



Pay respect to the elders: age, more than body mass, determines dominance in female beef cattle[☆]



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Dominance hierarchies in groups of social animals can be based either on asymmetries that are important for agonistic interactions (such as body mass) or on more 'conventional' cues (such as age), which are respected despite having little relationship to the animal's fighting abilities. We investigated how social dominance is influenced by age and body mass in a herd of 29–39 beef cows over a 10-year period, focusing on all levels of the dominance hierarchy (individual, dyadic and group). The results demonstrate that age prevails over body mass in the structuring of the dominance network in beef cattle. At the individual level, path analysis confirmed that the dominance index of a cow was more strongly associated with her age than with her body mass. At the dyadic level, age superiority had a stronger influence on the direction of social dominance in pairs than body mass superiority. Older cows were dominant in 73.6% of those dyads studied, even when the younger cow was heavier. At the group level, the strong influence of age on dominance produced a hierarchy that was very stable and strongly transitive. Our findings show that beef cows, for the most part, do not use their physical strength to attain dominance over older, but lighter, herdmates. This results in a stable age-based hierarchy, which might serve a universally shared function that promotes the smooth functioning of the herd and/or the expression of experience by older cows. Among the theoretical models of conflict resolution, the system most closely resembles the partial bourgeois evolutionarily stable strategy.

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Social dominance, defined as a lasting asymmetry in the outcomes of agonistic interactions between specific individuals (Bernstein 1981), is a ubiquitous phenomenon among animals of diverse taxa living in groups, including mammals, birds, fish and insects (Bonabeau et al. 1999; Chase et al. 2003; Wittemyer & Getz 2007; Lindquist & Chase 2009). Why did social dominance develop in so many species? The first possibility is that being socially dominant secures priority access to resources such as food, shelter, space for breeding or mating opportunities (Rowell 1974; Van Doorn et al. 2003; Ceacero et al. 2012). Therefore, social dominance may bring fitness benefits for the dominant (Ellis 1995; Pluháček et al. 2006) but not for the subordinate animals. If this is the main function of dominance, then individuals with larger resource-holding potential (RHP; Parker 1974; Taylor & Elwood

2003), that is, those in possession of phenotypic traits that enable them to prevail in agonistic interactions (such as large body mass), should use these traits to acquire dominance over animals that are less able to oppose them (such as lighter opponents; Arnott & Elwood 2009). This does not always need to be accomplished by escalated physical fights, since the weaker opponent often quits the contest soon after having assessed its own and/or the opponent's RHP in the initial phases (Rillich et al. 2007; Hsu et al. 2008; Arnott & Elwood 2009). A second possibility is that social dominance serves primarily to reduce within-group aggression through ritualization (Lorenz 1963; Huxley 1966; Maynard Smith 1984) and/or to facilitate the group's coordination (Šárová et al. 2010), thus bringing comparable, even if not identical, benefits to both the dominant and subordinate animals in the group. Restated in terms of individual selection, if the value of becoming dominant is not worth the effort for the physically stronger (yet subordinate) animal to strive for dominance, then the dominance relationships may be based on 'conventional' asymmetries, and respected even if they do not correspond to the differences in RHP, such as which animal is heavier. This view on dominance may be seen as a special case

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(Cant et al. 2006) of the intensively investigated conjecture that uncorrelated asymmetries in RHP (such as prior residence or ownership) decide contests over a resource (Hammerstein & Parker 1982; Grafen 1987; Kemp & Wiklund 2004; Eshel 2005; Kemp et al. 2006; Kokko et al. 2006; Kokko 2013).

This dual view on social dominance is linked to two empirical questions: (1) to what extent do the RHP phenotypic traits of an individual affect its dominance position in a group and (2) to what extent is the position determined by 'conventional' factors (Hammerstein 1981) unrelated to the individual RHP? The quantification of the relative strength of these two classes of factors could increase our understanding of the mechanisms and functions of social dominance. Such empirical quantification could also contribute to a resolution of the theoretical debate as to whether agonistic strategies based on uncorrelated asymmetries in RHP (such as the bourgeois strategy of prior ownership) can be evolutionarily stable (Hammerstein 1981; Korona 1991; Eshel & Sansone 2001; Kemp & Wiklund 2004; Wenseleers et al. 2013). Additionally, the strength of these factors can change during the lifetime of an individual; therefore, it is important also to assess social dominance in terms of its ontogeny (Pelletier & Festa-Bianchet 2006; Favre et al. 2008).

Body mass is an example of a phenotypic trait that may influence dominance in several taxa (see Arnott & Elwood 2009 for examples). On the other hand, age is not a body trait, but rather a time-related property that increases at the same rate for all animals. Therefore, differences in age between individuals may become unrelated to their phenotypic differences, such as body mass, especially after they reach adult body size (Pelletier & Festa-Bianchet 2006). Grafen (1987) and Korona (1991) noted that age may more often be used in natural populations for the 'conventional' settling of potential contests than are other uncorrelated RHP cues. This is because every young individual has a chance to become older, and hence this system does not create permanent losers who might attain a 'desperado' strategy of challenging at any cost because they have nothing to lose. The prospect for future reproductive success may be a very important factor in why age-based systems of peaceful queuing for a better dominance position can be stable (Kokko & Johnstone 1999).

Many studies have focused on body mass and/or age as predictors of social dominance in female ungulates (e.g. Rutberg 1983; Drickamer et al. 1999; Archie et al. 2006; Kemp et al. 2006; Pluháček et al. 2006). Nevertheless, most results are inconclusive, and they do not resolve which of the two factors has the decisive influence upon dominance. One problem is that body mass and age are correlated during the juvenile, adolescent and early adulthood periods of life (Favre et al. 2008), and the commonly used statistical procedures cannot handle such collinearity. Another problem is that only a few studies have collected data over the life span of individuals to investigate properly the ontogenetic mechanisms that underlie the dynamism of social dominance. This may be extremely important, since age may be correlated with body mass early in life but not at adulthood. That age may change from being a correlated RHP cue to being an uncorrelated RHP cue during an individual's lifetime may explain why age, but not other asymmetries between animals, can become established as the conventional cue that animals use for the nonaggressive settling of conflicts (Eshel 2005).

The aim of the present study was to use longitudinal social data to establish whether differences in body mass (an RHP-correlated dominance cue) or age (a 'conventional' dominance cue) primarily determine dominance relationships in a herd of female beef cattle, *Bos taurus*. Use of captive beef cows is suitable, because their hierarchical organization is similar to that of free-ranging cattle (Clutton-Brock et al. 1976). As recommended by Langbein & Puppe (2004), we analysed social dominance at three levels: group

(stability and linearity of the hierarchy); individual (dominance position of an individual); and dyadic (pairwise relationships). After quantifying the stability and transitivity of the dominance hierarchy at the group level, we first addressed the influence of age versus body mass at the individual level by studying the relative contributions of body mass and age to the actual dominance position using path analysis as a suitable (but scarcely used) statistical tool (Briffa et al. 2013). Then, at the dyadic level, we examined how frequently the initial age-determined pairwise relationships were reversed and the extent to which differences in age and/or body mass determine the direction of dominance in a dyad. At both levels, we took ontogenetic aspects into account by distinguishing between the first period of life, when body mass is increasing, and the second period of life, when cows reach their mature body mass.

METHODS

Animals and Housing

Observations were carried out in 1999–2009 (except 2003) in a herd of female dehorned cattle of the Gasconne breed, and their crossbred offspring with at least 50% Gasconne genes. The herd was stationed at the experimental farm of the Institute of Animal Science in Prague, Czech Republic (14°38'E, 50°02'N; elevation approximately 300 m above sea level). The herd size fluctuated between 29 and 39 animals, aged 2–16 years of age, with body mass between 368 and 910 kg. The proportion of growing and mature cows varied across years owing to inclusion of new heifers and/or selling and slaughtering of older cows. Calves were born between January and April and weaned and separated from their mothers in September. Yearling heifers were taken back to the herd in June. Calves were routinely eartagged after birth (up to 72 h postpartum) according to the EU and Czech law. The standardized plastic eartags for identification of individual cattle were distributed by Českomoravská společnost chovatelů (Hradištka, Czech Republic).

From November (2 months after the calves had been weaned and 2 months before the calving season started) until April, the herd was kept loose housed in a 279 m² barn with deep straw bedding connected to a 1145 m² concrete outdoor run. During this winter season, animals were fed silage and had ad libitum access to alfalfa hay, water and a mineral lick. For the rest of the year, the animals were kept on a pasture. Rotating grazing of four pasture plots ranging from 1.9 to 6.8 ha in size was used. Thus, the animals generally had plenty of food, water and lying areas, although some competition occurred immediately after fresh silage was provided in the morning during the winter season.

This kind of herd is especially suitable for studying the mechanisms underlying acquisition and maintenance of dominance rank in species in which recruitment of new herd members is mainly from the herd's own progeny. This pattern of animals leaving and entering the herd is common in several free-ranging large herbivores, including in pastured female cattle with no milk production and in feral cattle with no human interference (Lazo 1994).

The study was designed according to European and Czech laws and the ASAB/ABS guidelines for ethical use of animals in research. The protocol was approved by the Institutional Animal Care and Use Committee of the Institute of Animal Science (Permit Number: 11/99). All data were collected during standard husbandry procedures of feeding and weighing of the animals.

Data Collection

We observed the herd during a socially stable period (i.e. when no changes to herd structure occurred) between early November and first calving in January. At the time of observation, the youngest

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