

Postconflict Third-Party Affiliation in Rooks, *Corvus frugilegus*

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Summary

Conflict features in the lives of many animal species and induces social stress mediated by glucocorticoid hormones [1]. Postconflict affiliation, between former opponents (reconciliation) or between former opponents and a bystander (third-party affiliation), has been suggested as a behavioral mechanism for reducing such stress [2], but has been studied almost exclusively in primates [3]. As with many primates, several bird species live in social groups and form affiliative relationships [4]. Do these distantly related animals also use affiliative behavior to offset the costs of conflict? We studied postconflict affiliation in a captive group of rooks. Unlike polygamous primates, monogamous rooks did not reconcile with former opponents. However, we found clear evidence of third-party affiliation after conflicts. Both initiators and targets of aggression engaged in third-party affiliation with a social partner and employed a specific behavior, bill twining, during the postconflict period. Both former aggressors and uninvolved third parties initiated affiliative contacts. Despite the long history of evolutionary divergence, the pattern of third-party affiliation in rooks is strikingly similar to that observed in tolerant primate species. Furthermore, the absence of reconciliation in rooks makes sense in light of the species differences in social systems.

Results

Rooks, a highly social species of corvid, roost and nest communally and forage in flocks [5]. Although longitudinal studies of marked individuals have not been conducted, it has been reported that pairs, which associate outside of the breeding season and often mate for life, return to the same nest site year after year [5], so a degree of group permanence may be assumed. Group living may bring rooks advantages, such as enhanced predator vigilance and information sharing, but it is also likely to lead to conflict over space and resources. Observations of our captive colony have documented that individuals form long-term affiliative relationships

with specific group mates throughout the year, engaging in exclusive affiliative interactions (e.g., allopreening and food sharing) as well as giving aid to one another in agonistic interactions [4]. Agonistic interactions occur over food and perching position, and sometimes without obvious cause (though likely competition for dominance). We aimed to discover what, if any, mechanisms rooks employ to minimize the costs of such conflict.

We examined the postconflict affiliation of a captive group of ten rooks (four male-female pairs, and two single females) by using the PC-MC methodology developed by primatologists [6, 7]. We recorded the affiliative behavior (Table 1) of individuals involved in dyadic conflicts and looked at contacts both with the former combatant (reconciliation) and with an uninvolved bystander (third-party affiliation) for the 10 min postconflict (PC) period. We compared these data to those taken during a 10 min matched control (MC) period. If affiliation occurred between the focal individual and another bird only in the PC period, or sooner in the PC period than in the MC, that pair was labeled “attracted.” If the reverse was true, the pair was labeled “dispersed.” If no affiliation occurred in either period, or if the affiliation occurred in the same minute in the PC and the MC, the pair was labeled “neutral.” For contacts between a combatant and a bystander, we then calculated a triadic contact tendency (TCT; following [7, 8]), which is equal to the number of attracted pairs minus the number of dispersed pairs divided by the total number of pairs.

Conflicts occurred between rooks from different partnerships (we saw no within-partnership conflict). We found no evidence for reconciliation in our group of rooks; former opponents never contacted one another, either in the PC or MC periods. However, both victims and aggressors engaged in third-party affiliation with their social partner at higher levels after conflicts than during control periods, as revealed when the data from seven of the partnered birds were analyzed with the PC-MC method (the male from one pair did not take part in enough conflicts to be included in the analysis). The difference between the mean proportion of attracted and dispersed pairs for both aggressors and victims was significant (see Table 2 for results of Wilcoxon signed-ranks tests). Contacts between former combatants and group mates other than the partner were not seen.

In our group of rooks, the majority of affiliative behaviors were coded as mutual (defined as both birds approaching each other without an obvious initiator), as opposed to directional (defined as one bird remaining stationary while the other approached). This was the case both in the PC (both for when the focal bird was the aggressor and for when the bird was the victim) and in the MC periods (mean proportions of behaviors coded as mutual, calculated by dividing the number of mutual behaviors seen in a 10 min focal period by the total number of behaviors seen: MC = 0.54 ± 0.057 ; PC aggressors = 0.56 ± 0.077 ; and PC victims = 0.55 ± 0.86).

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Table 1. Ethogram of Rook Social Behavior

Behavior Category	Behavior	Description
Aggressive	Displacement	One individual approaches and the other retreats.
	Challenged displacement	The approach-retreat interaction involves threat posturing [5] and/or vocalization by the aggressor, the victim, or both.
	Aggression	One bird pecks, feather-pulls, or aerially attacks another.
Affiliative (Directed)	Allopreening	One bird nibbles or strokes the feathers of another with the beak.
	Food sharing	One bird initiates the transfer of food to another, from beak to beak, often inserting the food into the throat.
Affiliative (Mutual)	Bill twining	Two birds interlock the mandibles of their beaks. Often this is accompanied by simultaneous displaying (see below).
	Dual feeding	Two birds feed from the same source simultaneously, sometimes manipulating the same food items.
	Dual object manipulation	Two birds manipulate an object, such as a stick, stone, or toy, simultaneously, sometimes engaging in a “tug-of war.”
	Displaying	Two birds engage in a synchronized bowing and tail-fanning display, accompanied by harsh vocalizations, as described in [5].
	Dual caching	Two birds cache food together, sometimes moving the same piece of food with their bills simultaneously.

However, when the directional behaviors alone were analyzed with the PC-MC method, we found that both combatants and third parties initiated more behaviors in the PC than in the MC period. (See Table 2 for results of Wilcoxon signed-ranks tests.)

We examined the temporal distribution of the first affiliative contacts in the PC and MC data and found that the highest proportion of first contacts fell in the first minute of the PC period (Figure 1). A Wilcoxon signed-ranks test revealed that the difference between the proportion of behaviors seen in the first minute of the PC and in that of the MC was significant ($T = 0, n = 7, p < 0.02$). This temporal pattern is the same as that found for majority of postconflict behavior described for other species (e.g., [9]).

The type of behavior used for postconflict third-party affiliation may shed light on its function. We investigated whether rooks employ specific behaviors at a higher level during the PC than the MC period by comparing proportions of each behavior (of all those seen) in each

focal type (Figure 2). For those behaviors seen at a higher proportion in the PC than in the MC (bill twining and displaying), we used Wilcoxon signed-ranks tests to investigate whether the difference was statistically significant. This revealed that the mean proportions of both bill twining and displaying were significantly higher in the PC than the MC both when the focal animal was the aggressor and when it was the victim (for bill twining, aggressors versus MC: $T = 0, n = 7, p < 0.02$; victims versus MC: $T = 0, n = 7, p < 0.02$. For displaying, aggressors versus MC: $T = 0, n = 7, p < 0.02$; victims versus MC: $T = 0, n = 7, p < 0.02$). There was no significant difference between aggressors and victims in the proportion of either behavior during PC periods (for bill twining, $T = 8, n = 7, p > 0.02$; for displaying, $T = 8, n = 7, p > 0.05$).

Discussion

There is evidence that reconciliation serves to restore relationships between former opponents and therefore to reduce the risk of renewed attack and stress associated with the uncertainty of the relationship's future (see [10] for a review). Aureli and colleagues [10] have therefore suggested that in any group of social living animal, reconciliation is only likely to be favored if conflicts disrupt valuable relationships, the so-called “valuable relationship hypothesis.” This hypothesis is supported by the fact that levels of reconciliation are highest between individuals with valuable relationships (reviewed in [10]). The distribution of such relationships in social groups of mammals and birds is likely to be very different, largely because of their divergent reproductive and developmental biology. There is a much greater asymmetry between the sexes in mammals than in birds, both in the physiological propensity and in the selective advantage to give care to the young. Consequently, for the majority of birds, monogamy is favored, whereas for the majority of mammals, polygyny is optimal. In any given species, this evolutionary legacy interacts with ecological factors

Table 2. Results of PC-MC Analysis of Third-Party Affiliation

	n	Mean Proportion Attracted	Mean Proportion Dispersed	Mean TCT	T	p
Aggressors	7	0.85	0.06	0.78	0	0.02
Victims	7	0.86	0.06	0.80	0	0.02
Combatants	7	0.35	0.10	0.25	0	0.02
Initiate						
Third Parties	7	0.30	0.10	0.20	2	0.05
Initiate						

Mean triadic contact tendencies (TCT) between combatants ($n = 7$ birds) and their social partners, which were not involved in the conflict. TCTs are presented for when the combatant was the aggressor and for when it was the victim (top two rows), and for when contact was initiated by the combatant and by the third party (bottom two rows). Test statistics and p values are from Wilcoxon signed-ranks tests of the difference between the proportions of attracted and dispersed pairs.

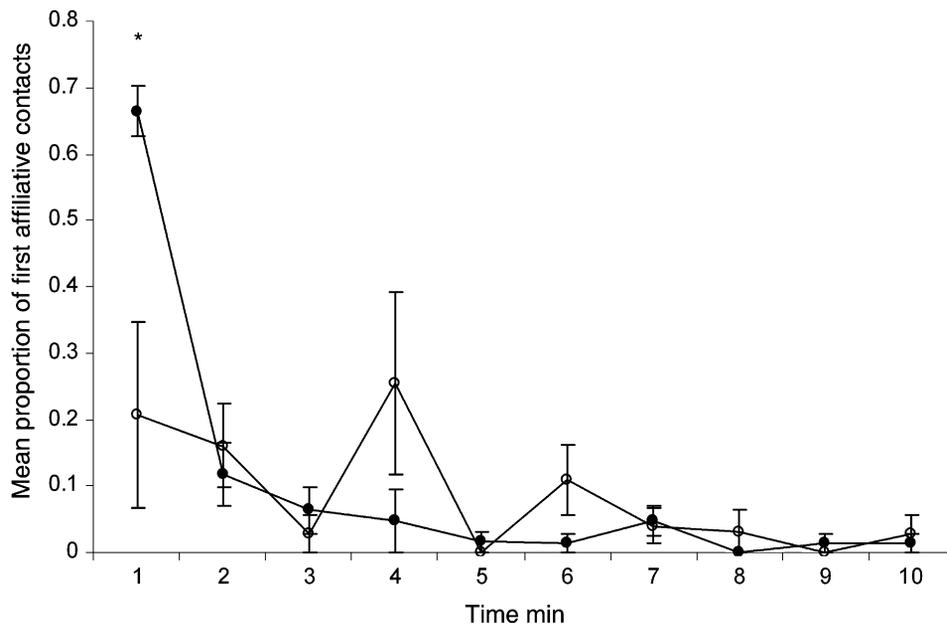


Figure 1. Temporal Distribution of First Affiliative Contacts

Mean proportion of first affiliative contacts between combatants and their social partners (which were not involved in the conflict), in the post-conflict period 10 min after a fight (PC, filled circles) and in a comparable matched-control period (MC, open circles). Error bars represent standard errors of the means (SEM). * indicates $p < 0.05$ (Wilcoxon signed ranks).

to dictate the social system, which in turn will dictate the distribution of valuable relationships within a social group.

For group-living polygamous mammals, maintaining valuable relationships with a wide range of individuals should be favored because several individuals may have value not only as potential mates, but also as cooperative partners for use in securing mates or defending offspring, as well as in the competition for food. Exactly which individuals form valuable relationships will depend on the species' social system [11]. For example, many species of macaque have social systems in which valuable relationships are seen between kin. However, for group-living monogamous birds, regardless of social system, the most valuable relationship is likely to be that with the mating partner (although in addition, birds living in cooperatively breeding social systems might be expected to maintain valuable relationships with helpers). In most birds, unlike most mammals, both parents provide care to the offspring. The partnership therefore derives value not only from the immediate benefits of reproduction, but also from the cooperative nature of brood care, as well as territory and nest defense. For species, such as rooks, that pair for life, there are also the benefits of future reproduction. In our captive group of monogamous rooks, we can therefore posit that valuable relationships exist between mating partners. The fact that affiliative behavior is seen exclusively within partnerships [4] reinforces this view.

The present study has shown that our rooks do not reconcile conflicts, probably because aggression was only observed between individuals with nonvaluable relationships. This result is similar to that from a study of cooperatively breeding red-bellied tamarins, in which conflicts are mild and do not disrupt valuable relationships; that study also reported an absence of

reconciliation [12]. These results are in accordance with the predictive framework of Aureli et al. [10].

Spectacled leaf monkeys, gorillas, chimpanzees, bonobos, and human children have been suggested to use postconflict third-party affiliation as an "alternative mechanism" for reducing stress after conflicts that are not reconciled [13–19]. As an extrapolation of this argument, for species in which reconciliation is not seen at all, third-party affiliation may be the only mechanism by which stress is countered. However, a recent study found no evidence that third-party affiliation serves to reduce stress in chimpanzees, nor that third-party affiliation is used as an alternative to reconciliation [20]. Postconflict third-party affiliation has also been suggested to strengthen bonds between allies and to signal allied status to other members of the group [21]. Das and colleagues [22] examined the function of third-party affiliation in long-tailed macaque aggressors (victims do not show third-party affiliation). Examination of stress-related behaviors revealed that conflicts were stressful, but that similar to the findings for chimpanzees, third-party affiliation did not serve to reduce stress levels, unlike reconciliation. The results were more consistent with the idea that third-party affiliation serves to strengthen bonds between allies and to signal the existence of these bonds to other group members [22]. An explicit test of the function of third-party affiliation in rooks was not possible in our study, largely because of the low proportion of conflicts that were not followed by this behavior (for comparison), but also because of the lack of a known behavioral indicator of stress in rooks. However, through a closer look at the pattern and form of the third-party affiliation we recorded, and comparison with the other species studied to date, we shall aim to assess possible functions of this behavior.

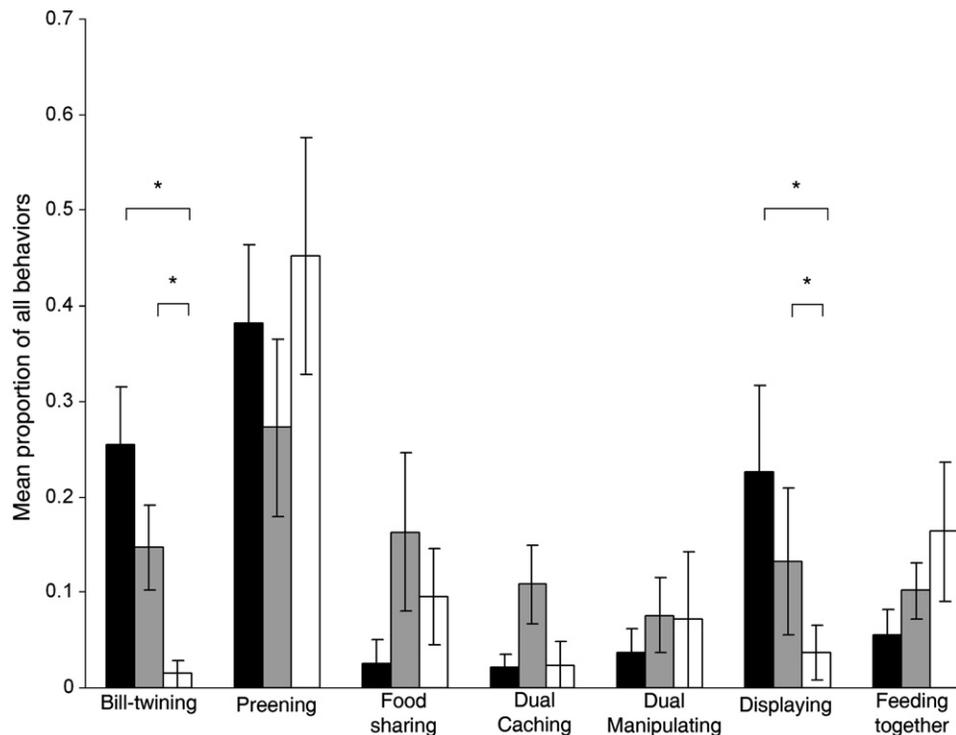


Figure 2. Proportions of Specific Affiliative Behaviors

Proportions of specific affiliative behaviors (bill twining, allopreening, food sharing, dual caching, dual manipulating, displaying, and feeding together) between combatants and their social partners, which were not involved in the conflict. Data shown for postconflict period for aggressors (black bars) and victims (gray bars) and during matched-control periods (clear bars). Error bars represent SEM. * indicates $p < 0.05$ (Wilcoxon signed ranks).

Which Opponent Is Involved?

With the exception of rhesus macaques, long-tailed macaques, and pig-tailed macaques, for which only the aggressor engaged in higher levels of affiliation with third parties [7, 9, 22, 23], the primate studies that examined the behavior of aggressors and victims separately found that both opponents engage in third-party affiliation [8, 13, 20, 24–26]. Importantly, for stump-tailed macaques, this result was only found when the identity of the third parties and the specific behaviors used were analyzed separately [8]; such an analysis was not performed in the earlier studies of the three other macaque species [7, 9, 22, 23]. In rooks and most primates, therefore, it would seem that third-party postconflict affiliation benefits both victims and aggressors. This would make sense if the function involves the reduction of stress, given that conflict induces stress in both initiators and recipients of aggression [27]. It is also consistent with the notion that the behavior serves to strengthen bonds, or to signal alliances to other group members.

Identity of the Third Party

The direction of postconflict affiliation by individuals exclusively to their social partner in our group of rooks is, at first glance, in contrast to that reported for primates, which are not known to restrict their postconflict affiliation to one other individual. However, all primate studies that analyzed third-party identity found that opponents did not affiliate at random, but instead showed selectivity. As Das [21] has pointed out, many of these patterns

are consistent with the idea that relationship value is a critical factor for third-party postconflict affiliation (as well as reconciliation), because the identities of the third party map on to the social systems of the different species. For example, gorilla females tend to affiliate with males [14] and immature gorillas with their mothers [28]; olive baboon females with males, particularly those that recently gave them support in agonistic encounters [29]; kin-bonded species of macaque with their own kin [9, 21, 30]; and egalitarian chimpanzees and spectacled leaf monkeys with preferred grooming partners [13, 25] (though see [18] for a contrasting result with chimpanzees). In these studies, the third party was therefore found to be a valuable individual that posed less risk of aggression than other group members. This observation suggests that the function of third-party affiliation in both rooks and primates is one best served by affiliation with valuable partners. Possibilities include strengthening bonds between social allies and dampening the stress response.

In some primate groups, there is evidence that third-party affiliation may serve a further function, namely indirect reconciliation, because studies of macaques and vervet monkeys have found that former aggressors engage in contact with the kin of their targets, which reduces the risk of future attack from the aggressor (discussed in [21]). This type of contact was not seen in our group of rooks. The number of focal samples in which further aggression was seen was low, and so the risk of attack by the former aggressor does not

seem to be high for rooks, which might explain the absence of this behavior.

Who Initiates?

In our rook group, the majority of contacts seen between former combatants and their social partner were mutual rather than directed, although both combatants and third parties initiated contacts. The behavior therefore seems likely to be underpinned by direct or indirect mutualism: Either the benefit of the behavior applies equally to former combatants and their social partners (signaling alliance; strengthening bond; or stress reduction, if watching the involvement of the social partner in a fight is stressful), or the benefits only apply to the combatant, in which case the behavior might be maintained by reciprocity.

Among primates, third-party-initiated postconflict affiliation is rare and has only been documented for chimpanzees, bonobos, stump-tailed macaques, and gorillas [2, 8, 17, 28], whose societies are relatively egalitarian. Studies of several despotic species of macaque have documented an absence of postconflict affiliative contacts initiated by third parties (reviewed in [31]). In these species, which are characterized by low levels of social tolerance, it has been suggested that greater risk of attack by the original aggressor may be one reason why uninvolved third parties do not initiate contacts [24]. Among corvids, communal-living rooks have a high level of social tolerance. A comparison with other corvid species, such as territorial carrion crows (*Corvus corone corone*), would provide further support for the importance of social tolerance in dictating the pattern of postconflict affiliation with bystanders.

Behavior Employed

A few primate studies have identified the use of a particular behavior for third-party affiliation. However, to our knowledge, the use of a behavior little seen outside of the postconflict context has only been reported for chimpanzees and spectacled leaf monkeys, which have been reported to use “embracing” for third-party postconflict affiliation [2, 13]. In our group of rooks, “bill twining” and “displaying” were employed at a significantly higher proportion in the postconflict period, and bill twining was only once recorded in a matched control. The use of a special behavior has been suggested to “advertise” third-party affiliation [13]. Perhaps this is an indication that postconflict affiliation in rooks serves to signal alliances to other group members.

Timing

All studies that analyze the temporal distribution of postconflict behavior in primates report that it is highest in the first 1–2 min after the aggressive bout. This pattern was also found in our group of rooks. It has been suggested that this is indicative of the potential stress-reducing role of the behavior, given that stress levels of former combatants peak during this time window [32].

Conclusions

Although several primatologists have hypothesized that the benefits of postconflict affiliation apply to any group of animal living in a permanent group with individualized relationships [10], this is the first study to confirm its

convergent evolution in an avian species. Furthermore, the pattern and distribution of postconflict behavior in our colony of rooks is consistent with the predictions drawn from studies of primates, once the differences in mating and social systems are taken into consideration. Similar to the findings for red-bellied tamarins [12], for which conflicts do not disrupt valuable relationships, we found no evidence for reconciliation in our captive group of rooks, in which aggression was only seen between nonvaluable partners. This result is therefore consistent with the valuable-relationship hypothesis, although other explanations for the absence of reconciliation in rooks are possible. Though the analysis was based on a relatively small sample size (37 conflicts) compared to other studies of reconciliation, the absolute absence of contact between former opponents is clear. We found clear evidence for third-party affiliation and furthermore report some striking similarities between this behavior in our rooks and that reported for primates; these similarities are consistent with the view that the function of the behavior in both rooks and primates is best served by affiliation with a valuable partner. The function of third-party affiliation remains to be explicitly tested, both for rooks and for most species of primate, although dampening the stress response, strengthening bonds, and advertising alliances seem to be likely candidates. Future studies examining stress-related behaviors are likely to shed more light on this point. Further investigation of postconflict behavior in groups of animals with different social systems (e.g., cooperative breeders, polygynous birds, and monogamous mammals) would be an interesting avenue for future research.

Experimental Procedures

Study Animals and Housing

The captive colony consisted of ten rooks, which were obtained as 15–18-day-old nestlings on April 21, 2002 from four nests in Cambridge and then subsequently hand-raised. At the time of the study, they were housed in an outdoor aviary at the Sub-department of Animal Behavior, Madingley (approximately 8 m × 10 m × 3 m). The group consisted of four male-female pairs and two single females. Food (a combination of fruit, dog biscuits, pasta, bread, birdseed, meat, and eggs) and water was available ad libitum, and the maintenance diet was typically provided between 9 and 11 a.m.

Data Collection and Analysis

Data were collected from 1 hr observations carried out by two observers almost daily between 2 and 4 p.m. Because competition over food has been found in other groups to result in different patterns of postconflict behavior, we purposefully chose a time during which little food competition was seen. Observations were carried out between October and December (and therefore outside of the breeding season) in 2004 and 2005. Observers were able to view the birds from an observation hut adjoining the aviary in order to avoid any effect of the presence of an observer on the birds' behavior. The birds were clearly visible in all but a small part of their aviary (which, fortunately, was visited rarely), and all vocalizations could easily be heard.

Data on the social behavior of the birds were taken ad lib [33] for use in analyzing affiliation patterns. Postconflict (PC) data were taken for 10 min after an instance of unambiguous aggression (challenged displacements or aggressive interactions, Table 1), during which both the aggressor and victim were followed as focal individuals for 10 min and any affiliative behavior was recorded. For behavioral bouts with clear directionality, and for unambiguous cases in which one bird flew to another and initiated a mutual behavior

such as bill twining, we recorded the identity of the initiator; any other behaviors were coded as mutual.

On the next available day and at precisely the same time (provided that no aggressive interaction had occurred in the 10 min preceding it, in which case at the nearest possible time), focal samples were taken of the same two individuals for use as a matched control (MC). PC or MC observations were aborted if another bout of aggression occurred, if the birds flew into the unobservable part of the aviary, or if there was an external disturbance (such as a low-flying plane). An aborted MC would be repeated on the next possible day.

There were 70 PC-MC pairs available for analysis (35 victims and 35 aggressors), with a mean of 8.25 conflicts for each individual included in the analysis. Because the fights were always between members of different partnerships, data from each member of a social partnership were independent. We analyzed the data following the PC-MC method developed by de Waal and Yoshihara [7], as described above. Nonparametric statistics were used throughout the analysis because, for the most part, the data did not satisfy the conditions of normality. Wilcoxon signed-ranks tests were conducted by hand because of the small sample size ($n = 7$) [34], following the method described in [35]. Alpha was set at 0.05. All tests were two-tailed.

This research adhered to all UK Home Office and University of Cambridge regulations concerning use of nonhuman animals in research.

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