

Ravens Intervene in Others' Bonding Attempts

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Summary

The competition for power in a complex social world is hypothesized to be a driving force in the evolution of intelligence [1]. More specifically, power may be obtained not only by brute force but also by social strategies resembling human politics [2]. Most empirical evidence comes from primate studies that report unprovoked aggression by dominants to maintain power by spreading fear [3] and third-party interventions in conflicts [4–6]. Coalitionary support has also been described in other animals [7, 8] and is often linked to social bonding [9, 10]. As coalitions can lead to a gain in power [5, 11] and fitness benefits [12], individuals may try to prevent coalitionary support or indirectly prevent others from forming social bonds that might lead to coalitions. Although there is some empirical evidence that coalitionary support can be manipulated [13], little is known about the indirect strategy. We show here that wild ravens (*Corvus corax*) regularly intervene in affiliative interactions of others even though such interventions are potentially risky and without immediate benefits. Moreover, the identities of both interveners and intervened pairs are not randomly distributed. Ravens with existing ties initiate most interventions, and ravens that are creating new ties are most likely to be the targets of interventions. These patterns are consistent with the idea that interventions function to prevent others from forming alliances and consequently becoming future competitors. We thus show previously undescribed social maneuvers in the struggle for power. These maneuvers are likely to be of importance in other social species as well.

Results and Discussion

Common ravens (*Corvus corax*) are renowned for their sophisticated social behavior, including affiliative interactions like allopreening and various types of third-party interactions [8, 14]. Although the structure of raven flocks is dynamic [15], there nevertheless exists considerable social structure, including differentiated social relations. Notably, dominance ranks are heavily dependent on the bonding status of male-female pairs [16], with established breeding pairs (pair-bonded) at the top of the hierarchy, followed by bonded individuals without a breeding territory (strongly bonded), which in turn outrank individuals that are in the process of establishing a bond (loosely bonded). At the bottom of the hierarchy we find those

individuals with no specific bonds (nonbonded). It has recently been shown that ravens can remember social bonds for years [17] and can even track the dominance relations of others (third-party understanding [18]). Here, we investigated whether ravens can also act upon their social knowledge and selectively intervene in affiliative interactions of conspecifics with a different bonding status. Using behavioral sampling methods, we studied all occurrences of affiliative interactions and all of the associated third-party interventions in a free-ranging population of about 300 wild ravens in the Austrian Alps, of which ~200 were individually marked (for detailed methods, see the [Supplemental Experimental Procedures](#) available online). The underlying assumption of our study was that repeated third-party interventions by a given individual toward a particular dyad might indicate attempts to manipulate the formation and/or maintenance of the bond between individuals in this dyad. Specifically, well-bonded ravens might preserve their high status by intervening in affiliative interactions between ravens that are about to form a bond. Nonbonded birds, in contrast, might face the risk of two-on-one aggression when intervening in affiliative interactions of bonded birds.

We show that intervening in affiliative interactions is a relatively common behavior in our population of wild ravens. Out of 564 affiliative interactions observed during a six-month period, 106 (18.8%) experienced intervention by a third party, with a total of 94 individually marked ravens contributing to the data set. Intervening ravens either showed aggression toward the affiliating individuals (75 instances, 70.8%) or merely placed themselves between them (31 instances, 29.2%). As expected, engaging in interventions posed some risk to the intervener. Although 52.8% of all interventions were successful (i.e., the birds engaging in affiliative interactions were separated), 22.6% of the interventions had an indecisive result (i.e., all three birds either stayed or left), and 24.5% resulted in joint aggression of the affiliating birds against the intervener, which then had to retreat. Aggressive interventions were significantly more likely to be successful than when birds merely placed themselves between the two affiliating birds (62.7% versus 29.0%, $\chi^2 = 68.18$, $p < 0.001$). Binomial analyses of whether or not an intervention was successful revealed marginal effects of the bonding status of both the third-party intervener and the individual experiencing the intervention, which were, however, not statistically significant ([Figure S1](#); [Tables S1](#) and [S2](#)).

Different effects of bonding status became more apparent when we focused on the two critical questions of (1) who intervenes and (2) which pairings are the targets of an intervention. Concerning the first question, the best-fitting model ([Table S3](#)) for the rate of interventions in affiliative interactions of each individual contained only a significant effect of bonding status ($F = 3.636$, $df_1 = 3$, $df_2 = 90$, $p = 0.016$), whereas we found no effect of sex or age class of the intervening individual. [Figure 1](#) illustrates the pattern, and post hoc tests revealed that pair-bonded and strongly bonded individuals intervened most often.

Concerning the second question, the best-fitting model ([Table S4](#)) for the proportion of each individual's affiliative interactions that were interrupted also showed a significant

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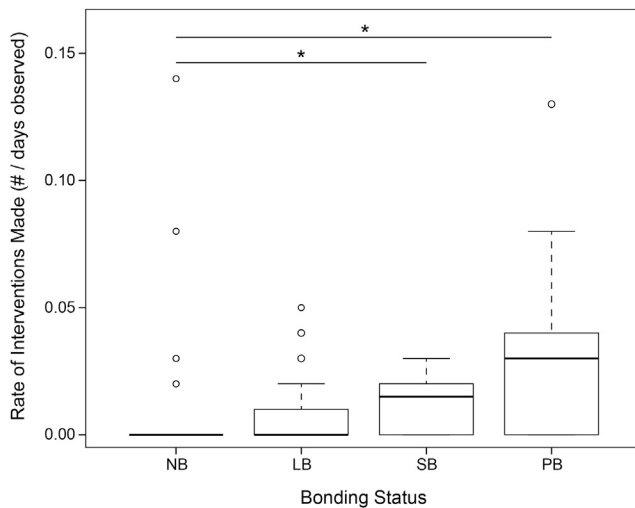


Figure 1. Who Intervenes?

Median rate (interquartile range \pm smallest and largest nonoutlier) of interventions in affiliative interactions of others made by nonbonded individuals (NB), loosely bonded individuals (LB), strongly bonded individuals (SB), and pair-bonded individuals (PB). * $p < 0.05$ by post hoc Mann-Whitney U tests with Holm-Bonferroni correction. See also Table S3.

effect of bonding status ($F = 3.261$, $df_1 = 3$, $df_2 = 68$, $p = 0.027$) and, again, no effect of sex or age class. Interestingly, post hoc tests revealed that the affiliative interactions of individuals that were trying to establish a bond (loosely bonded) were interrupted most often (Figure 2).

Finally, in an attempt to combine both questions, we investigated the amount of interventions that birds of different bonding status experienced depending on the bonding status of the third-party intervener (see Table 1). Binomial analyses revealed that nonbonded birds did not have a significant preference for targeting dyads of a particular bonding class, whereas loosely bonded, strongly bonded, and pair-bonded ravens preferentially intervened in interactions of loosely bonded birds (see also Supplemental Experimental Procedures and Figure S2).

Taken together, our results show that the stronger the bonding of the male and female raven pair, the more they intervene in affiliative interactions of others, irrespective of their individual sex and age class, and that interventions affect mainly those individuals that are trying to establish a bond themselves. It should be noted that because these results are derived from separate analyses, they cannot be integrated into one interpretation, namely, that strongly bonded individuals intervene particularly in the affiliative interactions of loosely bonded individuals. Unfortunately, our data set on wild ravens did not allow us to identify when birds did *not* intervene in affiliative interactions. However, analysis of the number of occurrences per bonding status indicates that as soon as ravens are bonded, they specifically target ravens that are loosely bonded.

Moreover, we show that interventions in affiliative interactions are risky and can cause counteraggression. Therefore, an opportunistic perspective would predict that the affiliative interactions of nonbonded individuals will experience the most interventions, much like how monkeys tend to support higher-ranking individuals against individuals they themselves already outrank [19], so-called status quo-maintaining, non-rank-changing, all-down coalitions [5]. Interestingly, however,

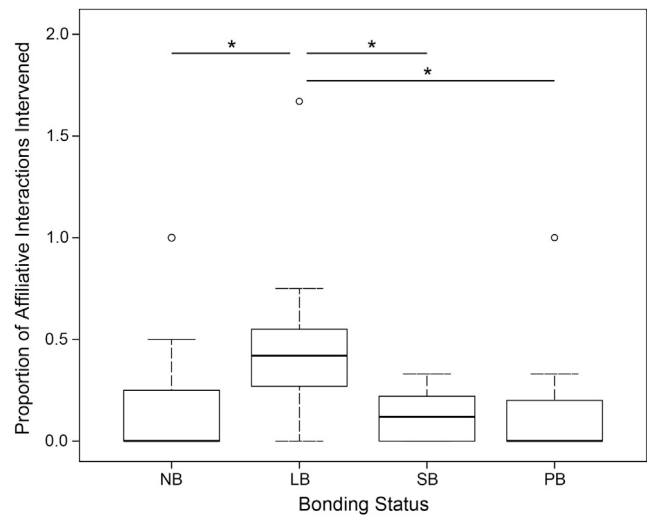


Figure 2. Who Is the Target of Interventions?

Median proportion (interquartile range \pm smallest and largest nonoutlier) of affiliative interactions of nonbonded individuals (NB), loosely bonded individuals (LB), strongly bonded individuals (SB), and pair-bonded individuals (PB) in which a third party intervened. Proportions above 1 represent individuals who had affiliative interactions in which a third party intervened more than once. * $p < 0.05$ by post hoc Mann-Whitney U tests with Holm-Bonferroni correction. See also Table S4.

it was not the affiliative interactions of the nonbonded ravens but rather those of the loosely bonded individuals that experienced the most interventions. Social bonds between ravens are created and maintained by affiliative interactions such as the ones we describe here, and over time, these affiliative interactions become more intense and reciprocal [8]. As a consequence, the bonded pair will rise in rank [16]. Selectively intervening in such interactions may hinder the formation of these bonds and the subsequent rise in rank. Future research should aim to investigate whether these interventions do in fact inhibit the formation of these particular bonds.

Possible Implications of Third-Party Interventions in Affiliative Interactions

That ravens specifically choose to intervene in the affiliative interactions of loosely bonded individuals seems suggestive of sociostrategic behavior. First, they do not need to break up the affiliative interactions of nonbonded individuals, since without a specific partner choice, these do not form a threat. Second, they are less likely to break up the affiliative interactions of strongly bonded individuals, either because it is already too late to do so or because the incurred costs might be too high compared to the gains. Consequently, we feel that the intervention in affiliative interactions of those individuals that are still forming their bonds may reflect a strategic behavior relating to the competition over power and associated resources, e.g., breeding territories and access to food. Additionally, as this behavior occurs rather often, it seems to be an important mechanism for reducing competition.

Although many nonhuman animals form differentiated social bonds [9, 20] characterized by close proximity and affiliative behavior such as preening and grooming [21–23], surprisingly little data is available on third-party interventions in those affiliative interactions, and hence it is difficult to compare the current findings in ravens with those of other animals. To our knowledge, apart from one descriptive study on stump-tailed

Table 1. Interventions per Bonding Class of Intervener and Targets

Intervener (Third Party)	Bonding Class	n Attempts	n Individuals	Bonding Class of Targeted Pair				Total
				NB	LB	SB	PB	
PB		25	10 (5 M, 5 F)	3	12	5	5	25
SB		20	7 (4 M, 3 F)	0	14	6	0	20
LB		12	8 (6 M, 2 F)	2	8	1	1	12
NB		9	8 (3 M, 5 F)	2	4	2	1	9
Total		66	33 (18 M, 15 F)	7	38	14	7	66

Number of attempted interventions in the affiliative interactions of individuals that were pair bonded (PB), strongly bonded (SB), loosely bonded (LB), or nonbonded (NB), by males (M) and females (F) of each of those four bonding classes. Note that this table refers to a subset of the data, as it reflects only those interventions in which both the identity of the third-party intervener and the identity of at least one of both affiliating individuals was known. See also Figure S2.

macaques [24], the phenomenon of third-party interventions in affiliative interactions has thus far received hardly any attention in the primate literature. In two reports published on horses, the focus was only on the interveners, and the results were conflicting (interveners were either high or low ranking) [25, 26]. Unfortunately, no data on the possible function of these interventions are available. We therefore encourage future studies to focus on the occurrence and function of third-party interventions in affiliative interactions. We expect that these behaviors may be present in any species that form social bonds and rely on coalitions in the struggle for power, including primates (e.g., [5, 11]), dolphins [27], hyenas [28], other corvids [29], and possibly fish [30].

Possible Mechanisms of Third-Party Interventions in Affiliative Interactions

As in primates [31], the bonding status of ravens cannot be observed directly but needs to be inferred from the quality and/or reciprocity of affiliative interactions [8, 16]. Affiliative behaviors per se are also shown by nonbonded birds, suggesting that ravens—much like their human observers—recognize others' social bonds on the basis of certain features (e.g., length or equity of allopreening bouts) and/or the history of interactions between particular dyads. Note that the ability to recognize others' bonds does not explain what makes ravens act on a particular bonding class. It could be that they have a predisposition to intervene in others' affiliative interactions in general and subsequently learn when this is appropriate. This is unlikely, because in that case young individuals should show most intervention attempts. However, age class did not influence the occurrence of interventions in our observations. It could also be that ravens follow a learned rule of thumb like "intervene in affiliative behaviors of those who become bonded." Interestingly, we never observed any direct benefit for the intervening ravens, except that they could succeed in stopping others from affiliating. Breaking up affiliation bouts of loosely bonded individuals may pay off in the long term, as it may prevent them from becoming close allies. At the time of intervention, however, individuals in loosely bonded pairs pose hardly any competition for resources, especially when compared to pair-bonded and strongly bonded individuals, which perform most interventions. Hence, there is hardly any temporal contingency between the intervention in affiliated interactions and the possible future status-related competition over resources that would be required for associatively learning. Finally, ravens may use cognitive inferences

based on some kind of mental representations of the social bonds and status of others. Ravens recognize their own social bonds with others [17], and we recently showed that they also have third-party knowledge of others' dominance ranks [18]. The current results suggest that, similar to baboons [32], ravens may use their third-party knowledge flexibly for rank and social relations. Future studies should reveal whether ravens, just like baboons and macaques [32, 33], can simultaneously classify their conspecifics based on rank and social relations, which is of particular interest since these categories are highly interdependent in ravens [16].

Supplemental Information

Supplemental Information includes two figures, four tables, and Supplemental Experimental Procedures and can be found with this article online at <http://dx.doi.org/10.1016/j.cub.2014.09.073>.

Author Contributions

T.B. and G.S. conceived the study. M.S. collected the data. J.J.M.M. analyzed the data. J.J.M.M., G.S., and T.B. wrote the manuscript.

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References

- Byrne, R.W., and Whiten, A. (1988). *Machiavellian Intelligence: Social Expertise and the Evolution of Intellect in Monkeys, Apes, and Humans* (Oxford: Oxford University Press).
- de Waal, F.B.M. (1982). *Chimpanzee Politics: Power and Sex among Apes* (New York: Johns Hopkins University Press).
- Maestriperi, D. (2007). *Macchiavellian Intelligence: How Rhesus Macaques and Humans Have Conquered the World* (Chicago: University of Chicago Press).
- Harcourt, A.H., and de Waal, F.B.M. (1992). *Coalitions and Alliances in Humans and Other Animals* (Oxford: Oxford University Press).
- van Schaik, C.P., Pandit, S.A., and Vogel, E.R. (2004). A model for within-group coalitional aggression among males. *Behav. Ecol. Sociobiol.* 57, 101–109.
- Byrne, R.W., and Bates, L.A. (2010). Primate social cognition: uniquely primate, uniquely social, or just unique? *Neuron* 65, 815–830.
- Smith, J.E., van Horn, R.C., Powning, K.S., Cole, A.R., Graham, K.E., Memenis, S.K., and Holekamp, K.E. (2010). Evolutionary forces favoring intragroup coalitions among spotted hyenas and other animals. *Behav. Ecol.* 21, 284–303.
- Fraser, O.N., and Bugnyar, T. (2012). Reciprocity of agonistic support in ravens. *Anim. Behav.* 83, 171–177.
- Massen, J.J.M., Sterck, E.H.M., and de Vos, H. (2010). Close social associations in animals and humans: functions and mechanisms of friendship. *Behaviour* 147, 1379–1412.

10. Silk, J., Cheney, D., and Seyfarth, R. (2013). A practical guide to the study of social relationships. *Evol. Anthropol.* **22**, 213–225.
11. Higham, J.P., and Maestripieri, D. (2010). Revolutionary coalitions in rhesus macaques. *Behaviour* **147**, 1889–1908.
12. Schülke, O., Bhagavatula, J., Vigilant, L., and Ostner, J. (2010). Social bonds enhance reproductive success in male macaques. *Curr. Biol.* **20**, 2207–2210.
13. Harcourt, A.H. (1992). Are primates more complex than non-primates? In *Coalitions and Alliances in Humans and Other Animals*, A.H. Harcourt and F.B.M. de Waal, eds. (Oxford: Oxford University Press), pp. 445–471.
14. Gwinner, E. (1964). Untersuchungen über das Ausdrucks- und Sozialverhalten des Kolkrahen (*Corvus corax corax* L.). *Z. Tierpsychol.* **21**, 657–748.
15. Heinrich, B. (1989). *Ravens in Winter* (New York: Summit Books).
16. Braun, A., and Bugnyar, T. (2012). Social bonds and rank acquisition in raven nonbreeder aggregations. *Anim. Behav.* **84**, 1507–1515.
17. Boeckle, M., and Bugnyar, T. (2012). Long-term memory for affiliates in ravens. *Curr. Biol.* **22**, 801–806.
18. Massen, J.J.M., Pasukonis, A., Schmidt, J., and Bugnyar, T. (2014). Ravens notice dominance reversals among conspecifics within and outside their social group. *Nat. Commun.* **5**, 3679.
19. Bernstein, I., and Ehardt, C. (1985). Agonistic aiding: Kinship, rank, age, and sexual influences. *Am. J. Primatol.* **8**, 37–52.
20. Seyfarth, R.M., and Cheney, D.L. (2012). The evolutionary origins of friendship. *Annu. Rev. Psychol.* **63**, 153–177.
21. Silk, J.B., Alberts, S.C., and Altmann, J. (2006). Social relationships among adult female baboons (*Papio cynocephalus*) II. Variation in the quality and stability of social bonds. *Behav. Ecol. Sociobiol.* **61**, 197–204.
22. Mitani, J.C. (2009). Male chimpanzees form enduring and equitable social bonds. *Anim. Behav.* **77**, 633–640.
23. Massen, J.J.M., and Sterck, E.H.M. (2013). Stability and durability of intra- and intersex social bonds of captive rhesus macaques (*Macaca mulatta*). *Int. J. Primatol.* **34**, 770–791.
24. Mondragón-Ceballos, R. (2001). Interfering in affiliations: sabotaging by stumptailed macaques, *Macaca arctoides*. *Anim. Behav.* **62**, 1179–1187.
25. van Dierendonck, M.C., de Vries, H., Schilder, M.B.H., Colenbrander, B., Thorhallsdóttir, A.G., and Sigurjónsdóttir, H. (2009). Interventions in social behaviour in a herd of mares and geldings. *Appl. Anim. Behav. Sci.* **116**, 67–73.
26. Schneider, G., and Krueger, K. (2012). Third-party interventions keep social partners from exchanging affiliative interactions with others. *Anim. Behav.* **83**, 377–387.
27. Conner, R.C. (2007). Dolphin social intelligence: complex alliance relationships in bottlenose dolphins and a consideration of selective environments for extreme brain size evolution in mammals. *Philos. Trans. R. Soc. Lond. B Biol. Sci.* **362**, 587–602.
28. Engh, A.L., Siebert, E.R., Greenberg, D.A., and Holekamp, K.E. (2005). Patterns of alliance formation and postconflict aggression indicate spotted hyenas recognize third-party relationships. *Anim. Behav.* **69**, 209–217.
29. Paz-Y-Miño C, G., Bond, A.B., Kamil, A.C., and Balda, R.P. (2004). Pinyon jays use transitive inference to predict social dominance. *Nature* **430**, 778–781.
30. Bshary, R., Gingins, S., and Vail, A.L. (2014). Social cognition in fishes. *Trends Cogn. Sci.* **18**, 465–471.
31. Hinde, R.A. (1983). *Primate Social Relationships: An Integrated Approach* (Oxford: Blackwell Scientific).
32. Bergman, T.J., Beehner, J.C., Cheney, D.L., and Seyfarth, R.M. (2003). Hierarchical classification by rank and kinship in baboons. *Science* **302**, 1234–1236.
33. Schino, G., Tiddi, B., and Di Sorrentino, E.P. (2006). Simultaneous classification by rank and kinship in Japanese macaques. *Anim. Behav.* **71**, 1069–1074.