



The influence of relationships on neophobia and exploration in wolves and dogs



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Exploration is important for animals to be able to gather information about features of their environment that may directly or indirectly influence survival and reproduction. Closely related to exploration is neophobia, which may reduce exposure to danger, but also constrain explorative behaviour. Here we investigated the effects of social relationships on neophobia and exploration in wolves, *Canis lupus*, and dogs, *Canis familiaris*. Eleven pack-living wolves reared by human foster parents and 13 identically raised and kept dogs were tested in a novel object test under three different conditions: (1) alone, (2) paired with a pack mate and (3) together with the entire pack. Dogs were less neophobic than wolves and interacted faster with the novel objects. However, the dogs showed overall less interest in the novel objects than wolves, which investigated the objects for longer than the dogs. Both wolves and dogs manipulated objects for longer when paired or in the pack than when alone. While kinship facilitated the investigation of novel objects in the pair condition in both wolves and dogs, rank distance had opposite effects. Our results suggest that the presence of conspecifics supported the exploration of novel objects in both wolves and dogs, particularly within kin and that this may be interpreted as risk sharing. The reduced latency to approach objects and less time spent exploring objects in dogs compared to wolves may be interpreted as an effect of domestication.

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Exploration is important for animals to be able to gather information about features of their environment that may directly or indirectly influence survival and reproduction. Exploring animals may collect information about food distribution and abundance, shelters, predators, escape routes or potential mates (Dall, Giraldeau, Olsson, McNamara, & Stephens, 2005; Heinrich, 1995; Mettke-Hofmann, Winkler, & Leisler, 2002; Renner, 1988; Schwagmeyer, 1995). To acquire such knowledge, an individual may assess its environment alone (Day, Kyriazakis, & Rogers, 1998), by social learning or by using public information (Swaney, Kendal, Capon, Brown, & Laland, 2001; Valone & Templeton, 2002; Visalberghi & Adessi, 2001; Visalberghi & Fragaszy, 1995).

Closely related to exploration is neophobia with highly neophilic animals being quick to approach and explore a novel object, while highly neophobic animals are slow to do so (Day, Coe, Kendal,

& Laland, 2003). Neophobia is linked to exploration because individuals only explore if they are interested in an object and the same is true for active avoidance. Thus objects can be neither explored nor avoided out of sheer disinterest/lack of perceived relevance. Accordingly, neophobia has been defined as ‘the avoidance of an object or other aspect of the environment solely because it has never been experienced and is dissimilar from what has been experienced in the individual's past’ (Stöwe, Bugnyar, Heinrich, & Kotrschal, 2006, p. 1079). Neophobic responses can therefore reduce exposure to danger but they can also constrain explorative behaviour and thus opportunities for learning and innovating (Stöwe, Bugnyar, Heinrich, et al., 2006; Stöwe, Bugnyar, Loretto, et al., 2006).

Depending on a species' ecology and the animal's motivation, individuals approach and investigate changes in their familiar environment with different latencies and for variable periods (Day et al., 2003; Mettke-Hofmann, Winkler, & Leisler, 2005; Mettke-Hofmann et al., 2002; Stöwe, Bugnyar, Heinrich, et al., 2006). This may also be affected by social context. For example, the

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presence or action (handling or food intake) of a conspecific facilitated the acceptance of novel food in gerbils, *Meriones unguiculatus* (Forkman, 1991), zebra finches, *Taeniopygia guttata* (Coleman & Mellgren, 1994), capuchin monkeys, *Cebus apella* (Visalberghi & Fragaszy, 1995; Visalberghi & Addessi, 2000), rats, *Rattus norvegicus* (Galef, 1996; Galef & Whiskin, 2000), keas, *Nestor notabilis* (Huber, Rechbergen, & Taborsky, 2001) and house mice, *Mus musculus domesticus* (Valsecchi, Bosellini, Sabatini, Mainardi, & Fiorito, 2002). In contrast, delay and inhibition of approach/acceptance of novel food in a social context have been observed in chum salmon, *Oncorhynchus keta* (Ryer & Olla, 1991), Atlantic salmon, *Salmo salar* (Brown & Laland, 2001, 2002) and great tits, *Parus major* (van Oers, Klunder, & Drent, 2005). It is not unlikely that the delay/inhibition reported in these studies was caused by dominance rank differences (and associated risk of agonistic interaction) between the participating individuals (Brown & Laland, 2001, 2002; van Oers et al., 2005; Ryer & Olla, 1991). Individual ravens, *Corvus corax*, for example, approached a novel object faster when tested alone than when paired with a conspecific, but they spent more time close to, and manipulating the novel object in dyads or in groups (Stöwe, Bugnyar, Loretto, et al., 2006). This study showed that social relationships mattered: ravens approached a novel object faster when paired with siblings than nonsiblings and dominant males approached the novel object first when in a dyad with a female, but not when with a male (Stöwe, Bugnyar, Loretto, et al., 2006).

Wolves, *Canis lupus*, are cooperative, group-hunting animals that provide communal care for the pups in a kind of helper system supporting the exclusive reproduction of the dominant pair (Mech & Boitani, 2003). Moreover, wolves also defend their territories (Mech & Boitani, 2003, 2004) and kills (Kaczensky, Hayes, & Promberger, 2005) together. A pack usually consists of the reproductive pair and their offspring of 1 or more years; however, many variations of this theme have been observed (Packard, 2003). The pack is structured according to a sex–age graded hierarchy that reflects the composition of the family group (Packard, 2003). Domestic dogs, *Canis familiaris*, although phylogenetically closely related to wolves (Pang et al., 2009; Savolainen, Zhang, Luo, Lundeberg & Leitner, 2002; Scott & Fuller, 1965), differ fundamentally not just genetically (Axelsson et al., 2013) in regard to their closeness to humans, but also in their breeding system and, possibly, other cooperative interactions (Boitani & Ciucci, 1995; Butler, du Toit & Bingham, 2004; but see Bonanni, Valsecchi, & Natoli, 2010). Similar to wolves, free-ranging dogs may form stable social groups (Cafazzo, Valsecchi, Bonanni, & Natoli, 2010) consisting of several unrelated males and females. Feral dogs form a relatively steep, sex–age graded dominance hierarchy (Cafazzo et al., 2010). Particularly during feeding on dumps or on carcasses, aggression tends to be high (Boitani, Francisci, Ciucci, & Andreoli, 1995; Macdonald & Carr, 1995), which may make it less costly for them to explore a new source of food alone rather than in a group. Moreover, while free-ranging dogs, similar to wolves, defend their territories together (Boitani et al., 1995; Macdonald & Carr, 1995), they usually do not raise pups cooperatively (Boitani et al., 1995; Daniels & Bekoff, 1989; but see Pal, 2005), nor is it clear how closely they cooperate during hunting (Boitani et al., 1995; Macdonald & Carr, 1995).

If dogs are indeed less cooperative than wolves within groups of conspecifics, it may be predicted that also with novel objects, potentially perceived as a source of danger, wolves might rely more on support from conspecifics than dogs. For example if the social context mediates the expression of an individual's personality by either synchronizing its behaviours to the behaviour of its partner or by increasing individual differences between the partners (King, Williams, & Mettke-Hofmann, 2015), wolves could be more prone to synchronize than dogs because, in general, cooperativeness with

conspecifics is more important for their daily survival than for dogs. On the other hand, in social mammals the presence of a familiar conspecific has been shown to be more effective for social buffering, namely in alleviating acute stress responses, compared to the presence of an unfamiliar conspecific (Kiyokawa, Honda, Takeuchi & Mori, 2014). Therefore in potentially stressful situations, as when confronted with a novel object, the presence of a conspecific might be a valuable resource reducing the potential stress, which might be the same for dogs and wolves.

While wolves have experienced various degrees of persecution and exploitation from humans during the last centuries, potentially selecting for greater neophobia (Fritts, Stephenson, Hayes, & Boitani, 2003), dogs have undergone the opposite selection through the domestication process (Clutton-Brock, 1995; Hare & Tomasello, 2005; Thorne, 1995). It has been argued that neophilia is an adaptive consequence of selection by living in association with humans (Kaulfuß & Mills, 2008), suggesting that dogs should be inherently less neophobic than wolves, which may also decrease the dependency on a group in their approach of novelty, as compared to wolves. Still, wolves may be more strongly interested in novelty than dogs, because the potential costs or benefits of contact with novelty may be greater in the former than in the latter because of their reliance on prey rather than relatively stable food resources.

In this study, we compared the responses of identically raised and kept pack-living wolves and dogs to novel objects presented in three different conditions: alone, as a pair with a pack mate and with the entire pack. The aim was to investigate how the social context and relationship between pack members influenced their neophobic responses and explorative behaviour. For reasons discussed above, we predicted that wolves would be overall more neophobic than dogs towards human-related objects (Clutton-Brock, 1995; Fritts et al., 2003; Hare & Tomasello, 2005; Thorne, 1995), approaching the objects slower than dogs, but possibly exploring novel objects more thoroughly than dogs as novelty may lead to potential benefits or costs that are greater for wolves than for dogs. Moreover, owing to the inherently higher cooperativeness of wolves towards conspecifics (Boitani et al., 1995; Kaczensky et al., 2005; Mech & Boitani, 2003, 2004; Pal, 2005; Range & Virányi, 2015), we expected a greater facilitating influence of the presence of conspecifics on the exploratory and neophobic behaviour of wolves than dogs, that is, wolves would approach the novel objects faster and explore the objects for longer when tested with a pack member or the entire pack. We also expected that when tested alone this effect would be larger in wolves than dogs; that is, there would be no or little influence of the presence of a pack member in dogs.

METHODS

Ethical Note

No special permission for use of animals (wolves and dogs) in such sociocognitive studies is required in Austria (Tierversuchsgesetz 2012 – TVG 2012). The relevant committee that allows running research without special permissions regarding animals is Tierversuchskommission am Bundesministerium für Wissenschaft und Forschung (Austria).

Subjects

We tested 11 wolves and 13 dogs raised and kept the same way at the Wolf Science Center, Austria (for details see Table 1). All animals were hand-raised after being separated from their mother at approximately 10 days after birth. During the first 5 months of

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