

BEHAVIOR OF INDIVIDUALS AND SOCIAL INTERACTIONS OF THE RED-FRONTED MACAW *ARA RUBROGENYS* IN THE WILD DURING THE MIDDAY REST

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Abstract. Behavior of the Red-fronted Macaw *Ara rubrogenys* was studied from September 1991 to March 1992 in south-central Bolivia. The macaws spent many hours at midday in groups of 2–30 individuals in quiet gorges and valleys. The birds always sat in pairs and spent most of the time sitting/resting or autopreening. Social interactions such as allopreening and playing/fighting took up 11–18 % of their time. Social activities appeared to increase up to the breeding period. Certain interactions such as allopreening, copulation and courtship feeding presumably serve to maintain the pair-bond. All types of interactions between pairs were rare. Individuals in the flock normally communicated by vocalizations and immediate copying of behavior, vocalization as well as movement, of one individual by another (social facilitation). Aggressive interaction between the pairs was exceptionally rare, and always sitting in pairs as well as performing allopreening seemed to keep the aggression at a low level. *Accepted 24 April 1997.*

Key words: Red-fronted Macaw, *Ara rubrogenys*, behavior, Bolivia, non-social interactions, social interactions.

INTRODUCTION

The Red-fronted Macaw is endemic to the valleys and montane basins within the eastern Cordillera in Bolivia (Lanning 1982, 1991; Forshaw 1989; Fjeldså & Krabbe 1990; Pitter & Christiansen 1995). It is threatened by habitat destruction, trapping for the pet trade and persecution as a pest on crops. The species is highly social (Boussekey *et al.* 1991) and during the day it was seen in flocks of 2–90 individuals. The flock size differed depending on time of year, area and type of activity (Pitter & Christiansen 1995).

According to previous studies parrots show few stereotyped sequences or distinct postures compared to many other bird groups (Jon Fjeldså, pers. comm.). However, extremely few published studies have been based on observations of the behavior of wild parrots.

The present paper focuses on the behavior during the long midday rest where the macaws gather in clusters of trees. The most commonly observed types of behavior performed during these hours are described as well as the social interactions within pairs and within the group.

STUDY AREA

The two main study areas were Camos, located 15 km south of Puente Arce along Río Chico (tributary to Río Grande) (between 18°37'–45'S and 65°08'–10'W) and Sucusuma, located 8 km north of Torotoro along Río Caine (between 18°02'–08'S and 65°38'–46'W). The numerous valleys in the area are arid to semi-arid, mesothermic valleys occupied by xerophytic thorn woodland (Hueck 1966, Solomon 1989). The woodland vegetation is composed of genera such as *Schinus*, *Prosopis*, *Tipuana*, *Aspidosperma*, *Loxopterygium*, *Schinopsis* and several species of cacti. The observations were made in a valley in Sucusuma and in a gorge on Río Chico.

The valley in Sucusuma was located in the vicinity of a large agricultural area, which was the main feeding area for the macaws at that time of the year. A stream ran through the valley, and the bottom of the valley was quite narrow (25–30 m) between 10 m tall slopes. The vegetation in the valley and on the hillsides was scrub and scattered 7–10 m tall trees. Most of the trees had a sparse foliage, but provided sufficient shade

for the macaws during the hottest hours of the day. Humans passed through the valley only rarely.

The gorge in Río Chico was 30 m long, 4 m wide at the bottom and with 10–12 m high slanting cliffs on both sides. The upper 3 m of the cliffs were vertical. The vegetation in the gorge was mostly grasses and bushes, but there were also a few 5–8 m tall trees on the hillsides, most of them on the edge of the gorge. The macaws prospected three holes in the vertical cliffs.

METHODS

The study was conducted from September 1991 to March 1992.

Birds always sat together in pairs during the midday rest. Judging from the behavior we assume that the pairs could comprise mated pairs, homosexual pairs and temporary pairs of immatures, either siblings or unrelated birds. The behavior of juveniles is treated in Christiansen & Pitter, 1993b.

Observations were made in Sucusuma during September and October. The groups observed included many juveniles as well as many immatures. The fieldwork in Río Chico took place from December to March and included the start of the breeding period. In Río Chico three pairs showed interest in nest holes, and one pair laid eggs during the last days of the study. Only one member of the flock was juvenile. The rest had adult plumage, but judging from behavioral characteristics, many were immatures.

The macaws were studied from a distance of 20–30 m with telescope, and the Scan Sampling method (Altmann 1974) was employed. In total we spent 68 hs scanning (4151 scan observations) in Sucusuma and 69 hs (2666 scan observations) in Río Chico. When Scan Sampling we noted the current behavior of each individual at five-minute intervals. Behavioral types with a duration of five or more minutes included sitting/resting, autopreening, interactions between individuals concerning allopreening the general plumage, cloacal region and beak (nonsimultaneous allopreening refers to one bird preening another. This may or may not be reciprocated by the preened individual. Simultaneous allopreening refers to two birds preening each other at the

same time) and playing/fighting. Using the scanning method a behavior is recorded at a certain moment and therefore no distinction has been made between sitting and resting or between playing and fighting as these behaviors often passed into each other.

The number of birds covered by each scanning varied from 2 to 20 individuals. During scanning the behavior of the individuals was noted in the same order for as long as possible, but it was difficult to identify individuals from a distance, and as they moved around the order changed. Therefore the results reflect the behavior of a group rather than of the individual birds. Behavioral types with a duration of less than five minutes are classified in the group "other". This group included locomotion (moving on the same branch, moving to another branch in the same tree, flying from one tree to another), acrobatics, chewing on different objects, copulation, courtship feeding. The frequencies of these shorter activities, noted during the scanning, are compared.

RESULTS

The midday rest of the macaws during the hot midday hours in Sucusuma normally lasted for 5–7 hs, from the time the macaws arrived in the valley after the morning feeding until they left for the afternoon feeding. In Río Chico the macaws flew in and out several times during the midday rest and were often seen in the gorge before the first feeding session in the morning (Pitter & Christiansen 1995). The composition of the flock changed during the day: some birds stayed only a few hours, while others stayed most of the day.

Usually the macaws gathered in groups. In Sucusuma we recorded up to 18 macaws and in Río Chico 30 macaws. Many birds usually rested in the same tree. In Sucusuma the mean group size in one tree was seven birds ($n = 58$, range 2–18) (Pitter & Christiansen 1995).

All adult and immature individuals in a resting flock usually remained together in pairs almost constantly. They changed between sitting together touching each other, sitting a few centimeters apart and more rarely, 20–50 cm apart. Once in a while, though, they separated, moving to other branches in the same tree or another

tree, but after a short while they rejoined. Separating was mostly seen after social interactions such as allopreening, playing/fighting or copulating.

During the midday rest, behavior varied depending on number of birds and composition of the group (number of juveniles, immatures and adults) resting in the same tree. The larger the group, the more active it was, and especially the activity of a group of noisy immatures could spread through the entire group.

TIME SPENT ON THE MAIN TYPES OF BEHAVIOR

The macaws were active in 23–42% of the time during the midday rest, performing auto- and allopreening and playing/fighting (Fig. 1). They spent 11–18% of the time on social interactions. However, the predominant behavior during the midday rest was sitting/resting. The birds in Río Chico were much more active than in Sucusuma and spent more time on both kinds of social interactions.

The group “other” was larger in Río Chico than in Sucusuma and indicated that the birds in Río Chico were more restless flying from tree to tree or circling in the gorge.

NON-SOCIAL INTERACTIONS, BEHAVIOR OF INDIVIDUAL BIRDS

Individual birds spent most of the time sitting/resting and autopreening (Fig. 1), but activities of shorter duration, such as different kinds of locomotion, chewing on objects, and acrobatics were often seen, as well.

Sitting/resting. Sitting/resting was the predominant behavior (Fig. 1). The macaws sat quietly in a relaxed and sometimes crouched posture. The behavior could last up to several hours or only a few seconds, interspersed with other behavior. Particularly in the middle of the midday rest, during the hottest hours, they rested for many hours with only few and short intervals of other behavior. During this period the eyes often were closed and they put the head backwards over the shoulder tucking the beak into the plumage of the back and often fluffing the plumage.

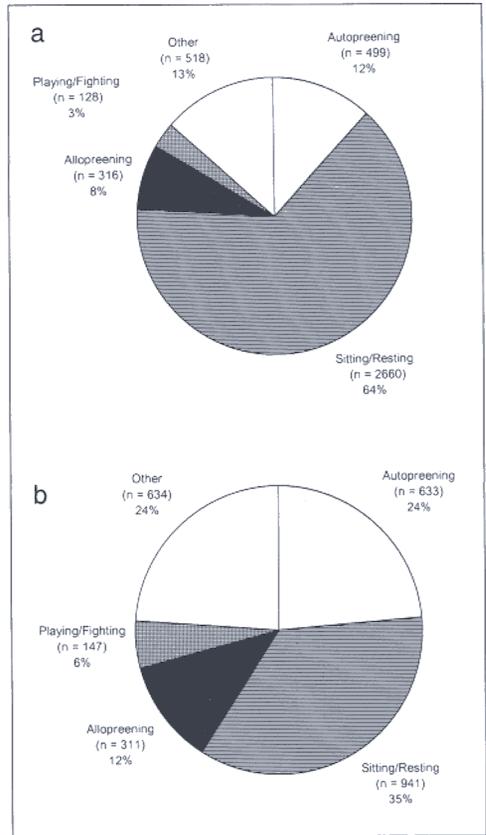


FIG. 1. Time spent on the main types of behavior in Sucusuma (a) and Río Chico (b).

Autopreening. In Río Chico the macaws often preened before the first feeding session but the main preening period was as in Sucusuma, during the midday rest. Autopreening was the second most commonly observed behavior (Fig. 1) and was seen throughout the entire midday rest. The macaw preened itself on most parts of the plumage, changing frequently between the different parts. The bird nibbled the feathers under the raised wing by putting the head below the wing from either the front or from behind. While preening the tail feathers the bird bent the head 180° to the tail and took one feather at a time in the beak and pulled it between the mandibles in a nibbling way. Sometimes the bird fanned its tail feathers, facilitating the preening

of individual feathers. When preening breast or back feathers the beak performed nibbling movements.

During a preening session the birds scratched the plumage, shook the plumage, stretched different parts of the body, and preened the feet or the beak.

The macaw scratched 'directly' the head and neck region as well as the breast region with either foot. Scratching and shaking of the plumage seldom lasted more than a few seconds.

The macaws stretched wings, tail, legs or jaws. They spread one wing at a time downwards, in a wing-to-foot movement combined with fanning that side of the tail, or showed a both wings stretch, with the tips of the wings folded. The jaw muscles were stretched by opening the beak as wide as possible either once or many times in succession.

The foot was nibbled by raising it to the beak, and the macaw cleaned each toe in a biting manner. This activity usually lasted less than a minute. The beak was cleaned by rubbing it with the foot or against a branch or cliff. Biting or chewing on branches and twigs probably served to keep the beak clean and fit. On a few occasions the macaws were seen rubbing the region behind the eye on a branch.

Locomotion. Sitting/resting and autopreening were often interspersed with locomotion of short duration. Locomotion was most frequently observed at the beginning or end of a rest period, when the birds were more restless. Most often the macaws only moved a short distance on the same branch (6 % of the activities noted on scan records in Sucusuma and 3 % in Río Chico). The macaws only moved rarely between branches in the same tree or between trees during the rest, and they often sat for hours on the same branch. Moving to another branch in the same tree accounted for 2 % of the activities in Sucusuma and 1 % in Río Chico. Flying from one tree to another accounted for 2 % of the activities in Sucusuma and 7 % in Río Chico. Circling in the valley or gorge was seen very few times in Sucusuma, while it was a common activity in Río Chico (8 % of the activities). In Río Chico the nest prospecting pairs also flew to the cliff near their nest holes many times a day (2 % of the activities).

Within the tree there was a clear tendency to travel short distances by climbing, sidling or walking rather than flying. When the macaws moved along branches they usually moved sideways one foot after the other. They normally walked slowly but while playing/fighting, they often moved fast. During a fast move through the canopy they sometimes kept their balance by grasping the branch with the beak.

Acrobatics. The macaws were several times observed hanging upside down. They sometimes hung for quite a long time, swinging slightly back and forth or bending the head backwards to look around. Sometimes they hung by only one leg. From this position at times they grabbed hold of a lower branch with the beak and swung around to hang underneath that branch before regaining foothold.

Chewing on different objects. The macaws in Sucusuma and Río Chico were often observed chewing on objects (3 % of the activities in Sucusuma and 2 % in Río Chico). In Sucusuma they chewed on bark, branches, twigs and leaves, while in Río Chico they also chewed on pieces of rock.

SOCIAL INTERACTIONS, BEHAVIOR WITHIN PAIRS

Social interactions made up 11–18 % of the macaws' activities (Fig. 1). Both agonistic and non-agonistic behavior occurred, but most of the time was spent on non-agonistic behavior. Besides allopreening and playing/fighting, several times we also observed social interactions of shorter duration within pairs, such as caressing, copulating and courtship feeding.

Allopreening. Allopreening was only seen between members of pairs and between juveniles and parents (Christiansen & Pitter 1993b), and not among groups of three or more.

The far most commonly observed type of allopreening was simultaneous allopreening (Fig. 2). More rarely one bird preened another which was sitting passively or autopreening. Usually, after some time the roles were reversed or they started simultaneous allopreening. Allopreening often lasted for 15–30 minutes interspersed with various other behavior types such as autopreening, sitting, etc.

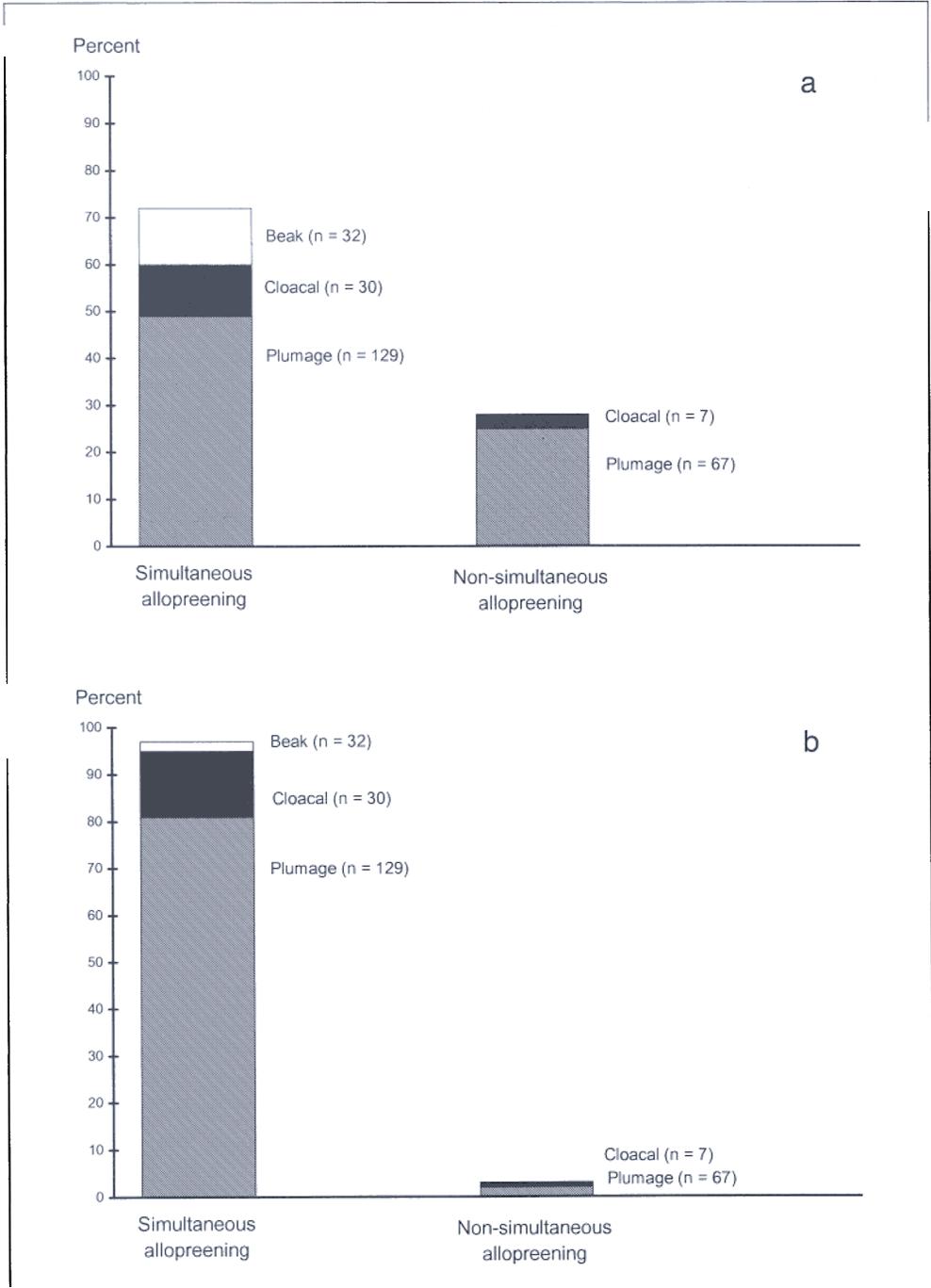


FIG. 2. Time spent on simultaneous allopreening and non-simultaneous allopreening on different parts of the body: beak, cloacal and plumage in Sucusuma (a) and Río Chico (b).

The birds faced in the same direction or opposite each other while allopreening. Often one of the birds crouched on the branch and raised the feathers on its head and neck, similar to begging behavior of juveniles (Christiansen & Pitter 1993b). The macaws allopreened all parts of the plumage.

During simultaneous allopreening they either preened each other in exactly corresponding parts of the body or they preened different parts dependent on where it was convenient in relation to their position.

The macaws were often seen sitting opposite each other on the branch preening each other's undertail coverts and around the cloaca. In between they grabbed the tail feathers and pulled them through the beak.

When the macaws alternated between allopreening and autopreening, the autopreening was often carried out as if the macaws imitated each other and preened exactly the same part of the body.

The mated pairs used allopreening as a greeting ceremony as well, e.g., when the female returned after a long stay in the nest hole or after a long rest without any interaction between the two.

Caressing. Pairs were observed nibbling each other very carefully in the plumage around the beak, on the chin, whiskers, lores and forehead. Pairs were also seen grasping each other's beak and then rubbing their tongues together.

Playing/fighting. The macaws spent more time on playing/fighting in Río Chico than in Sucusuma (Fig. 1). The intensity of aggression varied a lot and in most cases it was not serious fights, but play.

Four main types of agonistic displays were observed, three of them are shown in Fig. 3. These partly followed the pattern found by Serpell (1981) in captive birds belonging to the genus *Trichoglossus*. The macaws often alternated between these displays as well as other behavior. Intensity and type of display depended on the context in which it was performed.

(a) *Pecking* (Fig. 3a): This behavior was mostly composed of gaping and pecking vigorously at the partner's head or legs. The attacked bird would often rapidly reciprocate the pecking and

they often continued pecking alternately over a long period. Attack was avoided by turning the head aside or moving away or the bird defended itself by pushing a leg toward the attacker to keep it at a distance. The attacked party could escape by swinging down below the branch, often hanging by one leg, fluttering the wings and defending itself from this position. The attacker often pursued the escaping bird gaping while sidling rapidly along the branch, or while hanging upside down the attacker bent to peck the other in the head or continued pecking at the leg of the bird, which often had to release its grip. On one occasion two birds were seen pecking at each other, both of them hanging upside down. The pecking either stopped suddenly or it continued until one bird lost its balance. However, the birds never injured each other.

(b) *Beak wrestling and beak fencing* (Fig. 3b): The birds wrestled by taking hold of each other's beak and twisting their heads from side to side or they fenced with the beaks.

(c) *Alternating jerks* (Fig. 3c): In this display the birds demonstrated agitation by very rapid and sudden jerky movements. The partners nearly always coordinated and synchronized these movements. They both turned the head to the right, to the left, against each other or away from each other at the same time or bent the bodies forwards over the branch with an exaggerated peering at a possible disturber or out in the air. During the display they often cackled loudly and intensely.

(d) *Tearing up and tossing objects*: When agitated, the macaws were seen tearing up grass violently or picking up pieces of rock, only to toss them down the cliff.

Pecking was the most commonly seen display. The degree of pecking varied much. Beak wrestling and beak fencing, alternating jerks, tearing up and tossing of objects were seen more seldom and only when the birds were agitated.

Vigorous pecking and the other playing/fighting displays (b–d) were often seen before separation and immediately after very close interactions such as copulation and courtship feeding. They were also seen as a response to disturbance from outside. The effect of the cooperation within the pair was that the aggression directed

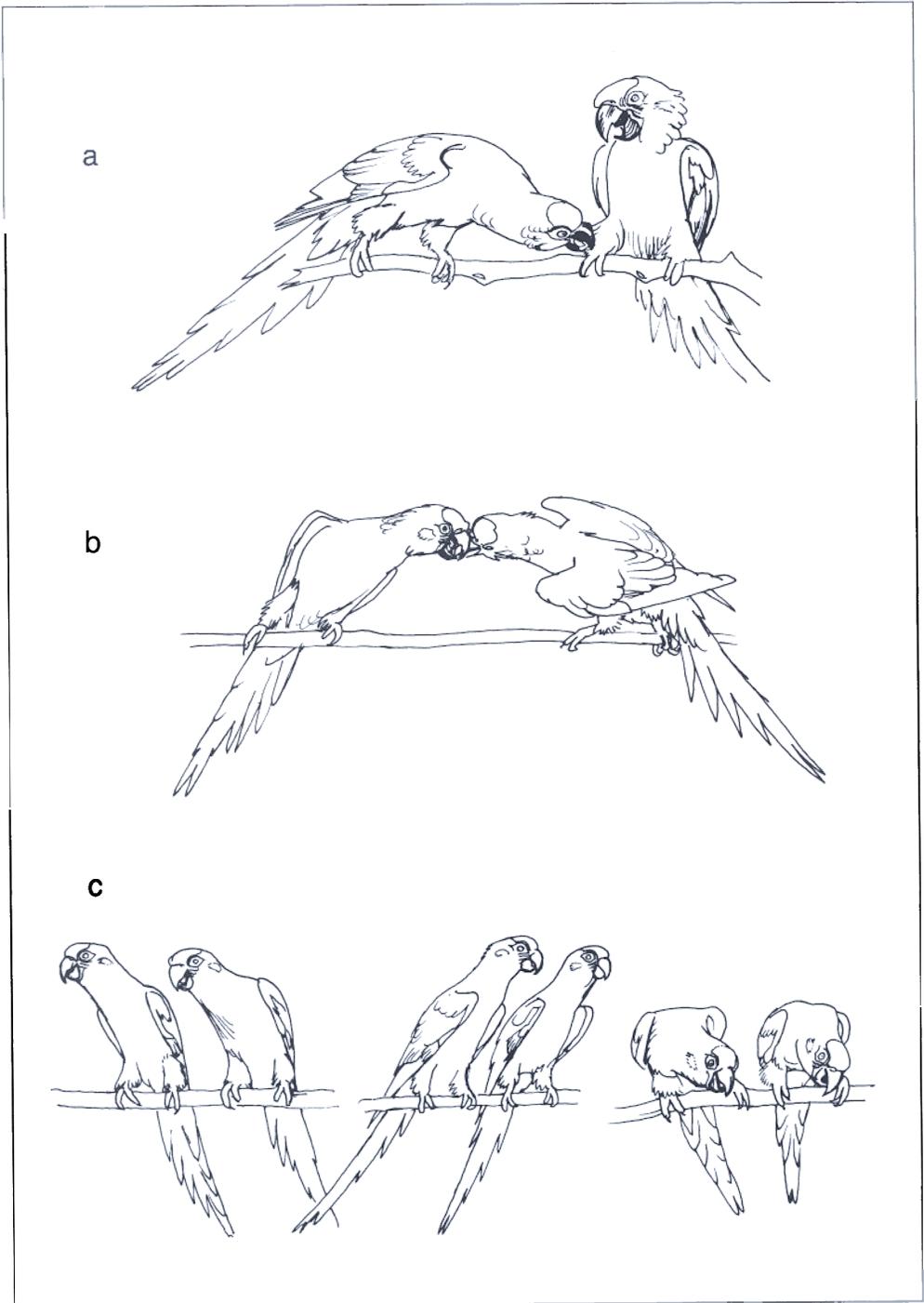


FIG. 3. Types of display of playing/fighting. 3a: pecking, 3b: beak wrestling and beak fencing, 3c: alternating jerks.

toward the disturber appeared more vigorous and impressive.

Pecking was the type of display that could have the longest duration. Beak wrestling and beak fencing, alternating jerks, tearing up and tossing of objects were all of shorter duration and were very often followed or seen alternating with other displays. After alternating jerks the macaws often suddenly turned their aggression toward each other and pecked at each other with quick and violent movements. Other displays, such as tossing of rocks, tearing up grass or violently rubbing the beak against branches often accompanied the jerks and pecking displays as well.

The macaws very often changed between agonistic and non-agonistic behavior. In stressful situations, where the birds became restless, the changes occurred more often, resulting in each display only lasting a few seconds.

In particular, alternating allopreening and pecking was frequently seen and could often last half an hour. While peacefully allopreening, two partners could suddenly start fighting without any obvious warning, but often allopreening was more intense and violent before it turned into aggression. After a short fight the birds usually quietly resumed auto- or allopreening, or sometimes they moved half a meter apart. Partners even alternated between caressing around the beak and fighting several times in succession.

Copulation. This behavior is described in Christiansen & Pitter (1993a). Few copulations were seen outside the breeding period. During the breeding period copulations were often seen (on 16 occasions in Río Chico).

Courtship feeding. This behavior is described in Christiansen & Pitter (1993a). Courtship feeding was seen both during the non-breeding and the breeding period (on 4 occasions in Sucusuma and on 3 in Río Chico).

SOCIAL INTERACTION, BEHAVIOR WITHIN THE GROUP

Only very few interactions took place outside the pairs, except that the group as a whole often communicated by immediate copying of behavior, vocalization as well as movement, of one individual by another (social facilitation). This

was seen before they left for the feeding area or as a response to disturbance and predators or during the rest. Very often we observed single birds or pairs initiating an activity which thereafter spread rapidly in mimetic fashion throughout the group. Many individuals could suddenly perform the same non-agonistic activity, such as preening, scratching, circling in the gorge, or the same agonistic activity, such as pecking or alternating jerks.

The vocal repertoire varied. Two types of vocalization commonly spread throughout the group.

Quiet twitter-vocalization: Partners were often seen flying to a particular branch or vertical cliff, crouching very close together for a long time while duetting. The loud jolly cackling and twittering passed into a quieter cooing and chuckle.

Alert-vocalization: A pair often simultaneously sat upright and vocalized loudly and intensely. At intervals they screeched stridently.

Alert-vocalization was performed in response to disturbances. Particularly in Río Chico the birds performed quiet twitter shortly after they had arrived in the morning. The nest-prospecting pairs flew to the cliffs close to their nest holes, and the other pairs sat in the trees and the entire gorge reverberated with vocalizations. Quiet twitter also followed arrival of conspecifics to the area or to the same tree.

At the end of the midday rest the macaws became restless and moved around on the branches or flew between the trees while vocalizing loudly. This restlessness coincided in Sucusuma with a daily change in the weather, which became windy and overcast and resulted in the whole group leaving for the same feeding area.

Agonistic behavior was usually seen within pairs. Only occasionally were the aggressions directed toward other pairs or individuals. During the breeding period, on nine occasions the nest-prospecting pairs were seen to defend their territory immediately around the nest hole against conspecifics. The defence was characterized by a fairly low level of aggression (Christiansen & Pitter 1993a).

DISCUSSION

Intrapair behavior. Cohesion within the pairs of Red-fronted Macaws is very strong as they act as a unit throughout the day doing almost everything together, while maintaining close proximity. This was also observed in mated pairs of Canary-winged Parakeets *Brotogeris v. versicolor* in captivity (Arrowood 1988).

The Red-fronted Macaw must be assumed to maintain sustained pair-bonds, as also with most other parrot species (Forshaw 1989). The increased amount of time that adult birds spent allopreening in the early breeding period probably indicated the importance of maintaining the relationship between the pair members in the beginning of and during the breeding period. Copulations and courtship feeding seen outside the breeding period supported the view that pair-bonds were maintained throughout the year.

The macaws allopreened almost any part of the body. Harrison (1964) stated that most allopreening in birds is restricted to head and throat, while especially preening under the wing is exceptional. Hardy (1963) suggested that allopreening directed to the head, wings and tail areas in pairs of Orange-fronted Parakeets (*Aratinga canicularis*) is the strongest behavioral device for maintenance of the pair-bond throughout the year. This may also be the case with the Red-fronted Macaw.

Simultaneous allopreening was by far the most common type of allopreening among the macaws and according to the interpretations of Harrison (1964), this indicates that there is no rank difference between the members of a pair. Allopreening among the Red-fronted Macaws very often passed into playing/fighting. This is very common among birds (Harrison 1964) and allopreening serves as an appeasement (Hardy 1963). Presumably allopreening replaces aggressive fighting in mated pairs. Social play has also been found in White-fronted Amazons *Amazona albifrons* (Levinson 1981) and in Green-winged Macaws *Ara chloroptera* (Deckert & Deckert 1982).

Arrowood (1988) stated that duetting between pair members does not promote bonding in Canary-winged Parakeets, but functions as a coordinated pair threat against conspecifics. In the Red-fronted Macaw we observed duetting in

response to disturbances. However, duetting performed by mated pairs close to their nest holes may be an activity that serve to strengthen the pair-bond in the early breeding season.

Communication in the flock. Despite the fact that the macaws rested in flocks, any interactions between members of different pairs were rare. Social interactions mostly took place within pairs, between parents and juveniles (Christiansen & Pitter 1993b), or between juveniles.

The entire flock often communicated either by vocalizing or performing the same movements synchronously. In general, movement imitation is highly developed among Psittaciformes (Moore 1992). Social facilitation as a means of flock coordination was also observed in Orange-fronted Parakeets *Aratinga canicularis* (Hardy 1965), African Lovebirds *Agapornis* spp. (Dilger 1960) and Budgerigars *Melopsittacus undulatus* (Brockway 1964). Levinson (1981) found periods of high activity in White-fronted Amazons during the day where all individuals in the flock were in a highly excited state. This appeared to function in increasing group cohesion.

Harrison (1964) suggested, that allopreening was often seen between neighbors in social groups of birds and reduced aggression between members of a group. Allopreening never extended outside the mated pair in Canary-winged Parakeet (Arrowood 1990), or in Budgerigars (Trillmich 1976), and pairs in Red-fronted Macaws. The spreading of allopreening probably reduced aggression to a low level between all pairs of a flock.

Aggressions between neighbors in the flocks were exceptionally few, and chasing of other individuals was seen on very few occasions. In the feeding grounds we only observed very few aggressions between conspecifics (Pitter & Christiansen 1995). This was also the case in a group of Hyacinth Macaws *Anodorhynchus hyacinthinus* (pers. obs.). Aggression between individuals in a group appears to be more common among smaller species of parrots. Serpell (1981) suggested that the genus *Trichoglossus* is exceptionally aggressive both in the wild and in captivity toward conspecifics and other species. The same was found for Orange-chinned Parakeets *Brotogeris jugularis*, where pairs were often seen fighting with other pairs or two flocks

against each other (Power 1966). Agonistic behavior was frequent in Budgerigars in captivity. However, in the wild there were few agonistic encounters between the birds and no peckorder or dominance hierarchy (Wyndham 1980). We observed no evidence of peckorder in flocks of Red-fronted Macaw, except for a breeding pair that seemed to be socially superior to non-breeding birds (Christiansen & Pitter 1993a).

Aggression between pairs of Red-fronted Macaw was probably reduced by the spreading out of the pairs when resting. Galahs *Eolophus roseicapillus* also space themselves out when roosting and feeding (Rowley 1990).

Furthermore, aggression was diminished by most individuals in a resting flock sitting in pairs, most aggression being kept within the pairs and often alternating with appeasing allopreening and caressing. A low degree of aggressive interaction between pairs contributed to strengthen the group.

Ward & Zahavi (1973) suggested that joint roosting and breeding areas serve as information centres where knowledge of good feeding places is passed on to conspecifics rather than as an anti-predator mechanism. The grouping of the Red-fronted Macaw during the midday rest probably serves both to avoid predators and exchange information on good feeding areas. The food of the macaws was in certain periods of the year rather sparse (Pitter & Christiansen 1995) and information on good feeding areas could be of great importance for the survival of the macaws. Peregrine Falcons (*Falco peregrinus*) occasionally were seen attacking the macaws and overflying raptors could cause a large group of macaws to take off (Pitter & Christiansen 1995) so the grouping of the macaws also may serve as an antipredator mechanism.

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REFERENCES

- Altmann, J. 1974. Observational study of behavior: Sampling methods. *Behaviour* 49: 227–267.
- Arrowood, P. C. 1988. Duetting, pair bonding and agonistic display in parakeet pairs. *Behaviour* 106: 129–157.
- Arrowood, P. C. 1990. Male-male, female-female and male-female interactions within captive Canary-winged Parakeet *Brotogeris v. versicolorurus* flocks. *Acta XX Congressus Internationalis Ornithologici*. Pp. 666–672 in Bell, B. D., Cossee, R. O., Flux, J. E. C., Heather, B. D., Hitchmough, R. A., Robertson, C. J. R., & M. J. Williams (eds.). New Zealand Ornithological Congress Trust Board, Wellington, New Zealand.
- Boussekey, M., Saint-Pie, J., & O. Morvan. 1991. Observations on a population of Red-fronted macaws *Ara rubrogenys* in the Río Caine valley, central Bolivia. *Bird Conserv. Intern.* 1: 335–350.
- Brockway, B. F. 1964. Ethological studies of the Budgerigar *Melopsittacus undulatus*: Non-reproductive behavior. *Behaviour* 22: 193–222.
- Christiansen, M. B., & E. Pitter. (1993a). Aspects of breeding behaviour of Red-fronted Macaws, *Ara rubrogenys*, in the wild. *Gerfaut* 82–83: 51–61.
- Christiansen, M. B., & E. Pitter. (1993b). Aspects of behaviour of juvenile Red-fronted Macaws, *Ara rubrogenys*, in the wild. *Gerfaut* 82–83: 63–69.
- Deckert, G., & K. Deckert. 1982. Spielverhalten und Komfortbewegungen beim Grünflügelara *Ara chloroptera* G. R. Gray. *Bonn. zool. Beitr.* 34: 269–281.
- Dilger, W. C. 1960. The comparative ethology of the African parrot genus *Agapornis*. *Z. Tierpsychol.* 17: 649–685.
- Fjeldså, J., & N. Krabbe. 1990. *Birds of the high Andes*. Copenhagen.
- Forshaw, J. 1989. *Parrots of the world*. Third revised edition. Willoughby, Australia.
- Hardy, J. W. 1963. Epigamic and reproductive behavior of the Orange-fronted Parakeet. *Condor* 65: 169–199.
- Hardy, J. W. 1965. Flock social behavior of the Orange-fronted Parakeet. *Condor* 67: 140–156.
- Harrison, C. J. O. 1964. Allopreening as agonistic behaviour. *Behaviour* 24: 161–209.
- Hueck, K. 1966. *Die Vegetation Südamerikas*. Die Wälder Südamerikas. Stuttgart.
- Lanning, D. 1982. Survey of the Red-fronted Macaw *Ara rubrogenys* and Caninde Macaw *Ara caninde* in Bolivia, December 1981 – March 1982. Unpublished report to the New York Zoological Society and International Council for Bird Preservation.

- Lanning, D. 1991. Distribution and breeding biology of the Red-fronted Macaw. *Wilson Bull.* 103: 357–365.
- Levinson, S. T. 1981. The social behavior of the White-fronted Amazon *Amazona albifrons*. Conservation of New World parrots (R. F. Pasquier, ed.). Washington, District of Colombia, Smithsonian Institution Press/International Council for Bird Preservation Tech. Publ. No. 1: 403–417.
- Moore, B. R. 1992. Avian movement imitation and a new form of mimicry: tracing the evolution of a complex form of learning. *Behaviour* 122: 231–263.
- Pitter, E., & M. B. Christiansen. 1995. Ecology, status and conservation of the Red-fronted Macaw *Ara rubrogenys*. *Bird Conserv. Intern.* 5: 61–78.
- Power, D. M. 1966. Agonistic behavior and vocalizations of Orange-chinned Parakeets in captivity. *Condor* 68: 562–581.
- Rowley, I. 1990. The Galah. Behavioural ecology of Galahs. NSW.
- Serpell, J. A. 1981. Duets, greetings and triumph ceremonies: Analogous displays in the parrot genus *Trichoglossus*. *Z. Tierpsychol.* 55: 268–283.
- Solomon, J. C. 1989. Floristic inventory of tropical countries. Pp. 455–463 in Campbell, D. G., & H. D. Hammond, (eds.). Bolivia. New York.
- Trillmich, F. 1976. Spatial proximity and mate-specific behaviour in a flock of Budgerigars *Melopsittacus undulatus*: Aves, Psittacidae. *Z. Tierpsychol.* 41: 307–331.
- Ward, P., & A. Zahavi. 1973. The importance of certain assemblages of birds as “information-centres” for food-finding. *Ibis* 115: 517–534.
- Wyndham, E. 1980. Diurnal cycle, behaviour and social organization of the Budgerigar *Melopsittacus undulatus*. *Emu* 80: 25–33.