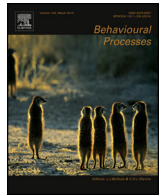




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Down but not out: Supine postures as facilitators of play in domestic dogs

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ABSTRACT

We used two sets of videotaped data of playing domestic dog dyads to determine whether rolling over during play served as a signal of submission or whether it was a combat maneuver adopted as part of an ongoing play sequence. Our results provide strong support for the latter. In the absence of any overt indication of agonism, the frequency with which rollovers occurred was determined primarily by play bout length. The discrepancy in partner size had no effect on the probability that rollovers would occur and there was no evidence that smaller dogs were more likely to rollover or to sustain a supine posture for longer, if they did. The supine phase of rollovers was significantly skewed to short durations. Most rollovers were either defensive (evading a nape bite) or offensive (launching an attack). None could be categorized as submissive. We conclude that asymmetries in the performance of rollovers cannot be assumed to point to asymmetries in the relationships between play partners.

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1. Introduction

The domestic dog (*Canis lupus familiaris*) is a subspecies of the gray wolf (*C. lupus*) that expresses high phenotypic diversification as a consequence of driving artificial selection by humans (Wayne and Ostreder, 1999). The relatively recent origin of the taxon (Freedman et al., 2014) has, in part, given rise to the assumption that the behavioral profile of domestic dogs (dogs, hereafter) is broadly mappable onto that of wolves (Mech, 1970; Bekoff, 1972; Abrantes, 2005. But see Coppinger and Coppinger, 2002 for a different perspective).

Associated with aggressive interactions between wolves (Mech, 1970), is a suite of ritualized agonistic displays that serve to curtail active aggression by signaling dominance and subordination. One famous exemplar of the latter is the ‘rollover’ (Lorenz, 1942), whereby a subordinate animal rolls over onto its back, often spontaneously, in an act of ‘passive submission’ or appeasement

(Packard, 2003) that inhibits attack by the dominant one. This behavior is coupled with other distinct postures and behaviors, indicative of ritualization, that include flattened ears, curved spine, tucked tail, reduced mobility and averted gaze (Schenkel, 1967; Mech, 1970; Abrantes, 2005).

Despite observed differences in social organization (Pal et al., 1998; Boitani et al., 2007), including the failure to observe the strong dominance relationships thought to be characteristic of wolf packs (Bradshaw et al., 2009), the observation that rollovers occur during play-fighting in dogs has also been assumed to indicate submission, and has led to their being used to identify play partners as dominant or subordinate (Bauer and Smuts, 2007; Ward et al., 2008; Fox, 1969). This suggests that, in the context of play-fighting, rollovers serve to prevent a shift to aggression, either by terminating the bout before escalation occurs, or by allowing the engagement to be recalibrated so that play can continue.

There are at least two other possibilities that may account for the occurrence of rollovers during play. Firstly, self-handicapping by a larger or more dominant animal has been reported as a means of soliciting play (Bekoff, 1974; Palagi, 2008), with rolling over onto the back in front of the potential play partner being one such gesture (e.g., LeResche, 1976; Pellis et al., 2014). Secondly, in both dogs and canids more generally, the nape of the neck, the throat and the snout (Aldis, 1975; Bekoff, 1976; Fox, 1969) are gently bitten during play

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fighting, and rolling over may be used as a combat tactic, either by the defender to block access to the play target or by the attacker to gain access to the target. Such combat uses of rollovers have also been reported in the play fighting of non-canid species of mammals (e.g., Pellis and Pellis, 1987; Pellis et al., 2014).

If rollovers during play are acts of submission, then we would expect them to be (i) triggered by behavior that is overtly aggressive or that causes detectable discomfort or pain, (ii) performed predominantly by one of the play partners, who will be disadvantaged by being smaller or weaker, and (iii) the supine position will be sustained, thereby (iv) inhibiting the play behavior or aggression of the other animal. If, on the other hand, they are executed tactically, for combat purposes, then they should (i) be triggered by an attack and (ii) serve to block it or (iii) lead to an immediate attack or counter-attack. They are therefore either likely (iv) to be performed by either partner or (v) by the larger animal in the context of soliciting play. They will therefore (v) not inhibit the continuation of play. Finally, if used for playful solicitation, rather than inhibiting attack, rollovers should elicit playful attack by the nearby partner. To test these predictions, we analyzed two sets of videotaped footage of the play bouts of adult dogs.

2. Methods

2.1. Data set 1: staged play with a target dog

2.1.1. Subjects

We paired a single medium-sized female dog with 33 play partners of differing sizes and breeds. This approach enabled the selection of test subjects that were bigger, smaller and the same size as the standardized play partner. Although this raises unavoidable issues of pseudoreplication, we did so for three reasons. First, we wished to ensure that all play partners were unacquainted with each other so that recorded rollovers could not be ascribed to any prior establishment of dominance. Second, and following this, by using a known dog with a placid temperament, we wanted to allow for the possibility that being paired with an unknown dog would elicit behaviors associated with dominance and subordination, while minimizing the risk of agonistic escalation. Third, by having a standard target dog for each of the subjects, it increased the chance that any differences among the dogs, due to differences in relative size to the play partner, was not due to possible individual differences in the partners used.

We used opportunistic sampling of owners at a pet store in Lethbridge, Alberta to recruit subjects. We asked the owner(s) if their dog was well-socialized (i.e., did it have experience of daycare centers or playgroups) and whether they could recall any instances in which the dog had been involved in aggression. Dogs with a history of overt fighting were excluded from the study. We obtained body weight and height data from the owners. All procedures were approved by the University of Lethbridge Animal Welfare Committee.

2.1.2. Procedure

Play sessions took place in an indoor laboratory containing a cordoned-off play arena measuring 5.5 m × 3.5 m. This area included a door that opened into a small room in which the target dog was placed before the session began. Each session involved only the target dog and a single partner. On arrival, owners brought their dogs into the laboratory, placed them in the arena and remained with them until they had settled in. Once the dogs were relaxed, the owners left the laboratory and the target dog was released from the holding room. Two researchers remained to record the session and to manage the dogs. A pilot study indicated that dyads that were left alone in the arena tended to focus their attention on the

researchers and so did not interact with each other. Accordingly, to overcome this, we spoke to the dogs or petted them until they either started playing or had ignored each other for 5 min. Data collection took place between 6pm and 8pm, from June to August 2011.

We used a Samsung SD camcorder to document sessions and began filming once the dogs engaged with each other, either by coming face-to-face and making prolonged eye contact or when one of the dogs sniffed the other. Filming was ceased if the dogs had not interacted with each other for more than five consecutive minutes.

2.2. Data set 2: YouTube videos of playing dogs

To obtain video footage of unique pairs of playing dogs, we searched YouTube, using the keywords dogs and playing, and selected 20 videos in which the beginning and end of play bouts were clearly discernible. We selected 10 videos in which partners were of approximately the same size and 10 in which the two dogs were judged to be different in size relative to one another.

2.3. Data extraction

We used the Free Video to JPEG Converter (v. 5.0.6. build 221) software to reconfigure the video as individual frames (25 fps). When viewing the recorded sessions, we used the ethograms provided by Bekoff (1972, 1974), Horowitz (2009) and Ward et al. (2008). Playful interactions varied from rough-and-tumble play to the chasing of one dog by the other. In the latter case, we used the descriptions of canine body language by Abrantes (2005) and Handelman (2008) to distinguish between play and avoidance behavior.

The converted footage allowed quantitative estimates to be made of the number of rollovers performed by each subject, the frequency with which rollovers occurred, the duration of the play bout, as well as the duration of the supine phase of the rollover, in which the animal was on its back with all four feet off the substrate. Moreover, the videotaped material also allowed Eshkol-Wachman Movement Notation (Golani, 1976) to be used for detailed qualitative analysis of the contexts in which rollovers occurred. The analyses of the videotaped material were in three phases.

2.4. Data analysis

2.4.1. Qualitative analyses

Eshkol-Wachman movement notation (EWMN) is a global system, designed to express relations and changes of relation between parts of the body, with the body (i.e., body and limb segments) treated as a system of articulated axes (Golani, 1976). An important feature of EWMN is that the same movements can be notated in several polar coordinate systems. The coordinates of each system are determined with reference to the environment, to the midline axis of the subject's body, and to the next proximal or distal limb or body segment. Its primary value in the study of social interactions is that the movement by one animal can be described as relative to the body of the other animal (Moran et al., 1981; and see Appendix A in Pellis et al., 2013 for a detailed outline of how the system is used to record the behavior of two interacting animals). By transforming the description of the same behavior from one coordinate system to the next, invariance in the behavior may emerge in some coordinates but not others (Golani, 1976).

We used EWMN to describe 20 rollovers occurring in playful interactions containing rollovers from data set 1 to identify when and how rollovers occurred. Then, EWMN was used to describe 20 rollovers in play fights from data set 2 were also notated as an independent evaluation of whether the contexts identified for the use of

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