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 (Sárová 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.
(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 spořitelna chovatelů (Hradisko, 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 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
animals we observed were pregnant heifers, aged 20–24 months (hereafter 2 year olds). Observations were carried out three times per week during feeding time (1000–1100 hours) as dominance relationships based on spontaneous interactions differ only slightly from those motivated by feeding in cattle (Jezierski & Podlužny 1984) and are highly repeatable (Gibbons et al. 2009). In addition to eartags, all animals had numerical collars during observations. The standardized textile numerical collars for cattle were supplied by Profarm (Hradec Králové, Czech Republic) and were worn by cows from October to January.

We used ad libitum sampling (Altmann 1974; Martin & Bateson 1986) to record three categories of agonistic interactions: butt; low-head threat; avoidance (Table 1). We considered a pairwise dominance relationship as ‘ascertained’ in a given year if the same animal was always the loser (i.e. the butted/threatened/avoiding animal) in all observed interactions. The dominance status of an animal was quantified through the dominance index (DI), calculated as $D = D + S$, where $D$ is the number of ‘ascertained’ relationships in which the animal was dominant and $S$ is the number of ‘ascertained’ relationships in which the animal was subordinate (Sambras 1975; Wierenga 1990). The index was computed for each year separately and only for animals that had at least five ascertained relationships in that year.

Animals were weighed monthly in a restrain box on a tensometric scale with a 1 kg resolution. In our analysis, we included all weights taken during the month we started to measure the dominance. If weights from that month were not available, then we used the weight from the closest observation in the analysis.

### Statistical Analyses

#### Dominance indexes

We quantified the ‘linearity’ of the dominance hierarchy using the triangle transitivity metric $t_{tri}$ defined previously by Shizuka & McDonald (2012) as $t_{tri} = 4(P_1 - 0.75)$, where $P_1$ is the proportion of transitive triangles among all recorded triangles. The $t_{tri}$ metric takes into account the fact that 75% of all triangles will be transitive if dyadic relationships are formed completely at random. The $t_{tri}$ metric ranges from 0 (no orderliness, $P_1 = 0.75$) to 1 (full orderliness, no cyclic triangles). We calculated the triad caucus and the statistical test of significant transitivity based on randomization procedure in R codes (R Development Core Team 2009), including the Statnet Package (Handcock 2003) as provided by Shizuka & McDonald (2012). We subsequently analysed the stability of dominance indexes across years through Pearson correlations.

#### Body mass

We used one-way ANOVA with post hoc Tukey test to compare body mass differences related to age. We distinguished two periods of lifetime: Period 1, which included growing cows, and Period 2, which included mature cows that reached full body mass (see Results). For this reason, we performed all the subsequent analyses at three levels: for all cows in the herd (to assess the total effects on social dominance) and separately for the two periods (to establish whether the mechanisms affecting acquisition and maintenance of social dominance change with age).

### Age, body mass and dominance index

We used Pearson correlations to examine relationships among these three variables since Kolmogorov–Smirnov tests showed normality in all data sets.

We initially analysed the relative influence of age, body mass and group structure on the dominance index of a cow through path analysis (structural equation modelling, SEM). Herd age structure (quantified as the proportion of growing cows present in the herd) was included in the models, and the indirect effect of age through its influence on body mass was also considered. Path analysis provides a set of univariate equations that are solved simultaneously and therefore are better suited for studying multiple processes in complicated systems (Shipley 2002), especially when the studied variables are highly correlated (Schumacker & Lomax 2004), as in our data set. Thus, this procedure is especially suited to study simultaneous effects of age and body mass (Landete-Castillejos et al. 2010). We tested the same model for the whole herd, for growing cows and for mature cows. All endogenous variables included in the models (dominance, body mass) showed a normal distribution in the three data sets tested and, thus, we used maximum likelihood as the estimation method (Shipley 2002). Sample sizes were in the ranges proposed by Hoyle (1995) to ensure adequate goodness-of-fit indices. We assessed statistical significance of the variables included in the models and their relationships through critical ratios (the ratio mean/SE, which gives a z score allowing assessment of the P value for each variable; Schumacker & Lomax 2004). As goodness-of-fit indices of the models, we used the Bentler–Bonett normed fit index (NFI), which compares the chi-square value of the proposed model with that of the null model and is adequate for models with low complexity (Bollen & Long 1993), and Bentler’s comparative fit index (CFI), which corrects for the complexity of the model (Bentler 1990). These indices should be above 0.9, but values closer to 1 are preferable. Other parsimony-adjusted indices were not considered because, in most of the analyses, the best model was also the saturated one, owing to their relative simplicity. Path analyses were performed in Amos 20.0 for IBM SPSS Statistics.

We then tested the influence of the quantitative within-dyad differences in age and body mass on dominance direction in pairs through a generalized linear mixed model. Since many dyads were observed in several years, we randomly chose one yearly observation from each dyad to avoid pseudoreplication and applied the model to this data set of unique dyads. In each dyad, we randomly chose a focal cow and tested whether age and/or body mass superiority (or inferiority) affected the probability of her being dominant in the pair. The identities of the focal cow and the other cow entered the model as random factors. The analyses described in this section were carried out in SAS v9.3 (SAS Institute, Cary, NC, U.S.A.).

Finally, to examine the relative strength of the effects of age and body mass on dyadic dominance, we focused on those dyads in which the younger animal was heavier. Using a chi-square goodness-of-fit test, we tested in these dyads whether the dominance direction was more frequently congruent with age superiority or body mass superiority.

### RESULTS

Over the duration of the study (10 years), we recorded 11,226 agonistic interactions between 92 different individual cows. The...
dominance index could be established for all animals in all years except for seven cases, which were discarded from the analysis because the number of ascertained pairwise relationships was lower than five for the given animal in the respective year. We ascertained 865 pairwise relationships, some of them only for 1 year and some of them for up to 8 years. Thus, our database contained 3195 records at the dyad × year level (Table 2). At any given year we could ascertain between 43% and 84% (Table 2) of the possible dyadic relationships.

The dominance hierarchy was strongly transitive in all years ($P < 0.001$ for all 10 matrices; randomization tests with 1000 permutations; Table 2). Between 82% and 96% of the relationships remained unchanged between two consecutive years (Table 2). As a result, dominance indices of individual cows were highly correlated between subsequent years ($r$ between 0.63 and 0.94; Table 2).

Body mass of cows increased during years 2–4 and remained stable from the fifth year onward (Fig. 1). One-way ANOVA with Tukey posthoc tests showed that animals that were older than 4 years were significantly heavier than those that were younger than 4 years (all $P < 0.01$), while 5-year-old animals did not differ significantly from any older age category (all $P > 0.05$). Therefore, two periods of cattle lifetime were distinguished: Period 1, in which cows increased in body mass during ages 2–4 years (hitherto labelled as ‘growing cows’), and Period 2, in which cows reached full body mass (i.e. were 5 years or older; hitherto labelled as ‘mature cows’). Both for the whole data set and for the two defined periods (growing and mature cows), our main variables (age, body mass, dominance index) were highly correlated (Table 3). However, we found no correlation between age and body mass among mature cows (Table 3). Thus, all further analytical procedures, both at the individual and the dyadic level, were selected to deal with this high correlation among the variables.

**Individual Level Dominance**

Figure 2 shows the standardized regression of body mass in the most plausible models for the whole herd (Fig. 2a), for growing cows (Fig. 2b) and for mature cows (Fig. 2c) among the 17 possible models analysed through path analysis. All of these models achieved adequate goodness-of-fit values (whole herd model: NFI = 0.971, CFI = 0.974; growing cows: NFI = 0.926, CFI = 0.938; mature cows: NFI = 0.987, CFI = 1.000). All of the critical ratios in the selected models showed highly significant $z$ scores (values not shown). None of the 16 additional models achieved adequate goodness-of-fit values in any of the studied groups.

All of the models explained a large amount of the observed variability in the dominance index. In the whole herd model, squared multiple correlations explained 79% of the variability observed in the dominance index (Fig. 2a). This model showed that age (standardized regression weight $= 0.59$; hereafter SRW) exerted more influence on the dominance index than body mass (SRW = 0.36) or group structure (SRW = 0.23). Age also exerted a highly indirect influence on dominance by explaining 36% of the observed variability in body mass (SRW = 0.60).

In growing cows, the selected model explained 53% of the observed variability in the dominance index (Fig. 2b). This model confirmed age (SRW = 0.60) as the most important factor affecting dominance in growing animals, but it also showed a high sensitivity to group structure (SRW = 0.41). Body mass (which was also strongly correlated with age) had no effect on dominance index in this age category.

Finally, the model for mature cows explained 56% of the observed variability in the dominance index (Fig. 2c). Age (SRW = 0.61) again exerted a greater influence on the dominance index than body mass (SRW = 0.34) or group structure (SRW = 0.28). In this case, age did not explain the observed variability in body mass and, thus, showed no indirect effect on the dominance index.

**Dyadic Level Dominance**

When the heifers were observed for the first time at 2 years of age, they were subordinate in 98.8% of their relationships with older cows. Later during ontogeny, some relationships were reversed, but even for the category of mature cows aged 5 or more years, the proportion of these age-reversed relationships amounted to only 18.9%. The age-reversed dominance relationships thus played a much smaller role in determining the dominance positions of individual cows than the age-congruent relationships.

The generalized linear mixed-model analysis investigated whether the direction of dominance in a dyad was affected by the quantitative difference between the two respective cows in age and body mass. The probability of being dominant increased strongly with the age superiority of the focal animal ($F_{1,138} = 161.1, P < 0.0001$; Fig. 3). As expected, this was also true in the subset of growing cows ($F_{1,207} = 29.7, P < 0.0001$), but this effect of age was also strong in the subset of dyads involving only mature cows ($F_{1,270} = 59.2, P < 0.0001$) where the difference in age was unrelated to the difference in body mass since these cows were no longer gaining body mass with age.

Table 2

| Year | No. of animals$^*$ | No. of possible relationships$^1$ | Triangle transitivity$^1$ | Stable relationships with respect to the previous year$^1$ | Correlation between dominance indices in two consecutive years$^1,2$ |
|------|-------------------|---------------------------------|--------------------------|----------------------------------------------------------|---------------------------------------------------------------|
| 1999 | 29 (59)           | 406 (54)                        | 0.877                    | 63 of 76 (83)                                            | $r_{22} = 0.63, P < 0.00009$                                    |
| 2000 | 35 (46)           | 595 (43)                        | 0.915                    | 82 of 93 (88)                                            | $r_{20} = 0.76, P < 0.0001$                                    |
| 2001 | 36 (42)           | 630 (59)                        | 0.988                    | 106 of 129 (82)                                          | $r_{29} = 0.83, P < 0.0001$                                    |
| 2002 | 31 (58)           | 463 (49)                        | 0.483                    |                                                          |                                                               |
| 2004 | 35 (49)           | 595 (52)                        | 0.942                    |                                                          |                                                               |
| 2005 | 34 (56)           | 561 (55)                        | 0.962                    | 156 of 163 (96)                                          | $r_{28} = 0.94, P < 0.0001$                                    |
| 2006 | 37 (51)           | 666 (46)                        | 0.956                    |                                                          |                                                               |
| 2007 | 39 (59)           | 741 (57)                        | 0.875                    | 181 of 207 (87)                                          | $r_{29} = 0.85, P < 0.0001$                                    |
| 2008 | 30 (70)           | 435 (82)                        | 0.968                    | 193 of 211 (91)                                          | $r_{20} = 0.62, P < 0.0001$                                    |
| 2009 | 32 (59)           | 496 (84)                        | 0.974                    | 137 of 167 (82)                                          | $r_{21} = 0.77, P < 0.0001$                                    |

$^*$ Numbers in parentheses show the percentage of mature cows (>5 years old, as defined in the text) in each group.

$^1$ Numbers in parentheses show the percentage of ascertained relationships.

$^1$ Triangle transitivity is a measure of the prevalence of transitive triangles among all recorded triangles in a linear dominance hierarchy, following Shizuka & McDonald (2012).

$^1$ If the dominant cow in a given dyad was also the dominant cow in the previous year. Numbers in parentheses show the percentage of unchanged relationships.

$^2$ Pearson $r$. 

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The difference in age-dependent dominance was steepest between 1 and 1 years with respect to the focal cow, increasing by a full 66%. Further increases in the age difference had much weaker effects on dominance direction. That is, age superiority, even by a mere 1 year, in a given dyad was the decisive factor for the direction of dominance.

The quantitative difference in body mass also played a role in the models (Fig. 4): the larger the body mass advantage of the focal cow in a pair, the greater was her probability of being dominant in the pair ($F_{1,1382} = 122.8, P < 0.001$; Fig. 4). This relationship was also highly significant for dyads of growing cows ($F_{1,207} = 26.2, P < 0.0001$) and mature cows ($F_{1,270} = 30.9, P < 0.001$). The $F$ values for the influence of age on dominance were higher than those for the influence of body mass, demonstrating that age also had a stronger effect than body mass on dominance in dyadic relationships.

This stronger role of age than body mass was also confirmed by simple counting statistics. There were 602 dyads in which the younger cow was heavier (i.e. the effects of age and body mass acted in opposite directions). In 443 of these dyads (73.6%, $P < 0.001$ for the difference from 50% by sign test), the older but lighter cow was dominant. When categorized by the difference in body mass, the percentage of dyads in which the lighter but older cow was dominant was 81% when she had a small disadvantage (between –1 and –100 kg), 58% when she had a moderate disadvantage (between –101 and –200 kg) and 43% when she had an extreme disadvantage (below –200 kg). Also, in the whole data set, age-reversed dominant relationships ($N = 264$) were much less frequent than mass-reversed dominance relationships ($N = 543$, $\chi^2 = 96.5, P < 0.001$ different from equal frequency).

**DISCUSSION**

This study shows, both at the dyadic and at the individual level, that age, rather than body mass, is the decisive factor influencing social dominance in female beef cattle. At the individual level, we demonstrated a predominant effect of age over body mass using path analysis (a method that has, so far, only rarely been applied to dominance data). Previous studies in cattle have reported relationships between social rank and both age and mass, but they were not able to distinguish which of the two relationships is decisive (Clutton-Brock et al. 1976; Reinhardt et al. 1986; Bennett & Holmes 1987). At the dyadic level, we obtained strong evidence that the direction of dominance is explained more by age superiority than by differences in body mass. Moreover, we found that age-reversed relationships occurred much less frequently than mass-reversed relationships within a dyad.

Thus, our results indicate that dominance relationships in adult female beef cattle are strongly influenced by age superiority. That is, as part of the process of dominance acquisition, from the beginning, young cows accept their subordinate role in relationships with older animals. In later years, age-reversed dominance may arise, but in our study these relationships made up less than 20% of all dyadic relationships. Importantly, even when the younger cow outgrew an older one, the dominance relationship did not change in 74% of the cases, which suggests a great stability in dominance maintenance (Bouissou et al. 2001). Thus, the dominance hierarchy system documented in our study is based on two simple rules of thumb working at the dyadic level during dominance acquisition and maintenance, respectively: (1) when a cow enters the herd, it accepts subordination to each cow present; (2) it then respects this subordination for life.

However, the second rule was not obeyed in all dyads, as age-reversed dominance relationships did arise, although infrequently. When young cows entered the herd, they were 120–300 kg lighter than the resident cows. As they grew, the difference in mass diminished in the dyads. This affected the probability of dominance reversal. The age-reversed dominance relationships were more probable in dyads where the younger cow had a mass advantage, indicating that being heavier increased the younger cow’s fighting ability and/or motivation to challenge the status quo (Pelletier & Festa-Blanchet 2006; Favre et al. 2008). Nevertheless, age superiority had a stronger influence on the direction of dominance than mass superiority, especially within the category of mature cows that were no longer growing (i.e. where age and mass were unrelated). Therefore, the major conclusion at the dyadic level is that dominance in any pair is more strongly determined by age superiority than by relative body mass.

Results obtained at the dyadic level were totally congruent with the results obtained at the individual level through path analysis. Models showed that age was the only factor with a significant effect on the dominance status in growing cows (2–4 years old).

**Figure 1.** Relationship between age and body mass in female beef cows. Triangles indicate growing cows (linear regression line is shown as a dashed line); squares indicate mature cows (linear regression line is shown as a solid line).
Nevertheless, the importance of body mass increased for mature cows (>4 years old) for which age and body mass were uncorrelated; however, the effect of age was still approximately two-fold greater. Few studies have used path analysis for distinguishing the simultaneous effects of age and body mass in ungulates (e.g. parasite load: Decristophoris et al. 2007; milk production: Landete-Castillejos et al. 2010). Only Favre et al. (2008) used a similar approach when studying the effects of horn size, age and body mass in a herd of bighorn sheep, \textit{Ovis canadensis}. Their results were similar to ours, since only age (but not body mass) was related to rank in young animals; while the effect of body mass increased in full-grown animals. Their paper does not provide information about the amount of variability in dominance explained by these factors, so a direct comparison with our results is not possible. Therefore, it seems that age, especially in physically immature individuals, is the main mechanism driving the establishment of dominance hierarchies in several social ungulate species.

This predominance of age over body mass may not hold for all beef cattle under all conditions. For instance, when unrelated, same-age beef calves are housed in high-density intensive feedlots, or when previously alien beef cows are intermixed, intensive aggression often occurs. When unfamiliar beef cows are grouped, body mass, possibly combined with loser/winner and personality effects, may have more influence on the resulting dominance in dyads than age differences (Landaeta-Hernandez et al. 2013). Also, our results do not apply to dominance in male beef cattle, for which social dynamics and dominance relations differ. Nevertheless, the conditions in our study correspond well with the natural social structure of free-roaming cattle. When naturally breeding cattle are allowed to roam freely, they form spatially cohesive (Reinhardt & Reinhardt 2011) and stable matrilineal herds of 10–35 females with progeny (Lazo 1994). Female philopatry seems to be the rule, and, according to the most detailed study (Lazo 1994), intermixing between herds is rare. The studies in free-roaming cattle agree with our study: that escalated aggression between adult females is rare (Hall 1989), as are dominance reversals. These similarities indicate that our findings may indeed reflect dominance structure in female beef cattle, as naturally evolved in \textit{B. taurus}. Nevertheless, it is highly probable that beef cows have the ability to adapt to less stable social situations using strategies other than age-based dominance reported here. Further research should investigate the effects of factors such as breed (Stricklin 1983). For example, in cattle breeds for which aggressiveness (Plusquellec & Bouissou 2001) or rapid body growth has been intensely selected, the role of various factors affecting dominance may differ.

\textit{Conventional Dominance: What Function?}

Our findings show that the physically strongest beef cows do not acquire the top dominance ranks, as predicted by the resource-holding potential hypothesis (Parker 1974; Kemp & Wiklund 2004). Rather, the system puts the oldest animals at the top. It has been shown theoretically (Maynard Smith & Parker 1976; Hammerstein & Parker 1982; Grafen 1987; Eshel & Sansone 2001) and empirically (Kokko et al. 2006; Wenseleers et al. 2013) that ‘conventional’ payoff-irrelevant cues may decide the outcome of animal contests under certain conditions. Elwood & Arnott (2012) showed that, independently of specific proximate mechanisms of agonistic behaviour, the decision whether to engage in a contest can be mapped on a two-dimensional space that plots the value of the contested resource \textit{V} against the (perceived) cost \textit{C} of the contest for the focal animal. The animal should not enter (or continue) a contest when \textit{C} > \textit{V}. The fitness costs and benefits of challenging an older female have not been measured in beef cattle. Nevertheless, a consideration of the ecology and social organization may indicate why the value of a somewhat higher dominance

\textbf{Table 3}

\begin{tabular}{|l|l|l|}
\hline
& \textbf{Age} & \textbf{Body mass} \\
\hline
\textbf{Whole data set (N=326)} & & \\
Dominance index & 0.796\textsuperscript{*} & 0.696\textsuperscript{*} \\
Body mass & 0.604\textsuperscript{*} & --- \\
\textbf{Growing cows (N=142)} & & \\
Dominance index & 0.522\textsuperscript{*} & 0.452\textsuperscript{*} \\
Body mass & 0.766\textsuperscript{*} & --- \\
\textbf{Mature cows (N=184)} & & \\
Dominance index & 0.595\textsuperscript{*} & 0.359\textsuperscript{*} \\
Body mass & 0.034 & --- \\
\hline
\end{tabular}

Values are shown for the whole data set and for the two periods studied (-growing cows 2–4 years old; mature cows >5 years old).

\textsuperscript{*} \textit{P} < 0.001.

\begin{figure}[h]
\centering
\includegraphics[width=\textwidth]{figure2}
\caption{Path analysis models of variables affecting dominance index in beef cows: (a) in the whole herd; (b) in the growing cows (2–4 years old); (c) in the mature cows (>5 years). Arrows show the standardized regression weights. Values in bold indicate the amount of variance explained in the exogenous variables. Symbols e1, e2 refer to errors in the measurement of dominance and body mass, respectively.}
\end{figure}
position in the herd may not be worth the struggle associated with a reversal of the established dyadic relationships.

First, most of the time, there are few defensible resources to which a high dominance status in female beef cattle will give priority access. Pasture-roaming beef cattle are, as were their ancestors thousands of years ago (Noe-Nygaard et al. 2005; Hall 2008), bulk feeders on a low-energy diet that is rarely concentrated in small patches; their reproduction is not dependent on shelters or dens, and there is no incentive to monopolize relationships with males, as bulls do not provide paternal care. Nevertheless, on specific occasions, such as competition over rare quality forage or during feeding from grass that has been cleared of snow in harsh winters, such small effects can accumulate to a biologically relevant effect, over time (American bison, Bison bison: Rutberg 1986; marginal advantages in access to resting places and preferred food items in dairy cows: Wierenga 1990; Val-Laillet et al. 2008; slight premiums in movement efficiency in more dominant beef cows on pasture: Sárová et al. 2010). Ultimately, it is important whether these differences result in any reproductive skew between the more and less dominant cows (Kokko & Johnstone 1999; Cant & Johnstone 2000). In the ecologically similar American bison, dominant cows enjoy little if any reproductive advantage (Vervaecke et al. 2005) in spite of having better access to forage during times of scarcity (Rutberg 1986).

Second, a younger cow may actually suffer a loss when she succeeds in becoming dominant over an older herdmate. Older cows presumably have accumulated more experience as to where to forage under the changing conditions of the pasture. Since more
dominant cows have more influence on the movement pattern of the herd (Sárová et al. 2010), the older cows, if dominant, can express this without restraint, with the other animals profiting from it (e.g. by following them during foraging and travelling). If a younger challenger becomes dominant over an older cow, this benefit from accumulated experience may diminish for each herd member, including the challenger itself. If this speculation is correct, then this would be a case where the value of the contested ‘resource’ (being dominant in a specific dyad) is higher for the ‘owner’ (the more experienced older cow) than for the ‘intruder’ (the younger cow; Arnott & Elwood 2008), which may stabilize the age-based dyadic relationships.

As the value of snatching dyadic dominance from one older cow is probably low, an attempt to do so may only be worth undertaking if the cost is even lower. Our results indicate that this is the case when the younger cow becomes more than 200 kg heavier than the older cow. This finding matches well the predictions of the model by Eschel & Sansone (2001), in which the bourgeois principle is accepted by contenders that are not too different in body size, and resembles the results of the model by Kokko et al. (2006), in which both an RHP-correlated and an RHP-uncorrelated asymmetry has an influence, the result being partial respect for the ownership.

The simple $C > V$ condition (Elwood & Arnott 2012) neatly summarizes when nonaggressive ‘concord’ (Eschel & Sansone 2001) solutions of dyadic disputes occur. What affects the actual costs of a conflict and the value of the resource will differ widely in different species and conditions, and also during ontogeny. Various theoretical models have investigated how differences in ecology, life history, social organization, cognitive abilities, the proximate nature of signalling and aggression (among others) affect the probability that an escalated conflict will occur, and the likelihood that the resolution will be based, fully or partially, on an RHP-uncorrelated asymmetry. Some of those models investigated age as a specific cue for conflict resolution (Kokko & Johnstone 1999), and a few focused specifically on the dyadic contests for dominance as a special case of conflict over resources (Cant et al. 2006). Although it is beyond the scope of this discussion to review the models in any detail, it is interesting to check the specific conclusions of the models against the specific situation of age-based dominance in stable female cattle herds (Table 4). Table 4 shows that at least seven conditions, which have been proposed to make RHP-uncorrelated solutions of conflicts more probable, are present in stable herds of female beef cattle. Thus, the presence of an age-based, rather than a mass-based, hierarchy in female beef cattle is in good accord with recent evolutionary theory on animal contests and dominance.

### Conclusion

In conclusion, dominance in beef cows is largely a conventional structure, in which dominance relationships are established through the initial asymmetry between young recruits and all older cows and develop into a highly transitive dominance structure. Thus, an individual’s dominance status increases with age along a highly predictable trajectory, with individual body mass playing a moderate modifying role. Therefore, dominance in female cows may be an example of contest resolution based upon prior residence. These findings might indicate that the dominance system of beef cattle not only provides advantages for the strongest animals, but may also serve a universally shared function that promotes the smooth functioning of the grazing herd and/or the expression of the experience gained by older cows.

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