Do wild tamarins reconcile? Two case reports from moustached tamarins

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Abstract
Mechanisms of conflict resolution, e.g. reconciliation, have been reported from a number of group-living animals, particularly primates. However, whether or not conflict resolution occurs in the cooperatively breeding callitrichids (marmosets and tamarins) remains a matter of debate. Captive studies provide contrasting evidence for the occurrence of reconciliation, and no evidence has been previously available for wild groups. Here, I present data on post-conflict behaviour in wild moustached tamarins, *Saguinus mystax*, which suggest that reconciliation occurs among wild callitrichids, too. However, reconciliation seems to occur very rarely among these primates, probably due to the generally peaceful nature of their social relations.

Keywords *Saguinus mystax* · Aggression · Affiliation · Post-conflict behaviour

Introduction
Group living provides benefits to group members, e.g. reduced predation risk, but also creates conflicts among group members over resources like food and mates (Danchin et al. 2008; Krause and Ruxton 2002). Conflicts may disrupt social relations thereby compromising the stability and integrity of groups. Therefore, mechanisms such as reconciliation have evolved to modulate and resolve conflicts (Aureli and de Waal 2000). Reconciliation occurs when former opponents interact non-agonistically after a conflict, thus reducing the probability of further conflicts (Aureli and van Schaik 1991; de Waal and van Roosmalen 1979). Reconciliation has been demonstrated in a number of different primate and non-primate species (Arnold and Aureli 2007; Fraser and Bugnyar 2011; Lazzaroni et al. 2017). For callitrichid primates (marmosets and tamarins), evidence for reconciliatory behaviour is conflicting: while it has not been observed in captive red-bellied tamarins, *Saguinus labiatus* (Schaffner and Caine 2000; Schaffner et al. 2005), it is present in captive common marmosets, *Callithrix jacchus*, and captive cotton-top tamarins, *Saguinus oedipus* (Peñate et al. 2009; Westlund et al. 2000). To date, no researchers have published accounts of reconciliatory behaviour among wild callitrichids.

In this paper, I report observations on two behavioural events in wild moustached tamarins, *Saguinus mystax*, where one individual acted aggressively towards a group mate and then immediately showed affiliative behaviour towards that same individual.

Moustached tamarins live in groups of 3–10, rarely more individuals with a high level of genetic relatedness (Heymann 2000; Huck et al. 2005; Löttker et al. 2004). Breeding is usually restricted to a single adult female, resulting in a high reproductive skew among females (Garber 1997). Breeding females may mate with multiple adult males in the group, and adult males are generally the main infant carriers (Garber 1997; Heymann 1990; Huck et al. 2004). Since other group members also participate in infant carrying, *S. mystax* are considered as cooperative breeders (Garber 1997). Allogrooming is the principal social interaction, and aggression is very rare (Heymann 1996). The anecdotal nature of the observations precludes the rigid statistical test demanded to demonstrate this is reconciliation (Kappeler and van Schaik 1992). However, I discuss these observations in the context of theoretical consideration on why reconciliation should be absent or rare in cooperatively breeding animals (Kutsukake and Clutton-Brock 2008; Schaffner and Caine 2000).
Methods

The observations reported here were made during field work at the Estación Biológica Quebrada Blanco (EBQB) in northeastern Peruvian Amazonia (4° 21′ S 73° 09′ W). At EBQB, behavioural and ecological research on tamarins is conducted since 1985. Groups of S. mystax at EBQB are very well habituated to the presence of human observers to observe them at close range.

The first observation was made in 1995 while collecting behavioural data of a group of S. mystax (2 adult males, 2 adult females, 1 subadult male, 1 juvenile male, and 1 juvenile female) through instantaneous scan sampling at 10-min intervals and continuous recording of social interactions. The second observation was made in 2010 during a field course while the author was video-recording a grooming session of three S. mystax, members of a group of 2 adult males, 1 adult female, 1 subadult male, and 1 subadult female.

Tamarins can be individually distinguished by body size; size, shape, and pigmentation of genitals; and permanent natural markings (Löttker et al. 2004). The group observed in 2010 did not include any of the animals of the group in 1995.

Results

I observed two cases in which an act of aggression was immediately followed by affiliative behaviour of the aggressor towards the target of the aggression.

Case 1 (28 August 1995)

1100 h The group starts resting and allogrooming.
1149 h Adult male B starts grooming the subadult male; other group members are resting and allogrooming, including the adult female who is about 2 m away.
1153 h Adult male B stops grooming the subadult male, and both move towards the adult female. Upon arrival at the adult female, adult male B lunges at the subadult male. Immediately after the lunge, adult male B starts grooming the subadult male and continues until 1205 h. Then, both males simultaneously groom the adult female.

Case 2 (5 October 2010)

At around 1200 h, the tamarin group started resting and grooming on a small treefall gap. The grooming session and associated events involved one adult male, the subadult male, and the subadult female. Timeline (minutes:seconds) from the video (available at https://zenodo.org/record/3237722).

00:00 Adult male grooms subadult male; subadult female forages on the same trunk some 40–50 cm away (Fig. 1a).
00:12 Subadult female stops foraging and approaches the grooming males (Fig. 1b).
00:14 Subadult female starts grooming adult male 2 (Fig. 1c).
00:20 Adult male stops grooming, grabs at the subadult female, and bites into her neck (Fig. 1d); subadult female gives a bared-teeth squeal (Coates and Poole 1983) (Fig. 1e).
00:22 Adult male and subadult female continue grooming of subadult male (Fig. 1f).
01:28 Adult male stops grooming, grabs at subadult female, and bites into her head/neck, more intensively than at 00:20 (Fig. 1g).
01:29 Subadult female gives a bared-teeth squeal, more intensively than at 00:20 (Fig. 1h).
01:33 Adult male starts grooming subadult female (Fig. 1i).

The grooming of the subadult female by the adult male continued for 3:25 min. Then, the adult male started to groom the subadult male while the subadult female remained resting in between the two males.

In neither case did I see an obvious stimulus that might have triggered the aggression.

Discussion

In their predictive framework of conflict resolution, Aureli et al. (2002) posited that reconciliation and other post-conflict reunions are not required in animal societies where aggression is rare. Furthermore, Kutsukake and Clutton-Brock (2008) argued that reconciliation and other mechanisms of conflict resolution are less important in animal societies with a high reproductive skew. In fact, aggression rates are very low in tamarins, both in captivity and the wild (Heymann 1996; Schaffner and Caine 2000), and reproductive skew is high in female tamarins, with breeding generally being monopolized by a single adult female per group (French 1997; but see Culot et al. 2011). Therefore, on theoretical grounds, reconciliation and other mechanisms of conflict resolution are expected to be are or absent in tamarins and other callitrichids. Captive studies demonstrated the occurrence of reconciliation in callitrichids (Peñate et al. 2009; Westlund et al. 2000), but previously, there were no reports of this behaviour occurring in wild groups. Albeit anecdotal in nature, this paper indicates that reconciliation occurs in wild callitrichids, too.

Aggressive acts immediately followed by grooming of the victim were observed in S. mystax by Laurence Culot (pers. comm.: 1 group, September 2005–May 2008, 2303 contact
hours [see Culot et al. 2010]) and Mojca Stojan-Dolar (pers. comm.: 4 groups, February 2006–March 2007, ca. 1800 contact hours [see Stojan-Dolar and Heymann 2010]). Since these studies did not focus on social behaviour, no details were recorded. In a study on the social behaviour and mating system of *S. mystax* (Maren Huck and Petra Löttker, pers. comm.; 2 groups, January–December 2001, 6261 contact hours [see Huck et al. 2004]), no reconciliation was observed. This suggests that reconciliation is extremely rare, in line with theoretical predictions. Reconciliation has not been observed in studies on social behaviour and communication of sympatrically living black-fronted tamarins, *Leontocebus nigrifrons* (Yvan Lledo-Ferrer, pers. comm.: 3 groups, 1363 contact hours [see Lledo Ferrer et al. 2011]; Darja Slana, pers. comm.: 5 groups, May 2012–August 2013, 3868.7 contact hours [see Slana 2019]). There are no marked differences in social organization and behaviour between *S. mystax* and *L. nigrifrons*, although the number of adult males and females per group seems to be lower in the latter and the two species differ in patterns of olfactory communication (Heymann 2000, 2001). The extent to which other wild callitrichids employ reconciliation as mechanism of conflict resolution and whether interspecific differences exist remains to be determined. In conclusion, the two cases reported here indicate that reconciliation is a behavioural option available to wild callitrichids, at least tamarins, but that it is an extremely rare behaviour, probably due to the generally peaceful nature of their social relations, so that many observation hours must be accumulated to be recorded at all.

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Availability of data and material The video recording of one of the cases reported in this manuscript is available at https://zenodo.org/record/3237722.

Compliance with ethical standards

Conflicts of interest The author declares that there are no conflicts of interest.

Ethics approval Field research adhered to the “Guidelines for the treatment of animals in behavioural research and teaching” of the Association for the Study of Animal Behaviour and the Animal Behavior Society and
to the “Code of Best Practices for Field Primatology” of the American Society of Primatologists.

Consent to participate  Not applicable

Consent for publication  Not applicable

Code availability  Not applicable

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