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The effects of fur rubbing on the social behavior of tufted capuchin monkeys

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Abstract

Fur rubbing has often been attributed a social as well as a medicinal function in capuchin monkeys, yet to date there have been no studies investigating the effects of fur rubbing on subsequent group dynamics. Here we report for the first time how social group cohesion is affected by fur rubbing in tufted capuchin monkeys. Fifteen captive capuchins were each observed 6 times for 45 minutes, three times following the provision of materials typically used for fur rubbing (onion) and three times following control food items (apple). When compared to the apple condition, monkeys significantly increased proximity to one another in the first 15 minutes of the onion condition, which is when most fur rubbing took place. Moreover, monkeys were more likely to spend time in groups when fur rubbing but less likely to spend time in groups when manipulating the onion in other ways. In subsequent periods monkeys were less likely to be in proximity to one another in the onion condition compared to the apple condition. Aggression between group members was elevated whereas affiliation was decreased throughout the onion condition. In short, capuchins spent more time further apart and engaged in more aggressive acts and shorter affiliative acts following fur rubbing bouts. It is possible that these differences in behavior could be due to differences in how the monkeys competed for and interacted with the items presented in each condition rather than due to fur rubbing as such. Alternatively, fur rubbing with pungent materials might interfere with olfactory cues used to regulate social interactions within a group and thereby cause increased levels of aggression.

Keywords

Cebus apella; affiliation; aggression; group cohesion; proximity

When given the opportunity, capuchin monkeys engage in fur rubbing using plants or tissues from soft–bodied invertebrates that are pungent and/or physically stimulating. Monkeys typically first manipulate the fur rub material, e.g. bite into it or tear it apart, then take a piece of material into one hand and rub it with swift arm movements all over their bodies including the arms, legs, tail, flank and back. White-faced capuchins may salivate excessively during such rubbing bouts (Fragaszy et al., 2004) and curl their tails around other individuals (Leca et al., 2007), whereas tufted capuchin monkeys often fur rub with their tails curled around themselves (pers. obs.). Fur rubbing can be performed by a single monkey or, more commonly, small groups or the entire troop. Materials for fur-rubbing include e.g. *Citrus, Clemantis, Piper,* and *Sloanea* in the wild (Baker, 1996) or vinegar, onions, and tobacco in captivity (Ludes & Anderson, 1995).

Fur-rubbing is generally associated with medicinal functions in capuchin monkeys as it appears to repel ectoparasites and improve general skin condition. Several lines of evidence support

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this view. For example, Baker (1996) observed that a wild troop of white-faced capuchin monkeys showed significantly more fur rubbing bouts during the wet season when high heat and humidity may increase the risk of bacterial infections. Furthermore, the plants selected for fur rubbing contain secondary compounds with insecticidal, antiseptic, and anti-inflammatory properties (Huffman, 1997). Other primate species have also been observed to engage in fur-rubbing, including owl monkeys (Zito et al., 2003) and spider monkeys (Campbell, 2000). The latter showed several differences to capuchin monkeys. Campbell (2000) reports no increase in fur-rubbing bouts during the wet season, rubbing of only a limited area of the body, and an increased probability of fur-rubbing in males. Campbell (2000) proposed that fur-rubbing may have a scent marking rather than a medicinal function in spider monkeys.

Might fur rubbing serve other purposes also in capuchin monkeys? Several alternative functions of fur rubbing have been suggested, including establishment of a group scent, reinforcement of social ties, or facilitation of social grooming (Baker, 1996; Huffman, 1997). Indeed, fur rubbing appears to be socially facilitated in white-faced capuchins (Meunier et al., 2007), and social aspects are often emphasized in observational reports. For example, Baker (1996) noted how white-faced capuchins without fur rub material clustered around monkeys that held material and rubbed themselves on monkeys that had already applied material to their own fur, resulting in “a mass of wet, drooling monkeys…, squirming and rolling over and around each other” (pp. 266). It is possible that the tolerance and social interactions inherent in these displays reinforce social ties and may lead to an increase in positive interactions between group members. Leca et al. (2007) compared fur rubbing behavior of tufted and white-faced capuchins in captivity, and found that the fur rub behavior of white-faced capuchins was more socially oriented than that of tufted capuchins. Leca et al. (2007) hypothesized that fur rubbing might enhance social cohesion in white-faced, but perhaps not in tufted capuchin monkeys. To date, there have been no studies investigating how capuchin monkeys interact with each other after fur rubbing bouts.

The current study was designed to assess whether the social behavior of captive tufted capuchin monkeys is affected by fur rubbing. We used three variables to evaluate social group cohesion, namely aggressive interactions, affiliative interactions, and proximity to other monkeys. We observed the monkeys’ social behavior in two conditions: after encounters with onions (both consumed and used for fur rubbing) and after encounters with apples (consumed only). We hypothesized that monkeys would show increased levels of affiliation and decreased levels of aggression after interactions with onions compared to interactions with apples.

METHODS

Subjects

Study animals were 15 tufted capuchin monkeys (*Cebus apella*), 7 sub-adult animals (4–5 years old, 4 male and 3 female) and 8 adult animals (6+ years old, 2 male and 6 female). In addition, 6 juveniles (1–3 years old) and 4 infants (<1year old) were part of the group; infants and juveniles were not observed as focal subjects, but were included in the proximity measures for focal animals. All study animals were captive born and housed at the NIH Animal Center, Poolesville, MD, in an outdoor enclosure (ca. 250 m^3) enriched with perches, ladders and swings. Monkeys were not food-deprived and received daily supplements of fresh fruits, seeds and nuts. Water and commercial monkey biscuits were available ad libitum.

Procedure

Monkeys were observed once a day, five times a week between May and Sept 2007. Using focal animal sampling, we collected data on each individual in 6 sessions, three times in the onion condition and three times in the apple condition. In onion sessions, one yellow onion

(*Allium cepa*) was cut into quarters and separated into individual layers making ca. 30 pieces, which were placed onto a prominent platform within the enclosure. In apple sessions, an apple was quartered and sliced so as to resemble the onion pieces, and was placed onto the same platform. In each session, a randomly selected focal animal was observed for 45 min following the provision of apple or onion pieces. Using the Pocket Observer (PDA HP iPAQ Pocket PC hx2190 and The Observer 5.0, Noldus), we continuously recorded proximity to other animals (within arm's reach, ca. 30 cm or less), the durations of affiliative behaviors (groom, mount/clasp, play) and, due to their relative short durations, the frequency of aggressive acts focal animals were involved in (supplant, threaten, chase, attack). Finally, we recorded the durations of focal animals' interactions with onion and apple pieces, and the duration of any fur rubbing.

This study was approved by the Animal Care and Use Committee of the National Institutes of Child Health and Human Development and is in compliance with the Animal Welfare Act.

Data analysis

For analysis, we split the 45 min observation period into 3 observation periods of 15 min each, thereby allowing us to investigate changes across time periods. We combined all affiliative and aggressive behaviors to form two distinct variables, affiliation and aggression. We also created three proximity variables: proximity to 1 and 2 other animals was combined to express time spent in small groups, proximity to 3, 4 or more animals was combined to express time spent in large groups, and not in proximity to other animals. Repeated measures ANOVAs indicated that these variables did not change across the three sessions of either condition (all $p>0.05$). We therefore calculated an average value for each variable and each animal for both conditions.

RESULTS

Interactions with materials

Monkeys interacted in different ways with onions and apples. Apples were strongly monopolized by the alpha male and female, who gathered arms full of apple pieces and then retreated to a distant platform to consume these pieces. Five monkeys (2 adult females, 2 sub-adult males, and 1 sub-adult female) never obtained apple pieces throughout the experiment. Apart from briefly clearing the apple of sawdust, monkeys never manipulated the apple but consumed it immediately, making the average duration of apple interactions 1 min 27 sec (SD 2 min 16 sec). Interactions with apple pieces were largely restricted to the first observation period (99.8%, 0% and 0.2% of interaction were observed during the first, second and third observation period respectively).

In contrast, the alpha male and female would take only 1 or 2 onion pieces and immediately start manipulating, eating and fur rubbing on the same platform. Monkeys would often tear larger onion pieces apart and drop smaller pieces, which were then picked up by other monkeys. All monkeys obtained onion pieces at least once throughout the experiment. In addition to using onions for fur rubbing, monkeys also ate the onion, or manipulated it by tearing it apart, sniffing it, or biting into it but spitting it out again. These non-fur rubbing manipulations were performed for 4 min 42 sec on average (SD 3 min 19 sec).

Fur rubbing

Seven monkeys engaged in fur rubbing during all of their three onion sessions. Five monkeys showed fur rubbing behavior in only one or two onion sessions; for these monkeys, sessions in which no fur rubbing occurred were discarded from the analysis. Three monkeys (all adult females) were never seen fur rubbing despite manipulating and eating pieces of onion. Of those monkeys that did fur rub, the average length of fur rubbing was 4 min 33 sec (SD 3 min 23

sec). The majority of fur rubbing occurred during the first observation period (93.5%). Four monkeys were seen to fur rub during the second observation period (6.4%), and only one monkey in the third period (0.1%).

Social behaviors

Proximity—Repeated measure ANOVAs with observation period and condition as within-subject factors revealed that the period x condition interaction was significant for the amount of time monkeys spent alone ($F(2, 28)=4.0$, $p=0.03$) and in large groups ($F(2, 28)=5.9$, $p=0.007$), but not in small groups ($F(2, 28)=1.68$, $p>0.05$). Post-hoc comparisons indicated that monkeys spent significantly more time in large groups in the onion condition compared to the apple condition during the first observation period ($t(14)=2.67$, $p=0.018$), but not in later observation periods ($p>0.05$ for both second and third observation period). At the same time, monkeys spent similar amount of time alone in both conditions during the first and second observation periods (both $p>0.05$), but more time alone in the onion condition during the third observation period ($t(14)=2.11$, $p=0.054$; see Figure 1).

To determine whether the proximity patterns of the first observation period could be attributed to fur rubbing, we further analyzed the data of the first observation period in the onion condition. Excluding the 3 monkeys that did not fur rub, we calculated a percentage of time that each monkey spent in small groups, large groups, and alone when fur rubbing or when manipulating the onion but not fur rubbing. Paired sample t-tests showed that monkeys spent significantly more time in small groups and significantly less time alone when fur rubbing ($t(11)=3.3$, $p=0.007$ and $t(11)=-3.49$, $p=0.005$ respectively), and no difference for time spent in large groups ($t(11)=1.15$, $p>0.05$; Figure 2).

Aggression

A repeated measures ANOVA with observation period and condition as within-subject factors revealed a significant main effect for condition ($F(1, 14)=4.9$, $p=0.044$), but no effect for observation period ($F(2, 28) = 2.8$, $p>0.05$) and no interaction ($F(2, 28)=0.17$, $p>0.05$). As Figure 3a shows, levels of aggression were significantly elevated throughout the onion condition.

Affiliation

Affiliative interactions showed a main effect for condition ($F(1, 14)=15.67$, $p=0.001$) and for observation period ($F(2, 28)=10.11$, $p<0.001$), but no interaction ($F(2, 28)=0.41$, $p>0.05$). Affiliative interactions were reduced during the first observation period and increased steadily during subsequent observation periods for both onion and apple conditions. However, there were significantly shorter affiliative interactions in the onion condition (Figure 3b).

DISCUSSION

Fur rubbing, but not manipulating an onion otherwise, increased proximity between tufted capuchin monkeys in the present study. This effect, however, was only short-lived: in subsequent observation periods, monkeys spent less time in proximity to others in the onion (fur rubbing) condition than in the apple (control) condition. At the same time, levels of aggression were elevated and levels of affiliation were suppressed during and following interactions with the onion compared to interactions with the apple.

These results may seem surprising since most previous studies emphasized the seemingly positive social interactions during fur rubbing bouts. It should be noted, however, that subjects in those studies were usually white-faced capuchin monkeys (*Cebus capucinus*), either in the wild (e.g. Baker, 1996) or in captivity (e.g. Meunier et al., 2007). Leca et al. (2007)

hypothesized that the more socially tolerant white-faced capuchins might derive social benefits from fur rubbing whereas the more dominance-based tufted capuchins might not. The present study is in line with this hypothesis in that fur rubbing in our tufted capuchin monkeys was not associated with increased group cohesion. Instead, fur rubbing in the onion condition was associated with significant decreases in group cohesion.

Can the observed behavioral differences between the onion and the apple condition be attributed to fur rubbing itself? It appears that this is certainly the case for proximity measures, at least during the first observation period where monkeys were more social when fur rubbing than when manipulating onions otherwise. It is not clear why monkeys congregate during fur rubbing bouts; it might be argued that the present findings are simply the result of the conditions of captivity where space is necessarily restricted and thereby potentially leading to closer proximity between individuals. Nevertheless, this line of argument cannot explain why higher levels of proximity were found only during fur rubbing, but not other onion manipulations. Possibly, fur rubbing is an attractive behavior because it might be easier to scrounge pieces of material from fur rubbing than from non-fur rubbing individuals.

For proximity after fur rubbing bouts and aggressive and affiliative interactions, the situation is less clear. While the presence or absence of fur rubbing behavior was one difference between conditions, other factors should also be considered. For example, monkeys interacted differently with onions and apples. Apples were strongly monopolized by the alpha male and female, and several monkeys were never able to obtain apple pieces. On the other hand, all monkeys gained access to onion pieces. It could be argued that these different types of intra-group competition rather than fur rubbing might have caused the observed differences in proximity, aggression and affiliation. It could also be argued that monkeys might attach different values to apples and onion pieces. Potentially, onions caused more excitement among group members and as a result led to more aggressive interactions.

An alternative explanation might attribute a more causal role to fur rubbing. Tufted capuchins engage in urine washing where an animal urinates onto one hand and rubs the urine onto the sole of the ipsilateral foot (Fragaszy et al., 2004). Recent studies have suggested that urine washing might be used as an appeasement gesture since it is preferentially performed after aggression has been received (Miller et al., 2007). These findings indicate that in addition to visual and auditory cues, tufted capuchins might also use olfactory cues to regulate social group dynamics. Fur rubbing with pungent material might interfere with such olfactory cues, and therefore lead to disruptions of otherwise regulated social interactions. In other words, olfactory signals used by subordinate individuals to express submission might be overpowered by the pungent smell of fur rub material, and, potentially in addition to higher levels of intra-group competition for materials, might have attracted higher levels of aggression from dominant individuals. If this hypothesis is correct, tufted capuchins face a trade-off between the medicinal advantages and social disadvantages of fur rubbing behavior.

The results of the present study cannot support any of these hypotheses unequivocally. For example, there was considerable excitement in both conditions as evidenced by frequent food calls (pers. obs.). Baker (1996) used the expression ‘almost frenzied’ (p. 264) to describe the fur rubbing behavior of white-faced capuchins, which may be interpreted as heightened excitement during fur rubbing bouts. However, we did not observe any fur rubbing or other behavior throughout the present study that we would merit this description. Moreover, it should be noted that these captive monkeys did not have any external parasites or other fur conditions that might have biased the respective value of items. Data from other studies also fail to strongly support any one hypothesis. For example, situations such as the apple condition in which resources are monopolized have been associated with higher, not lower levels of aggression in wild tufted capuchin monkeys (Janson, 1985). Finally, very little is known about olfactory

communication between tufted capuchins. If fur rubbing with pungent materials interferes with olfactory cues and thereby increases the probability of aggressive interactions, it could be predicted that subordinate monkeys might be less likely to engage in fur rubbing because they are more likely to receive aggression from dominant individuals. To our knowledge, previous studies relating engagement in fur rubbing to dominance rank in tufted capuchins failed to find an association between the two (e.g. Leca et al., 2007).

In conclusion, the current results suggest that fur rubbing does not increase affiliative interactions between tufted capuchins; instead, fur rubbing was associated with an increase in aggressive interactions. Future studies might clarify whether it was the items provided for fur rubbing or fur rubbing itself that led to the observed decreases in social group cohesion. Failure to find increases in social group cohesion further reinforces the view that fur rubbing in tufted capuchin monkeys serves medicinal rather than communicative purposes.

Acknowledgements

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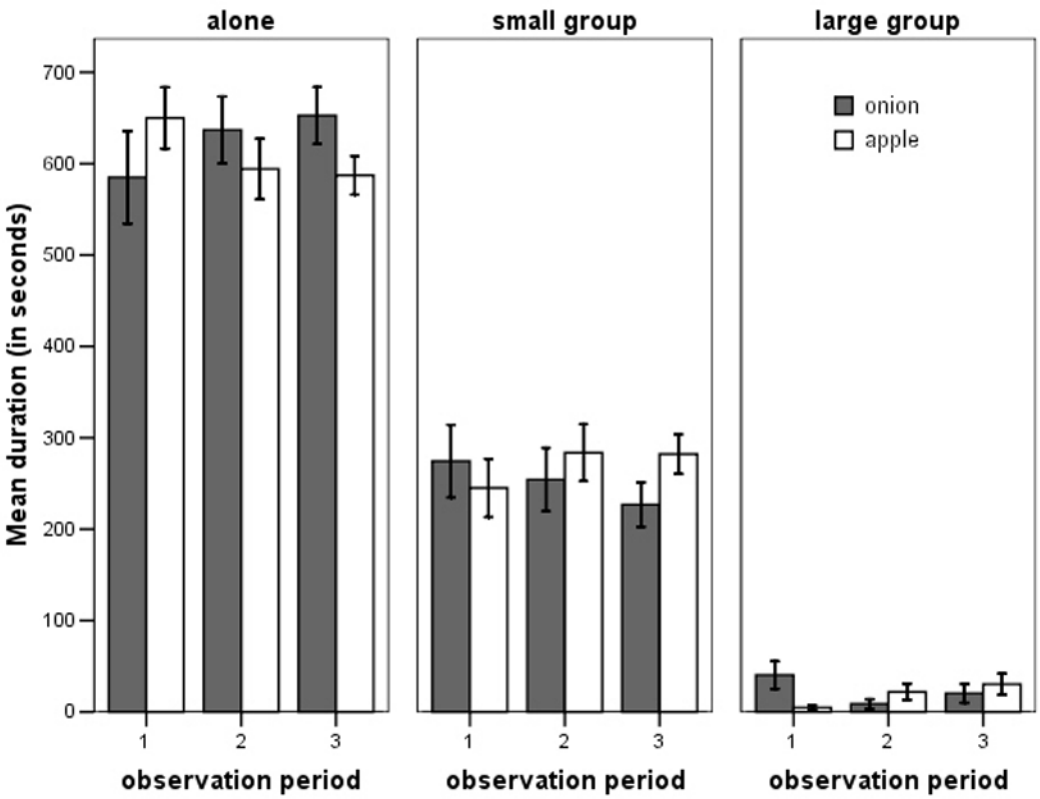

Figure 1.
Average durations spent alone, in proximity to 1–2 other animals (small group) and 3 or more other animals (large group) across observation periods. Grey bars represent onion condition, white bars represent apple condition, error bars represent standard errors.

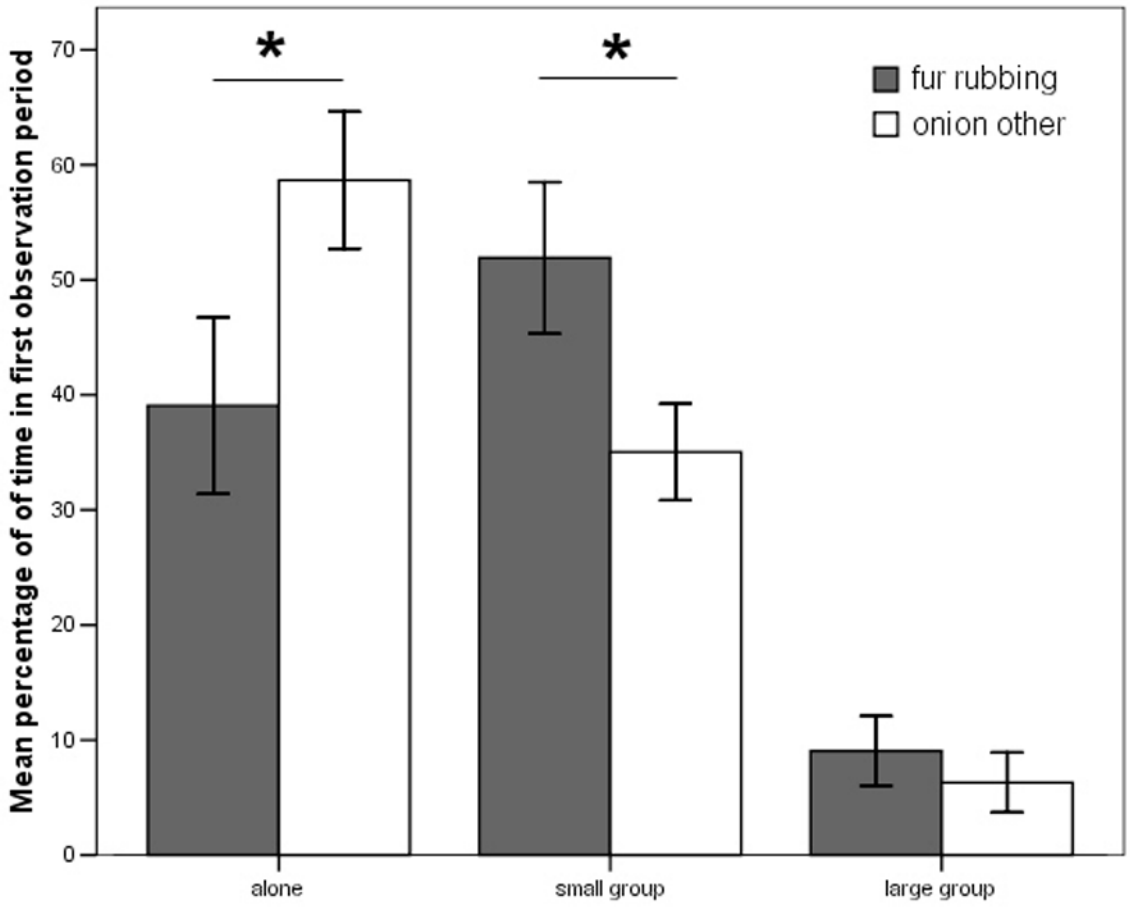

Figure 2.
Average percentages of time spent alone, in proximity to 1–2 other animals (small group) and 3 and more other animals (large group) whilst fur rubbing (grey bars) and whilst manipulating onions otherwise (white bars) during the first observation period. Error bars represent standard error, asterisk indicates $p<0.01$.

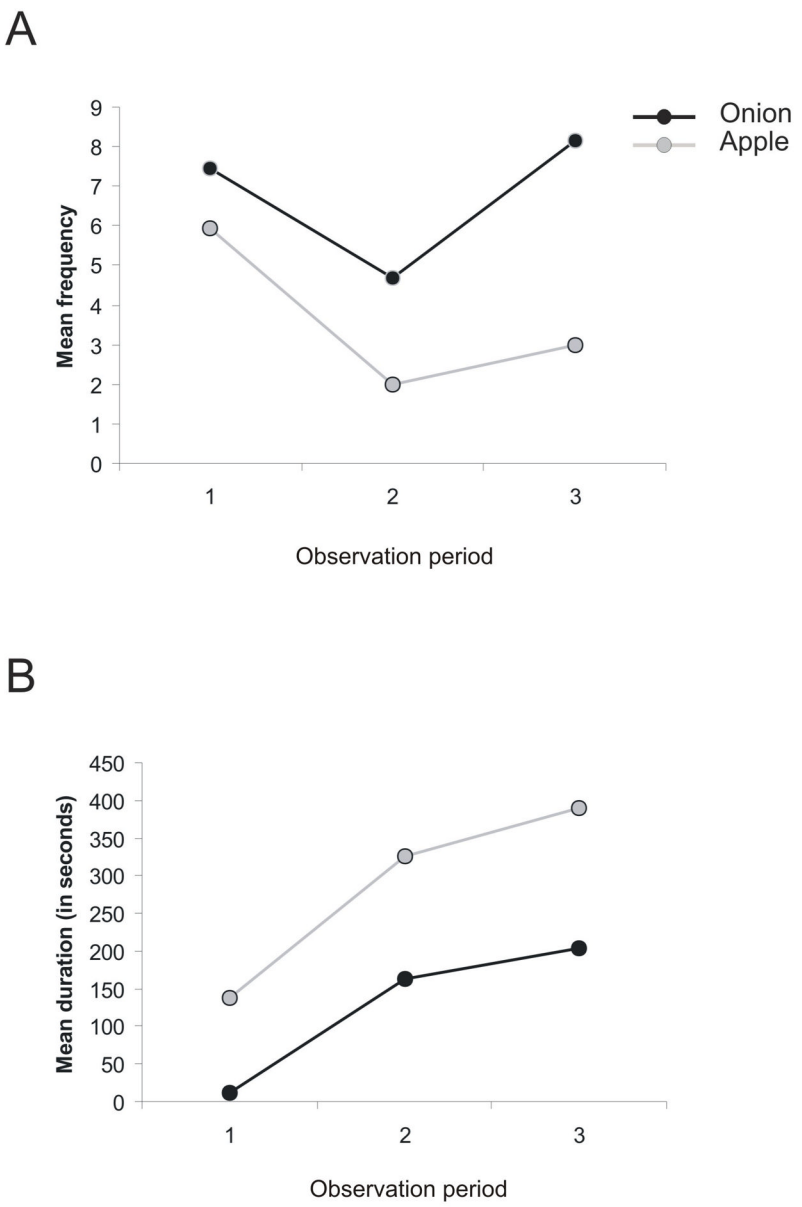

Figure 3.
Average frequency per individual of aggressive behaviors (a) and average duration per individual of affiliative behaviors (b) across observation periods. Black line represents onion condition, and grey line represents apple condition.