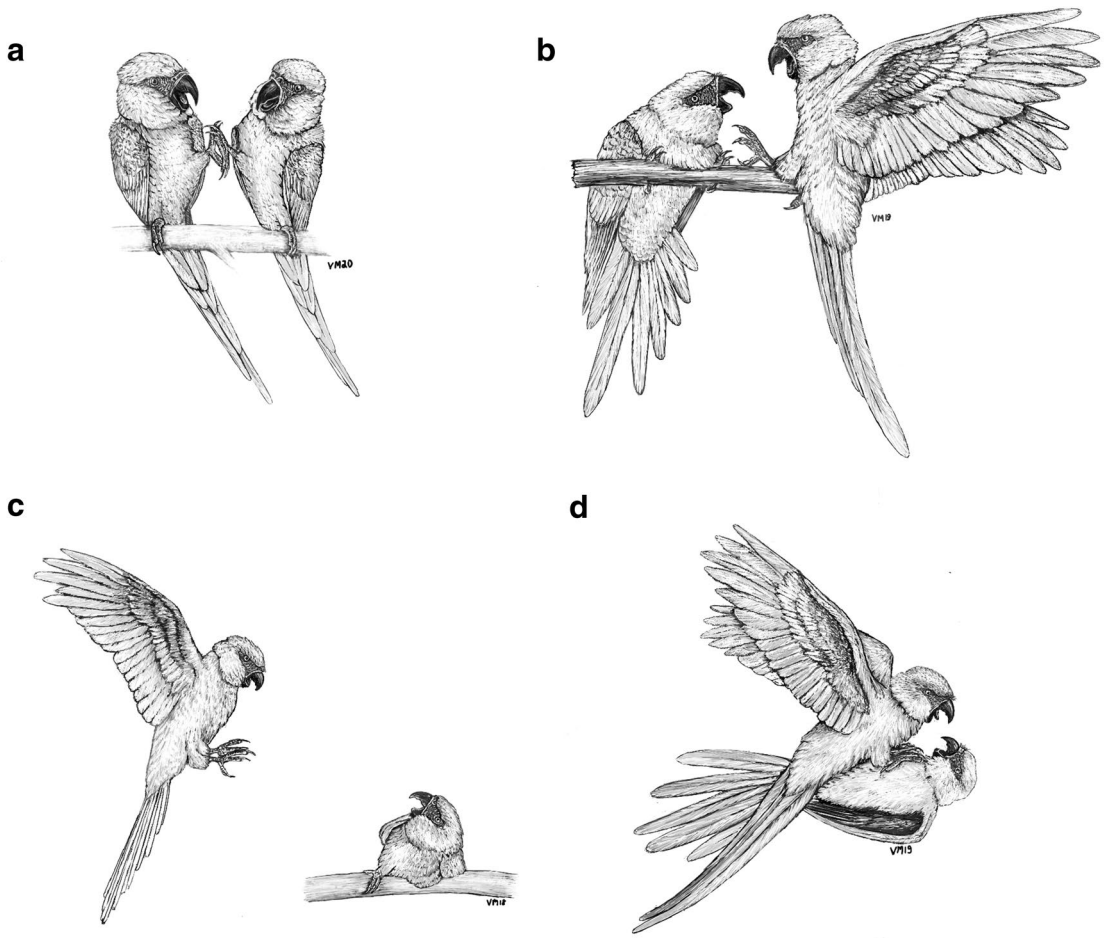

Fig. 4 **a** Claw, **b** flight approach, **c** flight attack, **d** fight

by eye-blazing or territorial calls. The food item will usually be crushed or only partly eaten. This display is performed close to the feeding bowl in front of an intruder.

2.3 Displacement rub (Fig. 5c) Pretended beak rubbing demonstrated as a part of a territorial display, performed in an exaggerated way, with beak rubbed on a solid surface in all available directions (on average 2 shakes to one side, duration c. 0.3–0.4 s). Neck and head feathers are raised, display performed solely or accompanied by other displacement behaviors like displacement hold-biting.

2.4 Displacement head scratch (as shown in video Fig. 7c counter time 00:02–00.06 http://www.momo-p.com/showdetail-e.php?movieid=momo200416sm04a*)* Identical to the normal maintenance behavior but performed with ruffled plumage and in another functional context. Usually slower than ordinary head scratch, duration 0.51 ± 0.16 s ($r = 0.19$–0.75; $n = 25$). Associated with displacement preening or displacement rubbing.

2.5 Displacement hold bite (Fig. 5d) Part of a territorial display, was not observed in younger birds (< 2 years). Performed more frequently (65 of 78 total observations) by males. Hold bite is usually directed toward a solid surface, like mesh or a perch and normally lasts between 1 and 3 s. Performing individual will chew or move head while beak remains fixed on target surface. If disturbance persists, it will redirect hold bite or attack intruder. Display can be accompanied by territorial calls, with head and neck feathers raised.

2.6 Displacement head-down shake (Fig. 6a) Given in response to mild disturbance, which is shorter in duration; 0.28 ± 0.06 s ($r = 0.20$–0.38; $n = 15$) and performed more vertically than sideward directed. Habitually not performed bilateral, normally executed to only one side.

2.7 Displacement yawn (Fig. 6b, as shown in video Fig. 7b http://www.momo-p.com/showdetail-e.php?movieid=momo200416sm06a*)* Identical in execution to the yawning performed usually after a prolonged period of inactivity or in response to thermal stress (e.g., cold). Observed frequently in force-mate attempts or in response of mild disturbance (duration c. 2.5–3.5 s).

2.8 Displacement allo-preen (as shown in Fig. 9a http://www.momo-p.com/showdetail-e.php?movieid=momo200417sm02a*)* Exceptionally rare display, seen in members

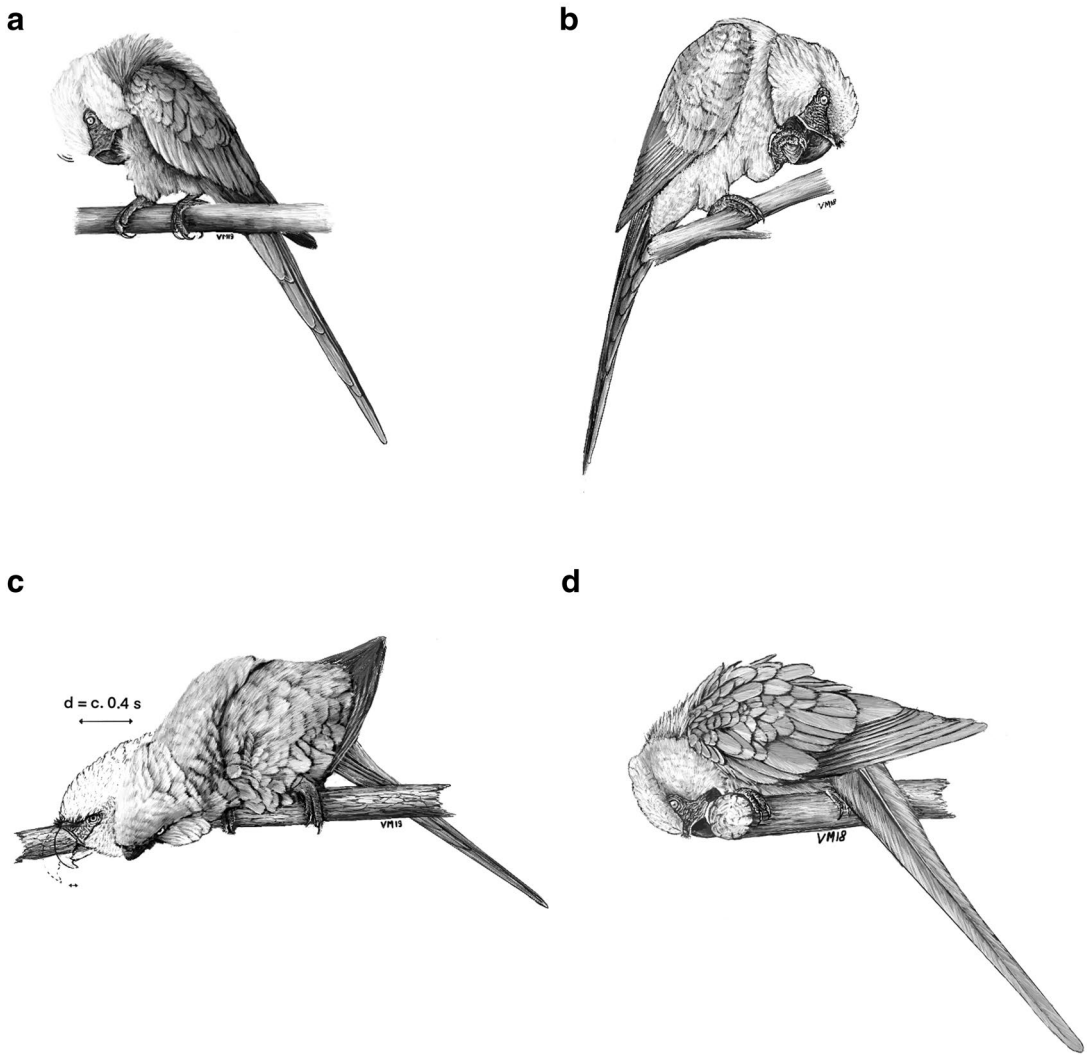

Fig. 5 **a** Displacement preening, **b** displacement food intake, **c** displacement rub, **d** displacement hold bite

of a pair exposed to physical stress (e.g., post-catching) or during a territorial encounter to convey the impressions of a strong cohesion between the pair to the intruder. Can be initiated by both genders but more likely by the female. Reciprocal displacement preening was not observed during study period.

2.9 Displacement mutual feed (Fig. 6d, as shown in video Fig. 7c counter time 00:09–00:14 http://www.momo-p.com/showdetail-e.php?movieid=momo200417sm03a*)* Extremely rare, with visible differences from sexual behavior associated mutual feeding. Normally initiated by the acceptor (commonly the female, while a mutual feeding is initiated by the donor). Observed only between members of a pair, usually close to an intruder. Function probably equivalent to the displacement copulation of *Anodorhynchus* spp. Interspersed with bill-clasping and sometimes mild intraspecific aggression, female/acceptor usually grasps the lower beak of the male/donor, forcing both beaks to interlock and stimulate a feeding response. Male/Donor starts to simulate mutual feeding by performing multiple head bobs (c. 0.2 s per head bob, $n = 25$), without passing pre-digested food to the female/acceptor. Behavior is accompanied by eye-blazing and territorial calls.

2.10 Irritated body shake (Fig. 8a, as shown in Fig. 9b http://www.momo-p.com/showdetail-e.php?movieid=momo200416sm05a*)* Given in response to mild disturbance, frequently observed in force-mate attempts (in $n = 49$ of 70 attempts). Duration in average 2.15 ± 0.30 s ($r = 1.53$–2.63 s; $n = 25$). A displacement display that is found in the behavioral repertoire of immature or adult birds as a reaction to a potential threat or mild disturbance.

2.11 Bill clasp (Fig. 6c) Interspecific display performed by two birds which are part of a social unit (also occurs in

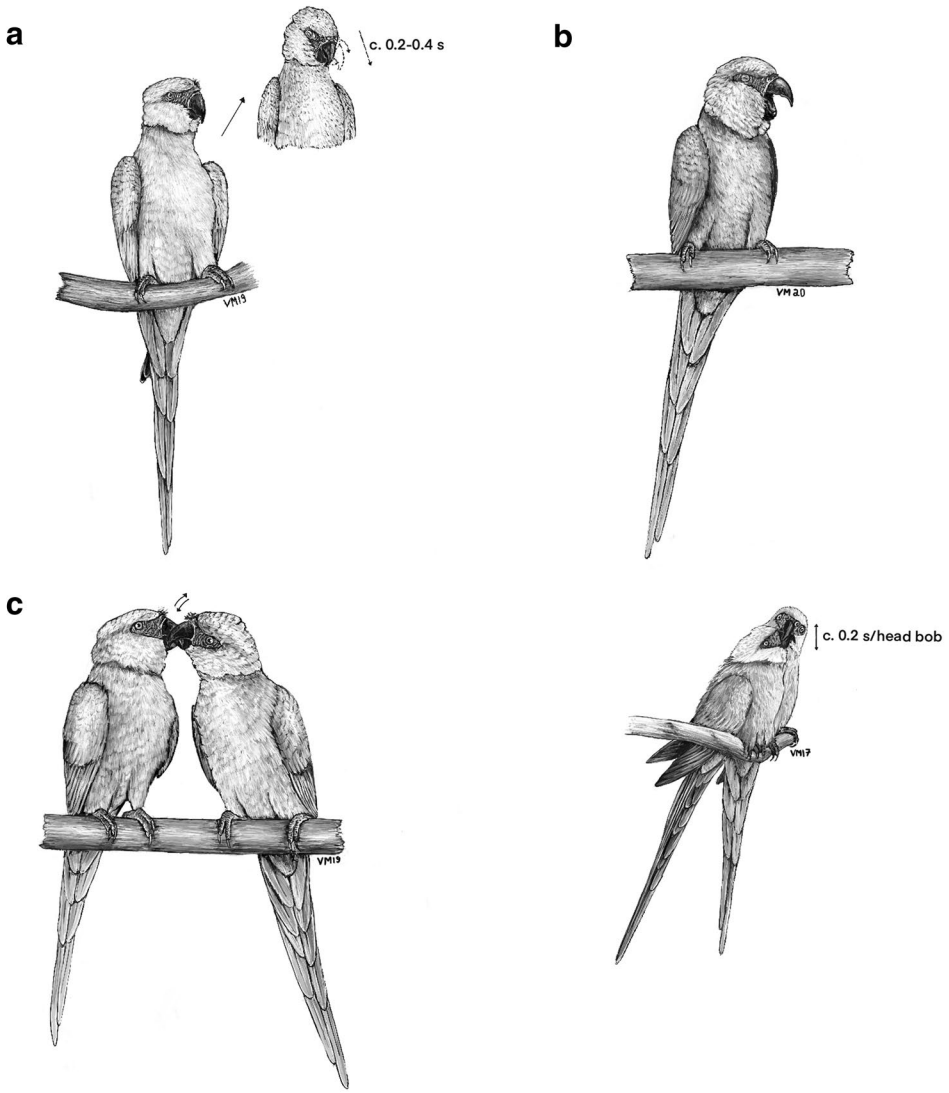

Fig. 6 **a** Displacement head-down shake, **b** displacement yawn, **c** bill clasp **d** displacement mutual feed

same-sex pairings). Both birds start almost simultaneously to grab the beak of the partner, interlock them, push and twist them shortly, using their body mass and follow-back to the initial posture. Sometimes repeated multiple times, with association with mild aggression.

Submission behavior

3.1 Turn away Active form of aggression avoidance or de-escalation. Follow-up aggression is unusual unless intense aggression occurred before. Forms with the behavior element slide away (see 3.2) the most common form of aggression avoidance (observed in 244 of 411; $f = 0.59$).

3.2 Slide away Bird moves away from aggressor to increase the inter-individual distance and decrease likelihood of a physical encounter. Most common form of aggression avoidance (in 391 of 411 conflicts; $f = 0.95$).

3.3 Alert-and-fear display Given in response to a potential threat. During the display, the carpal joints slightly raised and held away from body—to ensure a quick retreat in flight. Alert posture rarely accompanied by submissive calls. If threat retreats, birds gradually start to show normal activity. If risk or threat persists, bird will retreat in flight and emit alert calls. Birds nearby will show similar reaction, even without a visual contact to the source of disturbance.

3.4 Apparent death display (Fig. 8c) Anti-predator display observed in young birds during mid or late post-natal period. Can occur if individual is exposed to physical stress (e.g., catching attempt) or are threatened by sudden approach of a potential predator. Display connotes a muscular rigidity, as performing bird will fall on the back, with legs, tail, head and wings remaining completely motionless. In addition, the respiratory rate is reduced slightly.

Fig. 7 **a** displacement food intake demonstrated by a male and accompanied by a singleton jerk http://www.momo-p.com/showdetail-e.php?movieid=momo200417sm06a, **b** displacement yawn http://www.momo-p.com/showdetail-e.php?movieid=momo200416sm06a and **c** displacement preening performed by a male http://www.momo-p.com/showdetail-e.php?movieid=momo200416sm04a, **d** displacement scratching (00:02–00:06) and displacement mutual feed (00:09–00:14) performed by pair in response to mild disturbance http://www.momo-p.com/showdetail-e.php?movieid=momo200417sm03a

3.5 Bob (Fig. 8b, as shown in video Fig. 9c http://www.momo-p.com/showdetail-e.php?movieid=momo200417sm04a*)* Observed predominately in younger birds. Individual jerks with a rather small amplitude (~ 15 cm; duration 1.22 ± 0.22 s; $n = 72$), while remaining perched. Head and upper body pointed to the source of disturbance. Display accompanied by series of alert calls. Sometimes associated with displacement head shaking or displacement preening.

3.6 Head-tilt solidarity display (Fig. 10a, as shown in video Fig. 11a http://www.momo-p.com/showdetail-e.php?movieid=momo200416sm02a*)* Reaction to agitation, mild disturbance or in rare cases a post-aggression display; observed also in immature birds (> 1 year old); with an average duration of 0.94 ± 0.15 s ($r = 0.71$–1.25; $n = 60$). The duration does not differ significantly between male and female (Mann–Whitney U test; $z = 0.29$; $n_{male} = 34$, $n_{female} = 26$; $p = 0.77$). Display performed silently and repeated multiple times. Persistence of this behavior and repetition is closely associated with presence of disturbance.

3.7 Crouch-quiver solidarity display; after Serpell 1979 (Fig. 10b, as shown in video Fig. 11b http://www.momo-p.com/showdetail-e.php?movieid=momo200416sm03a*)* Describes a submissive posture given in response to high-intensity aggression or mild disturbance (usually during the presence of an animal keeper). Performing bird assumes a horizontal body position with head and tail positioned downwards and carpal joints held away from the body. Head is usually directed to source of aggression/disturbance. Performing individual will start to quiver both wings partly unfolded, at a moderate to rapid rate (in average 0.59 ± 0.12 s/wing quiver, $n = 210$) for short to extended periods until disturbance desists, remaining crouched following short interruptions. Frequency of wing-quivering does not differ significantly between male

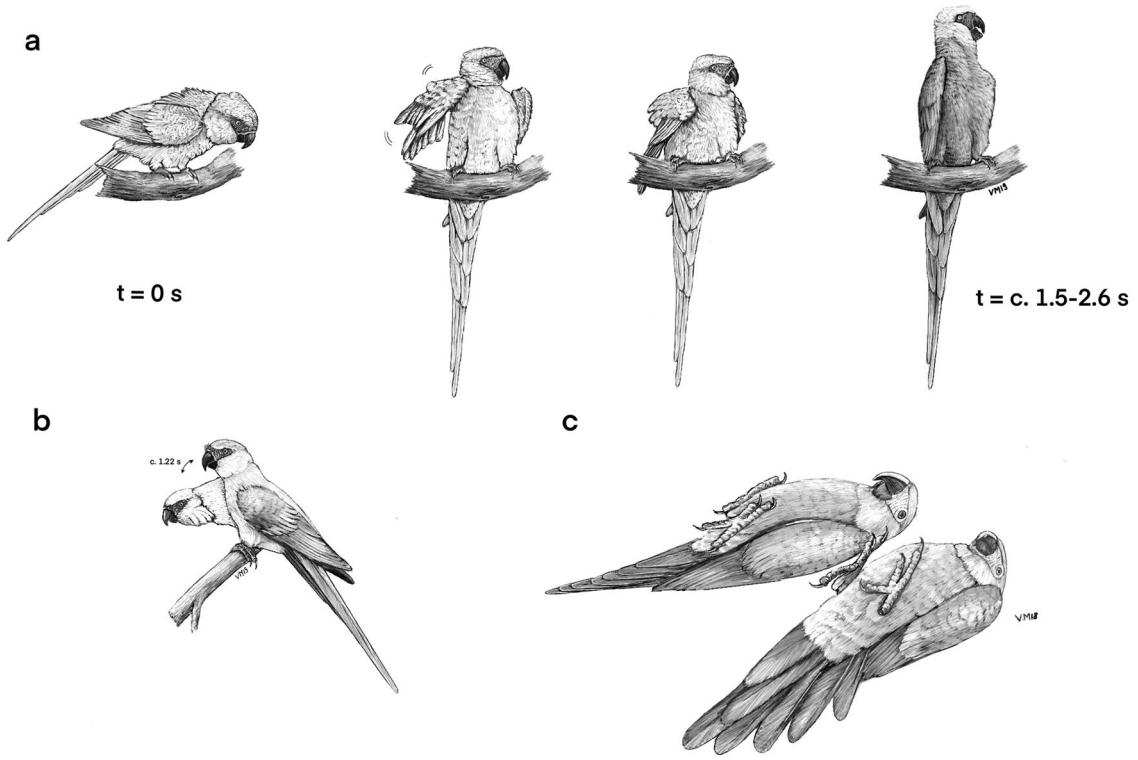

Fig. 8 **a** Irritated body shake, **b** bob, **c** apparent death display

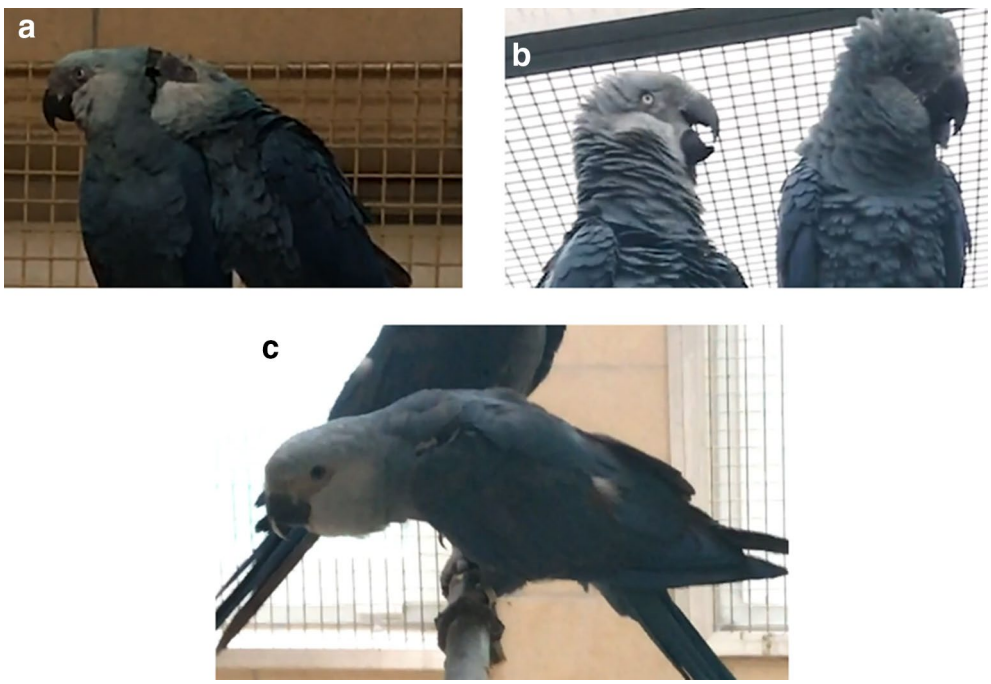

Fig. 9 **a** Displacement allo-preen observed in a pair during force-mate attempt http://www.momo-p.com/showdetail-e.php?movieid=momo200417sm02a, **b** irritated body shake performed by a male http://www.momo-p.com/showdetail-e.php?movieid=momo200416sm05a, **c** two siblings bob in response to mild disturbance http://www.momo-p.com/showdetail-e.php?movieid=momo200417sm04a

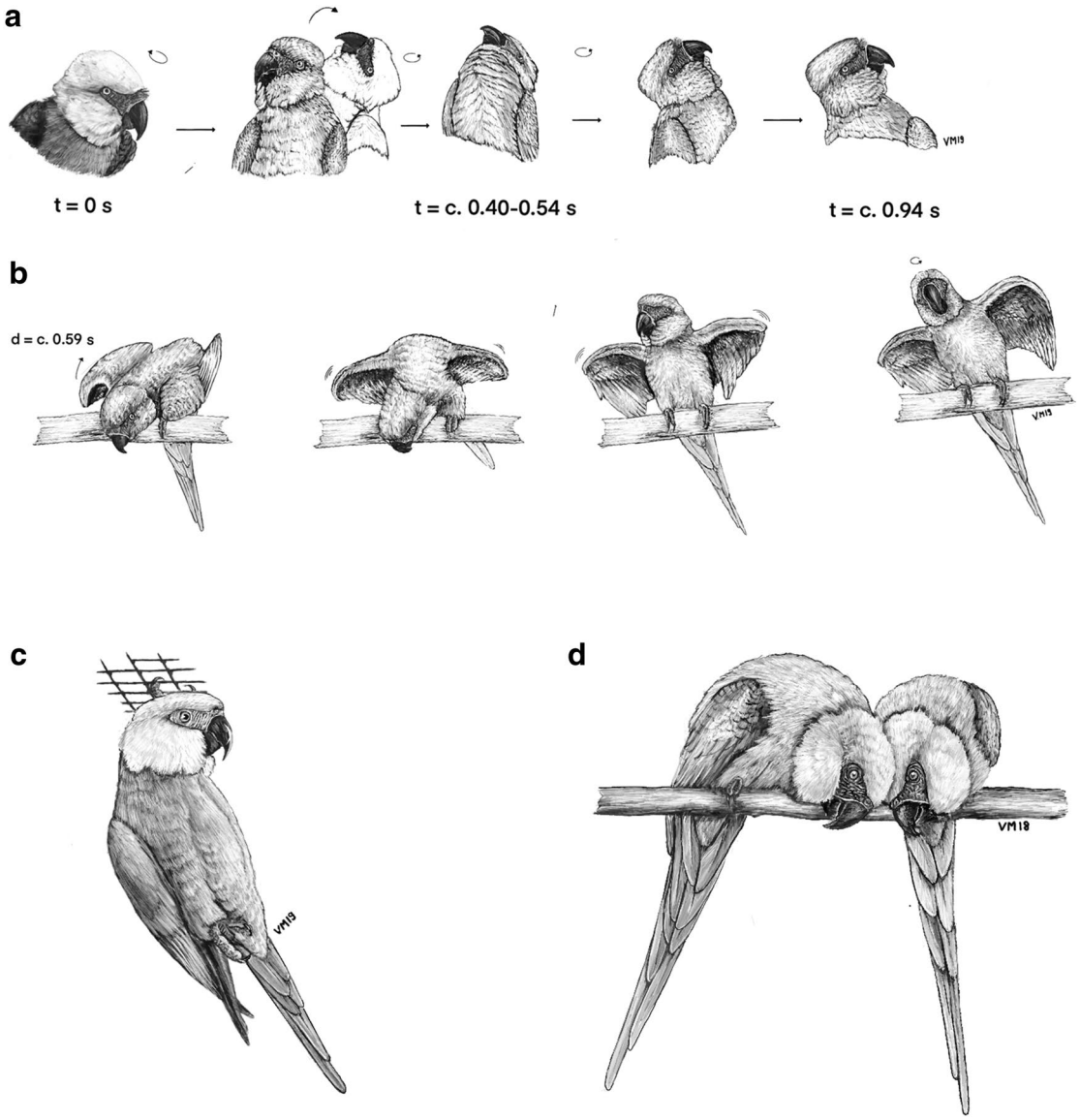

Fig. 10 **a** Head-tilt solidarity display, **b** crouch-quiver solidarity display, **c** upside-down lift solidarity display **d** peer

and female (Mann–Whitney *U* test; $z = 1.09$; $n_{male} = 90$, $n_{female} = 120$; $p = 0.27$). Display is accompanied by submissive calls, head-tilts or occasionally performed in silence.

3.8 Upside-down lift solidarity display (Fig. 10c) A submissive display observed in both, younger and older birds. Display probably accompanied by crouch-quiver solidarity display.

3.9 Peer (Fig. 10d) Mutual display performed by territorial pairs in response to a sudden disturbance, usually from a high perch site initiated by convergent directed head jerks. Head position is held nearly parallel to the perch (remaining there for 1–2 s), while both birds perching in a crouched body position. Interspersed with bill-clasping. Head directed laterally toward source of disturbance.

3.10 Unison jerk (Fig. 12a–e, as shown in video Fig. 13 http://www.momo-p.com/showdetail-e.php?movieid=momo200417sm01a) Predominately given by bonded pairs in response to agitation or apprehension. Single gestures of the display are highly coordinated between social members and are initiated by one bird, following the second within a short time interval of 2–5 s (Fig. 12a). Initial steps include the slow (rarely sudden) movement of the head downwards to take a crouched body posture for a short period before instigating a jerk (c. 1–2 s; Fig. 12b). Tail remains stationary or is moved upward; in that case, body axis is arranged nearly parallel to the perch. Head of both birds is directed in convergent direction, and wings are slightly held away from body. This stage is usually

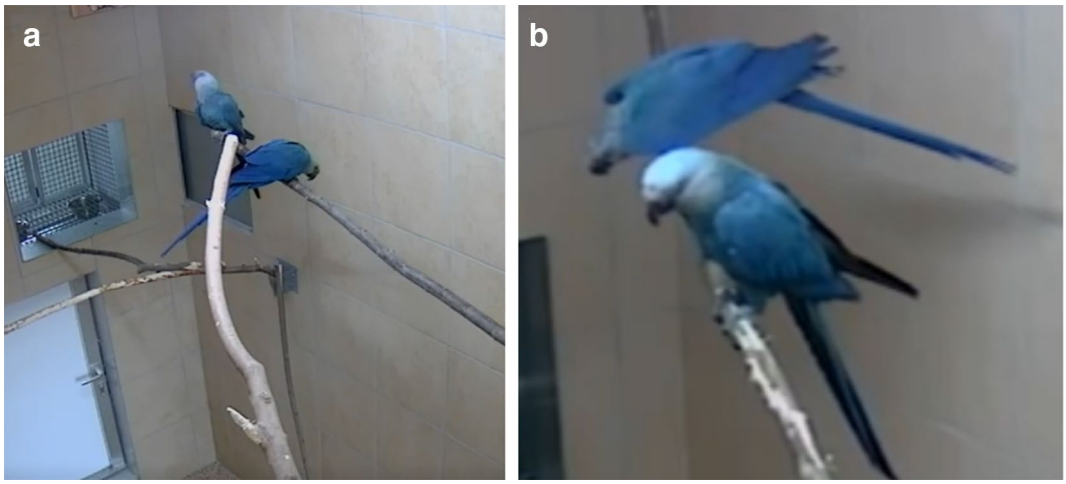

Fig. 11 **a** Video sequence with individual performing the head-tilt solidarity display http://www.momo-p.com/showdetail-e.php?movieid=momo200416sm02a, **b** female performing crouch-quiver solidarity display in front of an intruder http://www.momo-p.com/showdetail-e.php?movieid=momo200416sm03a

accompanied by simultaneous eye-blazing. Subsequently, both birds perform either a single sudden jerk or multiple jerks often by accelerating the initial steps, with body and head rapidly extended vertically and held there for a few seconds (Fig. 12c, e). Wings are partly (never fully) extended and held away from the body when the body is arranged vertically. Furthermore, once body is extended to the maximum, both birds simultaneous emit a unison call (in long-term bonded pairs, call structure is highly analogous). Unison jerks were observed when new birds were added to a flock (in 119 of 119 observations) or during force-mate attempts (in 47 out of 47 observations). They are commonly seen shortly after the sudden approach of an intruder (for example shortly after the approach of a bird keeper).

3.11 Singleton jerk (as shown in video Fig. 13 http://www.momo-p.com/showdetail-e.php?movieid=momo200417sm01a) Occurs under identical circumstances to the unison jerk but performed solely by a single individual, seen often in flocks of immature individuals.

Discussion

A comprehensive analysis of the behavioral repertoire can contribute to a better understanding of the animal welfare, social compatibility, species ability to adapt to environmental changes and serves as an important component of the long-term health management of the respective species (Luecher 2006). Behavior studies were conducted for a variety of psittacine species, including detailed observations for both wild and captivity parrot populations (Dilger 1960; Hardy 1963; Serpell 1979; Rowley 1990; Lantermann 1993; Higgins et al. 1999; Prestes 2000; Luecher 2006; Favoretto 2016; Ayeres-Peres and Silva 2017). However, information on the general behavior is lacking for many species, and husbandry manuals are only established for a handful of species.

Agonistic behavior

Socio-negative interactions have been described for solitary and para-social parrots, including many of the behavior elements documented during this study period for the Spix's macaw (Dilger 1960; Hardy 1963; Buckley 1968; Serpell 1979; Rowley 1990; Lantermann 1993; Pitter and Christiansen 1997; Higgins et al. 1999; Prestes 2000; Schneider et al. 2006; Luescher 2006; Queiroz et al. 2014; Favoretto 2016; Ayeres-Peres and Silva 2017). High intense aggression with physical encounters resulting in serious beak or head injuries is extremely rare and was never observed in flocks of immature birds during our study period. Bill thrusting, biting, lunging and bill fencing were documented in larger and smaller psittacines (Dilger 1960; Hardy 1963; Rowley 1990; Lantermann 1993; Higgins et al. 1999; Luescher 2006). Form, function and execution do not differ from the descriptions in this study.

Furthermore, in this study, we observed that immature birds tolerate direct approach of other flock members, unless competition for food, perch site or roosting sites is present. Once single individuals reach their maturity and establish a breeding territory, formed pairs start to defend their breeding

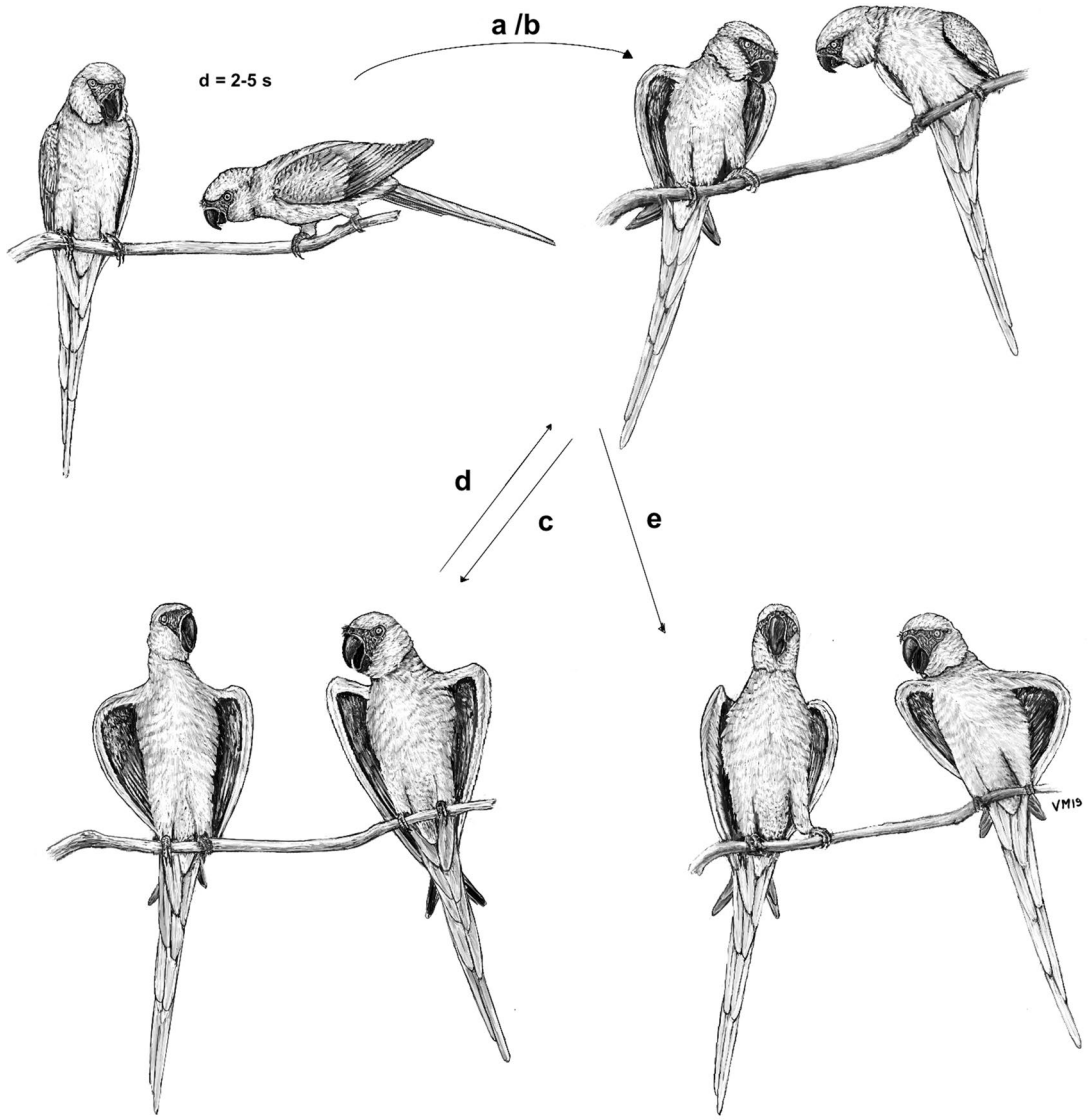

Fig. 12 Behavioral elements of the unison jerk **a** synchronization and **b** simultaneous head downside-lift accompanied by eye-blazing **c** unison jerk **d**, **e** repeat, by skipping step

territory against conspecific intruders using different visual displays and specific calls to insinuate physical dominance.

The wing-raise display symbolizes a characteristic element of the intimidatory behavior in many neotropical species (including most amazons and macaws) and furthermore was observed in species of the genus *Calyptorhynchus*, in *Nestor* sp. and in members of the genus *Cacatua* (Lantermann 1993; Higgins et al. 1999, authors *pers. obs.*). In congeneric species (*Ara* spp.), this display is performed solely or in duet by pairs as a visual display in response to a sudden approach of an intruder close to their breeding territory (authors *pers. obs.*). Recorded in captive pairs of *Ara glaucogularis, A. rubrogenys* (rare), *A. militaris, A. ambiguus, A. ararauna, A. macao* and *A. chloropterus* (Marcuk *pers. obs.*). The wing-raise display was described also in *Amazona aestiva* and *A. albifrons* (under the term *wing-shrug display;* Levinson 1980; Lantermann 1993). In comparison to macaws, amazons rarely tend to unfold the wings fully but rather expose the red wing converts to the opponent. In addition, the wing-raise display was observed in *Amazona guildingii* and *Amazona versicolor* (Marcuk *pers. obs.*). In *Calyptorhynchus lathami* and *C. banksii,* the wing-raise display was used as a defense posture, when birds were exposed to a potential threat (e. g., following a catching attempt or intra-specific aggression). Wings in both species are fully extended towards the intruder (Marcuk *pers. obs*).

Flying approach, flying attack and fights were recorded in both; smaller and larger psittacines (Hardy 1965; Buckley

Fig. 13 Video shows individuals in free-mate choice aviary performing unison and singleton jerks http://www.momo-p.com/showdetail-e.php?movieid=momo200417sm01a

1968; Lantermann 1993; Higgins et al. 1999). Accordingly, these behavior elements represent high-intensity forms of aggression and occurrence is extraordinarily rare. Direct evidence of mate trauma among wild living parrots are not directly recorded (Romagnano 2006 in Luescher 2006). Likely escalations (e.g., mate trauma) are more an outcome of an inappropriate set-up of a captive environment or inadequate avicultural techniques (e.g., the concentration of too many conspecific pairings within a small territory, constant disturbance, small flight areas). Inappropriate hand-rearing techniques and imprinting can promote the development of temporary or permanent stereotypic behavior or psychological disorders (Fox 2006 in Luescher 2006; authors *pers. obs.*). Furthermore, it equally can also contribute to an increased attack readiness towards conspecific individuals, once the imprinted individual has reached sexual maturity (Fox 2006 in Luescher 2006; authors *pers. obs.*).

Redirected aggression has been observed in all species of the genus *Ara, Anodorhynchus* and in some members of the genus *Primolius* under captive conditions (authors *pers. obs.*). An attack that is redirected to the mate always occurred under similar circumstances as described above, often close to an intruder as a side event while a pair vigorously defends a territory. Redirected aggression correlates with seasonal changes and peak during the breeding season, where pairs show an increased aggression potential. Intensity is not only considerably lower than reported in Amazons and several species of the genus *Cacatua*, but also usually instigated from the dominant partner (predominately male; Romagnano 2006 in Luescher 2006).

Displacement behavior

Displacement behavior is in general poorly documented in parrots. The specific function of displacement displays is not adequately understood. Displacement displays serve in accordance to our observation in two functional directions; the intentional distraction or confusion of an intruder as an element of the territorial defense and the probable strengthening of a social bond (some displacement displays disguise socio-positive interactions). Prevalence of single displays is difficult to interpret as usually inter-individual differences are present. Displacement displays interfere often with behavior elements from comfort, social or maintenance behavior (see 2.1–2.11). Ritualized forms of some displacement displays are also found in the sexual behavior of this species. Serpell (1979) provided a comparative study with a detailed account on the communicatory behavior for different members of the genus *Trichoglossus*, including a description of the displacement behavior (see Table 2; for comparison of quantitative aspects of some behavior elements). Moreover, displacement behavior was also noted in *Amazona aestiva* (Lantermann 1993). During field work; displacement behavior and mutual displaying of the wild Red-fronted macaws were recorded (Pitter and Christiansen 1997).

Displacement preening has been observed frequently by the authors in territorial Lear's and Hyacinth macaw pairs. However, eye-blazing is not evident in both species probably due to the dark coloration of the iris. Displacement preening was also observed in *Ara macao, A. chloropterus* and *A. ararauna* (Marcuk *pers. obs.*).

Displacement rubbing, displacement food intake and displacement biting have been reported in *Amazona aestiva* and several *Trichoglossus* species (Serpell 1979; Lantermann 1993). All three displacement display forms were observed moreover in *Ara glaucogularis, A. rubrogenys; A. militaris, A. ambiguus, A. chloropterus A. ararauna, A. macao* and both species of *Anodorhynchus* in identical functional context (Marcuk *pers. obs.).* A further displacement behavior; herein defined as a displacement copulation; was seen for example in territorial *A. hyacinthus* and *A. leari* pairs (Favorrito 2016; Marcuk *pers. obs*). This displacement behavior was not observed in the Spix's macaw during this study period. Displacement mutual feedings were observed only in the Spix's macaws that are most likely analogous to the displacement copulation reported in *Anodorhynchus*.

Bobbing and displacement shaking are reported in *Trichoglossus* (Serpell 1979). Bobbing and displacement shaking were observed in *Primolius maracana*, with form essentially similar to the Spix's macaw (authors *pers. obs.*). Peering was seen in *Ara* spp. and has been observed also in *P. maracana* and *P. auricollis* (Marcuk *pers. obs.*). In larger macaws, peering was frequently observed by the authors and given in response to a sudden disturbance. The behavior is performed in a more exaggerated and jerkier manner than reported in this study, and normally combined with other territorial displays like the wing-raise display or displacement preening (authors *pers. obs.*)

Submission behavior

The crouch-quiver solidarity display was documented in members of the genus *Trichoglossus* (Serpell 1979; Purchase *pers. obs.*), in *Amazona* spp. (Levinson 1980; described as "shake display"; Lantermann 1993) and in various species in captively managed flocks by the authors. In contrast, no definitive records were given in literature for wild parrots. Thus, recorded in *A. glaucogularis, A. ambiguus, A. macao, A. ararauna* and *P. maracana* and also in *Amazona* spp., *Callocephalon fimbriatum*, *Zanda latirostris, Psittacus* spp. and *Pionus* spp. (Marcuk *pers. obs.*).

Head-tilt solidarity display was occasionally observed in Lear's and Red-fronted macaws as a submission posture, normally during mild disturbance. In Lear's macaws, the head-tilts are performed more linearly; the movement is executed in a lateral direction; while in Red-fronted macaws, this behavior was identical to the described behavior in this study (Marcuk *pers. obs.*). Likely an equivalent submission behavior occurs in both *Calyptorhynchus* species and was also observed in all three *Zanda* species (Marcuk *pers. obs.*). A displacement head-down shake was recorded in Lear's macaws in equal functional context like documented in this study (Marcuk *pers. obs.*).

Apparent death display was reported in both *Anodorhynchus* species (Antas et al. 2010; Pacifico de Assis 2012; Purchase *pers. obs.*). In both species, the apparent death display does not differ from the description provided above. *Prima facia,* the eyes remain wide open during the display in both Lear's and Spix's Macaw, which is obviously contraindicative, thus a display intended for distraction. A possible explanation of this ambivalent element is that this defense behavior is performed by chicks prior to fledging. In the dark environment of a nest log, the overall darker iris of young birds is not visible. Furthermore, vision could represent an advantage for young birds to track the movement of a predator and enable additional options for auto-protection. Lear's Macaw juveniles will eventually perform an apparent death display, when birds are put in a closed transport box or equivalent, dark environment, where light and spatial conditions are similar to that of a nest log or during disturbance in the brooder of hand-reared chicks (Purchase *pers. obs.*). An apparent death display was not observed in mature birds.

Unison jerks were not described in the literature for any other smaller macaws. Our observations indicate that these play a substantial role in audio-visual communication between members of social groups or pairs, probably representing a functional element in individual recognition. The high-pitched call in single individuals associated with that behavior often differs from calls produced during a unison jerk. In flocks, different subtypes of duet calls can be distinguished. Calls associated with that behavior show a high inter-pair variation and general plasticity. Duet calls in unison jerks of re-paired birds can undergo structural changes; while, subordinate birds tend to adapt to the call structure of the dominant partner (requires further investigation).

We could record unison jerks in Blue-winged macaws without any visible differences from unison jerks of Spix's Macaws. Alternate jerks; an analogous behavior element was reported in Red-fronted macaws (Pitter and Christiansen 1997), serving probably a similar functional role. Alternate jerks were observed in several larger macaws including *Ara glaucogularis, A. militaris, A. ambiguus, A. chloropterus A. ararauna, A. macao* (Marcuk *pers. obs*). Alternate jerks in *Anodorhynchus* differs from members of the genus Ara, execution is more static and staggered, and is observed rarely in comparison to the Spix's macaw (Marcuk *pers. obs.*). Mutual territory displays with a high level of synchronization were observed for members of the *Trichoglossus* genus (Serpell 1979) and were observed in *Amazona guildingii*, *A. versicolor, A. arausiaca* and *A. imperialis* (Marcuk *pers. obs*.).

Acknowledgements We would like to thank Mr. Martin Guth for allowing us to conduct the research, including providing the funding that makes this long-term study possible. We would like to thank João Amador for proof-reading the paper and the anonymous reviewers for

their suggested improvements and comments on the early draft of the manuscript.

Compliance with ethical standards

Conflict of interest The authors declare that they have no conflict of interest.

References

Antas PTZ, Carrara LA, Yabe RS, Ubaid FK, Oliveira-Júnior S, Vasques ER, Ferreira LP (2010) A arara-azul na Reserva Particular do patrimônio natural Sesc Pantanal. SESC, Departamento Nacional. Conhecendo o Pantanal, Rio de Janeiro, p 6

Ayres-Peres L, da Silva CC (2017) Etograma da caturrita, *Myiopsitta monachus* (Boddaert, 1783) em ambiente natural. Revista de Ciência e Inovação 2(1):115–127. https://doi.org/10.26669/2448-4091132

Berkunsky I, Quillfeldt P, Brightsmith DJ, Abbud MC, Alemán-Zelaya AJMRE, Barberena JB (2017) Current threats faced by neotropical parrot populations. Biol Cons 214:278–287. https://doi.org/10.1016/j.biocon.2017.08.016

BirdLife International (2020) Species factsheet: *Cyanopsitta spixii*. https://www.birdlife.org. Accessed 14 Mar 2020

Buckley FG (1968) Behavior of the Blue-crowned hanging parrot *Loriculus galgulus* with comparative notes on the Vernal hanging parrot *L. vernalis*. IBIS 110(2):145–164

Burger J, Gochfeld M (2003) Parrot behavior at a Rio Manu (Peru) clay lick: temporal patterns, associations, and antipredator responses. Acta Ethologica 6(1):23–34

Butchart SHM, Lowe S, Martin RW, Symes A, Westrip JRS, Wheatley H (2018) Which bird species have gone extinct? A novel quantitative classification approach. Biol Cons 227:9–18. https://doi.org/10.1016/j.biocon.2018.08.014

Dilger WC (1960) The comparative ethology of the African parrot genus Agapornis. Zeitschrift für Tierpsychologie 17:649–685

Favoretto GR (2016) Comportamento de arara-azul-de-lear (*Anodorhynchus leari*, Bonaparte, 1856) em cativeiro e a influência da técnica flocking na interação de pares. M.Sc. Thesis

Fischer D, Neumann D, Purchase C, Bouts T, Meinecke-Tillmann S, Wehrend A, Lierz M (2014) The use of semen evaluation and assisted reproduction in Spix's macaws in terms of species conservation: assisted reproduction in Spix's macaws. Zool Biol 33(3):234–244. https://doi.org/10.1002/zoo.21129

Fox R (2006) Hand-rearing: behavioral impacts and implications for captive parrot welfare. In: Luescher AU (ed) Manual of parrot behavior. Wiley, Hoboken, pp 83–91

Hardy JW (1963) Epigamic and reproductive behavior of the orange-fronted parakeet. Condor 65(3):169–199

Hardy JW (1965) Flock social behavior of the orange-fronted Parakeet. Condor 67(2):140–156

Higgins PJ (1999) Handbook of Australian, New Zealand & Antarctic birds, vol 4, Parrots to Dollarbird. Oxford University Press, South Melbourne

Lantermann W (1993) Beobachtungen zum Aggressionsverhalten männlicher Blaustirnarnazonen (*Amazona aestiva*) unter Volierenbedingungen. Bonn zoll Beitr 44(1–2):57–62

Levinson ST (1980) The social behavior of the white-fronted Amazon (*Amazona albifrons*). In Conservation of new world parrots: proceedings of the ICBP parrot working group meeting, pp 403–417

Luescher AU (2006) Manual of parrot behavior. Wiley, Hoboken

Pacifico de Assis EC (2012) Biologia reprodutiva da arara-azul-de-lear *Anodorhynchus leari* (Aves: Psittacidae) na Estação Biológica de Canudos, BA. Ph.D Thesis. Universidade de São Paulo

Pitter E, Christiansen MB (1997) Behavior of individuals and social interactions of the red–fronted macaw *Ara rubrogenys* in the wild during the midday rest. Ornitol Neotrop 8(2):133–143

Prestes NP (2000) Descrição e análise quantitativa do etograma de *Amazona pretrei* em cativeiro. Ararajuba 8(1):25–42

Purchase C (2018) Spix's Macaw (*Cyanopsitta spixii*) international studbook. Annual Report 2018 and Recommendations for 2019. ICMBio National Action Plan

Queiroz BC, Genaro G, Queiroz VDS, Tokumaru RS (2014) Quantificação e descrição dos principais comportamentos de papagaios-chauá (*Amazona rhodocorytha*, Salvadori, 1890) cativos. Revista de Etologia 13(1):1–9

Romagnano A (2006) Mate trauma. In: Luescher AU (ed) Manual of parrot behavior. Wiley, Hoboken, pp 247–253

Rowley I (1990) Behavioural ecology of the galah, *Eolophus roseicapillus*, in the wheatbelt of Western Australia. Surrey Beatty & Sons Pty Limited

Schneider L, Serbena AL, Guedes NMR (2006) Behavioral categories of hyacinth macaws (*Anodorhynchus hyacinthinus*) during the reproductive period, at South Pantanal. Brazil Revista de Etologia 8(2):71–80

Serpell JA (1979) Comparative ethology and evolution of communicatory behavior in the loriine parrot genus *Trichoglossus*. Unpublished Ph.D. University of Liverpool

Skeate ST (1984) Courtship and reproductive behavior of captive white-fronted amazon parrots *Amazona albifrons*. Bird Behav 5(2–1):103–109

Snyder NF, Wiley JW, Kepler CB, Wiley BN, Taapken J, Snyder H, Kepler AK (1987) The parrots of Luquillo: natural history and conservation of the Puerto Rican Parrot. Western Foundation of Vertebrate Zoology, Los Angeles