



Redefining dominance calculation: Increased competition flattens the dominance hierarchy in dairy cows

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ABSTRACT

Dominance hierarchies are known for mitigating conflicts and guiding priority of access to limited resources in gregarious animals. The dominance hierarchy of dairy cows is typically investigated using agonistic interactions, often monitored at the feed bunk right after fresh feed delivery when competition is high, resulting in frequent interactions. Yet, the outcome of agonistic interactions during times of high competition may be more influenced by cows' high valuation of fresh feed than their intrinsic attributes, such that the dominance hierarchy constructed using agonistic interactions under high versus low competition times might differ. We tested how the structure of the dominance hierarchy changes in relation to different levels of competition in a dynamic group of 48 lactating dairy cows over 10 mo, with 6 cows exchanged every 16 d, for a total of 159 cows. Using a validated algorithm, we continuously detected the actor and reactor of replacement behaviors in 30 feed bins as cows competed for feed. We also calculated the percentage of occupied feed bins to characterize competition at the moment of each replacement. These data were combined to create hierarchies using Elo ratings, separately for 25 occupancy levels ranging from 13% to 100%. For each 1% rise in feeder occupancy, hierarchy steepness fell by $2.41 \times 10^{-3} \pm 9.71 \times 10^{-5}$ (SE), and the percentage of dyads where both cows replaced each other rose by $0.13\% \pm 0.01\%$. At the highest feeder occupancy level in comparison to the lowest one, we observed 7.57% more dyads in which the dominant individual (those that won more interactions at the lowest feeder occupancy) started to lose proportionally more. The magnitude of decrease in the winning rate of the dominant individual in those dyads also got amplified by $1.06 \times 10^{-3}\% \pm 1.37 \times 10^{-4}\%$ (SE) for each 1% increase in feeder occupancy.

These findings illustrate how inferred hierarchies vary with competition, with high competition flattening the hierarchy due to increased success of subordinate animals. We suggest that during heightened competition, increased valuation of resources can affect competitive success more than the individual's intrinsic dominance attributes. We recommend against calculating dominance hierarchies based on agonistic interactions during periods of high competition alone, and more generally urge researchers to differentiate agonistic interactions based on context when constructing dominance hierarchies.

Key words: dominance hierarchy calculation, agonistic interactions, resource availability, feed valuation, intrinsic dominance attributes

INTRODUCTION

Dairy cows are social animals, and dominance hierarchies within the group are assumed to regulate resource access and reduce aggression (Kondo and Hurnik, 1990; Wagner and Gauthreaux, 1990; Drews, 1993). Dominance has been referred to as the asymmetric relationship that emerges from dyadic agonistic interactions in which the animal that repeatedly outcompetes the other member of the dyad is considered to be more dominant (Drews, 1993). Agonistic interactions establish, maintain, and, in some cases, reverse previous ranks within a hierarchy (reviewed in Strauss and Shizuka, 2022). An individual cow's rank within the hierarchy can affect health (Phillips and Rind, 2002; Chebel et al., 2016), feeding strategies (DeVries and von Keyserlingk, 2006), and access to lying stalls and mechanical brushes (Wierenga, 1990; Foris et al., 2021).

The dominance hierarchy of dairy cows is often described using agonistic interactions, often at the feed bunk right after fresh feed delivery, when competition is the highest and a large quantity of interactions can be recorded in a short time (e.g., 0.5 h after feeding: Rioja-Lang, et al., 2009; 1 h after feeding: Gibbons et al., 2009; 2 h after feeding: Collings et al., 2011). This type of competition can be referred to as "exploitative," defined as when animals vie for shared resources, resulting in one

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The list of standard abbreviations for JDS is available at adsa.org/jds-abbreviations-24. Nonstandard abbreviations are available in the Notes.

individual diminishing the availability of those resources for another (Holdridge et al., 2016).

Estimating the dominance hierarchy during times of high competition should not be a problem if we assume that dominance is stable over time (Hausfater et al., 1982; Forkman and Haskell, 2004; Tibbetts et al., 2022) or if the outcomes of agonistic interactions are solely influenced by the animal's intrinsic attributes (e.g., strength, weaponry), which also remain consistent over time. However, outcomes can also be affected by how animals perceive the value of a resource (reviewed in Dehnen et al., 2022a), and this resource potential valuation can vary based on factors including resource availability and hunger (Arnott and Elwood, 2008; Edmunds et al., 2021). For instance, in cattle, the frequency of agonistic interactions increased after fresh feed delivery (Brakel and Leis, 1976; DeVries et al., 2004) and when animals had limited access to food (Lobeck-Lucherhand et al., 2015). Previous research has also shown increased agonistic interactions in other species following food deprivation (fruit flies, *Drosophila melanogaster*: Edmunds et al., 2021) and restricted access to food (common waxbills, *Estrilda astrild*: Beltrão et al., 2022).

The dominance hierarchy constructed based on agonistic interactions during periods of heightened competition may differ from that established in times of low competition. If resource potential valuation is the primary driver of agonistic interactions, subordinates might initiate more interactions against dominant counterparts (i.e., aberrant interactions; Wierenga 1990) to obtain access to fresh food, which cows are highly motivated to access (DeVries et al., 2003). This behavior may disregard established dominance relationships in pursuit of a valued resource (Pimentel et al., 2022), resulting in a more egalitarian (shallow) hierarchy. In such a hierarchy, individuals with adjacent ranks exhibit minor differences in their cumulative success in agonistic interactions (Neumann and Fischer, 2022). As the resource value increases, aberrant interactions may be especially prevalent because the cost of losing is low relative to the cost of not engaging in competition for the resource (Grafen, 1987; Elias et al., 2010; Edmunds et al., 2021).

The effects of competition on the dominance hierarchy are not well investigated. In dairy systems, feed availability and quality are both expected to fluctuate over the day due to the routine practice of feeding twice daily. Nutritional quality of feed is known to be highest right after delivery and wane over time due to selective feeding of specific components (e.g., grains) within a mixed ration (Leonardi and Armentano, 2003; Hosseinkhani et al., 2008; Miller-Cushon and DeVries, 2009). These changes in feed availability and quality are associated with fluctuations in the number of cows present (i.e., feeder occupancy) and agonistic interactions in the feeding area

(DeVries et al., 2004; Gibbons et al., 2010), which can be monitored to reflect changes in competition.

The objective of this study was to investigate how the dominance hierarchy changes in response to escalating competition, as reflected by changes in feeder occupancy. We hypothesized that with increasing competition (1) the dominance hierarchy would flatten; (2) there would be more 2-way dyads (i.e., where both members of a pair win in agonistic interactions against one another), and the winning percentage within the same dyad would become closer to 50:50 as previously subordinate animals become more successful in replacing dominants; and (3) the emergence of new dyads (dyads that were not observed at lower levels of feeder occupancy) would be more frequent.

MATERIALS AND METHODS

Animals, Housing, and Diet

This study was conducted from July 2020 to May 2021 at The University of British Columbia (UBC) Dairy Education and Research Centre in Agassiz, BC, Canada. Data collection and experimental procedures were approved by the UBC Animal Ethics Committee (protocol number A19-0299). During the 10-mo study, 159 lactating Holstein dairy cows were enrolled, of which 12 were primiparous and 147 were multiparous (parity = 3.0 ± 1.1 ; mean \pm SD). The study duration was limited for practical reasons, but we hoped to capture data on social behavior of cattle across a range of environmental changes that routinely happens on commercial farms. The number of cows assessed was determined by pen capacity and the duration of the study period. Cows were housed in a dynamic group of 48 (i.e., the study pen). The initial group of 48 cows was introduced to the experimental pen 12 d before the trial began, after which 6 ± 2 cows were removed from the pen and replaced with new animals (regrouping event) on average every 16 ± 3 d. Cows remained in the trial for an average of 86 ± 54 d. The regular regrouping was not specifically planned for this study but was due to regular removal of lame and sick cows.

Farm staff performed general health checks during the daily milking routine as per standard operating procedures adopted by the farm. A trained expert assessed lameness once every week, following a 5-level scale scoring method (Flower and Weary, 2006). Cows scoring 3 or higher for 2 consecutive weeks (Eriksson et al., 2020) were classified as lame and separated from the study pen. Cows showing signs of illness ($n = 8$) were also removed from the group and kept in a hospital pen; if a cow recovered within 5 d it was returned to the study pen ($n = 5$), otherwise the cow was replaced with a

healthy cow (i.e., no clinical diseases for 2 consecutive weeks; Eriksson et al., 2020). In an effort to minimize social disturbances, we prioritized re-enrolling cows that had been previously removed in a regrouping event ($n = 3$) and thus habituated with the pen to replace cows that were sick for more than 5 d.

The study pen provided access to 48 lying stalls (2.6 × 1.2 m) covered with 0.4 m of sand bedding. The pen was equipped with 30 electronic feed bins and 5 water bins (Insentec, Hokofarm, Emmeloord, the Netherlands; Figure 1). The electronic feed and water bins identified individual cows by radio frequency identification detections (Allflex, Rahway, NJ). For each visit to the feed bins, the system recorded the cow identification (**ID**), bin number, the visit start and end time, and the start and end weight of the feed in the bin (see Chapinal et al., 2007). Cows left the pen for milking twice daily (on average from 0515 to 0626 h and from 1511 to 1611 h). All cows departed for milking as a group, but returned to the pen in groups of 12 (at roughly 10-min intervals) due to the milking parlor's capacity. Fresh TMR (9% alfalfa hay, 39% corn silage, 28% grass silage, 24% concentrate and mineral mix) was delivered twice daily (on average 0607 h and 1538 h) throughout the trial while cows were away for milking. Feed bins were cleaned daily at approximately 1430 h and were empty for approximately 1 h before fresh feed was delivered. Animals had access to water ad libitum.

A portion of the data gathered in this research was previously published by Foris et al., (2023) as part of an analysis focusing on the establishment of dominance hierarchies using data from water bins in comparison to feed bins.

Data Analyses

Data collected from the electronic feeder were used to investigate the relationship between feeder occupancy and dominance hierarchy throughout the study. All data preparation and analysis were conducted using R (version 4.0.5; R Core Team, 2021).

Data Cleaning and Preparation. We recorded a total of 1,073,308 feeder visits over 10 mo. Data were summarized by day with no visit overlap between days, as bins were automatically shut down just before midnight (2345 h) and then reopened just after midnight (0003 h). A cumulative total of 24 d was omitted from the final evaluation due to technical malfunctions with the electronic bin system ($n = 19$ d) and human-induced disturbances within the pen ($n = 5$ d). We investigated the distribution of visit duration and noted that 0.03% of visits lasted longer than 30 min. These visits were retained following previous research (Foris et al., 2019) that validated events of similar length as true feeding events. In 0.66% of feeding visits the same cow was detected at 2 bins at the same time (due to a bin not detecting one cow leav-

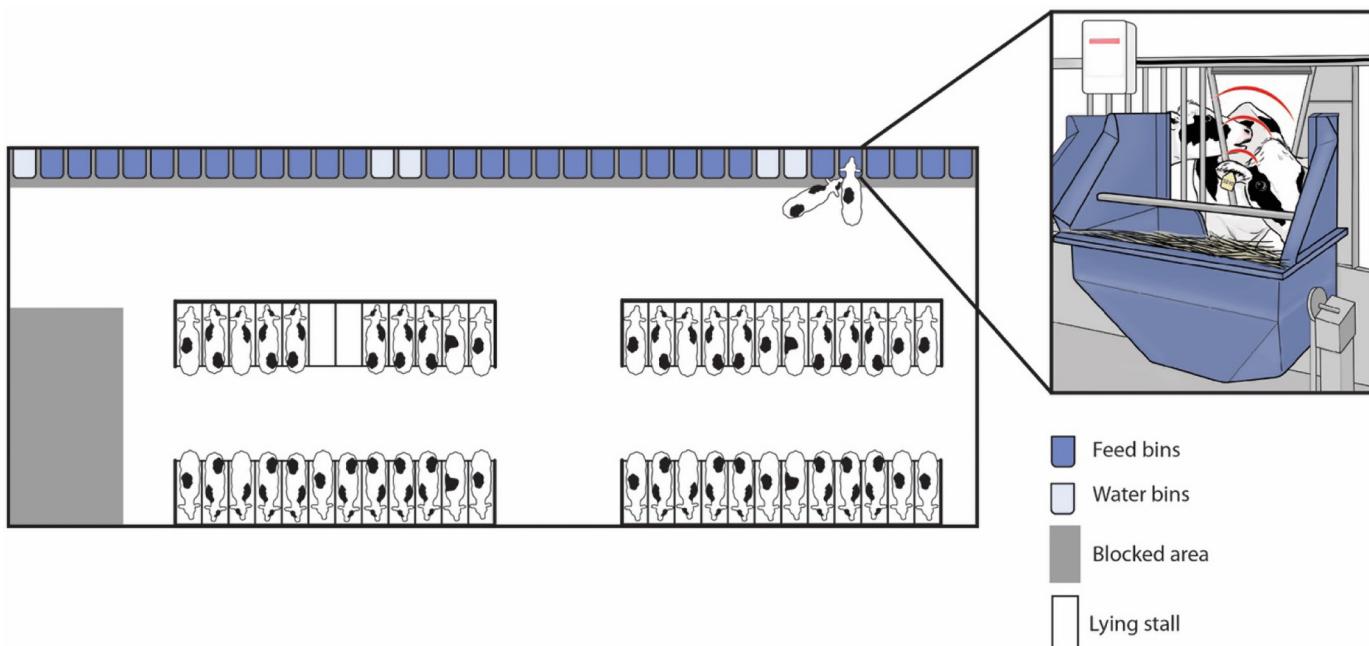


Figure 1. The layout of the experimental pen housing a dynamic group of 48 cows monitored over 10 mo ($n = 159$ cows in total). The setup comprised 30 electronic feed bins and 5 water bins. An illustrative instance of replacement behavior is shown in the right-hand section of the figure.

ing and another entering); these visits were adjusted so that the end time of the first visit was 1 s before the start time of the second visit. Visits with negative feed intake (0.11% of the visits) were removed. If the start or end weight of a bin at a visit was negative (<0.01% of the visits), the value was considered 0. After data cleaning, 1,061,638 feeding visits (98.91% of all recorded visits) were retained.

Measuring Feeder Occupancy. In our preliminary data analysis, we calculated a dominance hierarchy based on replacements that occurred during peak feeding times (approximately 90 min after fresh feed delivery), and a second hierarchy based on replacements at other times of the day and found a shallower hierarchy during peak feeding periods. We hypothesized that this difference was due to differences in competition, but also recognized that our initial comparison was inadequate as competition was likely to vary within both periods. Thus, we elected to measure feeder occupancy at each second to quantify competition directly when a replacement behavior was recorded. Specifically, we used data from feed bins to determine the level of feeder occupancy based on the feed availability in each bin and the number of cows present (Equation 1). For each second within a visit, the feed amount in the bin was calculated as a linear reduction with constant rate over time based on the start and end weight and visit duration. For seconds when the bins were not occupied, the end weight of the last visit was assigned. We also calculated the amount of feed in each bin at each second to distinguish empty bins (feed ≤ 0.5 kg; reflective of the measurement accuracy of the feed bin system) from those not empty, as empty bins should not be regarded as resources available for competing access. Then, we calculated feeder occupancy at each second when agonistic interactions happened as the percentage of feed bins occupied by the cows, excluding the number of unoccupied empty bins.

$$\text{no. of occupied feed bins} \\ \text{total no. of feed bins} - \text{no. of unoccupied bins with no feed} \\ \times 100\% \\ [1]$$

In the equation, “no. of occupied feed bins” refers to the total number of bins that were occupied by cows, “total no. of feed bins” refers to the 30 feed bins used in the trial. “no. of unoccupied bins with no feed” refers to the total number of bins that were not occupied by cows and were empty. By using this equation to define feeder occupancy, we choose to include empty but occupied feeders to account for (1) cows still occupying bins that just became empty as they finished consuming feed at that visit, and (2) cows that may have been unable to

visually estimate the quantity of feed within an occupied bin, but still had the ability to infer the availability of feed by observing the presence of another cow at the bin.

Detecting Agonistic Interactions. We aimed at detecting replacements at the feeder for dominance hierarchy construction. Replacement behavior is when one cow (i.e., actor) physically pushes another cow (i.e., reactor) away from the feed bin and occupies her place (Huzzey et al., 2014; Supplemental Movie S1, see Notes). To longitudinally gather a vast amount of replacement data, we used a validated algorithm to serve as a proxy for observing replacement behaviors. We identified an event as a replacement if the time between when one cow exits a bin and another cow enters the same bin was ≤ 26 s (Huzzey et al., 2014; Foris et al., 2019). We recorded the reactor (i.e., the cow that exits the bin), actor (i.e., the cow that enters the same bin in ≤ 26 s), the time of each replacement (i.e., reactor leaving the bin), the bin number, and the feeder occupancy when a replacement occurred. We discarded replacement events when the presumed “actor” cow was detected feeding at a different bin at the time the presumed “reactor” cow exited the bin where the replacement event was recorded (Foris et al., 2019). If the presumed “actor” cow was feeding at a different bin when the “reactor” cow exited, it is unlikely that the “actor” cow physically pushed the “reactor” cow to cause her to exit. These events likely reflect the “reactor” cow ending her feeding session and vacating the bin voluntarily, and the “actor” cow only coincidentally entering the vacated bin within 26 s.

To evaluate changes in competition within a day, we calculated the average feeder occupancy per hour, and the average number of replacements per hour across all trial days ($n = 285$) using replacements grouped by hour of the day.

Group Level Analysis. Using the EloSteepness package (function “elo_steeplness_from_sequence”; Neumann and Fischer, 2022), we calculated Elo ratings and summed Elo winning probabilities as estimates of individual’s dominance and computed the steepness of the dominance hierarchy. This method has the advantage of continuous dominance assessment in a dynamic group (Neumann and Kulik, 2020). This approach operates on a Bayesian framework, and it is more reliable in groups with many unknown relationships, compared with steepness determined using David’s scores. This method also allows for uncertainty assessment by providing the likelihood distribution of the steepness coefficient and each individual’s summed Elo winning probability (Neumann and Fischer, 2022). Because the initial Elo ratings of individuals are unknown at the start of the interaction sequence, EloSteepness estimates the initial Elo rating of each animal (Goffe et al., 2018). The Elo rating was

determined by considering replacements in the sequence of occurrence and updating the score after each interaction based on Equations 2 and 3 (Neumann et al., 2011):

$$\text{WinnerRating}_{\text{new}} = \text{WinnerRating}_{\text{old}} + (1 - p) \times k, \quad [2]$$

$$\text{LoserRating}_{\text{new}} = \text{LoserRating}_{\text{old}} - (1 - p) \times k. \quad [3]$$

After each interaction, the Elo rating of the actor (i.e., winner) increased by $(1 - p) \times k$ and decreased by the same magnitude for the reactor (i.e., the loser), where p refers to the probability of the actor to win over the reactor based on the Elo rating differences between the 2 before the current interaction, and k represents the maximum points that could be gained or lost in the single interaction (Goffe et al., 2018). The actor gained fewer points for expected wins (i.e., replacing another animal with a lower Elo rating) than unexpected ones (i.e., replacing another animal with a higher Elo rating).

This method takes into account previous interactions and Elo ratings of cows within the group, which are factored in when determining the Elo ratings of newly introduced individuals. The EloSteepness method sets each individual's final Elo rating at the end of the interaction sequence ($n = 159$ cows). To calculate an individual's winning probability against any potential opponent, the EloSteepness method employed Equation 4 (Neumann and Fischer, 2022):

$$p_{AB} = \frac{1}{1 + \exp(Elo_B - Elo_A)}. \quad [4]$$

The winning probability of cow A against cow B is denoted as p_{AB} , and Elo_A and Elo_B represent the Elo rating of cow A and cow B, respectively. To calculate the summed winning probabilities of each individual, their winning probability against all potential opponents were added up, as shown in Equation 5:

$$s_i = \left(\sum_{j=1}^n \frac{1}{1 + \exp(Elo_j - Elo_i)} \right) - 0.5. \quad [5]$$

Cow i 's summed winning probability is denoted as s_i , where Elo_i and Elo_j represent the Elo rating of cow i and cow j , respectively; n is the total number of cows in the trial ($n = 159$). To determine the steepness coefficient, a regression model was used with the summed winning probabilities as a function of the ordinal ranks, and the value of the slope was calculated. The steepness of the dominance hierarchy was used as the dependent variable in a linear model that considered feeder occupancy as a fixed effect.

Using the method described above, we constructed 25 dominance hierarchies based on subsets of data corresponding to replacements occurring at different levels of feeder occupancy during the study period and calculated the hierarchy steepness for each. We created 25 levels based on the percentage of feeder occupancy (level 1: 0%–13.33%; levels 2–24: 13.33%–90% of feeders occupied with 3.33% increment per level; level 25: 90%–100%) so that each of the 25 levels contained more than the minimum number of replacements required for the calculation of a reliable dominance hierarchy (i.e., at least 20 times the number of all cows housed in the group during the trial assuming a moderately steep hierarchy; Sánchez-Tójar et al., 2018). To ensure the comparability of the dominance hierarchies calculated for different feeder occupancy levels, we randomly selected the same number of replacements from each level to calculate the hierarchy ($n = 5,114$ per level; i.e., the lowest number of replacements across the 25 levels, corresponding to an interaction to individual ratio of 32).

We opted for 25 levels, rather than fewer levels with more replacements per level, to allow for better fit of a linear model while still ensuring that each level met the required minimum number of observations.

Dyadic Analysis. We analyzed the effect of feeder occupancy on dyadic relationships after sampling the same number of replacements from each level. This standardization was crucial for unbiased comparisons across various feeder occupancy levels, as an increase in the number of replacements leads to a higher likelihood of 2-way dyads occurring and a reduction in the proportion of unknown dyads (i.e., pairs of cows that have no recorded interactions between them).

Because the percentage of unknown dyads could potentially affect the estimation of hierarchy steepness (Klass and Cords, 2011; Balasubramaniam et al., 2014), we analyzed variations in the proportion of unknown dyads in relation to feeder occupancy. The proportion was determined by dividing the number of dyads without observed interactions by the total number of dyads that could have potentially interacted (assuming they were present in the experimental pen on the same day).

We further examined the influence of feeder occupancy on the proportion of 2-way dyads among dyads with more than one interaction observed at the given feeder occupancy level, as the formation of 2-way dyads requires the occurrence of more than one interaction. Among dyads with more than one interaction, there were 2.98 ± 1.48 (mean \pm SD) interactions recorded per dyad at each of the 25 feeder occupancy levels. The percentage of unknown dyads and 2-way dyads were considered as dependent variables, while feeder occupancy was treated as a fixed effect in linear models. To discern whether new relationships were emerging

with an increase in feeder occupancy, we also computed the percentage of unique dyads (i.e., dyads that were observed only at the corresponding feeder occupancy level and not at any other levels) among all observed dyads (i.e., dyads with at least 1 interaction noted at the particular feeder occupancy level) at each feeder occupancy level.

To investigate the influence of feeder occupancy on the changes in winning percentage within each dyad, we first singled out the dyads that were observed across all levels of feeder occupancy. However, only a small number of dyads ($n = 102$, 1.33% of all possible dyads) were present in all of the 25 levels of feeder occupancy. To address this challenge, we used 5 levels of feeder occupancy (0%, 26.67%], (26.67%, 43.33%], (43.33%, 60%], (60%, 76.67%], and (76.67%, 100%]. This approach increased the number of dyads present in all feeder occupancy levels ($n = 3,272$, 42.69% of all potential dyads). We recorded 6.56 ± 5.81 (mean \pm SD) interactions per dyad at each of the 5 feeder occupancy levels. Using these dyads, we computed the winning percentage for each cow within a dyad at each of the 5 levels. For example, for a dyad consisting of cows A and B, cow A's winning percentage was calculated as the frequency of A replacing B divided by the total number of replacements between the pair, separately for each of the 5 levels of occupancy. To understand how the winning percentage within each dyad changes as feeder occupancy increases, we calculated the changes in winning percentage relative to that at the lowest feeder occupancy level: (0%, 26.67%]. We anchored the winning percentage of each dyad to the cow that initiated more replacements at the lowest feeder occupancy level (i.e., reference animal). In instances where both cows initiated an equal number of replacements at the lowest feeder occupancy, we chose the cow with a greater numerical ID as the reference animal. We computed the percentage of dyads with negative changes in winning percentage (i.e., the dominant individual in a dyad was observed losing proportionally more interactions) at each level of feeder occupancy. We visualized the distribution of negative changes in winning percentage using violin boxplots. We employed mixed-effect linear models, treating the negative changes in winning percentage within the same dyad as dependent variables, feeder occupancy as a fixed effect, and dyad ID as a random effect with both random intercepts and slopes. This allowed us to statistically quantify the effect of feeder occupancy on the changes in winning percentage.

Data Sharing. Data and code for the data analysis are available as an R project on GitHub at: https://github.com/skysheng7/competition_dominance_analysis.git. It is also published at <https://doi.org/10.5683/SP3-HT9EHX>.

RESULTS

We observed a total of 194,631 replacements at the feed bins, with 636.05 ± 201.87 (mean \pm SD) replacements per day. Of these replacements, 53.9% took place when feeder occupancy was less than 50% (which was the case for the majority of the day; Figure 2). All 159 cows were involved in at least one replacement when feeder occupancy was less than 80%. A few cows (ranging from 1 to 7, depending on feeder occupancy levels) were not involved in replacements when feeder occupancy exceeded 80%.

We observed more replacements after morning and afternoon fresh feed deliveries compared with the other times of the day, corresponding to the times when feeder occupancy peaked; 12.1% of replacements took place in the hour after morning feed delivery (when feeder occupancy averaged 64.8%), and 24.1% of the daily replacements occurred in the hour after afternoon feed delivery (when average feeder occupancy was 74.1%; Figure 2).

As feeder occupancy increased, individual summed Elo winning probabilities became less certain (i.e., wider distribution), and the overlap between the summed Elo winning probabilities distributions of different cows increased (Figure 3; Supplemental Movie S2, see Notes). Our linear model revealed that the Elo steepness decreased by $2.41 \times 10^{-3} \pm 9.71 \times 10^{-5}$ (SE) for every 1% increase in feeder occupancy ($R^2 = 0.96$; Figure 4A). In other words, the dominance hierarchy was the steepest at low feeder occupancy (steepness = 0.61 when feeder occupancy was 20%–23.33%; Figure 4A) and the shallowest at high feeder occupancy (steepness = 0.39 when feeder occupancy was 90%–100%; Figure 4A; Supplemental Figure S1 and Movie S3, see Notes). For every 1% increase of feeder occupancy, the percentage of unknown dyads increased by $0.07\% \pm$



Figure 2. The average number of replacements (i.e., one cow pushing another away from the feed bin and occupying her place) per day grouped by hour of the day, in a dynamic group of 48 cows monitored over 10 mo ($n = 159$ cows in total). Color indicates average feeder occupancy (i.e., percentage of feed bins occupied by the cows; unoccupied empty bins were excluded from the calculation) during that hour of the day.

0.01% (SE; $R^2 = 0.48$; Figure 4B), and the percentage of 2-way dyads increased by $0.13\% \pm 0.01\%$ ($R^2 = 0.84$; Figure 4C). The percentage of unique dyads among all observed dyads remained low and constant (ranging from 0.09% to 0.50%) as feeder occupancy increased.

To track changes in winning percentage of the same dyads in relation to changes in feeder occupancy, we used a total of 5 occupancy levels. At the highest feeder occupancy level in comparison to the lowest one, we observed 7.57% (i.e., from 35.61% to 43.18%) more dyads in which the dominant individual (those that won more interactions at the lowest feeder occupancy) started to lose proportionally more. Among those dyads, the winning rate of the dominant individual decreased by $1.06 \times 10^{-3}\% \pm 1.37 \times 10^{-4}\%$ (SE) for each 1% increase in feeder occupancy (Figure 5). Some one-way dyads (i.e., those in which the more dominant individual in a dyad won all interactions at the lowest feeder occupancy) transitioned into 2-way dyads or even completely flipped directionality, with the previously subordinate animal now winning interactions at higher levels of feeder occupancy.

DISCUSSION

We found a decline in dominance hierarchy steepness with increasing competition. The increase in feeder occupancy corresponded to a slight but negligible rise in the percentage of unknown dyads, but the EloSteepness method is robust in accommodating the prevalence of unknown dyads (Neumann and Fischer, 2022). The decrease in steepness is more likely attributable to increased number of 2-way dyads with increased feeder occupancy. The increase in 2-way dyads resulted from formerly more subordinate individuals (identified at low feeder occupancy) becoming more successful in replacing the more dominant counterpart when feeder occupancy increased.

Studies have reported that dominance hierarchies remain stable over time (Hausfater et al., 1982; Forkman and Haskell, 2004; Tibbetts et al., 2022), but to our knowledge, only one previous study assessed the changes of hierarchy steepness within a day (Pimentel et al., 2022); this study concluded that hierarchy steepness decreased in cichlid fish when they were competing for limited resources. Our findings support this conclusion but go further by quantifying competition using feeder occupancy at the time of replacements and showing how this relates to hierarchy steepness. Thus we conclude that the constructed dominance hierarchy can fluctuate under different competitive conditions throughout the day, even within a stable group.

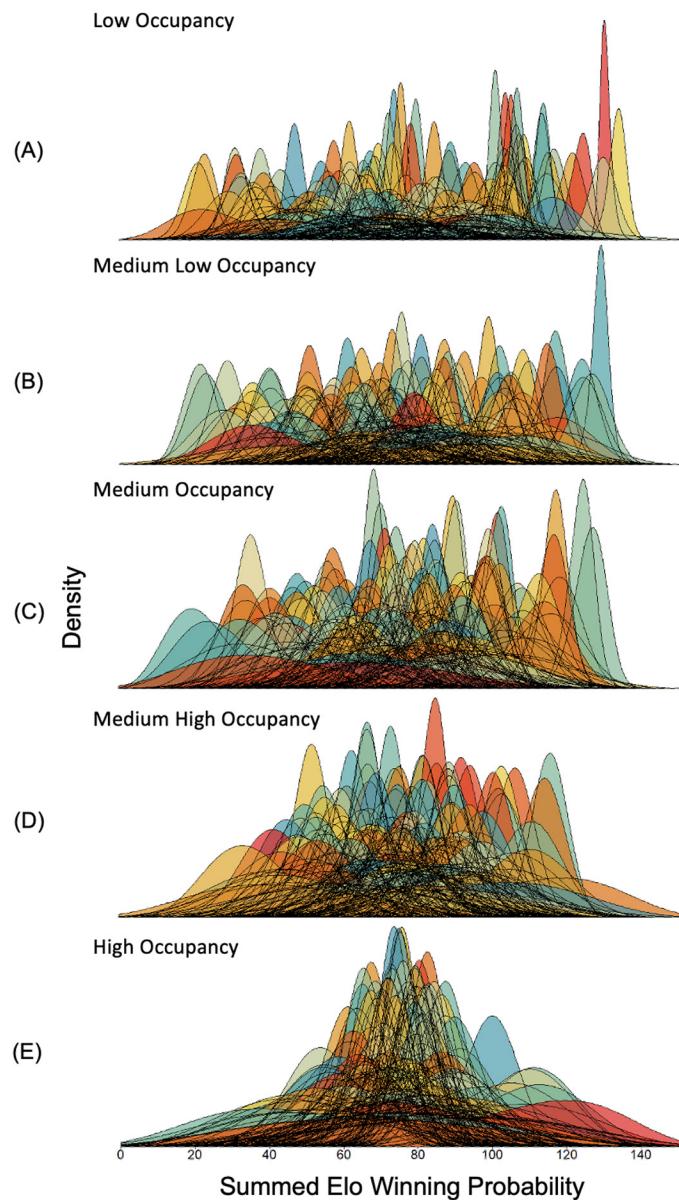


Figure 3. Distribution of summed Elo winning probability for individuals in a dynamic group of 48 cows over 10 mo ($n = 159$ cows in total) under 5 levels of feeder occupancy (i.e., the percentage of feed bins occupied by the cows, but excluding the number of unoccupied empty bins from the calculation) selected to represent trend seen across 25 levels: (A) low: 0%–13.33% feeder occupancy, (B) medium low: 23.33%–26.67%, (C) medium: 50%–53.33% feeder occupancy, (D) medium high: 73.33%–76.67% feeder occupancy, and (E) high: 90%–100% feeder occupancy. Elo rating is a measure of cattle dominance at the feeder, and the summed Elo winning probability represents the likelihood of success for an individual against any potential opponents at any stage in the evaluation process, as determined by their Elo rating. Summed Elo winning probability ranges from 0 to 159 on the x-axis to indicate the dominance position of each cow within the hierarchy. Each cow is represented by a unique color.

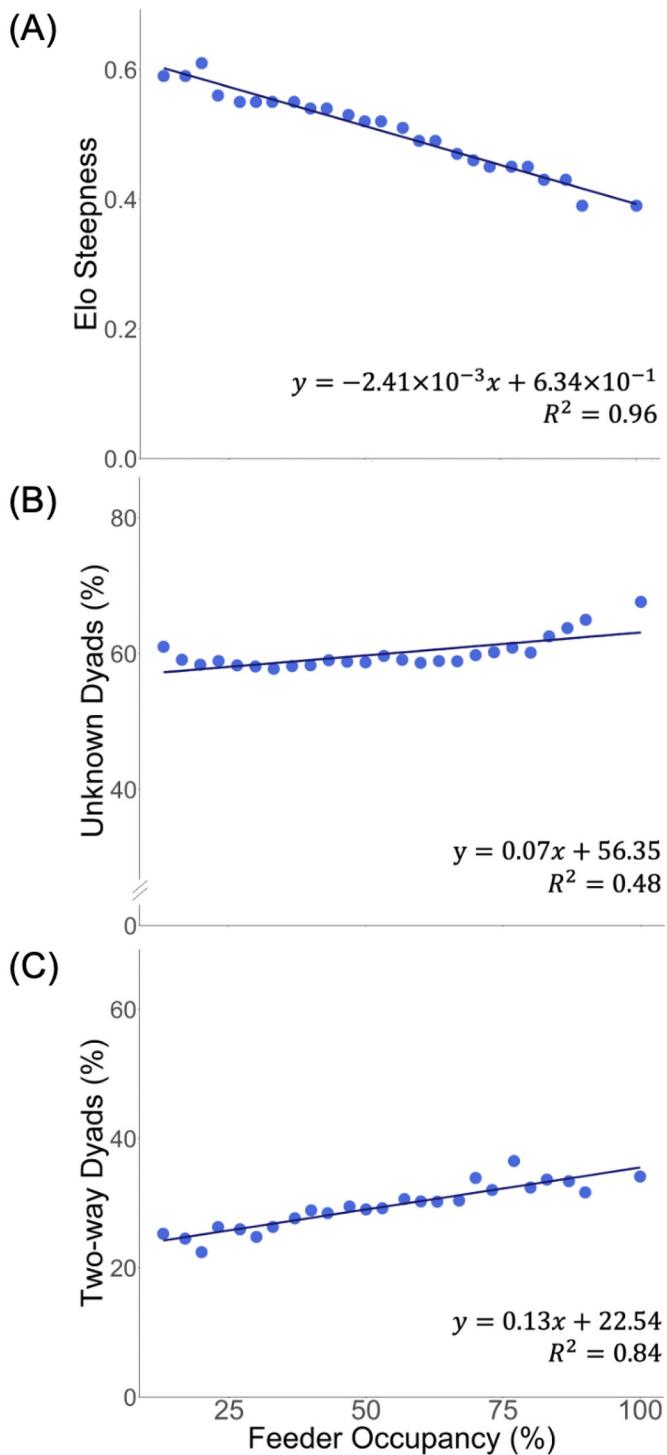


Figure 4. The results of linear models to assessing changes in (A) the Elo steepness of dominance hierarchy, (B) the percentage of unknown dyads, and (C) the percentage of 2-way dyads, in relation to changes in feeder occupancy (i.e., the percentage of feed bins occupied by the cows, but excluding the number of unoccupied empty bins from the calculation). Data were recorded in a dynamic group of 48 cows monitored over 10 mo ($n = 159$ cows in total).

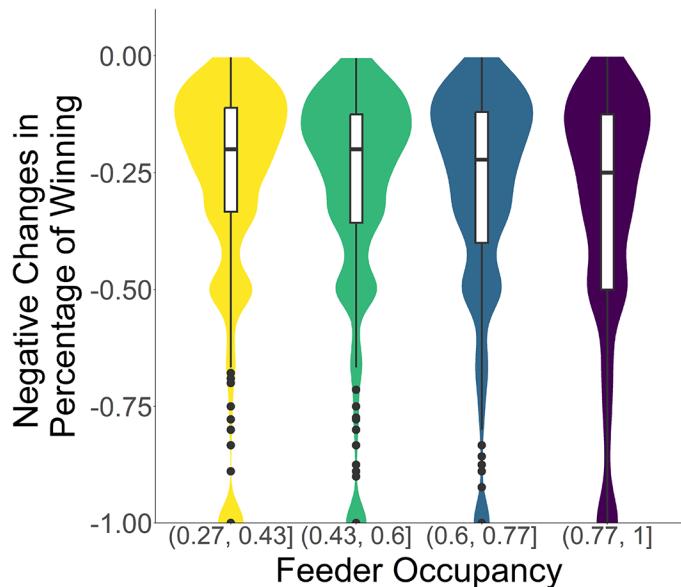


Figure 5. This violin boxplot illustrates the distribution of negative changes (i.e., situations where the more dominant individual in a dyad is observed losing more often as feeder occupancy increases) in the winning percentage within each dyad that was observed across all feeder occupancy levels ($n = 3,272$, 42.69% of all potential dyads). Changes in winning percentage at each feeder occupancy level were computed relative to the lowest feeder occupancy level: (0%–26.67%). The color coding represents different feeder occupancy levels.

Why a Flattened Dominance Hierarchy?

Change in resource potential valuation may explain the flattened dominance hierarchy under high competition. The outcome of agonistic interactions can be explained by intrinsic attributes and resource value asymmetry (Dehnen et al., 2022a). Intrinsic attributes refer to the prior attribute of an individual, such as an individual's size, strength, body condition, and personality. Resource value asymmetry describes the differences in how 2 individuals perceive the value of a resource, which varies based on context. Individuals scale their investment in contests as the perceived value of a resource changes (Dehnen et al., 2022a). We propose that resource potential valuation is sufficiently high during periods of high competition that the cost of avoiding agonistic interactions (e.g., forgoing access to fresh feed) is greater than the potential cost of losing to opponents with superior intrinsic attributes, leading to a type of "desperado" effect as demonstrated in fruit flies (Grafen, 1987) and jumping spiders (Elias et al., 2010).

Others have argued that in guineafowl, displacing another individual from a food source is relatively low-cost given that minimal physical contact is required (Dehnen et al., 2022b). Likewise, we presume that the cost of re-

placement is low for dairy cows. This, combined with the higher nutritional value of feed after fresh delivery (Miller-Cushon and DeVries, 2017), suggests that benefits to access feed after fresh feed delivery may outweigh any cost of competition for access (Parker, 1974).

An alternative explanation for the less steep dominance hierarchy could be that dominant cows accessed fresh feed sooner, thus creating an asymmetry in resource valuation (Pimentel et al., 2022). Dominance can be related to milking order in dairy cows (Soffié et al., 1976), so more dominant animals may have returned from milking (and access fresh feed) before their more subordinate group mates. In addition, the cost of being replaced from the feeder may be lower for more dominant cows, as they could more easily displace another cow to gain access to feed.

Applications on Dominance Hierarchy Calculation

Previous work by our research group and others has recorded agonistic interactions during a few hours of a day (e.g., 1 h/d; Arave et al., 1977; 3 h/d; Phillips and Rind, 2002; 4.5 h/d; Galindo and Broom, 2002), especially following fresh feed delivery (Gibbons et al., 2009; Rioja-Lang et al., 2009; Collings et al., 2011). This approach has primarily been motivated by the need to minimize the time spent observing the behavior. The results of our study indicate that the outcome of agonistic interactions, and thus the resulting hierarchy, is influenced by resource valuation of animals. We advise researchers to be wary of dominance hierarchies based on agonistic interactions measured only at times of high competition at the feeding area.

Despite the high frequency of replacements under high feeder occupancy, most replacements took place when feeder occupancy was low (accounting for about 20 h daily). The number of interactions used to calculate dominance hierarchy has previously been reported to affect the accuracy of dominance analysis (Sánchez-Tójar et al., 2018). However, our results demonstrate that the context of interactions (e.g., level of feeder occupancy) also affects the hierarchy construction (see also Krahn et al., 2023). We suggest also sampling replacements under low competition times to minimize bias caused by animals' high valuation of feed.

Limitations

Resource potential valuation during fresh feed delivery may have been amplified by environmental factors and management procedures in our study. Cows were away from feed for approximately 1 h during the milking before feed delivery. The feed bins were cleaned about 40 min before the afternoon milking, such that

cows spent about 60 to 90 min each day with no access to feed in the afternoon. These periods likely increased cows' motivation to access feed, as evidenced by the high number of replacements associated with afternoon fresh feed delivery.

The feeding area was overstocked in this study, as only 30 bins were available for 48 cows. Overstocking increases the frequency of displacements, especially during peak feeding time (Huzzey et al., 2006; Collings et al., 2011). The subordinate cows may spend longer time standing and waiting to access resources in a competitive situation, increasing the cost of trying to access feed (Huzzey et al., 2006; Foris et al., 2021). Another limitation is the feeding system employed in this study. Physical escalation in agonistic interactions can often be avoided through non-physical threats and unprovoked submissive behaviors in stable groups where individuals can recognize one another and remember previous interactions (Barrette and Vandal, 1986; Drews, 1993; Hobson, 2022). The feeding system used in this study partially blocked peripheral vision of cows when feeding, potentially compromising their ability to respond to nonphysical cues. We recommend others to conduct external validation studies to verify the applicability of our results in different settings. It is conceivable that in scenarios such as an open feed bunk or with reduced stocking density that the dominance hierarchy might be less flattened during peak feeding time.

The physical design of the electronic feed bins (Figure 1) may have made it difficult for cows to see how much feed was available. Feed was easily visible following fresh feed delivery, but as feed was consumed it likely became harder for the cows to gauge how much feed was in each bin. Our use of the feeder occupancy equation Equation 1 assumed that cows were able to differentiate between a bin that had some feed and a bin that was completely empty. We note that cows may also have been able to smell the presence of feed, including when only a small quantity remained. However, exactly when and if cows were able to perceive the presence of feed in bin is not clear.

Presently there is no ideal method to estimate steepness changes longitudinally in a dynamic group. In our preliminary investigations we used both Elo-rating and EloSteepness to establish dominance hierarchy, finding consistent results (both show that the hierarchy flattens with increasing feeder occupancy). In the current paper we chose to focus on EloSteepness due to its direct steepness calculation. However, the current EloSteepness package does not support dynamic steepness calculation; it only offers a single steepness measure at the end of the trial and considers all animals from the 10-mo span, even if some departed midway. Future research should focus on developing methods for dynamic steepness calculation.

The dependence on automatic data collection from the electronic feed bins could also be a limitation of the current study. Physical and nonphysical agonistic interactions in the other areas of the pen, and unsuccessful attempts of replacements were not recorded in this trial. This might have compromised our ability to accurately estimate the dominance hierarchy. Agonistic interactions in the feeding area are also more influenced by cows' valuation of feed than those occurring elsewhere in the pen.

Despite the high precision of the replacement algorithm used in this trial (Huzzey et al., 2014; Foris et al., 2019), there may have been some false positive and false negative interactions between cows based on the current algorithm. In an earlier study our group found 12.4% false positives and 0.8% false negatives in the same feeding area (Foris et al., 2019). False positives and negatives can stem from various sources. Huzzey et al. (2014) found that the optimal threshold ranges from 15 to 47 s for different individuals in identifying replacement events. This variability indicates that we might have incorrectly categorized some events. Nonetheless, the application of a single threshold across a herd is a pragmatic approach when using sensor data for large-scale, herd-level analysis. The choice of a 26 s threshold in this study was informed by previous validation studies (26 s: Huzzey et al., 2014; 25 s: Foris et al., 2019) conducted under similar stocking densities (i.e., 20 cows with access to 12 feed bins, 0.6 bin per cow).

Changes in competition (i.e., feeder occupancy) could influence the optimal threshold for replacement detection using the current algorithm. Among replacements detected using the 26 s threshold, we found a decrease in the median of time interval between 2 consecutive feeding visits as feeder occupancy increased (Supplemental Figure S2, see Notes). This result suggests that a lower threshold may be suitable under high feeder occupancy. Despite this limitation, the 26 s threshold was validated across various levels of feeder occupancy in previous validation studies using 24-h video observations across multiple days, providing a broadly applicable criterion across different competition contexts (Huzzey et al., 2014; Foris et al., 2019). Notably, the majority of detected replacements (77.12%) at high occupancy (feeder occupancy >83.33%) fell within the 10 to 12 s range, which has been shown to accurately represent true replacement events (Foris et al., 2019).

We also tested 2 lower thresholds for identifying replacement events (12 and 15 s) during the highest feeder occupancy level (90%–100%). Using both of these thresholds, we reconstructed 2 dominance hierarchies. This preliminary analyses indicated that changing the threshold (to 12 or 15 s, compared with 26 s) had little effect on the dominance hierarchy steepness (which

changed from 0.39 ± 0.02 to 0.41 ± 0.02 and 0.40 ± 0.02 , when the threshold was 26, 15, and 12 s, respectively). This result suggests that changing the detection threshold for replacement events under high competition is unlikely to change the study's conclusions. However, we recommend future research to explore the effect of feeder occupancy on the optimal threshold for detecting replacement events.

Some authors have argued that affectionate cows share feed bins together by taking turns feeding (Stricklin and Gonyou, 1981; Wasilewski, 2003). The algorithm we used would have labeled this type of affiliative behavior as replacement events, increasing false positive detections, and potentially biasing dominance calculations. We advocate for research to explore the development of computer vision models for the automatic monitoring of agonistic behaviors (Oczak et al., 2014) that address limitations of sensor-based detection systems and provide a more nuanced understanding of social dynamics of animals.

Welfare Concerns

Previous research has argued that high synchronicity of feeding could be an indicator of high animal welfare (Metz, 1983; Mattiello, et al., 2019; Mee and Boyle, 2020). However, we observed that periods of high feeding synchronicity were associated with increased feeder occupancy, coinciding with a rise in the frequency of agonistic interactions. It is difficult for the subordinate cows to avoid the more dominant conspecifics when competition is high in an overstocked indoor environment (Kondo and Hurnik, 1990; Wierenga, 1990). In more natural environments, such as pasture, cattle have greater freedom to avoid dominant peers. Cattle on pasture also have the opportunity to form subgroups organically, in contrast to the managed grouping practices in indoor environments that may interfere with the formation of long-term social bonds (Marino and Allen, 2017; Hodgson et al., 2024). It has been shown in mice that chronic agonistic interactions induce a depressive-like state in defeated animals (Kudryavtseva et al., 1991; Berton et al., 2006). We encourage future research to investigate farm management practices that could mitigate conflicts, and endorse the adoption of farm practice that reduces the frequency of agonistic interactions.

CONCLUSIONS

The structure of dairy cow dominance hierarchies is influenced by the level of competition. Periods of high competition were associated with decreased hierarchy steepness and an increase in the number of 2-way dyads, as previously subordinate animals became more success-

ful in replacing group mates. These results suggest that agonistic interactions and the constructed dominance hierarchy under high competition time are driven by the animals' high valuation of resources more than by their intrinsic dominance attributes. We advise researchers to avoid establishing dominance hierarchies based solely on agonistic interactions at the feeder during high competition and highlight the importance of distinguishing agonistic interactions based on context.

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Nonstandard abbreviations used: ID = identification; UBC = University of British Columbia.

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