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Interspecific cooperation in human (*Homo sapiens*) hunting: the benefits of a barking dog (*Canis familiaris*)

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The first wild animal humans domesticated was the wolf (*Canis lupus*). The benefits of dog presence for human hunting success is often mentioned as a probable factor initiating the domestication of the wolf. We compared the per-hunter moose (*Alces alces*) hunting success of four hunter groups of different sizes with and without a dog. Groups with a dog had a higher hunting success for every group size. The difference was most pronounced for the smallest group (< 10 hunters) — hunters with a dog obtained 56% more prey than those without a dog. Indeed, the mean hunting success was the highest for the smallest groups with a dog. Among larger groups, hunting success was independent of the group size regardless of whether or not a dog was present. In groups over ten hunters, hunting success correlated with the number of dogs. The benefit of hunting with a dog had a density-dependent pattern: the benefit increased when moose density was low. Our results give quantitative support to the hypothesis that the benefits of cooperative hunting was a potentially important factor in the wolf domestication process.

Introduction

Cooperation between humans (*Homo sapiens*) and wild animals may have originated as early as 20 000–100 000 years ago (Vilá *et al.* 1997, Leonard *et al.* 2002, Savolainen *et al.* 2002), specifically with the domestication of the wolf (*Canis lupus*). Ever since, both dog (*Canis familiaris*) and human behaviour have been modified through natural selection, artificial selection (i.e., breeding) and/or cultural evolution. Today dogs are one of the most popular pets all over the world. Several breeds of dogs are specialised in different tasks, e.g., guidance, hunting, protection or companionship (Naderi *et al.* 2001). For hunting, strains are bred with the intent to assist in hunting a specific game, like grouse, hares or large ungulates.

Hunting large prey is suggested to have played a major role in promoting domestication of the wolf (Clutton-Brock 1977, 1996; but *see* e.g., Naderi *et al.* 2001). In the northern hemisphere, large ungulates have been an important resource for humans, and moose (*Alces alces*) is one of the most important prey species for wolf (e.g. Messier 1994). For a hunter to be effective in killing a prey larger than itself requires skills of cooperation and communication among cooperative hunters (Clutton-Brock 1977, 1996), which are typical behavioural patterns for both humans and wolves. During the process of domestication, dogs have also acquired social-communicative skills used with humans (Hare *et al*. 2002), increasing chances of cooperation in different tasks, e.g. hunting. Consequently, it has been suggested that the decrease in the wild animal populations at the end of the Pleistocene may have been caused by increased hunting success of humans with early domesticated dogs (Clutton-Brock 1980, 1992).

The dense and intensively exploited moose populations of Fennoscandia are regulated by licence harvesting (Nygrén & Pesonen 1993, Ericsson & Wallin 1999, Solberg & Sæther 1999). Moose hunters most often work in groups, and the groups can differ significantly in size. While hunting with a dog is the most common practice (Ball *et al*. 1999, Koskela & Nygrén 2002), moose is regularly hunted without dogs as well. The value of a hunting dog is often suggested in terms of finding game and tracking wounded animals, but studies on the actual effect on hunting success are lacking.

Here we study the unique relationship between a human and a dog by comparing the per-hunter moose hunting success for hunting groups that differ in size and in the use of a dog. Dogs are universally utilized in hunting, which suggests that they may have an influence on hunting success. In this study we test the following hypotheses: (i) moose hunting groups using dogs have better hunting success than groups without dogs; (ii) hunting success increases with effort, i.e. with the group size and number of dogs available. In addition, we compare the hunting success of groups with and without dogs in conditions of different prey densities.

Material and methods

Our data is based on 5250 observation cards filled by moose hunting groups (mhg). These data cover the 15 Game Management Districts (GMD) of Finland (Nygrén & Pesonen 1993) during the moose hunting season in 2001 (29 September–15 December). Although voluntary for hunters, national coverage of observation cards is very good; 89% of total moose harvest was reported in observation cards. Observation cards were not completely filled by every mhg, thus causing variation in sample sizes. Each mhg organized their hunting practice independently within the area specified in the licence permit. Mhgs reported their main hunting practice on a daily basis, and for this study we categorised the methods according to the use of a dog. If without a dog, part of the mhg works to direct and/or track the moose towards a line of hunters (the remaining mhg). In mhgs using a dog, hunters wait for a released dog to direct moose towards them, or, if the dog has halted the moose by barking at it, one hunter approaches the moose within a shooting range (*see* also Ball *et al*. 1999). Only mhgs that used either practice (dog/no dog) for at least two days during the season were included in the analysis. From groups that used both methods, only days without a dog were selected to balance for the unequal sample size. Correspondingly, each hunting group was used only once in each test.

Mhgs also reported the daily number of hunters and the number of moose killed. Accordingly, the daily group size and number of moose killed per hunter per day were obtained, and as an observation unit for the analysis, mean values from each mhg covering the season were obtained. The mhg size, categorized into four classes and hunting practice (dog/no dog), were used as independent variables for hunting success, i.e. moose killed/hunter/day. Daily number of hunters in most mhgs varied during the season, and the mean mhg size was categorized as 1 = 1–9.9, 2 = 10–19.9, 3 = 20–29.9 and 4 = > 30 hunters. Weight of moose is indicated as carcass weight, i.e. without head, skin, lower legs, blood and viscera.

In addition to reporting the size of their licensed hunting area, mhgs estimated the number of live moose left in the area after the hunting season. From these estimates, we calculated moose density as the number of moose per 1000 ha. Because our data did not meet the assumptions of parametric tests, corresponding nonparametric tests were applied. Nonparametric multiple comparisons subsequent to Kruskall-Wallis tests were conducted according to Zar (1996). All tests are two-tailed.

Results

The presence of a dog increased hunting success in all group sizes (Kruskall-Wallis, group 1: $\chi^2_1 = 98.592$, $p < 0.0001$; group 2: $\chi^2_1 = 74.289$, $p < 0.0001$; group 3: $\chi^2_1 = 25.402$, $p < 0.0001$; group 4: $\chi^2_1 = 26.352$, $p < 0.0001$; Fig. 1a). The difference between hunting practices was most pronounced in the smallest groups (Fig. 1a).

We examined the effect of a dog number on hunting success within each group size. With increasing number of dogs, hunting success increased except in the smallest mhg size (group 1: $r_S = -0.013$, $n = 1968$, $p = 0.57$; group 2: $r_S = 0.105$, $n = 1556$, $p < 0.0001$; group 3: $r_S = 0.174$, $n = 325$, $p = 0.0016$; group 4: $r_S = 0.368$, $n = 95$, $p = 0.0002$).

We also studied the effect of the group size on hunting success per hunter. In groups without a dog, group size was associated with hunting success (Kruskall-Wallis: $\chi^2_3 = 12.438$, $p = 0.006$; Fig. 1a). Hunting success for the smallest group was lower as compared with groups 2 and 3 (2 *vs.* 1: $Q = 2.686$, $k = 4$, $p < 0.05$; 3 *vs.* 1: $Q = 3.253$, $k = 4$, $p < 0.05$). Hunting success did not differ, however, between group sizes 2–4 (Fig. 1a).

Hunting success was also associated with the mhg size when a dog was used (Kruskall-Wallis $\chi^2_3 = 8.317$, $p = 0.04$; Fig. 1a). Mean hunting success was highest for the smallest group, but differed significantly only from the next largest group (2 *vs.* 1: $Q = 2.761$, $k = 4$, $p < 0.05$). Among groups 2–4 hunting success remained constant (Fig. 1a).

The effect of a dog on hunting success differed with different moose densities. We related the difference in hunting success between the practices to moose density of the GMD. When the benefit of a dog on hunting success was compared in different moose densities among the GMDs, the advantage of a dog increased with decreasing moose density ($r_S = -0.536$, $n = 15$, $p = 0.04$) (Fig. 1b).

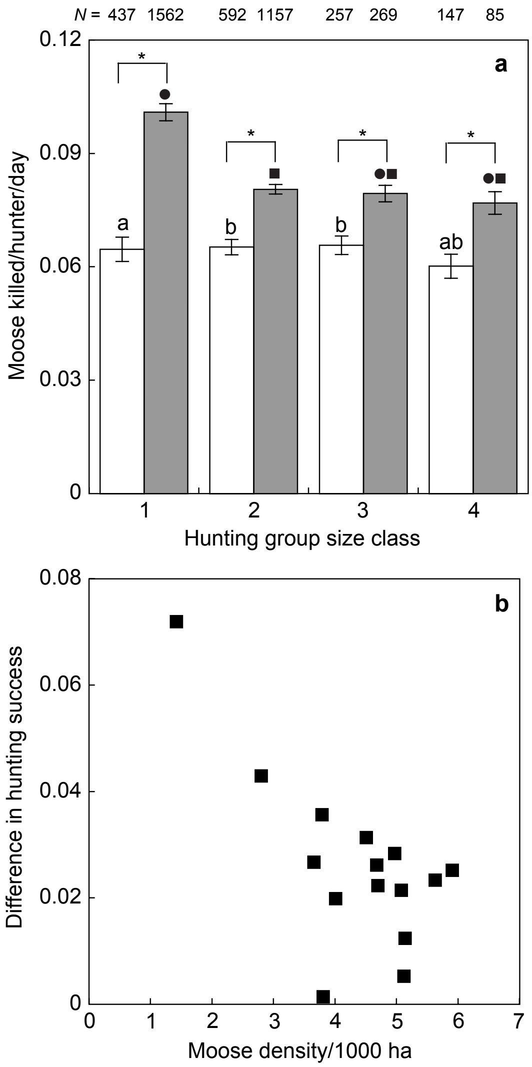

Fig. 1. — **a**: Mean hunting success (mean ± SE) in different sized groups without a dog (white bars) and with a dog (grey bars). Statistically significant differences ($p < 0.05$) between groups are indicated as different letters, symbols or an asterisks above the bars. — **b**: Correlation between moose density and difference in hunting success between mhgs with and without a dog ($r_S = -0.536$, $n = 15$, $p = 0.04$). All group sizes were pooled within each GMD.

Discussion

Our study provides empirical support to the hypothesis that dogs increase human hunting success. As hypothesized, when compared with groups of humans only, hunting success with a dog was higher for all mhg sizes and this benefit increased with the decreasing prey density. In Sweden, Ball *et al.* (1999) discovered that mhgs using dogs had a higher rate of detecting female moose, but they did not measure the hunting success of groups with and without dogs. If the benefit of a dog observed in this study (measured as moose killed per day per hunter) is transformed to carcass weight of moose obtained per hunter in the smallest mhg (mean carcass weight of moose 130 kg (Anonymous 2002)), it equals 8.4 kg and 13.1 kg per hunter per day in groups without and with a dog, respectively.

Group size was also associated with hunting success. For groups without a dog, hunting success was significantly lower in the smallest group. The difference in mean success was very small, however, and may have been due to high variance of the data (e.g., CV of group size 1 for both methods is 93%). Hunting with humans alone may require a minimum number of hunters to be effective, since success among larger groups did not differ significantly. For groups using a dog, in contrast, the smallest group size was markedly more efficient than the second largest group (Fig. 1a). If the dog has halted the moose by barking, one hunter can approach it within a shooting range and kill the animal, while other group members can be strategically placed in the likely directions of the moose escape pattern. Consequently, with a good dog, even a small number of hunters can be very successful. Corresponding to 'no-dog' groups, hunting success among groups over 10 hunters with a dog did not differ. This indicates that even though larger groups killed more prey overall (with or without a dog), success for the individual hunter remained unchanged.

Hunting success also increased with the number of dogs except in the smallest group size. The more dogs associated with the hunting group, the larger the area that can be simultaneously searched. However, with larger areas more hunters are required on stands waiting for the approaching moose. This stresses the importance of cooperation and good knowledge of the area. In small groups, coordination of hunting with more than one dog becomes difficult, since fewer hunters can be placed on stands.

Difference in hunting success between groups depending on their use of dogs had an interesting density-dependent pattern. The benefit of a dog increased with decreasing moose density (Fig. 1b). This result makes intuitive sense: the more moose there are, the more opportunities to meet and kill a moose exist. Accordingly, use of hunting dogs is particularly advantageous during periods of low prey density. Wolf domestication was initiated in early hunter-gatherer societies where hunting success played a vital role in humans' protein acquisition. Presuming the corresponding effect outlined in this study, groups using a dog might have had an increased survival, thereby reinforcing wolf domestication.

Our results have also conservation and management implications. Control of hunting effort is one way of regulating the harvest (Caughley & Sinclair 1994). Sustainable hunting in low density populations and/or populations with low growth rates requires special attention, where restrictions of more effective hunting methods (e.g., dog use) might be in order. Control of hunting group size can also be used to limit hunting pressure, since large groups kill more prey even if the gain per hunter does not increase. On the other hand, attempts at reducing population size to, for example, decrease damage done by a species, might be more effectively carried out by increasing hunting efficiency with the use of dogs and increasing hunting group size.

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