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Friendships in Animals

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Synonyms

Animal social relations; Relationship quality

Introduction

Friendship in animals has long been considered an anthropomorphism, and the use of the term was consequently a taboo. Joan Silk, while advocating the use of term, even referred to it as the "F"-word in primatology (Silk 2002). The debate about animal friendship originates, at least partly, by the lack of a proper definition. The Oxford dictionary of English defines friendship as *a relationship between friends* and more broadly as *the emotions or conduct of friends*. Whereas the former provides little help as to compare the social relationships of humans and other animals, the latter is rather subjective, be it while comparing the emotions involved in friendships of humans and other animals, or even when comparing the emotions involved in friendships of different people. Rather than discussing semantics, however, it may be useful to first have a look what friends, be it human or non-human, are actually doing.

From a more behavioral point of view, Robert Hinde (1976) defined a relationship as a series of interactions in time, and based on the nature of these interactions, in their specific context, these relationships can be defined as good or bad. Good relationships are thus defined as a series of positive interactions, and the measures that are often used to quantify such good relationships are (tolerance for) close proximity and social grooming or other forms of gentle body contact (e.g., embracing and preening) (Massen et al. 2010). As these objective measures are comparable for humans and other animals, first primatologists, and later also researchers that work on different species, have started to adopt the term friendship for such good relationships or close social bonds.

In an attempt to reconcile "costly" investments such as grooming with the theory of evolution, Hans Kummer (1978) recognized that such differential relationships do not emerge randomly, but that specific relationships have specific value. In particular, the value of a relationship may be the support or protection of the individual with whom one has such a good relationship. Later, this value of a relationship has been integrated in a more detailed and overarching description of relationship *quality* that also includes the security or consistency of a relationship, and the compatibility of a relationship (Cords and Aureli 2000). Nevertheless, this value of relationships has incited a long-

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lasting debate among biologists, as well as between biologists and psychologists about the comparability of human friendships and those of other animals. Because, such short-term "business partnerships" (Barrett and Henzi 2002) are *clearly* different from the unconditional friendships of humans. In fact, Hinde's definition of a relationship as a series of interactions *in time*, makes it inevitably dynamic and subject to short-term changes. Consequently, it is indeed important to distinguish short-term relationships that only cater current needs from long-term stable social relationships.

Many relationships of animals, including those of humans, are short-term, and interest and investment in particular relationships may follow economic market forces like supply and demand (a.k.a. biological markets: Noë and Hammerstein 1994). For example, males start entertaining affiliative relationships with females only when they are in estrous, and their investment in that female (e.g., the amount of time they groom them) depends on how many other females are in estrous (supply) and how many other males are interested (demand). Nevertheless, not all relationships follow such patterns. Some relationships remain stable over long periods of time, and these are what we call friendships, at least in humans. However, not only humans have such long-term stable affiliative relationships with others, and by now we know that, for example, chimpanzees can have stable friendships that last at least 10 years (Mitani 2009), and similar patterns have been observed in other primates, but also in elephants (Moss et al. 2010), dolphins (Connor et al., 2000), and several bird species (Bugnyar and Massen 2017). With evidence accumulating that animals do not merely have short-term goal-orientated relationships but also show long-term stable relationships, by now the term animal friendship has been accepted in the academic world (e.g., Seyfarth and Cheney; 2012).

The Adaptive Value of Friendships

If these enduring friendships are not contingent on current needs, why do we humans and all those other animals nonetheless entertain such costly long-term investments? A common answer to that question is that a friendship is rewarding in itself; i.e., we experience joy when spending time with friends. Indeed, such emotional responses to proximity to friends can easily be detected, yet from an evolutionary point of view such endorphin peaks do not constitute any fitness benefit (i.e., ultimate causation), but instead provide "merely" the system (i.e., proximate causation) that entices us to form such friendships (c.f. Tinbergen 1963). However, for a behavior like forming and maintaining friendships to evolve it should also have direct (i.e., an increase in survival/longevity and or reproductive success) or indirect fitness benefits.

Many of the long-term and stable relationships we observe in both animals and humans alike are among kin; by helping our relatives (i.e., nepotism), we *indirectly* promote the contribution of (part of) our own genes to the next generation (i.e., kin-selection: Hamilton 1964). Nevertheless, some of the friendships we observe among humans and other animals are with unrelated conspecifics, or even with individuals of a different species (e.g., human bonds with their dogs), and recent research has elucidated that those friendship also have fitness benefits. In fact, having friends is shown to increase people's odds of survival by an equal amount as quitting to smoke does (Holt-Lunstad et al. 2010). In non-human animals having friends may be paramount to, for example, surviving a harsh winter (MacFarland and Majolo 2013) or to gain access to mating opportunities (Schülke et al. 2010). Indeed, in the last decade, evidence for fitness benefits of friendship has been accumulating; be it increased access to food or mates, or protection for both the animal itself or its offspring against extreme weather conditions, predators or aggressive conspecifics. Moreover, this evidence does not just include studies on humans and other primates, but encompasses a range of species including, for example, horses, elephants, hyraxes, dolphins, hyenas, kangaroos, but also birds like, for example, geese and ravens.

Cooperation

Many of the fitness benefits related to friendship arise through cooperation. For example, animals

may cooperate while hunting, thereby gaining access to high-value food sources, or team up to fight conspecifics in competition over resources, be it food or mates, or to fend off predators or aggressive conspecifics. Long-term studies on a range of species have now shown that it is specifically friends that form such alliances and support each other in conflicts (e.g., Schino 2007). Additionally, several behavioral experiments testing cooperation in a range of species have shown that the strength of the social bond is indeed the main predictor for success in such cooperation tasks, and that, if given the choice, animals prefer to cooperate with friends rather than with just anybody (e.g., Asakawa-Haas et al. 2016). Relying specifically on friends while cooperating may be beneficial as your long history with them makes them more predictable and trustworthy. Consequently, not only humans but also, for example, chimpanzees place greater trust in their friends than in non-friends (Engelmann and Herrmann 2016).

Trust in a partner becomes really important when the benefits of cooperation are not acquired at the same time for both partners; i.e., when one individual helps another now, and the other reciprocates that help when the former individual needs it at a different point in time (i.e., reciprocal altruism: Trivers 1971). Such an interaction carries a form of uncertainty because you do not know if the other keeps up to his/her part of "the deal," as there is the possibility of freeriding. To prevail, one needs to keep track of such cheaters and not interact with them anymore and only maintain interactions with those that reciprocate. However, the cognitive requirements underlying such tit-for-tat reasoning have been subject of debate (e.g., Brosnan and de Waal 2002), as many animals are considered unable to keep track of everything given and received from all their group members, especially when living in large groups. Whereas humans may be able to do so (which can be debated considering the large-scale societies we live in), in fact, humans tend not to revert to such "calculated reciprocity" (see Brosnan and de Waal 2002) in their everyday interactions. Instead, in their decisions on whether to invest they rely on the feelings they have for a certain interaction partner. Such emotionally based reciprocity (Schino and Aureli 2010) relies on series of interactions with a partner to create such specific emotions and is not necessary contingent on the short-term but rather on the long-term. Whereas such a system may be exposed to short-term inequality, it is constantly updated, and that friend that never buys a round of drinks may slowly become less of a friend and consequently will also receive fewer drinks from his/her "friends" after a while. Observational data on exchange patterns among a variety of species shows that also among non-human animals, these exchanges are mostly not contingent on the short-term but rather on the long-term. Moreover, it has been shown experimentally that animals base their decisions of, for example, food sharing on the more long-term qualities of a relationship, rather than on immediate reciprocation.

The Requirements of Friendships

In contrast to when we interact with strangers, when dealing with friends we do not seem to actively keep track of what is given and received (Massen et al. 2010). Consequently, having friends may sound like one of the simplest things there is. Nevertheless, creating and maintaining such unique social bonds does require some cognitive skills and some biochemical regulations. However, by now many studies have shown that not only humans have the cognitive requirements for friendships, and moreover, that the biochemical mechanisms that allow for such relationships seem evolutionary old and are shared among many animal species (Brent et al. 2014).

Cognitive Requirements

To have friends, you need to know who they are; i.e., distinguish them from other individuals. Individual recognition may seem a given, but not all animal species have it, or at least for some there is no proof so far (Sheehan et al. 2014). Nevertheless, it is widespread in the animal kingdom with examples in both vertebrates and invertebrates, which are using either visual, vocal, or olfactory cues or a combination of those to distinguish individuals from each other (Tibbetts and Dale

2007). Next you need to understand your relationship with that other and, if separated for a while, also remember the nature of that relationship. Because it could be harmful if you start treating your former enemies as friends, many species do indeed remember and understand the nature of their relationships with others.

Besides knowing who your friends are, it may also be beneficial to know who the friends of your enemy are. For example, you don't want to pick a fight with someone, if at that moment that individual has multiple friends standing next to him/her. Thus, to have an understanding of the relationships of others can be very important for surviving in large social groups, and it is the need for such social intelligence that is hypothesized to be the driving force in the evolution of large brains (Byrne and Whiten 1999). Having such knowledge may be particularly beneficial if used to ones own advantage in a Machiavellian way (see "► Machiavellian Intelligence"). For example, ravens seem to monitor the affiliative relationships of their conspecifics, and when they notice that others attempt to become friends and thus potentially form a powerful competitive alliance, they intervene in the affiliative behaviors of those two birds thereby preventing them from forming that bond (Massen et al. 2014).

Biochemical Mechanisms

As mentioned before, friendships seem to be regulated, at least partly, by emotions. The emotions involved in friendship do not only have a behavioral and cognitive component, but also, like any emotion, require a certain physiological infrastructure. Not surprisingly, oxytocin (which has sometimes been dubbed the "love hormone," but see De Drue and Kret 2015) does seem to play a major role. Oxytocin, mesotocin (the oxytocin homologue in amphibians, reptiles, and birds), or isotocin (the oxytocin homologue in fish) promote and facilitate different aspects of social bonding like for example trust and cooperation, in both humans (De Drue and Kret 2015) and other animals (Young and Wang 2004). Additionally, β-endorphins, which are involved in the reward system, are released during certain social behavior. As these β-endorphins induce positive affect, this mechanism may be a crucial driving force in the initiation of friendships (Keverne et al. 1989). In contrast, a lack of social contact may be stressful (e.g., Stocker et al. 2016), and the avoidance of associated high cortisol levels, may form an alternative reason for the initiation of friendships. Finally, a combination of different biochemicals and their interactions with each other play important roles in, for example, the perception of social stimuli and social memory but also in aggressive behavior (see Brent et al. 2014 for a nice overview).

The Development of Friendships

Relatively little is known about how friendships start and develop over time, as it is rather difficult to pinpoint the exact start of "a series of interactions" and to check whether there is actual partner choice at play. Many social relationships seem structured by the society the animal lives in. For example, in societies that are based around matrilines friends are often kin. Also, just by avoiding aggression, hierarchical societies are structured such that dominance status leads to spatial centrality in the group (Hemelrijk 2000). Thus, dominant individuals spend most of their time close to each other in the center of the group, whereas more subordinate individuals spend most of their time with other subordinates at the periphery of a social group. As a consequence, many friendships are based on similarities in traits like dominance rank, but also for example age (e.g., Silk et al. 2006). Likewise, having similar interests can influence the spatial structure of a social group in such a way that you end up next to each other. For example, curious individuals are always at the forefront of a population and just by association may become friends (Croft et al. 2009). Alternatively, you may actively choose to spend your time with individuals that have similar interests and or personality. Similarity increases predictability (as you know what you would do in a given situation) and could consequently increase trust in cooperation. Recent research does indeed show that, like humans, animals choose their friends based on similarity in personality (Massen and Koski 2014).

Conclusions

After some controversy in the early days of animal cognition and behavior studies, by now the term animal friendship is accepted across the field. Studies on a multitude of species show that animals entertain differentiated relationships with their group members, and like human friendships, the affiliate relationships between animals are not just short term "business deals" but instead can be stable over long time periods.

Friendships of humans and other animals are adaptive as they provide clear fitness benefits, be it survival or increased reproductive success. Most of these benefits are acquired by cooperation, and animals indeed do cooperate more often and more successfully with their friends in comparison to with other conspecifics, and consequently, also seem to actively choose to cooperate with their friends. If cooperation concerns the reciprocal exchange of goods and services, animals, and in particular friends, do not keep an active count of what has been given and received. Instead, they rely on an emotionally based mechanism, in which decisions to give are based on the long-term qualities of the relationship with the interaction partner.

To have friends requires some cognitive capacities. First off you need to be able to recognize and differentiate individuals from each other, and second, you need to recognize and remember the specific relationship you have with certain individuals. Additionally, understanding the relationships of others may also be beneficial when maneuvering in a complex social world. From a physiological perspective, friendship concerns a mix of biochemicals that operate different systems within the brain. And like the cognitive aspects, these systems seem evolutionary old and shared among a range of different species.

Finally, the ontogeny of friendship is relatively understudied, particularly because it is difficult to observe the actual start of a friendship. Nevertheless, some retrospective studies are showing that many friendships are based on homophily; i.e., love of the same. Friends may be similar with regard to rank or age simply by association. Alternatively, animals actively choose to befriend individuals that are similar with regard to personality, since these are more predictable and may consequently be trustworthier in future cooperation. As the saying goes, it does indeed seem like that "birds of a feather flock together."

Cross-References

- ▶ Altruism
- ▶ Andy Whiten
- ▶ Dorothy Cheney
- ▶ Frans de Waal
- ▶ Joan Silk
- ▶ Kin Selection
- ▶ Machiavellian Intelligence
- ▶ Oxytocin
- ▶ Primate Social Structure
- ▶ Prosocial Behavior
- ▶ Proximate Causation
- ▶ Reciprocity
- ▶ Richard Byrne
- ▶ Robert Hinde
- ▶ Robert Seyfarth
- ▶ Robert Trivers
- ▶ Sarah Brosnan
- ▶ Social Behavior
- ▶ Social Grooming
- ▶ Social Intelligence Hypothesis
- ▶ Social Network Analysis
- ▶ Sociobiology
- ▶ Ultimate Causation
- ▶ William Donald Hamilton

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