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It's All About the Climb: Consistent Individual Differences in Cattle Behavior and How they Relate to Grazing Distribution on Extensive Rangelands

By

MAGGIE CREAMER
DISSERTATION

Submitted in partial satisfaction of the requirements for the degree of

DOCTOR OF PHILOSOPHY

in

Animal Behavior

in the

OFFICE OF GRADUATE STUDIES

of the

UNIVERSITY OF CALIFORNIA

DAVIS

Approved:

Kristina Horback, Chair

Kate Laskowski

Kenneth Tate

Committee in Charge

2024

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Abstract

Consistent individual differences (CIDs) in animal behavior can be measured in assays that target specific behaviors which are assumed to represent underlying stable traits. These are linked to various outcome measures, such as how animals use space and/or forage in natural environments. Consistent individual behavioral variation in beef cattle has been previously studied, however, traditional assays involve stressful contexts, subjective rating scales, and short-term assessments. CIDs measured in multidimensional behavior assays with extensively managed beef cattle have not yet been linked to grazing patterns by previous studies. The grazing patterns of beef cattle that forage on extensive rangeland landscapes have implications for the environmental sustainability of cattle production and conservation of rangeland ecosystems. The objectives of this dissertation were to measure CIDs in behavior in cattle using broad scope, yet practical, assays and investigate how these relate to relevant feeding behaviors (Chapter 1), identify consistent grazing patterns of cattle on rangeland (Chapter 2), and examine the relationship between CIDs measured in assays and grazing patterns (Chapter 3). I found that cattle showed consistency in behaviors observed across short-term and long-term time frames in a management context (handling cows through an open chute) without using physical restraint (Chapter 1). Behaviors measured in distinct locations of the assay loaded onto different principal components (e.g. time to traverse the concrete chute while isolated and time to traverse the hydraulic squeeze chute while isolated), which may indicate different mechanisms from which these behaviors arise. Less active and less excitable cows during the assay chose to feed from supplement rather than be in proximity to groupmates in a social-feed tradeoff task (Chapter 1). Individual cows were consistent in grazing patterns across two summers despite cattle having access to a new, high-elevation watering site during the second summer of grazing the same

rangeland pasture (Chapter 2). This provides evidence that consistent individual differences in grazing are robust and persist between two years and despite a management tool (off-stream water) added to the rangeland environment, which is a commonly used method to achieve better distribution of cows. Cows that were using higher elevation and were further from water were also more variable in their elevation and distance from water, thus behavioral flexibility coincides with overall rangeland use patterns in cattle (Chapter 2). Ultimately, cattle that appeared more cautious and passive in the narrow cement chute while isolated were those that were grazing higher elevation areas, further from water, and closer to upland supplement sites (Chapter 3). This could signify that cows that have a reactive (also called a passive) response when coping with mildly stressful contexts (i.e. isolation and handling) also notice environmental fluctuations over the grazing season and respond by grazing wider and higher, less utilized areas of the pasture. These passive cows are thought to be using the rangeland more sustainably (or optimally) because they are not clumping near water resources or preferred grazing areas, but rather grazing vegetation that is more difficult to travel to and may otherwise go under-grazed. Altogether, temperature was the most influential animal or environmental factor on grazing patterns; cows conserved energy by not traveling as far or on high elevation and prioritized being closer to water and resting sites on hotter days or weeks (Chapter 2 and 3). Neither grazing patterns nor behaviors exhibited during the management context assay related to cows' approach to a novel feeding opportunity (Chapters 1 and 3). This dissertation (a) informs the design and utilization of behavior assays for identifying CIDs in beef cattle (Chapter 1), (b) fills literature gaps in how management tools used to optimize cattle distribution alter grazing patterns of *individual* cows (Chapter 2), and (c) demonstrates the potential to select cattle that exhibit certain behaviors (i.e. more passive cows) to shape a herd with more desirable grazing patterns (i.e. use higher elevation areas further from water; Chapter 3).

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"Nothing of Significance was Ever Achieved by an Individual Acting Alone" …not that my dissertation is itself significant, but accomplishing it feels significant to me, and I could not have done it without everyone that supported me along the way. Thank you.

Dedication

I cannot, on good conscious, dedicate this to a single human or animal, so…

To my wonderful siblings and their partners: Vaughn and Alexis, Katie and Callum

To my supportive parents and stepparents: Kurt and Melissa, Nancy and Peter

To my partner Devin McHugh and my best friend Katie Stanton

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General Background & Introduction

1. *Consistent Individual Differences in Behavior*

Consistent individual differences (CIDs) in behavior among non-human animals is thought to be somewhat permanent and manifest early in life via genetics, developmental environment, the interaction between genetics and environment, or even ‘developmental stochasticity’ (Dall et al., 2004; Laskowski et al., 2022a,b; Sih et al., 2004). CIDs are thought to be relatively stable throughout development, and often coincide with biological (i.e. genotypes and gene expression) and physiological (i.e. hormones, immune response) characteristics of the animal (Gosling, 2001; Dall et al., 2004; Koolhaas, 2008). Differences in behaviors of animals are often evaluated via exposing animals to repeated assessments of relevant (i.e. species-specific) situations and contexts and quantifying reactions (e.g. response latency; Laskowski et al., 2022b; Réale et al., 2007; Sih et al., 2004; Stamps & Groothuis, 2010). Common terms used to describe the same or similar phenomena of relatively consistent traits that are stable across time and context are consistent individual behavior variation, animal personality, coping style, and temperament (Beekman & Jordan, 2017; Laskowski et al., 2022b; Mackay & Haskell, 2015; Réale et al., 2007; Roche et al., 2016; Sánchez-Tójar et al., 2022).

Though all of these aforementioned terms do have slightly distinct definitions, researchers do not always use terms appropriately and cautiously, muddying formulation of specific hypotheses and the interpretation of results of these studies (Laskowski et al., 2022b; MacKay & Haskell, 2015). For example, many animal scientists use temperament, personality, or CIDs interchangeably for livestock. However, in this particular case, it should be noted that temperament is used to describe how animals react to a ’challenging event’, especially restraint or human handling/presence, and refers to the traits of docility, aggressiveness, and excitability of animals (Finkemeier et al., 2018; Mackay & Haskell, 2015). Although the term personality may be relatable to a broader audience because it is used in human literature, the term also receives criticism for anthropomorphizing animal traits and assigning value to personality types like is done with humans (Finkemeier et al., 2018; Jones & Gosling, 2005). To simplify language and encompass the broader definition of this phenomenon of persistent traits in animals, in this review and throughout the chapters of my dissertation, I will refer to consistent individual behavior variation and consistent individual differences (CIDs) in behavior to discuss correlated behavior traits across time and context.

1.1 Measuring Consistent Individual Differences with Behavior Assessments/Assays

CIDs in behavior can be determined through ethological coding of the animal's daily life or through experimental assessments that present animals with specific situations or contexts (Laskowski et al., 2022b; Sih et al., 2004). Both approaches require researchers to have a clear understanding of what behaviors are expressed by their species of interest and what these behaviors might mean for the species or individual in a broader sense (i.e. latency to emerge from a hiding place has implications for predation). It is important to abstain from assigning *a priori* trait names (like 'boldness' or 'exploration') to behaviors that might be expressed during behavior assays. This is because it can create bias and subjectivity upon analysis, wherein researchers are linking different assumptions to behaviors that might be measuring the same propensity in animals (Laskowski et al., 2022b; Réale et al., 2007). For example, in many behavior assessments for certain species, the traits of fear, boldness, exploration, emotionality, neophobia and gregariousness that researchers assume are expressed via distinct observable behaviors are very easily conflated with one another (Carter et al., 2012, 2013; Greggor et al., 2015; Le Neindre, 1989; Perals et al., 2017; Walsh & Cummins, 1976). Two methodologies used to record individual differences in behavior assays are via subjective ratings of animals for certain traits and continuous sampling of behaviors displayed within assays (Gosling, 2008). If the goal is to identify traits in animals from behaviors, continuous scoring of behaviors that may aggregate to represent a consistent behavior trait is a more robust measure of individual differences that is not as vulnerable to human subjectivity or bias (Gosling, 2008).

The application and interpretation of behavior assessments used to measure individual differences are difficult to generalize across species. This is because situations and contexts introduced to animals to gauge unique responses provoke specialized meanings based on evolutionary history and current ecological roles (Finkemeier et al., 2018). For example, a common behavior assessment, the open field test, has been used to study CIDs in mice and other rodents since the 1930s (Hall & Ballachey, 1932) and its use has been applied to other animals to study similar individual differences in traits. This application to other animals receives criticism due to the fact that the open field test was developed to identify a species-specific reaction from a prey animal (mice or other rodents) that is evolved to hide from aerial predators, which would not directly translate to its use in livestock and other species (Boissy & Bouissou, 1995; de Passillé et al., 1995; Forkman et al., 2007; Munksgaard, 1996; Romeyer & Bouissou, 1992; Warnick et al., 1977). However, this does not mean that these types of tests developed in other species are not useful for determining CIDs; for example individual variation in reaction to isolation and novelty is still observed in the open field test in livestock species, but behaviors should perhaps not be attributed to exploration and boldness traits and rather anxiety related behaviors and sociality (Boivin et al., 1992; Boissy & Bouissou, 1995; de Passillé et al., 1995; Forkman et al., 2007).

Individual traits in gregarious species that participate in collective behavior can be relatively consistent across both individual and group contexts (Magnhagen & Bunnefeld, 2009; Magnhagen & Staffan, 2005), however because individuals vary in sociability, this consistency across contexts should be closely examined (Koolhaas & Van Reenen, 2016; Webster & Ward, 2011). Fear of isolation and lack of social buffers during individual behavior assessments, especially for individuals with highly social behavior, alter the animal's response to stimuli during the assessments (Atkinson et al., 2024; Boissy & Bouissou, 1995; Boissy & Le Neindre, 1997; Forkman et al., 2007; Koolhaas & Van Reenen, 2016). A multidimensional approach to measuring CIDs across time and contexts (such as when individuals are isolated versus when they have contact with conspecifics; Atkinson et al., 2024) can mitigate incorrect conclusions drawn from unidimensional situations and is crucial to our understanding of consistent behavior traits in animals (behavioral types; Graunke et al., 2013b; Graunke, 2014; Koolhaas et al., 2007; Koolhaas & Van Reenen, 2016; Sih et al., 2004).

1.2 Preference Assays in Animals

Because animals cannot directly communicate with humans, preferences are difficult to assess without the assistance of standardized assays, which allow researchers to objectively and quantitatively measure preferences in animals (Kirkden & Pajor, 2006). Some preferences are deduced through observations and time budgets, where an animal is assumed to prefer an item or situation over another if they spend more time with that item or in that situation (e.g. Bubier, 1996; Gaskill et al., 2009). Another way to determine preferences are through choice assays, which often employ a T- or Y-maze to examine a discrete choice of an individual animal to gain access to or engage with only one of the options (Dawkins, 1997; Kirkden & Pajor, 2006). For example, Pollard and colleagues (1994) concluded red deer preferred to not be restrained rather than restrained in an individual choice assay with a Y-maze design. Motivation tests are different in that they ask how *much* an animal wants (or wants to avoid) a preferred item or situation, or in other words the strength of the value of an opportunity for an animal (Kirkden & Pajor 2006). For example, motivation is commonly assessed in dairy cattle by using a progressively heavier weighted door or gate to measure motivation to access pasture (von Keyserlingk et al., 2017), calf contact (Wenker et al., 2020), or enrichment (McConnachie et al., 2018). Preference assays between feeding opportunities and social companionship are especially important in social grazers and browsers where often animals within a herd are making decisions whether to remain by other members of the herd or seek foraging opportunities independently (Hirata et al., 2013; Neave et al., 2018; Sibbald & Hooper, 2004). The trait of sociality (Réale et al., 2007) could influence an animal's choice in this type of preference assay; with the assumption being that highly social animals prefer to be near conspecifics rather than access feed. From a behavioral syndrome framework, 'fast' behavior types also tend to have broad and 'loose' social networks with weak bonds (Sih & Del Giudice, 2012). Beyond relying less on social mates, fast behavior types exhibit riskier behavior and have higher energy demands all of which can contribute to an observed preference to feed rather than remain close to social mates (Réale et al., 2007; Sih & Del Giudice, 2012).

Examining the relationship between CIDs and preferences presents methodological and logistical obstacles that must be carefully considered in experimental design (Kirkden & Pajor, 2006; Griffin et al., 2015). Implementing repeated measures and being intentional about the context and measurement of preference assays or motivation tests (stimulus used, response of animal, outcome that is measured) are ways of circumventing these obstacles to draw the correct conclusions about the animal (Dougherty & Guillette, 2018; Kirkden & Pajor, 2006; Griffin et al., 2015).

1.3 Consistent Individual Differences and How They Relate to Foraging

Consistent individual differences in behavior have animal and ecological implications because they relate to cognition, social niches, antipredator behavior, reproductive success, sexual selection, habitat use, movement and dispersal, and foraging (Bergvall et al., 2011; Carere & Locurto, 2011; Cote et al., 2010; Dingemanse et al., 2004; Dingemanse & Réale, 2005; Réale et al., 2007; Schuett et al., 2010; Spiegel et al., 2017; Toscano et al., 2016; Wolf & Weissing, 2012; Zuckerman & Kuhlman, 2000). Despite ample evidence that there are indeed individual differences in fine-scale movements such as feeding behavior and habitat use (Bonnot et al., 2015; Ciuti et al., 2012; Farwell et al., 2014; Harrison et al., 2015; Leclerc et al., 2016; Spiegel et al., 2015; Toscano et al., 2016), with regards to CIDs and wide-scale movement and foraging patterns, more empirical evidence of the mechanisms driving differences are needed in the literature (Nilsson et al., 2014; Spiegel et al., 2017). Toscano and colleagues (2016) recognized this gap in integration between CIDs and specialization in foraging and provided five theoretical mechanistic links between individual behavior traits and foraging behavior: activity level, decisions within a landscape of fear, social aspects, spatial aspects, and physiological drivers.

Pace-of-life syndrome, the concept that metabolic factors, fecundity, growth, and mortality co-vary with observed differences in behavior, could be an underlying framework for the relationship between CIDs, dispersal strategies, foraging patterns, and rates of consumption (Biro & Stamps, 2010; Montiglio et al., 2018; Toscano et al., 2016). For instance, animals with a faster pace-of-life syndrome may exhibit correlated bold, exploratory, aggressive, and active behavior traits in assays and also forage more to keep up with faster metabolic and growth rates

(Réale et al., 2010; Wolf et al., 2007). However, lack of empirical evidence supporting the pace-of-life syndrome hypothesis has been noted by recent meta-analyses and the predictions of this theory should perhaps not be generally assumed (Moiron et al., 2020; Royauté et al., 2018). Another example of an underlying framework to explain behaviors across assays and while foraging is proactive and reactive coping styles (Koolhaas et al., 1999). Proactive individuals are considered to be bolder, more exploratory, more active and more aggressive than others, exhibited in behavior assays, and also have distinctive routine responses to environmental stressors and change, thus they might be less observant of changing quality in foraging resources (Benus & Röndigs 1997; Hessing et al. 1993; Koolhaas et al., 1999; Koolhaas & Van Reenen, 2016; Sih et al., 2004). Results from both empirical studies and theoretical models exemplify that consistent behavior traits can be linked across behavior assays and foraging environments. Non-captive animals that have more bold and exploratory behavior types are more likely to forage in riskier habitats and move further from social mates or their home range (Bergvall et al., 2011; Gonzalez-Bernal et al., 2014; McArthur et al., 2014; Minderman et al., 2010; Sih et al., 2012; Toscano et al., 2016; Werner et al., 1981; Wilson, 1998; Wolf & Weissing, 2012). Similarly, Boon et al., (2008) found that more active red squirrels traveled further outside of home ranges.

2. *Beef Cattle Production System*

There are four main types of beef cattle operations extant in the United States: cow-calf, seedstock, stocker/background, and feedlot operations (Drouillard, 2018). Typically, these operations differ not only in composition of cattle (gender, age), but also geographically and temporally, meaning they occur in distinct areas of the United States and host different stages of the cow's life. Cow-calf operations are operations where ranchers own one to several herds of mature female cattle and are maintained by selling weaned calves to stocker operations, backgrounding lots, or feedlots (Drouillard, 2018). Some female calves will be selected to remain in the herd as ‘replacement heifers’ and replace older, less productive, cows that are culled (removed from the herd and sold to feedlots or abattoirs). This selection favors calves from dams that have produced consistently larger calves and have not required assistance during calving. Most (60%) of weaned female and castrated male calves (steers) will be sold to stocker operations or backgrounding lots, which raise the weaned calves on pasture or a diet that is typically at least partially forage until they are approximately one year of age or more (yearlings). They will then join the other 40% of weaned calves that are sold directly to feedlots for fattening before eventual slaughter at the abattoir (Drouillard, 2018).

There are variations within these operations, but cow-calf and stocker operations are predominantly pastorally based, thus the majority of cattle life is spent grazing on pasture. Seed-stock operations raise bulls to service female cattle. Most operations breed via ‘natural service’ meaning that female cattle are exposed to bulls for a brief period of time while females are in heat in order to reproduce. Much fewer operations (~6%) use artificial insemination to breed their female cattle (Karisch, 2020). Because the beef production system is predominantly pastorally based, 320 million hectares (41% of the total land area) in the U.S. are used for livestock grazing (Drouillard, 2018; USDA, 2018). Much of this livestock grazing occurs on expansive rangelands in the western U.S. that cover 163 million hectares of the western region (USFS, 1989; Cameron et al., 2014). The research described in this dissertation regards cow-calf operations because these host female herds in relatively stable social groups for long periods of time on extensive, heterogenous rangelands unlike other beef cattle production sectors.

3. *Consistent Individual Differences in Cattle*

Despite thousands of years of selective breeding of beef cattle to achieve a higher-producing and relatively homogeneous beef product as well as ease of handling and management, consistent individual differences in behavior traits of cattle persist, raising intriguing questions about the adaptive nature of CIDs and their function in animals (Haskell et al., 2014; Hirata et al., 2016; Kilgour et al., 2006; Marino & Allen, 2017; Koolhaas & Van Reenen, 2016). Cattle CIDs are typically measured in tests that involve some kind of restraint (like a squeeze chute) or restriction of movement, but can be measured without the use of restraint or restriction (Burrow, 1997; Creamer et al., 2021; Forkman et al., 2007). Measures of CIDs are often labeled ‘temperament’ traits in cattle, and many of these studies pair behavior reactions to stress and/or challenge to physiological responses (like heart rate variability or cortisol levels e.g. Graunke et al., 2013b; Kovács et al., 2015; MacKay et al., 2013; Müller & Schrader, 2005). Although CIDs have been assessed in species ranging from water-striders to dogs to primates (Pederson et al., 2005; Svartberg et al., 2005; Wey et al., 2015) behavior assessments have not yet been standardized for most livestock species including cattle (Briffa & Weiss, 2010; Finkemeier et al., 2018; Forkman et al., 2007; Gosling & John, 1999).

3.1 Behavior Assays/Assessments in Cattle

Often consistent individual differences in cattle are assessed via behaviors exhibited in stressful contexts, such as while cattle are restrained in a hydraulic squeeze chute and their subsequent velocity while exiting restraint (i.e. chute scoring and exit velocity; Burrow, 1997; Burrow et al., 1999; Café et al., 2011; Curley et al., 2006; Gibbons et al., 2011; Hoppe et al., 2010; Mackay et al., 2013). Assessments of cattle behavior alternatively or additionally involve an element of human approach, interaction, or handling (Cooke et al., 2012; Kilgour et al., 2006; King et al., 2006; Le Neindre et al., 1995). Studies that replicate these measures across populations of cattle are inconsistent in their findings and some find repeatability of measures over time, while others do not. These discrepancies can be attributed to unintentional bias of behavior scoring and non-trivial variation in human handlers of differing characteristics and approaches (Burrow, 1997; Burrow & Corbet, 2000; Dickson et al., 1970; Gibbons et al., 2011; Graunke, 2014; Kilgour, 1975; Kilgour et al., 2006; King et al., 2006; Tulloh, 1961). Other studies of cattle CIDs adapt standard assessments for livestock animals that are otherwise commonly used in ecological studies in order to identify exploratory, bold, social, aggressive, and active behaviors (Réale et al., 2007). These tests evaluate animal responses to novelty, startle, and social situations (i.e. isolation, resource use among herd mates, familiarity of herd mates) and often employ objective and continuous coding of behaviors to aggregate behaviors that are consistent across tests into meaningful traits (Forkman et al., 2007; Gibbons et al., 2009, 2010, 2011; Graunke et al., 2013 a,b; Hirata et al., 2016; Hirata & Arimoto, 2018; Kilgour et al., 2006). Based on these experiments, beef and dairy cattle have been shown to vary in exploratory, bold, social, aggressive, and active behaviors (Costa et al., 2020; Gibbons et al., 2009; Graunke et al., 2013b; Hirata & Arimoto, 2018; Neave et al., 2020; reviewed by Finkemeier et al., 2018). As has been pointed out in the limitations of these studies, though, many have inadequate sample sizes, are not replicated across other populations of cattle, are not practical to implement on most farms, and lack application to relevant extensive management outcomes for beef cattle.

3.2 Preference Assays in Cattle

Preference assays in beef and dairy cattle have been primarily used to explore food/vegetation preferences (Hirata et al., 2008; Hosoi et al., 1995), recognition of social mates (Hagen & Broom, 2003; Patison et al., 2010); space use and other environmental aspects (Rioja-Lang et al., 2012; pasture versus stalls: Legrand et al., 2009), and enrichment preferences

(Dickson et al., 2022; Wilson et al., 2002; Zhang et al., 2022). Free-grazing beef cattle on extensive pastures are constantly making decisions on a spectrum between foraging and remaining close to conspecifics, presenting a very relevant preference test for researchers to investigate between social companions and foraging opportunities (Hirata et al., 2013; Searle et al., 2010). This tradeoff is generally prevalent in herd and flock species and has been thoroughly explored by Sibbald and colleagues in sheep (Sibblad & Hooper, 2003, 2004; Sibbald et al., 2006; Michelena et al., 2009). Hirata and colleagues (2013) implemented a social-feed tradeoff based on the set up presented by Sibbald et al., (2006) to have cattle choose between visiting buckets of feed versus remaining close to a pen of conspecifics, of which they found results to be consistent in the short-term, but not in the long-term. Patison et al., (2010) also conducted a similar social-feed tradeoff assay and manipulated the element of familiarity of the social mate. Both Hirata's study and Patison's study suffered consequences of ceiling effects (Hirata et al., 2013) and concluded that a larger test arena, or perhaps a different set up, is necessary to study individual differences in this tradeoff. Ishiwata et al., (2007) looked at cattle preferences after brief restraint between a bare pen, a pen with food, and a pen with social mates and found that more cattle chose the pen with peers over food, however this was not repeated across individuals and evaluated for consistency.

3.3 Individual Grazing Patterns in Beef Cattle

Rangeland cattle make foraging decisions on heterogeneous, extensive landscapes with challenging topography and fluctuating vegetation composition and quality, similar to situations faced by wild ungulates. Although cattle managers implement rotational grazing, fencing, and other practices to alter or constrict grazing patterns to certain targeted areas on range, cattle are still given large areas of land to graze (on the scale of thousands of acres; Bailey et al., 2015;

Drouillard, 2018). Aspects of the environment (temperature, topography, vegetation quality, access to water) and the individual animal (experience, perception, memory, cognition, social learning) affect how domestic beef cattle graze on rangelands and contribute to variation across animals and herds (Bailey et al., 1996; García et al., 2020; Howery et al., 1998; Searle et al., 2010; Rivero et al., 2021).

Beef cattle exhibit consistent individual foraging patterns called ‘grazing personalities’ (Bailey et al., 2004, 2006, 2010a; García et al., 2020), that persist beyond reported differences in grazing due to breed, sex, age, and weight (Bailey et al., 2001; Bailey et al., 2005; Funston et al., 1991; Schottler et al., 1975; VanWagoner et al., 2006). These individual differences in foraging and movement patterns appear to be influenced by several proximate and ultimate factors including genetics (Bailey et al., 2015; Pierce et al., 2020), epigenetics, ontogeny, cognition, and emotional state (Carere & Locurto, 2011; García et al., 2020), but also collective movement of the herd and the social environment of cattle (García et al., 2020; Howery et al., 1998; Searle et al., 2010). Consistent individual differences in grazing as well as variation observed in behavior assessments are hypothesized to be the result of underlying behavior types of cattle predisposed by genes and the environment (García et al., 2020; Sih et al., 2004). Therefore, it is likely that cattle reactions during behavior assays and observable differences in grazing patterns of beef cattle are correlated, however the specific details of these relationships remain unknown. One study by Wesley et al. (2012) (expanded upon by Goodman et al., [2016]), and another by Wyffels et al., (2021a) examined grazing patterns on rangelands through the framework of behavioral syndromes. Wesley et al., (2012) found that cattle more willing to consume supplement in a behavior assay also grazed wider areas on rangeland, however Wyffels et al., (2021a) did not find this result. Their studies focused solely on supplement consumption rate as a proxy for foraging behavior and did not measure more practical, multidimensional behaviors across a variety of assessments (Wesley et al., 2012). Notable other contributions to this specific topic are from Bailey et al., (2010b) that did not find a link between maternal temperament and grazing distribution and Neave et al., (2022) that found relationships between calm cattle and time spent grazing and milk yield of dairy cattle. No studies to date have attempted to use standardized and practical behavior assessments in beef cattle and relate the results of these CID tests to preference assays and grazing behavior on rangeland.

Additionally, only few studies in cattle have assessed the relationship between CIDs in behavior assays and sociality in collective, group environments. Cattle are a socially complex herd species, therefore foraging decisions are influenced not only by internal motivations of the individual, but also the social environment (Costa et al., 2016; García et al., 2020; Gueron et al., 1996; Mainardes & DeVries, 2016; Searle et al., 2010; Stutz et al., 2018; Sueur et al., 2018), much like in sheep, a flocking species (Michelena et al., 2009; Sibbald et al., 2009). As mentioned previously, responses in individual assessments may be influenced by the fear of isolation from social mates and the animal's ability to cope with isolation (Boissy & Bouissou, 1995; Boissy & Le Neindre, 1997; Koolhaas & Van Reenen, 2016). Studies that have attempted to relate individual assessments with group environments in cattle either do not measure the trait of sociality in group environments, although relate other traits like displacements at a feeder (dominance behavior; MacKay et al., 2013) or only measure behavior at the group level and fail to relate this to tests at the individual level (Dumont et al., 2005; Hirata & Arimoto, 2018; Stephenson et al., 2016; Sueur et al., 2018). Sociability may influence behavior in assays where animals are isolated (Boissy & Bouissou, 1995), and data from such assessments should be corroborated by relating consistent traits with sociality in group contexts, for example while cattle are grazing on rangeland (Koolhaas & Van Reenen, 2016). This information will be useful in understanding cattle's relative responses in individual assessments (relative meaning how their behavior responses compare to the rest of the population) standardized by how social that individual appears to be in group contexts.

4. *Human, Cattle, and Environmental Context of Research*

Cattle in cow-calf operations in California (and other regions of the world where rangelands are abundant, like Australia) spend the majority of their lives grazing on extensive rangelands, which are defined as grasslands, savannas, and shrublands that are not cultivated or developed, but are suitable for livestock grazing (Lund, 2007; Sayre, 2017). Extensive rangelands cover large swaths of land, altogether about fifty-six million acres in California, which is approximately 53% of the total land area (Banwarth et al., 2023; Drouillard, 2018; Svejcar et al., 2014). Because of the immense spatial scope of cattle grazing and humans' reliance on cattle protein products, responsible and sustainable management of cattle is necessary to conserve rangelands (Svejcar et al., 2014) and abate growing global food demand.

Efficient cattle grazing on rangeland provides benefits to humans, animals, and the environment. For example, sustainable grazing can allow for an increase in animals per usable land (Bailey, 2004) which provides a larger amount of quality beef for the growing population (Greenwood, 2021) and increases profitability for ranchers. An increase in profitability of ranches also retains land that might otherwise be developed for residential areas if financial control is lost, which conserves rangeland habitats (Cameron et al., 2014). It is not enough to acknowledge that simply utilizing extensive rangelands for grazing livestock benefits the environment, but specifically '*even' or 'optimal'* grazing on extensive rangelands improves the sustainability of land and water resources. 'Even' grazing refers to cattle that are evenly distributed among land and resources in a manner that gives cattle access to all vegetation, nutrients, and water needed, but does not exceed the grazing capacity in an unsustainable way (Bailey et al., 1996). Rangelands on their own are hosts of several ecosystem services such as carbon sequestration, nutrient cycling, pollination, and high-quality habitats (Maczko et al., 2011;2022), which is why their conservation is critical. Optimal distribution of wild or domestic ungulate grazing on rangelands upholds these benefits to the ecosystem by maintaining habitats for native rangeland species, sustaining vegetation quality, and reducing fuel load for destructive wildfires (Bailey et al., 1996; Cameron et al., 2014; Davies et al., 2015; Delcurto et al., 2005; Rouet-Leduc et al., 2021; Svejcar et al., 2014). Unmanaged or unchecked cattle grazing can negatively interfere with ecosystem services. Uneven grazing distribution can result in issues from diminished water quality to streambank erosion in sensitive riparian areas (Bailey et al., 1996; Delcurto et al., 2005).

Due to the *potential* negative impacts of uneven grazing on rangelands, the beef cattle industry has been the target of major criticism regarding the detriments of livestock on the environment (Beschta et al., 2013). To counter criticism and achieve sustainable cattle management, ranchers in the western U.S. employ grazing management techniques to alter or interfere with the foraging patterns of their cattle herds (Roche et al., 2015; Svejcar et al., 2014). There are several tools a rancher may implement to achieve more optimal grazing distribution such as off-stream water, targeted grazing with supplement, low-stress herding, or rotational grazing (Bailey, 2004; Creamer et al., 2020; Delcurto et al., 2005). Most of these tools that have traditionally been used on rangeland, such as those listed above, have included some modification of the animal's environment or surroundings to achieve improved grazing distribution (Bailey, 2004; Creamer et al., 2020). However, some studies have begun to consider the implications of individual animal behavior on grazing distribution, such as nuanced animal selection to shape herd movement (Creamer et al., 2020). Due to the fact that cattle spend much of their lives grazing on rangeland, rangeland health and sustainability is contingent upon grazing patterns of cattle, and, an immense amount of land is dedicated to livestock grazing in California (56 million acres, >50%; Banwarth et al., 2023), improving the spatial and temporal distribution of cattle grazing is essential to prolong economic, social, and environmental sustainability of beef cattle production.

5. Theoretical and Applied Implications of Research Objectives

We have created and conducted three studies to address the gaps in the literature identified by the above review and to investigate the potential for this applied work to contribute to our understanding of consistent individual differences in beef cattle, the sustainability of beef production, and rangeland conservation. The overall objectives of this dissertation, broken up by chapters, are to:

1. (Chapter 1) (a) Apply repeated short-term and long-term (across days and over one year) practical behavior assessments in a management context and preference assays, (b) define and record behaviors expressed in these assessments, (c) identify consistent behaviors across the management assay that may or may not cluster into coherent traits in cattle and (d) examine how these traits may explain cattle responses in preference assays along with other factors (i.e. age, temperature, positionality of a social group).
2. (Chapter 2) Identify consistent foraging patterns of cattle between two years of summer grazing seasons while cattle are on extensive, complex rangeland. In this study we seek to identify distinct 'grazing personalities' of cattle and understand factors that might be affecting grazing patterns (i.e. age, pregnancy status, temperature, temporal components)

3. (Chapter 3) Explore the relationship between consistent behaviors we have identified in Chapter 1 and grazing patterns of cattle while on extensive rangeland.

This research will fill knowledge gaps in both ecological and animal science literature. Graunke (2014) highlights the need for standardized, practical, repeatable, and applicable behavior assessments in beef cattle, and Searle et al., (2010) discusses the general necessity to understand traits of individuals of herd species that are consistent when individuals are in a larger group context (i.e. social behavior on rangeland). Spiegel et al., (2017) emphasizes the importance of empirical literature to back up theoretical frameworks and identify how personality traits are linked to movement and foraging patterns of animals. Current multidimensional measures of CIDs in cattle are difficult to apply in a practical management setting as they involve the use of an open arenas, novel objects, forms of restraint, or other infrastructure that is not found on many ranches. This study observes isolated cattle in only corrals and a working chute (narrow alley, restraint not necessary), which is infrastructure that can be found on almost all ranches. In this study, we will not be assigning *a priori* assumptions of behaviors that could indicate traits nor scoring cattle subjectively, but rather using raw operant definitions of expressed behaviors from an ethogram to sample behaviors from assays. This research will also examine the relationship between CIDs and behaviors expressed in a repeated preference assay, avoiding limitations in experimental design that inhibit making inferences about consistent preferences (i.e. that unless these tests are repeated, it is difficult to conclude that the preference is inherent to the animal and not the circumstances at the time of testing, brought up by Griffin et al., 2015 and Kirkden & Pajor, 2006).

Current literature regarding measuring cattle CIDs through standardized tests (Hirata et al., 2016; Hirata & Arimoto, 2018) lack the application to grazing, while other studies of ‘grazing personalities’ (Bailey et al., 2004; Bailey et al., 2015; García et al., 2020; Wesley et al., 2012) measure the cow’s average slope, distance to water, or walking rate and relate results to cattle genetics and production traits rather than to standardized behavior assessments. Studies explicitly examining grazing in cattle are often describing factors that contribute to observed patterns (e.g. Schoenbaum et al., 2017; Rivero et al., 2021; Wyffels et al., 2021b), consistency of individual grazing patterns and categorization of ‘hill-climber’ cows and ‘bottom-dwelling’ cows (e.g. Bailey et al., 2004, 2006, 2010a), and efficacy of management tools (e.g. Bailey & Jensen, 2008; George et al., 2008; Stephenson et al., 2016). No studies to our knowledge have combined all three goals. We know that individual cattle vary in grazing patterns (García et al., 2020) and the composition of individuals influence herd dynamics (Searle et al., 2010). Thus, understanding individual responses to management tools could inspire customized management plans that feature selecting individuals for a herd that ‘match’ the characteristics of the rangeland environment and initiate a big step towards achieving optimal grazing distribution.

6. References for General Introduction

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Chapter one: Consistent individual differences in behavior among beef cattle in handling contexts and social-feed preference testing

1. *Introduction*

Consistent individual behavioral variation describes behavior in a population of animals that is relatively similar across time and in different contexts or situations and is typically assessed by calculating repeatability of behavior in multiple assays (Laskowski et al., 2022; MacKay & Haskell, 2015; Sih et al., 2004). The terms consistent individual variation or consistent individual differences (CIDs) in behavior broadly encompass behaviors that are measured in a variety of tests and described with a range of terminology depending on the field of study (i.e. temperament, personality traits, behavior syndromes, coping styles; Laskowski et al., 2022; MacKay & Haskell, 2015). One universal assumption of assays that are presumed to be measuring *stable* traits of individual animals is that there is some level of consistency of behavior across short and long-term repetitions of tests (Bell et al., 2009), as well as across contexts or situations (MacKay & Haskell, 2015; Sih et al., 2004). CIDs in behavior often relate to relevant outcome measures in animals, such as fitness consequences in wild animals (reviewed by Moiron et al., 2020), or growth and fertility rates in livestock animals (reviewed by Haskell et al., 2014). In the current study, we seek to measure consistent individual differences in behavior in a population of rangeland beef cattle, relating behaviors across short and long-term timeframes in an assay that is novel to the literature and practical to implement. We then relate behaviors in this assay to a feeding versus social choice assay and a novel approach assay to measure how CIDs relate to relevant outcome measures.

Consistent individual differences (CIDs) in cattle behavior have been a topic of interest since the 1960s and have historically been measured in restrained and unrestrained tests (Burrow, 1997; Forkman et al., 2007), which have also been linked to physiological responses (e.g. Graunke et al., 2013; Kovács et al., 2015; MacKay et al., 2013). Three of the most common tests used in cattle CID literature are the chute score (i.e. crush test), the docility test, and the flight speed test (Burrow, 1997; empirical examples: Curley et al., 2006; Hoppe et al., 2010; Kilgour et al., 2006; King et al., 2006). Chute scoring relies on an ordinal scale (typically 1-5) of cattle behavior while restrained in a squeeze chute (Grandin, 1993; Tulloh, 1961). Chute scoring is a subjective measure of cattle reactions while in the chute, which could be vulnerable to both human bias and cattle memory of previous chute restraint (often used for stressful and painful procedures; Grandin, 2007; McLennan & Chapman, 2017). Docility tests range in methods in the literature, but always have an element of human interaction where a human attempts to constrain a cow to a specific area or location by halter, handling, or mere presence (Burrow, 1997; Grignard et al., 2001). Flight speed tests are a measurement of the amount of time it takes for a cow to exit a constraint, most often a squeeze chute, measured within a pre-determined distance so that velocity can be calculated (Burrow et al., 1988; Petherick et al., 2002). Despite being commonly used in cattle behavior research, studies utilizing these tests have found widely varied results in their inter and intra-assay consistency (Kilgour et al., 2006; King et al., 2006; Parham et al., 2019), which is likely caused by subjective, biased, and non-standardized scoring and interference by human presence (Burrow, 1997). Recent studies of cattle CIDs have begun to apply a wider variety of tests adapted from other fields of literature for livestock research, such as responses to challenge, novelty, startle, and social contexts (e.g. reactions to isolation or conspecifics; reviewed by: Forkman et al., 2007; Finkemeier et al., 2018; empirical examples in both dairy and beef cattle: Gibbons et al., 2009; Hirata et al., 2016; Kilgour et al., 2006). These tests, however, fall short in their on-farm practicality, standardization, sample sizes, replication, and further application to cattle management (linking to how animals use spatial cognition to forage or how socially cohesive they are within the herd; Hirata et al., 2016; Forkman et al., 2007).

There is evidence that consistent individual differences predict preferences and choice in animals, such as those related to habitats (Holtmann et al., 2017; Rey et al., 2015) and foraging (Bergvall et al., 2011; Herath et al., 2021). According to Kirkden & Pajor (2006), preferences in animals can be deduced by measuring motivation to avoid or obtain one resource over another resource. Although they argue that determining preferences between 'non-substitutes' (e.g. enrichment item versus litter access) is not as meaningful as between substitutes (e.g. two different enrichment items), we argue that in the specific case of social ruminants that form herds or flocks, preference between feed and social mates is meaningful to test (Sibbald et al., 2006; Hirata et al., 2013). For beef cattle specifically, a preference assay in which cows choose between a feeding opportunity and conspecifics may indicate how cattle form grazing patterns on extensive rangelands, clumping close to social groups or grazing vegetation that is further from the herd (Hirata et al., 2013; Moreno García et al., 2020; Searle et al., 2010). Additionally, introducing novelty to the feeding opportunity in a preference assay can indicate whether some animals might be unwilling to approach novel environments or novel vegetation types on rangeland (such as the case with deer Bergvall et al., 2011; and possums Herath et al., 2021). A crucial pitfall of preference assays is that they are generally not repeated in order to avoid a habituated response, which makes conclusions about consistency in preferences difficult to make (Griffin et al., 2015).

In beef cattle, consistent individual behaviors in a management context (e.g., physical touching, or herding through a narrow passage [chute]) have been related to both feeding (Black et al., 2013; Hoppe et al., 2010; Llonch et al., 2018) and social behavior (Bruno et al., 2018; Hirata et al., 2016). For example, more excitable cows in chute restraint and that were faster upon exiting a chute restraint had less feed intake and lower daily gain (Bruno et al., 2016; Café et al., 2011; Hoppe et al., 2010). Hirata et al. (2016) reported that cows with an active response in restraint displayed faster approach to conspecifics upon release as compared to inactive cows. Although Hirata and colleagues found short-term consistency in their social-feed tradeoff paradigm (2013), they did not find a relationship between cattle behavior in assessments and performance in the social-feed tradeoff test (Hirata et al., 2016), however they had a limited sample size (n=15 cows). No other studies to our knowledge have compared management-related behaviors to a social-feed preference assay.

Consistent individual differences have primarily been called either 'temperament' or 'personality traits' in cattle, however these two terms can have slightly different meanings (MacKay & Haskell, 2015). In the current study, we did not pre-determine behaviors that we expect to align with temperament or a specific personality trait. We therefore refrain from using these terms and rather define consistent individual differences as repeatable behavior responses to practical challenges in mildly stressful, but not entirely novel, situations. Mildly stressful situations allow for consistent behavior measures better than non-stressful or extremely aversive experiences (Budaev et al., 1999; Toms et al., 2010).

We observed the behavioral responses of cattle in three different repeated behavioral assays: a practical, management assay (containing a handle and chute situation) and two preference assays (social-feed tradeoff assay and novel approach assay). This allowed us to estimate consistent individual behavioral variation within assays (i.e. whether behaviors are repeatable across repetitions and correlated between years) and also determine if behavior traits in the management assay were predictive of behaviors in the preference assays. If the management assay and preference assays are an appropriate assessment of consistent individual behavior variation, we would expect behavior responses to be a) repeatable across repetitions within an assay, b) correlated between years, and c) cluster to form behavior traits. If behavior traits measured in the management assay are indicative of how cow's respond to stressful situations and their willingness to be isolated, we predict that cattle that show lower-arousal to being handled and while isolated in the chute will choose supplement over conspecifics and have lower latencies to supplement in both the social-feed tradeoff assay and novel approach assay.

2. *Methods*

2.1 Animals and Environment

All selected study cows were housed at the Sierra Foothills Research and Extension Center (SFREC) in Browns Valley, CA managed by University of California Animal and Natural Resources (UCANR). We selected fifty cattle from a herd of available cattle housed at the research center (approximately 150 total available) to participate in this study if they had at least one calf (at least parity 1) and were within the range of 80-100 days pregnant at the time of the pregnancy check (determined via ultrasound). Ages of selected cattle ranged from 2 to 8 years old with an average of 4.96 years old, weight ranged from 1009 pounds to 1890 pounds with an average of 1340.55 pounds. The same cattle participated in behavior assessments in year two (however one cow of the same age was added in year two to replace a culled cow after year one). All research methods were approved by the Institutional Animal Care and Use Committee of UC Davis, protocol #22672.

We split cattle into four groups of 12 or 13 individuals for behavior testing that were balanced by age (m = 4.5, 4.9, 5.0, 5.0 years) and pregnancy status (m = 93.3, 91.8, 93.1, 93.3

days pregnant). We did this for logistical reasons, for all cattle in a group to participate in assays in the morning before the temperature became too hot to conduct assays safely. Groups were kept consistent between years. One cow in both years did not complete all repetitions of the behavior assays due to avoidant behavior (fence-jumping) and one cow in year one was also excluded because she was used as a social mate in the corral and chute to dissuade fence-jumping. In year one, the first group of cows had a slightly different novel approach assay that was ultimately changed for the other three groups, so were excluded from analysis for that year. Sample sizes of cows to participate in all repetitions of assessments (full data) are summarized in Table 1.

Behavior tests began one week after fence-line weaning to avoid the post-weaning balking period (based on observations by facility managers and supported by articles about cattle behavior during fence-line weaning; Price et al., 2003). The order in which subgroups were assessed was reversed in year two of the study to balance the effects of testing earlier or later in the season as well as sooner or later after weaning. Behavior tests occurred between 0730 and 1100 at the handling corral and chute infrastructure which included a hydraulic squeeze chute.

The management assay was repeated 4 times each year for 2 consecutive years (8 times total) and contained two separate situations where behaviors were observed: while handled (corral) and while isolated in the chute (cement chute, hydraulic squeeze, and exit; Figure 1). The preference assays in which cattle chose between proximity to social mates versus consuming a mineral supplement in both a familiar (i.e. a social-feed tradeoff assay) and novel bucket (i.e. a novel approach assay) were also repeated. The social-feed tradeoff assay was repeated 3 times each year for 2 consecutive years (6 times total) and the novel approach assay was repeated once each year (2 times total).

2.2 Behavior observations in the management assay (handling and chute)

We assessed individual differences in behavior within a management assay, which contained two distinct situations where cattle were 1) handled and 2) isolated in the chute. At the beginning of each day of behavior observations, an experienced facility manager herded cows from two subgroups (of the four mentioned previously) into a corral from a nearby 0.18 sq. kilometer pasture on which they were housed at the research center. The subgroup that was participating in assays that day was then sorted by the same experienced facility manager into the holding pen before the chute system and the other subgroup was divided into a social group (n = 10) and a social buffer group (n = 2 or 3 depending on the size of the subgroup). The study group (n = 12 or 13) and the social buffer group were placed in the corral that holds cattle before they are moved into the chute and hydraulic squeeze chute (i.e. infrastructure that catches cattle for processing events). The handler for behavior assessments, which was not the same handler that sorted cattle, remained the same across each day and with each subgroup, and kept their appearance exactly the same across tests. The handler approached and moved with maximal speed of one step per second, hands at sides. If the cow turned and attempted to move behind the handler, the handler would place their hands out to the side of their body, perpendicular to the ground, to dissuade the cow from turning. If cows showed aggression toward the handler (e.g., kicking, charging) at least two times or escaped back into the social group at least two times, the handler used a flag, waving it behind and to the sides of the cow’s body, to move the cow up toward the chute. One cow at a time was moved to enter the cement chute through a gate that separated the corrals from the cement chute. The handling of the cattle individually into the chute was referred to as the ‘handle situation’ within the management assay.

The order at which cows entered the chute was recorded as this has been linked to stress response and cortisol levels in previous studies (Bristow & Holmes, 2007; Chen et al., 2016) and has been found to be consistent across repetitions (Andrade et al., 2001). Cattle walked individually through the cement chute and awaited at the doors of the hydraulic squeeze chute for 30s (seconds). Squeeze chute doors were opened at the same speed for each cow after the 30s, cattle walked through the hydraulic squeeze chute and exited on the other side of the squeeze chute where a spray-painted line indicated 2.5m from the exit doors of the squeeze chute. From when the cow entered the cement chute until she crossed the 2.5m line was denoted the ‘chute situation’. Markers placed along the chute enabled observers to identify the time it took cattle to move through specified areas of the chute (i.e. the narrow cement chute ‘chute’, hydraulic squeeze ‘squeeze’, and exit ‘exit’; Figure 1; Table 2). The corral, cement chute, hydraulic squeeze chute, and exit were recorded on video cameras from an above angle so that cattle positions and distance markers could be seen clearly when behaviors were coded from video using The Observer XT software v.11 (Noldus Information Technology, Wageningen, The Netherlands).

2.3 Social-feed tradeoff assays (familiar and novel)

At the exit of the chute, the preference assay (social-feed trade-off or novel approach) was set up as shown in Figure 1. The ten conspecifics from the other (non-test) subgroup that were sorted from the herd initially were corralled in the alleyway on one side of the cattle that were exiting. Conspecifics were within at least 30m of the test paradigm (an appropriate distance that is biologically relevant to herd cohesion according to Stephenson et al., 2016) and separated by a gate, that still allowed visual contact, from the focal animal exiting into the preference assay alleyway. Across three consecutive days, cattle entered a T-maze after exiting the chute to approach their conspecifics on one side or to move towards a familiar bucket filled with supplement (~16 kg) to the opposite side. The bucket was at a position 6m away from conspecifics on day 1, moved to 12m away from conspecifics on day 2, and 18m away from conspecifics on day 3. Cattle then had one day of rest between the social-feed tradeoff assay and novel approach assay. The preference assays were loosely based on those conducted by Sibbald and colleagues (2006), Hirata and colleagues (2013), and the supplement consumption rate assessment conducted by Wesley and colleagues (2012), but modified to obtain repeated measures of a dynamic preference. The novel approach assay was set up the same as the social-feed tradeoff assay when the bucket was at 6m (Figure 1), however, cattle were presented with the same amount of familiar supplement in a bucket that was now covered with an unfamiliar pattern and color that changed between years and subgroups.

As soon as cattle crossed a designated threshold distance from the chute (2.5 m), observers started a timer, counting down from five minutes. This procedure was the same across all trials of the social-feed tradeoff assay with the bucket at varying distances and for the novel approach assay. Camcorders (DCR SX85, Sony Corporation of America, New York, NY, USA) on tripods (4m high) recorded the assays from three angles to ensure that the entire test alleyway was in view. After five minutes passed, the cow was escorted to a separate pen away from the testing area.

All video footage of the tests were coded for specific behaviors with all-occurrence continuous sampling of states and events (Altmann, 1974) using The Observer XT software v.11 (Noldus Information Technology, Wageningen, The Netherlands). All coders achieved an ICC greater than 0.80 for continuous behavior data and Cohen's kappa > 0.75 on count data (icc function in the performance package in R statistical software; Lüdecke et al., 2021). Behaviors were recorded as durations and proportions (See Table 2). Running occurred too infrequently (1 or 2 cows performing this behavior each year), thus was excluded from further analysis. Social-feed choice was calculated as a binary variable where a 'group choice' meant cows displayed a shorter latency to approach the group than they did to supplement and a 'supplement choice' meant the cows displayed a shorter latency to supplement bucket than to the conspecifics. If latencies to supplement and group (operational definitions in Table 2) were both the full duration of the assay (300 seconds), they received an 'NA' for choice. The proximity of the conspecifics to the gate (i.e. group location in assays in Table 2) was also recorded continuously throughout observation of the social-feed tradeoff and novel approach assays. All behaviors recorded from videos and definitions can be found in the behavioral ethogram (Table 2).

2.4 Statistical Analysis

We intentionally took more than two repeated measures within and between years in assays to assess consistent individual behavioral variation, however this design creates greater complexity upon analysis. We created a comprehensive, statistical plan to explore the data we have across measures, but also reduce the complexity so that measures could be representative and practical on commercial settings. With this goal in mind, we analyzed data to (a) identify repeatability of behaviors across repetitions of assays within a given year and correlations between years (n=2 years), b) cluster repeatable behavior measures using principal component analysis (PCA), and c) identify if traits in the management assay predicted behavior in the preference assays.

2.4.1 Repeatabilities and between-year correlations

Consistent individual behavioral variation in populations of animals is often identified via calculating repeatability of behaviors (also called the intra-class correlation coefficient [icc] in mixed models and variance partitioning component; MacKay & Haskell, 2015; Nakagawa & Schielzeth, 2010). The repeatability of a given behavior is calculated as a proportion of variance such that the amount of between group variance (also known as among individual variance) σ_{α}^{2} is divided by the total variance, or between group variance plus within group (within individual) variance $\sigma_{\alpha}^{2} + \sigma_{\epsilon}^{2}$

$$\frac{\sigma_{\alpha}^{2}}{\sigma_{\alpha}^{2} + \sigma_{\epsilon}^{2}}$$

(Nakagawa & Schielzeth, 2010). We ran Bayesian multilevel models to examine repeatability of behaviors across repetitions of behavior assays adjusted for year (i.e. year was the only predictor variable) in the brms package in R (Bürkner, 2017; R Core Team, 2022), which is an interface to Stan (Stan Development Team, 2022). We adjusted for year in these models to get broad-sense repeatability of behavior in these measures while accounting for contributors to major differences in behavior between years (habituation, different testing order of groups, each individual was one year older; Biro & Stamps, 2015). Bayesian models in brms were used in this case because they provided greater flexibility in modeling data with unusual distributions (i.e. gamma, truncated negative binomial, cumulative logit). We used relatively weak, uninformative priors for these data. Repeatability was calculated for the random effects using the variance_decomposition function in the performance package (Lüdecke et al., 2021), which is the recommended way to estimate repeatability for Bayesian models using the posterior predictive distribution.

To assess how behaviors were correlated between years, we ran multivariate Bayesian mixed models also using the brms package in R. We ran separate multivariate models for all behaviors between years (the two separate years made up the multivariate model) which included duration walking or being stationary in the chute and during handling, latency to enter, traverse, and exit the chute, entry order, and choice (Table 2 & 3). We estimated behavioral consistency between years using among-individual correlations between multivariate models for each of the same behaviors which we calculated repeatabilities. This approach examines the correlation between behaviors while taking into account the variation occurring within repeated measures of behavior (Dingemanse & Dochtermann, 2013; Sih et al., 2004) and avoiding reducing the importance of that error variance as is the case with using BLUPs (Houslay & Wilson, 2017). Much like our broad-sense repeatability models, we used intercept-only models with a random effect of cow ID to assess correlated behaviors between years. Multivariate models were run with specific families that matched the data type and enhanced posterior predictive checks and trace plots of the model and with relatively weak, uninformative priors. Repeatabilities adjusted for year and correlations between years using multivariate models are reported in Table 3. To examine consistency of behavior response in the social-feed tradeoff assay, repeatability of choice was calculated as described above (using the variance_decomposition function and multivariate models). Between-year correlations of latencies to the group and to supplement across bucket distances and novel approach were calculated with spearman rank correlations (Table 3). Because each 'repetition' of the social-feed tradeoff assay was a distinct manipulation of the distance from the social group to the supplement, we treated latency to group and supplement correlations between years separately per bucket distance (6m, 12m, and 18m).

Behaviors were deemed repeatable and used for further analysis if the lower bound of the confidence interval of the repeatability estimate was not close to zero (at least > 0.10) and correlated if the confidence interval of the correlation coefficient did not cross zero. Repeatability is constrained to be positive, unlike correlation coefficients, thus repeatability confidence interval estimates that are negative or close to zero indicate that the behavior is not repeatable (Table 3).

2.4.2 Principal component analyses (PCA)

The values from the first day of behavior assays for only repeatable and correlated (between year) behaviors were input into a PCA to examine how behaviors cluster across the management assay. Data from the first test day was used because behaviors were repeatable and correlated between years, thus we assume that day one should represent relative differences between cows, and ranchers are more likely to only examine behaviors once to determine behavior traits (pointed out also by Neave et al., [2022] in a similar study). The first exposure to a stressful situation is also thought to be the most representative of 'temperament' in animals (MacKay & Haskell, 2015). Principal components were retained if eigenvalues were greater than or equal to one. We also visualized the scree plot to identify components contributing most to the overall variance of the data. The first three components in our principal components analysis explained 66% of the data and all had eigenvalues greater than one, thus were kept for further regression analysis.

2.4.3 Predictive models for social-feed tradeoff assay and novel approach assay

We used linear mixed models with the glmmTMB package to predict responses in both the social-feed tradeoff assay and novel approach assay of both years. We wanted to know both if behaviors in the management assay would predict group versus food choice in cattle across repetitions of the social-feed tradeoff assay and willingness to approach food in the social-feed tradeoff assay and when the bucket was novel to cattle. To accomplish this goal, we extracted individual scores from the first three dimensions of the principal component analysis to input into three different models with response variables: 1) choice, 2) latency to supplement in the social-feed tradeoff assay and 3) latency to supplement in the novel approach assay. Other predictors along with the component scores in these models accounted for year, bucket distance (for the social-feed tradeoff assay only), age of focal cows, position of the social group (whether they were closer than 10m to the assay set-up), temperature during testing, and random effects for the individual cow and the testing group to which they belonged.

Social-feed choice was modeled as a betabinomial logistic regression model where a ‘group’ choice received a dummy code of 0 and a supplement choice received a dummy code of 1; if they did not approach the group nor supplement during the assay, they were excluded from this model. Latency to supplement for both the social-feed tradeoff and novel approach assays was transformed for hurdle models where the conditional component of the model explained latency to supplement when supplement was consumed, while the zero-inflated component of the model explained supplement not being consumed at all. We used the glmmTMB function in the glmmTMB package (Brooks et al., 2017) to analyze truncated negative binomial models with latency to supplement as the response variable. We checked models via QQ plots in the DHARMa package (Hartig, 2022) which indicated no issues with dispersion, deviance from normality, or outliers. We also checked dispersion of our negative binomial models with the testOverdispersion function in the DHARMa package (Hartig, 2022) and no tests were significant, indicating there was no issue with overdispersion. Finally, we visualized residual versus predicted values of the model, which did not show any obvious patterns in the residuals.

3. *Results*

3.1 Behaviors were repeatable across repetitions and between years.

Most behaviors from the management assay were repeatable and correlated between years, including durations to be handled into the chute, traverse the cement chute, and traverse and exit the hydraulic squeeze (Table 3). Entry order was considered repeatable given that the lower bound of the confidence interval was not close to zero, although the ratio of among individual variance was lower than other behaviors. Although the behavior ‘change directions in the chute' had a high repeatability estimate and was correlated between years, it also had a lower bound of the confidence interval that was nearly zero and thus was not considered repeatable for further analysis. Proportion of time walking and stationary during handling, urge weighted, and choice in the social-feed tradeoff assay were not repeatable nor correlated between years.

3.2 Behaviors clustered into traits deemed 'activity', 'fearfulness', and 'excitability'

Behaviors that were repeatable and correlated from the assays, and thus included in the principle component analysis (PCA), were: squeeze duration, exit duration, chute duration, handle duration, enter squeeze duration, proportions of time walking and stationary through the chute situation, and order (Table 3). The PCA revealed three components or 'traits' of cattle from the management assay that explained 66% of the data (more than comparable other studies like Neave et al., 2022 and Kilgour et al., 2006) and traits mostly clustered within respective situations (Table 4). Behaviors that loaded strongest on the first component (explained 31.3% of the variation in the data) were: proportion of time spent stationary, proportion of time spent walking, and duration to traverse the chute (Table 4). Cows scoring higher on component one were labeled 'less active', given that this component identified cows that spent more or less time stationary versus walking through the chute. The second component (explained 18.2% of the variation in the data) was comprised of the behaviors: time to enter squeeze chute, time taken to handle cattle into the chute, and entry order (Table 4). Cows scoring higher on this trait were labeled as 'less fearful' because it identified cows more willing to be separated from groupmates in the corral, less reactive to human handling, and less active when entering the squeeze chute. Behaviors that loaded strongest on the third component (explained 16.3% of the variation in the data) were time in the squeeze and time to exit the squeeze (Table 4). Cows that received higher component three scores were labeled 'less excitable', as previous studies have reported calmer chute behavior and lower velocity upon exiting the chute are indicative of lower arousal or excitability (Burrow, 1997; Forkman et al., 2007).

3.3 Predictive models

We found evidence that at least some of the behaviors exhibited in the management assay predicted an individual's response in the social-feed tradeoff assay. Specifically, cows scoring higher on component three (i.e. less excitable cows) tended to have higher latency to supplement (Table 5). In terms of other overall effects, we found that cows took longer to approach the supplement as the bucket distance moved further from conspecifics, and, cows approached the supplement quicker in year two than in year one (Table 5). Cows were more likely to never approach supplement as the bucket moved further from conspecifics, at distances 12m and 18m compared to 6m (Table 5).

We also found evidence that management behaviors predicted the choices individuals made within the social-feed tradeoff assay. Cows that scored higher on component one (cows that were less active) were more likely to choose supplement over proximity to conspecifics, and, cows that scored higher on component three (less excitable) were also more likely to choose supplement over proximity to conspecifics (Table 5). In the choice model, similarly to the zero-inflated latency to supplement model, cows were less likely to choose supplement over conspecifics as the bucket distance moved further from conspecifics. Interestingly, cows were less likely to choose supplement over conspecifics when it was hotter (Table 5).

In the latency to the novel bucket assay, we did not find any strong evidence that behaviors in the management assay predicted an individual's latency to approach the novel bucket. However, overall, we found that cows were significantly quicker to approach the novel bucket in year two, and there was a tendency for older cows to take longer to approach the novel bucket than younger cows. Proximity of the social group during the tradeoff assays did not significantly predict cattle responses in any of the three models (i.e. latency to supplement in social-feed tradeoff and novel approach models nor the social-feed choice model).

4. *Discussion*

This study was conducted to examine consistent individual behavior variation in beef cattle across short and long-term repeated, practical assessments and to determine whether this behavior variation related to feeding versus social proximity preferences. Cattle displayed consistent behavior in assessments as indicated by repeatability of behavior across repetitions and correlation of behaviors between years. Principal component analysis demonstrated cattle were clustering mostly within situations in the management assay and revealed behavior traits of cattle along active, fearful, and excitability spectrums. Predictive models provided evidence that less active and less excitable cattle in management assays are more feed-centric in social-feed tradeoff assays.

4.1 Cows were consistent in behavior over time.

Many observed behaviors were deemed consistent by our repeatability criteria and were correlated between years, suggesting that cattle were not merely responding to immediate conditions on a particular day or even within a particular year. This study is among very few to look at long-term consistency (between years) of behavior in multivariate models that account for error within year and responds to gaps in the literature addressing appropriate sample size retention across long-term repeated measures (Hirata et al., 2016).

Many chute-related behaviors, especially those related to duration to move through the chute and squeeze, activity (i.e. walking) and entry order, were correlated between years. Time to traverse and exit through the open squeeze chute were repeatable and correlated between years in our study. Relative consistency between repeated restrained tests has been found in other studies involving chute-related behaviors (chute score and exit velocity; Bruno et al., 2016; Curley et al., 2006; Vetters et al., 2013; Parham et al., 2019), but many of these studies reported either only consistency in exit velocity and none in squeeze chute behaviors or higher repeatabilities or correlations in exit velocity than squeeze chute behaviors (Curley et al., 2006; Gibbons et al., 2011; Kilgour et al., 2006; King et al., 2006; MacKay et al., 2013; Parham et al., 2019). Interestingly, in our study, time to traverse through the squeeze unrestrained had a notably higher correlation coefficient between years than exit duration. In contrast to our study where we did not restrain cattle in the squeeze, these studies measured cattle behavior responses to restraint while in the squeeze chute and subsequent exit velocity. This suggests that future researchers could obtain consistent behavior by simply allowing cattle to move through the chute without interference or operating the physical restraint and avoid issues that arise from aversive situations in cattle (e.g. animal welfare, worker safety; Grandin, 2007; McLennan & Chapman, 2017). Grignard et al., (2001) also found evidence of 'general reactivity' in beef cattle to handling instances regardless of restraint.

Entry order, essentially a measure of cows' willingness to enter the chute from handling in the corral (i.e. cows self-selected to enter), was also repeatable (although weakly) and correlated between years even though this measure involved human interference and responses of other cows in the same testing group. Other studies found entry order to be consistent and relate to physiological measures like serum cortisol and glucose (Andrade et al., 2001; Bristow & Holmes, 2007; Chen et al., 2016). Our study provides further evidence that entry order is a valid, and practical, measure of consistent individual differences in cattle behavior.

Both latency to group and latency to supplement behaviors in the novel approach assay were consistent between years, which was not found in several other studies examining response to novelty in beef cattle (Gibbons et al., 2011; Hirata et al., 2016; Forkman et al., 2007; Kilgour et al., 2006). One way to measure fear in cattle is with assays involving response to novel items and is denoted often as neophobia and boldness (Costa et al., 2020; MacKay et al., 2014). The collective traits of fearfulness, neophobia, and boldness, although compounded together in some studies, are important for cattle in our production systems because their environment changes frequently, including their diet, and the animal's ability to cope with changes (Costa et al., 2020; Neave et al., 2018) as well as certain production traits (e.g. average daily gain; Café et al., 2011; Neave et al., 2018) coincide with these traits (reviewed by Haskell et al., 2014). Consistency in this study gives credibility to our novel approach assay and warrants replication and validation via physiological measures by other researchers interested in long-term fearful, neophobic or bold responses in cattle. We found that group versus food choice was not repeatable nor correlated between years in the social-feed tradeoff assay, yet latency to consume supplement between years of the 6m and 12m bucket distances were correlated. Hirata et al. (2013) found inconsistency in long-term social-feed tradeoff measures in their version of the assay, which perhaps suggests an advantage to measuring latency to supplement across 6m and 12m distances like we did rather than how many buckets were approached, which was their measure of food choice. Latency to approach the group was not consistent between years of differing bucket distance locations, which probably was driving the fact that choice was not correlated between years. Approach to conspecifics in this preference assay is perhaps not representative of long-term consistent behavior, while the latency to approach supplement could be representative of a trait. This result should encourage future researchers to conduct repeated preference assays because *choice* in an assay with an arbitrary set up may not be representative of a consistent preference. However, our familiar supplement set-up may be an appropriate measure of long-term consistent feeding behavior (rather than choice) for at least the 6m and 12m bucket distances.

4.2 Behaviors clustered primarily by situation and indicate behavior traits.

Based on component analyses, behaviors were clumped mostly in their respective situations of the management assay yet are informative for classifying cattle reactions to handling and isolation. The durations of time to traverse the cement alley, time to handle cattle into the chute, and time to traverse the squeeze and exit were each separated into the three components. This may indicate that there are different mechanisms contributing to different behaviors in these three areas of the chute. We anticipated handling and the chute to represent different situations for cattle, but perhaps, handling, the chute, and the squeeze and exit manifest distinct behavior reactions and should be considered separately. Hirata and colleagues (2016) found high within-test consistency of behavior in restrained and unrestrained tests but did not find correlations across tests. Kilgour et al. (2006) also found components to separate behaviors of general agitation versus reactivity towards humans, which might explain why we found components to represent behaviors mostly within our pre-determined situations (handling versus chute).

Component one clustered behaviors related to ‘activity’, differentiating cattle that were more or less stationary in the chute as a whole, and those that took longer to traverse the narrow cement part of the chute. The underlying trait of component two was less apparent and comprised behaviors related to fearfulness and sensitivity of flight zones. Cattle that scored higher on this component took longer to be handled into the chute and enter the squeeze, however were lower in entry order (i.e. less hesitant to be isolated from groupmates in the corral). Animals that are more fearful of human interaction move to the back of the herd during handling (Lawrence et al., 1991 [pigs]; Syme & Elphick, 1982 [sheep]), and later entry order has been linked to higher cortisol levels in previous studies (Bristow & Holmes, 2007; Chen et al., 2016). Cattle that experience reduced stress may be one of the first animals to enter the chute (Chen et al., 2016) and take longer to enter the chute and the squeeze because the motivation to avoid human proximity is lower than other cows which are one of the last animals to enter the chute and traverse the chute quickly (Grandin, 2021). Hirata et al. (2016) also found that cows more willing to enter the chute were also more reactive while in the restraint and moved quickly to social mates afterwards. While these authors argued that this behavioral difference was due to the cattle being unprepared for physical restraint, it could be argued that cows which took longer to enter the squeeze/chute are less reactive and slower moving overall.

The third component clustered behaviors that related to duration of time spent in the hydraulic squeeze, and speed of exiting the chute, and thus could represent cattle reactivity to potential restraint. Cattle learn to associate sights, sounds and smells with aversive events, like showing fear at just the buzz of an electric cattle prod (Croney et al., 2000), and associating handling with certain locations and people (Cote, 2003; Rushen et al., 1998; Grandin, 2007; Grandin & Shivley, 2015). Cattle exhibit long-term memory especially for aversive events like those that occur in the hydraulic squeeze (e.g. hot-iron branding, ear-tagging, disbudding; Burdick et al., 2011; Grandin, 2018; Marino & Allen, 2017; Markus et al., 2014). Although previous experience is a main contributor of cattle's physiological and behavioral response in restraint and handling (Grandin & Shivley, 2015), restraint by itself can produce physiological indicators of stress even in the absence of other painful procedures (Lay et al., 1992b; Mitchell et al 1988). This may be due to several mechanisms: emotional reactivity to novel events, full-body excessive pressure, and isolation from conspecifics (Grandin, 2007; Grandin & Shivley, 2015; Grignard et al., 2001). Escape-avoidance behaviors have been validated as indicators of pain and fear (Morton & Griffiths, 1985; Lay et al., 1992a; Schwartzkopf-Genswein et al., 1997), which is why squeeze and exit behaviors are common 'fear tests' often considered together to represent reactivity or excitability in cattle (Burrow, 1997; Forkman et al., 2007; King et al., 2006).

Anecdotally, cattle that took a long time to traverse the squeeze nosed the sides and bottom, exploring the squeeze as they walked slowly through, where cows that were quicker sprinted through the squeeze seemingly to avoid restraint. Interestingly, our PCA clustered unrestrained squeeze and exit durations together where some studies using restraint found that chute score and exit velocity did not relate to each other nor relate in the same way to behavioral or physiological measurements (Bruno et al., 2018; Kilgour et al., 2006; MacKay et al., 2013). In our scenario where we did not restrain cattle, it is possible that the squeeze and exit durations were more similar to each other and both were measures of anticipating aversive experiences and reacting to isolation. Our results that duration to traverse and exit the squeeze were consistent (discussed above) and the fact that these behaviors clustered together reiterates that restraint does not seem necessary to measure reactivity in cattle. The novelty of the situation and potential for restraint appears enough to provoke individual differences in escape-avoidance behavior like duration to traverse and exit the squeeze (similar to Grignard et al., 2001).

4.3 Evidence for less excitable/feed-centric cattle

Predictive models in our study provided evidence that traits exhibited in the management assay related to feeding behavior in the social-feed tradeoff assay. Cows that were less active in the chute, slower to traverse the squeeze, and slower upon exiting the squeeze (i.e., 'lower excitability': Burrow, 1997; Curley et al., 2006) were more likely to choose supplement over conspecifics in the social-feed tradeoff assay and vice versa more active and excitable cows were less likely to choose supplement. Physical isolation from conspecifics is stressful for individuals of socially cohesive herd or flock species (Boissy & Le Neindre, 1997; Hirata et al., 2016; Forkman et al., 2007; de Passillé et al., 1995; Kilgour et al., 2006). Cows that were spending the least amount of time in an isolated context (shorter duration in the chute, squeeze and exit) were choosing conspecifics in the tradeoff assay, which distinguishes cattle that had a more active response to isolation than a passive response (i.e. pacing and walking instead of freezing, Müller & Schrader, 2005; Forkman et al., 2007). These results support previous literature that cows that were less reactive during management procedures and handling were those exhibiting more feed-centric behavior (Black et al., 2013; Llonch et al., 2018; Café et al., 2011; Neave et al., 2018). Similarly, cows that showed more fearful reactions to restraint (Hirata et al., 2016) and humans (Fisher et al., 2000) also rejoined herd mates faster after isolation. Intriguingly, cows that scored higher on component three (i.e. were slower in the squeeze and while exiting) had higher latencies to supplement overall *if* supplement was consumed. This could mean that cattle that had low reactivity and arousal in the management assay, though they moved toward the supplement over social mates, were just slower moving in general and walked toward supplement at a slower pace than conspecifics.

We did not find a relationship between any component scores and the novel approach assay. This result corroborates other studies which reported no relationship between novel response assays and chute behaviors among cattle (Hirata et al., 2016; Gibbons et al., 2009,2011, Kilgour et al., 2006; Schrader, 2002). Thus, although novel approach behaviors were consistent in the long-term (discussed above), if researchers are interested in predicting neophobia or boldness in cattle using behaviors observed during management events, a different novel approach assay, perhaps one that does not conflate feeding and social behavior with novel response, should be utilized. We did find a statistical trend for older cows to take longer to approach the novel supplement. Age groups not only represented ages of cattle in this herd, but also potentially genetic and environmental similarities as cattle are bred from the same bulls and exposed to the same developmental conditions within a given birth year. Consistent individual differences in behavior, such as boldness in approach to novelty, has been linked to genetic and developmental environment in fish and spiders (Edenbrow & Croft, 2013; Liedtke et al., 2015; reviewed by Biro & Stamps, 2008, Stamps & Groothuis, 2010; and Cabrera et al., 2021). Because older cows were slower to approach supplement, this could mean that as cows age in this herd, they become less bold than younger conspecifics. Behavior traits have been found to change with life stage, and younger animals have been found, in some studies, to be bolder than older individuals (Starling et al., 2013 in dogs) or less neophobic (Mackay et al., 2014 in dairy cattle). Age should be considered when evaluating consistent individual differences in preference assays. Additionally, whether the conspecifics were closer (within 10m) or further (within 30m) from the test location did not contribute to social-feed choices nor latencies to supplement. This result gives further validation to 30m as a biologically relevant herd distance (Stephenson et al., 2016) within which cows are not visually isolated from the herd. Ranchers could use this practical distance threshold to provide a social buffer to cows while isolated.

5. *Conclusion*

There was evidence for consistent individual behavior variation across days and between years within the management assay, however, behaviors clustered within situations involving humans (handling situation) versus isolation (chute and activity) versus potential restraint (squeeze and exit). This does not negate the importance of understanding these behavior traits to classify cattle reactions to challenges and how they might relate to other characteristics of the animal (production traits, immune function, fertility, affective state, etc.). We found consistent individual differences in behavior across short and long-term time frames in the chute situation while cattle are not restrained, which could improve animal welfare and safety of handlers during these types of experiments. We found that the latency to familiar supplement for bucket distances of 6 and 12m were consistent between years and latencies to supplement and conspecifics in our novel approach assay were consistent between years. Inter-assay results demonstrate less-excitable/feed-centric cattle adding to ample literature about temperament in cows and how it relates to feeding behavior, but in two unique tradeoff paradigms (social-feed tradeoff and novel approach assay). Very few studies implement such a comprehensive battery of tests like the one presented in this study repeated after one year.

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Chapter Two: Where's The Beef? Consistent Individual Differences in Cattle Grazing Patterns

1. *Abstract*

Cattle grazing patterns can have a significant impact on the economic and environmental sustainability of rangelands and cattle production. Grazing patterns appear to be driven by consistent individual differences in cattle, deemed 'grazing personalities'. Optimal distribution of cattle on rangelands can be manipulated by alteration of the environment, like adding water, supplement, or fencing to targeted sites, but few studies address how these management tools are impacting grazing patterns of individual cattle. Our study sought to fill this gap in knowledge by investigating consistency of grazing patterns among fifty cattle, fitted with GPS collars, across two years given the addition of a water site at higher elevation prior to year two. We used Bayesian multivariate mixed models to evaluate consistency, evidenced by among-individual correlations across years with confidence intervals that do not cross 0. We found that cattle were consistent in all rangeland use metrics across years after the addition of the new water site: elevation (Estimate = 0.38, CI = [0.07,0.64]), slope (Estimate = 0.59, CI = [0.21,0.86]), distance to water (Estimate = 0.38 CI = [0.03,0.67]), distance to supplement (Estimate = 0.42, CI = [0.04,0.72]), distance to loafing sites (Estimate = 0.68, CI = [0.24,0.95]), except for distance traveled (Estimate = 0.16,CI = [-0.18, 0.48]). Cows that ventured higher on rangeland in year one (Estimate = 0.84 CI = [0.59,0.98]) and year two (Estimate = 0.93 CI = [0.79,0.99]) and further from watering sites in year two (Estimate = 0.72 CI = [0.41,0.92]) also had more within-individual variability in their grazing patterns than those that stayed at lower elevation and closer to water. These results indicate differences in plasticity or variability can be linked to grazing personalities. There was strong evidence that temperature affected grazing distribution such that

on hotter days, cows clumped closer to water and loafing sites, were found at lower elevation, and traveled less far, not reaching supplement sites that were placed at the higher elevations. Based on results of this study, ranchers should consider the effectiveness of management tools on individual cattle and conduct cost-benefit analyses of tools implemented for specific behavior types of cattle. Cattle with behavior types demonstrating more within-cow variability and more ‘hill-climbing’ will impact how cattle graze especially patchy landscapes where resources are distributed across elevation, thus ranchers could potentially match cattle types to rangeland characteristics.

2. *Introduction*

Extensive rangelands used for livestock grazing cover more than half of the western U.S and fifty-six million acres in California (>50% of the total land area; Banwarth et al., 2023; Drouillard, 2018; Svejcar et al., 2014). Rangeland conservation is extremely important, as rangelands provide a host of ecosystem services such as carbon sequestration, nutrient cycling, pollination, and high-quality habitats for native vegetation and animals (Maczko et al., 2011; 2022), in addition to grazeable land for cattle. Optimal grazing on rangelands is environmentally sustainable because it provides direct and indirect benefits to the ecosystem such as maintaining vegetation quality, habitats, and preventing the spread and intensity of wildfires by reducing fuel load (Cameron et al., 2014; Davies et al., 2015; Svejcar et al., 2014). Conversely, uneven grazing distribution can result in a host of issues such as diminished water quality, streambank erosion, reduced soil health, and degradation of keystone species or habitats (Bailey et al., 1996; Delcurto et al., 2005).

Ranchers in the western U.S. implement grazing management techniques to increase productivity of cattle, profitability of land, and environmental sustainability (Bailey, 2004;

Delcurto et al., 2005; Roche et al., 2015). Historically, grazing management has relied upon altering the animals' surroundings and external environment to achieve better grazing distribution (Bailey, 2004; Creamer et al., 2020; Delcurto et al., 2005). Examples of these techniques include strategic placement of supplements and off-stream livestock drinking water, fencing, and rotational grazing, many of which are temporary and/or extremely costly (e.g. fencing wide areas or installing new water sources; Bailey, 2004). More recent studies, however few, have begun to consider the implications of manipulating endogenous, behavioral factors of the animals and individual animal selection to achieve better grazing distribution (Bailey et al., 2006; Bailey et al, 2015a; Moreno García et al., 2020). Even fewer studies have combined altering aspects of animal surroundings *and* evaluating endogenous behavioral motivators of grazing patterns in tandem to improve grazing distribution (Creamer et al., 2020).

Rangeland cattle select preferred habitats and make foraging decisions on a complex and heterogeneous range landscape with differing topography and vegetation quality (Bailey et al., 1996; Howery et al, 1998). Domestic rangeland beef cattle exhibit variations in grazing patterns based on a variety of environmental (heterogeneity of landscape, access to water, temperature; Bailey et al., 2015b; Schoenbaum et al., 2017), biological (age, pregnancy status; Bailey et al., 2004; Vanzant et al., 1991; Walburger et al., 2009) and behavioral (perception, memory, cognition, social) factors (Bailey et al., 1996, Howery et al., 1998; Sowell et al., 1999). Although animal age, weight, and other biological characteristics have an unclear effect on grazing patterns (Walburger et al., 2009; Wyffels et al., 2020b), temperature seems to have a ubiquitous effect on grazing distribution (Rivero et al., 2021; Larson-Praplan et al., 2015; Schoenbaum et al., 2017) such that cattle are at resting sites and shade for longer periods of time and travel shorter distances around areas of rest in hotter temperatures. Beyond these factors that may influence grazing, we know from recent literature that individuals constituting herds of social herbivores are paramount in shaping movement and foraging patterns (Bergvall et al., 2011; Michelena et al., 2009; Nilsson et al., 2014; Spiegel et al., 2017). Thus, the characteristics of individual cattle must be considered in conjunction with other optimal grazing techniques.

Beef cattle have been shown to exhibit ‘grazing personalities’, which refer to unique inter-individual foraging patterns (Bailey et al., 2004, 2006, 2010; Moreno García et al., 2020), and are distinct from differences in grazing patterns that exist between breeds (Bailey et al., 2005; Funston et al., 1991; VanWagoner et al., 2006). These individual differences in foraging and movement patterns are influenced by genetics (Bailey et al., 2015a; Pierce et al., 2020), the developmental environment, epigenetics, cognitive abilities, social environment, and emotional state (Carere & Locurto, 2011; Howery et al., 1998; Moreno García et al., 2020; Searle et al., 2010). Although personality traits may be influenced by an animal’s immediate environment or state (e.g., age, life-stage: Mathot & Dingemanse, 2014; Stamps & Biro, 2016), it is necessary to decouple stable inherent behavior traits that result from genetic and environmental interaction or even just ‘developmental noise’ (Laskowski et al., 2022) from the influence of environment or state-dependence.

Management tool effectiveness has, so far, been extensively explored on the herd level (Bailey, 2004; Creamer et al., 2020; Delcurto et al., 2005), yet still little is known about how these interventions are shaping individual cattle grazing patterns. Given that more studies are suggesting individual factors are likely the drivers of variation in grazing patterns (Moreno García et al., 2020; Wyffels et al., 2020a,b), more research that explores individual-level responses to management tools is warranted. This study was implemented to 1) evaluate consistency of individual grazing patterns of cattle across two years, 2) explore alternative factors that could explain individual grazing patterns, and 3) determine the impact of an environmental management tool on individual grazing patterns. We hypothesize 1) that cattle will be relatively consistent in overall rangeland use across years (i.e. individuals that use higher elevation in year one will also use higher elevation in year two) and will be relatively consistent in within-individual variability of rangeland use across years (i.e. individuals that fluctuate in elevation in year one will also fluctuate in elevation in year two) despite the addition of a water trough and while accounting for age, pregnancy status, temperature, and day of the summer grazing season and, 2) that temperature will influence grazing patterns such that higher temperatures will result in reduced use of the pasture and more time spent near water sites, while age and pregnancy status will not influence grazing patterns.

3. *Methods*

3.1 Animals and housing

All study cows were housed at the Sierra Foothill Research and Extension Center (SFREC) in Browns Valley, CA administered and managed by the University of California Agricultural and Natural Resources (UCANR). This research was approved by the Institutional Animal Care and Use Committee of UC Davis, protocol #22672. Fifty Angus x Hereford black and brown cattle were recruited for the study in 2021 if they had at least one calf (at least parity 1) and were 80-100 days pregnant determined via ultrasound. Ages of selected cattle ranged from 2 to 8 years old with an average of 4.96 years old, weight ranged from 1009 pounds to 1890 pounds with an average of 1340.55 pounds. Forty-nine of the same cattle grazed the pasture in year two (2022; one cow was added in year two to replace a culled cow after year one). All study cows were familiar with the climate and environment (vegetation, topography) of SFREC. This herd represents similar breed composition and age to herds in the surrounding Sierra foothill region and in California and was grazed at a low stocking rate which is typical on California rangeland. However, as a herd that is utilized for research, this herd was more familiar to human presence than other rangeland cattle.

3.2 Study Pasture

For this study, cattle grazed the same 2.53 sq. kilometer (625 acre), fenced, oak woodland rangeland pasture across two years. Approximately 19% of this pasture was classified as open grassland versus 81% tree cover and prominent vegetation species (native and invasive, nutritive and noxious) included fescue (*Vulpia octoflora*), crested wheatgrass (*Agropyron cristatum*), dogtail Grass (*Cynosurus echinatus*), soft chess (*Bromus mollis*), wild oat grasses (*Avena fatua*), false brome (*Brachypodium distachyon*), ryegrass (*Lolium perenne*), purple needlegrass (*Nassella pulchra*), red brome (*Bromus rubens*), medusa head (*Taeniatherum caput-medusae*), ripgut brome (*Bromus diandrus*), Italian thistle (*Carduus pycnocephalus*) and starthistle (*Centaurea solstitialis*). Given that 70 cattle were grazing this pasture, the stocking density was 0.26 AUM per acre (according to UC Rangelands Animal Unit Calculator, 2023). Elevation in this pasture ranged from 201.4 to 618 meters and slope ranged from 0 to 47 degrees, with an average slope of 16 degrees. Lower elevation areas of the pasture were fairly steep with rugged, rocky terrain and a few areas near the top of the pasture were also steep and rocky.

During the summer grazing season, this region experienced intense sunlight and little cloud cover with occasional haziness from wildfire smoke. The temperature during the grazing period in 2021 had an average minimum daily recorded temperature of 71°F, an average maximum daily recorded temperature of 103°F, and an average mean daily recorded temperature of 84°F. In 2022, the average minimum recorded daily temperature was 68°F, the average maximum recorded daily temperature was 103°F, and an average mean daily recorded temperature of 82°F.

Eleven loafing sites were identified by ranch managers that had observed loafing sites across years of grazing and by direct behavioral observation in the first 4 weeks of data collection. Loafing sites, supplement sites (both mineral supplement and low moisture protein blocks), and water sites can be visualized in Figure 1 along with topographical information about the rangeland pasture. Supplement sites were chosen based on the grazing goals of facility managers for cattle grazing higher elevation in the rangeland pasture and location and type were kept relatively consistent across years. Water sites were fixed pipe-fed troughs that had previously been established in the rangeland pasture with the exception of the pipe-fed trough that was added in year two at a higher elevation.

3.3 GPS tracking

Each study cow was collared with a custom-built GPS collar (Knight Collars, Knight et al., 2018) and were released to graze the pasture described in the previous section. Cattle grazed this pasture between June - August 2021 and June - August 2022. GPS collars consisted of a GT-120 iGotU GPS tracker (Mobile Action, Taiwan), a rechargeable Li-ion battery pack, a PVC box and insulation to house the GPS unit and battery pack, and a thick, leather collar (Knight et al., 2018). The GT-120 iGotU GPS trackers have a location error of less than 10m and a mean 50% circular error probable of less than 7m (Morris & Conner, 2017). Fix success rate of these particular trackers is not significantly affected by cover (Morris & Conner, 2017). GPS collars were programmed to sample location every 10 minutes. Onset HOBO data loggers^{TM} were placed in a solar radiation shield in the pasture and set to collect temperature data every 30 minutes in order to obtain accurate minimum, maximum and average daily temperature in the pasture.

3.4 Data Cleaning

Raw GPS data were visualized and cleaned with ArcPro GIS software (GIS software by ESRI^{TM}, Version 2.5.0, Redlands, CA) and R statistical software (R Core Team, 2022). GPS data for both years were imported into ArcPro along with the accurate rangeland pasture boundary which was acquired via Trimble GEO 7x handheld GNSS receiver. All GPS points outside of 27m of the rangeland pasture boundary were removed from the dataset according to a previous methods study indicating that 27m is the 95% circular error probable when dense cover is possible of these specific iGotU 120 devices (Morris & Conner, 2017). Thus, points within 27m were considered possible to have occurred inside the bounding fence, while points outside of 27m were considered outlier points. This process removed 1,068 points in 2021 (0.003% of total points) and 996 points (0.003% of total points) in 2022. Further, outliers that indicated the cow was moving at greater than 3 m/s speed between two fixes (~10 minutes) were removed based on biological evidence of cattle speeds while running (Café et al., 2011). This removed 291 points in 2021 (0.0009% of total points) and 335 points in 2022 (0.0009% of total points). Though estimates of these outliers may be considered conservative, outliers were also checked before and after this process of removing outliers with the R package ctmm (Fleming & Calabrese, 2022), and this process was effective in removing all outliers identified by the package as interfering with analysis of the data.

GPS metrics were calculated through both ArcPro GIS tools and movement packages in R from cleaned GPS data output by the process described above. Using the Near tool in ArcPro GIS software (GIS software by ESRI^{TM}, Version 2.5.0, Redlands, CA), distances to water sites, supplement sites, and loafing sites were calculated for each GPS data point. Elevation and slope data was also calculated for each GPS data point with a Digital Elevation Model with 1/3 arc second (approximately 10m) resolution of the study area. Elevation and slope were appended to each point with the ArcPro Extract Values to Point tool (GIS software by ESRI^{TM}, Version 2.5.0, Redlands, CA). The AdehabitatLT package was used to calculate daily trajectories (distance traveled) by cattle from GPS points (Calenge, 2011). Elevation, slope use, and distances to water sites, supplement sites, and loafing sites were averaged by day to evaluate daily grazing patterns and to account for temporal autocorrelation of data.

3.5 Statistical Analysis

We used the brms package in R (Bürkner, 2017; R Core Team, 2022), which is an interface to Stan (Stan Development Team, 2022) to run multivariate, hierarchical Bayesian mixed models for analysis of these data. We ran six separate multivariate models for the six rangeland metrics across years (the two separate years made up the multivariate model): average daily elevation, daily distance traveled, average daily slope, average daily distance to water, average daily distance to loafing sites, and average daily distance to supplement sites. Statistical models accounted for animal (i.e. age, pregnancy status) and environmental (i.e. temperature) fixed effects in a given year that may have predicted rangeland use metrics (i.e. elevation, distance to water, etc.) and contained cow ID as the random effect to account for individual variation. We estimated behavioral consistency across years using among-individual correlations for each rangeland metric extracted from multivariate models. This unique way of looking at consistency across years was adapted for this use from suggested statistical analysis of behavioral syndromes (Dingemanse & Dochtermann, 2013; Sih et al., 2004), examining the correlation between behaviors while taking into account the variation occurring within repeated measures of behavior (in this case across days within a year) and avoiding reducing the importance of that error variance as is the case with using BLUPs (Houslay & Wilson, 2017). Correlations between years indicate that among individual variation is greater than within-individual variation and a significant (determined by 95% confidence intervals) correlation, either positive or negative, can be detected.

We used a smoothing spline with the predictor variable of day to accommodate non-linear relationships between the progression of the summer season (days) and the rangeland use metrics. Pregnancy status was added as a monotonic variable because it represents the ordinal variable of stage of pregnancy of the cows at the start of grazing. Monotonic specification allows for ordinal variables to have varying distances between levels of the variable (Bürkner & Charpentier, 2020) which is best for pregnancy status where different stages of pregnancy could indicate substantial differences in hormone production between them. Other factors included in the model besides date and pregnancy status were the age of the cows and average daily temperature. We used weak, uninformative priors for the intercept, parameters, and standard deviation, however for the monotonic variable of pregnancy status, a larger difference between cows in year two that were not pregnant versus the rest of pregnancy status levels was specified in the prior (dirichlet prior distribution; Bürkner & Charpentier, 2020). We centered and scaled all predictor variables, except for day of grazing season, to standard deviations (i.e. standardized) to aid in the interpretation of relative effect of the predictor variables on the rangeland use metrics (Schielzeth, 2010). Day of grazing season was only centered and not scaled to aid in interpretability of the intercept (intercept is interpreted at half-way through the grazing season rather than at day 0) and because it represented time in the model. We checked collinearity on a linear model of the same predictor variables with the vif function in the car package (Fox &

Weisberg, 2019), all VIFs (variance inflation factor) were around 1, indicating no issues with collinearity between predictors.

We conducted much of this statistical analysis following guidance from the tutorial provided by Hertel et al. (2020) about evaluating among and within individual variation in animals from movement data. A double hierarchical mixed effects model was used to allow residual variation (sigma) to vary per cow subject (the random effect). This method allowed us to obtain estimates of within-cow variability in daily grazing patterns of rangeland use metrics (similar to animal 'predictability') in a given year and how within-cow variability might correlate between years and with intercepts in each year. Predictability or unpredictability, adopted from language used by Hertel et al. (2020), is an estimate of the within-individual variation of the response variable after accounting for fixed effects, which in our case included day as a smoothed spline rather than a reaction norm slope. Double hierarchical general linear models (DHGLMs) are the best way to assess such 'predictability' according to Cleasby et al. (2015) and Hertel et al. (2020). A higher sigma value estimate of the individual cow (random effect) signifies more 'unpredictability' in cows (i.e. more within-cow variability), while a lower sigma value estimate of the individual signifies 'less unpredictability' in cows (i.e. less within-cow variability). Standard deviations of residual error (sigma values) indicate if there are overall differences in within-individual variation and are constrained to be positive, so it is not enough to evaluate the credible interval as not overlapping with 0, however if the estimate and credible interval are not close to zero, there is evidence for differences in within-animal behavioral variation (Hertel et al., 2020). Throughout this article, we will use the terms within-cow (or within-individual) variation or variability to refer to these sigma values in place of predictability and unpredictability to describe results in more accessible terms and because in the case described by Hertel et al., (2020), they included a random slope in these models to model reaction norms and we did not.

Models were run with specification of the lognormal family in brms due to the fact that all rangeland metrics were bounded to be positive and continuous, and this improved posterior distribution checks from use of the gaussian distribution. We assessed model fit using R-hat values, inspection of chain mixing, trace plots, and posterior predictive checks. All R-hat values were at 1.00, there were no warnings or divergent solutions, and all model plots looked adequate for chain mixing and posterior sample distributions. Model fit was evaluated via the loo criterion and for all models, pareto k estimates were below 0.5 (Vehtari et al., 2017).

Smooth terms and unpenalized regression coefficients of splines for the date variable are reported in tables, however significant unpenalized coefficients are not interpreted because there was no clear trend in conditional plots and confidence intervals of smooth terms did not cross 0, indicating unpenalized coefficients cannot be interpreted. Because the predictor variables were centered, intercepts are the given rangeland metric at average age, pregnancy status, temperature, and in the middle of the grazing season; all data and confidence intervals in tables are presented on the log scale.

4. *Results*

In year one, the selected 50 study cattle and 20 cohorts grazed on rangeland pasture for 70 days total (June 22, 2021 – Aug 30, 2021), although some collars failed before the end of the grazing season (mean days tracked = 66.6, SD = 7 days). In year two, 69 of the same cattle (with one replacement cow to make 70 total) grazed on rangeland pasture for 77 days total (June 15, 2022 – Aug 30, 2022; mean days tracked = 75.4, SD = 5.3 days). There were 47 cows with analyzable GPS datasets within each year (mean age year one = 4.96, SD = 1.92; year two =

5.97, SD = 1.90), and 43 of the same cows with analyzable GPS datasets between both years. The mean and standard deviation of each rangeland use metric per year are included in Table 2.1.

4.1 Animal and environmental effects within year

We found that temperature influenced all rangeland use metrics for at least one of the years of the study, however only the effect of temperature on distance to supplement sites was found across both years (Table 2.2). In year one, higher average daily temperature meant more gradual average daily slope use among cattle and cattle were, on average, closer to loafing sites and further from supplement sites (Table 2.2). Temperature in year two affected average daily elevation use such that higher mean temperatures meant cattle utilized lower average daily elevation. In year two as average daily temperature increased, cattle traveled significantly shorter daily distances, were further from supplement sites, and were closer to water sites. Individuals further along in gestation in year two were, on average, closer to water sites on a given day (Tables 2.2). All results reported are shown in Table 2.2.

4.2 Variability of cattle grazing patterns within and between years

Cattle differed in intra-individual variability within year for various rangeland use metrics as indicated by standard deviations of the sigma estimates of cows (the random effect; Hertel et al., 2020; Table 2.3). There was evidence for differences in within-cow variability (i.e. within-cow variation was different per individual) in daily distance traveled (Estimate = 0.20, CI = [0.15, 0.26]), and elevation (Estimate = 0.12, CI = [0.08, 0.16]) in year one, but not in other rangeland use metrics (Figure 2). In year two, there was evidence for differences in within-cow variability for daily distance traveled (Estimate = 0.12, CI = [0.08, 0.16), elevation (Estimate =0.14 CI = [0.10, 0.19]), and distance to water sites (Estimate = 0.15 CI = [0.10,0.20]), but not in other rangeland use metrics (Figure 2). Here, a conservative threshold of the lower C.I. to be at least above 0.05 was set to indicate evidence of differences in within-cow variation, but elevation in year 1 and daily distance in year 2 should be interpreted cautiously.

Results regarding the relationship between within-individual variability and cattle grazing patterns are estimated via correlations between residual variation (sigma) and individual intercepts. A higher standard deviation of the sigma estimate of cow (the random effect) indicates more within-individual variability for that rangeland use metric. Thus, a positive correlation between intercept and sigma means cows with higher values with regards to rangeland use metrics are also those cows that exhibit more variability in that same metric. Generally, if there was evidence of significant correlations between individual residual variations and intercepts, they were positive. This was evident in the rangeland use metrics of elevation use and distance to water. For the metric of average daily elevation use, there was a correlation between higher average daily elevation use and more within-cow variability in average daily elevation use in year one (Estimate = 0.84 CI = [0.59,0.98]) and year two (Estimate = 0.93 CI = [0.79,0.99]). Additionally, there were correlations between a higher average daily elevation use in year one and more within-cow variability in year two (Estimate = 0.45 CI = [0.10,0.73]) and vice versa, higher average daily elevation use in year two and more within-cow variability in year one (Estimate = 0.44, CI = [0.10,0.72]). Cows that were more variable in average daily elevation use for year one were also more variable for year two (Estimate = 0.56, CI = [0.21, 0.83]). Cows that had average daily distances further from water were also more variable in year two (Estimate = 0.72 CI = [0.41,0.92]) and cows that were on average further from water on a given day in year one were also more variable in year two (Estimate = 0.48 CI = [0.12,0.78]). Notably, one negative correlation between residual variation (sigma) and intercept was found for the rangeland use metric of distance to loafing sites. Cows that were on average further from loafing sites on a given day in year two were less variable in year two (Estimate = -0.50, CI = [-0.87, -0.03]). There were no correlations between intercepts and within-cow variability or within-cow variability between years in slope, distance traveled, and distance to supplement (Figure 2).

4.3 Consistency of cattle grazing patterns between years

Cows were consistent in rangeland use metrics as indicated by among-individual positive correlations between years in average daily elevation use (Estimate = 0.38, CI = [0.07,0.64]), average daily slope use (Estimate = 0.59, CI = [0.21,0.86]), average daily distance to water (Estimate = 0.38 CI = [0.03,0.67]), average daily distance to loafing sites (Estimate = 0.68, CI = [0.24,0.95]), and average daily distance to supplement sites (Estimate = 0.42, CI = [0.04,0.72]). Confidence intervals did not indicate a correlation in daily distance traveled (Estimate = 0.16, CI = [-0.18, 0.48]) (Figure 3). It should be generally noted with this analysis that credible intervals are wide because these models are ‘data hungry’, in other words Bayesian multivariate models need large datasets to make meaningful inferences about variables because they are estimating complex relationships and uncertainty in parameters by creating posterior distributions, and especially because correlations account for variation across daily repeated measures. However, 95% credible intervals for variance components are still an overly conservative measure (Royauté & Dochtermann, 2021). Correlations are not constrained to be negative, so credible intervals that do not overlap with 0 are thought to signify an important or noteworthy result.

5. *Discussion*

This study explored the factors that influence grazing patterns within and among cattle and assessed the consistency and variability of grazing patterns between two years given the addition of a new water trough at higher elevation. Cattle remained consistent between years in all rangeland use metrics except for daily distance traveled despite the addition of a new water trough while accounting for age, pregnancy status, the passage of days of the grazing season, and temperature. Average daily temperature influenced rangeland use metrics such that cattle did not travel as far or as high when days were hotter. Cattle that ventured to higher elevation on the range and were further from water were also more variable in their grazing patterns, suggesting differences in variability of rangeland use among "hill-climbing" and "bottom-dwelling" cows.

5.1 Temperature affected cattle grazing patterns

Temperature influenced cattle grazing such that higher temperatures meant shorter daily distances traveled, more gradual daily slope use, closer distances to loaf sites and water, lower elevation use, and farther distances to supplement. These results are likely due to the longer duration of time spent near watering sites and/or resting sites (where cattle loaf), which are mostly at lower elevation and where slope was more gradual. Supplement sites were at higher elevations in the rangeland pasture and further from loafing and water sites (Figure 1). Cattle truncate grazing bouts on days where temperature is hotter during the summer and spend more time resting (Larson-Praplan et al., 2015; Schoenbaum et al., 2017), they also tend to group and rest on areas of more gradual slope (Bailey et al., 2015a; Mueggler, 1965). As time passed in the grazing season, cattle used areas of the rangeland pasture variably as evidenced by the significant smooth terms (Table 2.2). This could provide support for using penalized splines to represent how grazing patterns vary across days of a grazing season based on endogenous and exogenous factors. These findings generally support methods of achieving optimal distribution on rangeland that involve implementing water sites and training cattle to use certain loafing sites early in the season. Because cattle are more likely to clump near water and loafing sites with increased temperature, enticing cattle to use upland water sites and establishing manmade loafing sites at specific locations (with shade, water, dirt to keep cool, positive rewards) at the beginning of the season may prime cattle to use them on hot days. Low-stress herding is another strategy utilized to achieve optimal grazing (Stephenson et al., 2016). Given that temperature influences cattle use of rangeland, ranchers could use low-stress, targeted herding on the hottest days when it matters the most rather than at random time points throughout the season.

Interestingly, age of cows did not significantly relate to any rangeland metrics. This is contradictory to findings by Bailey et al. (2006), Walburger et al. (2009), and Parsons et al. (2021) that found older cows used areas farther from water, and younger cows used areas at lower elevation. Cattle age and its relationship with supplement intake has been equivocal in the literature as some studies, with age ranges very similar to ours in the current study, have found older cows to have higher supplement intake than younger cows (Kincheloe et al., 2004; Sowell et al., 2003), while others have found the opposite (Wyffels et al., 2020a; Parsons et al., 2021). In at least a few of these studies on cattle age, age is conflated with grazing experience in the pasture (as noted by Wyffels et al., 2020a in their study). In this study, cattle had variable experience with this grazed pasture despite age, which might be why we did not find an effect of age in either year. More pregnant cows were, on average, closer to water on a given day. This finding is supported by a general necessity for more water intake during later stages of pregnancy seen in grazing mammals like cows and sheep (Forbes, 1968; Winchester & Morris, 1956). The results of this study that indicate age does not influence grazing should encourage ranchers to focus more on how to manipulate or exploit individual variation in grazing patterns in their herd to achieve optimal distribution rather than focusing on age of the herd. More watering sites for herds of cattle that are farther along in pregnancy could also improve distribution.

Overall, a few more estimates of animal or environmental factors with confidence intervals that indicated a significant result were found in year two. This may be because there was more statistical power to detect significance as there were more data points per individual in year two (i.e. data was collected for a slightly longer sampling period than in year one). There was also more variability in the response variables of rangeland metrics in year two (Table 2.1) and more variability in predictor variables of temperature and pregnancy status, both which may have increased the signal-to-noise ratio of the model. Researchers conducting studies that utilize GPS collars to track grazing distribution should carefully consider how to compromise logistical and experimental hurdles such as obtaining enough data to have the power to detect significance and having collars that will last on remote batteries without interference.

5.2 Cows were consistent in most rangeland use metrics

Cattle displayed consistent grazing patterns between years. Literature from other species corroborates this finding; use of foraging areas and habitat selection/preference is distinct among individuals and related to personality (Bonnot et al., 2015; Boon et al., 2008; Cote et al., 2010; Leclerc et al., 2016; Nilsson et al., 2014; Spiegel et al., 2015). However, this finding is interesting in this specific case with genetically similar individuals developed on similar terrain. The consistency of cattle in average daily slope use, average daily distance to water, average daily distance to supplement, and average daily distance to loafing sites provides evidence for the existence of grazing styles or grazing personalities and preference to be closer to, or further from, important resources (Bailey et al., 2004; Moreno García et al., 2020). Notably, cattle were correlated with a tight confidence interval in their elevation use, which is similar to other literature indicating there may be consistent grazing styles of “hill-climbing” and “bottom-dwelling” cattle (Bailey et al., 2004; Bailey et al., 2006; Moreno García et al., 2020).

The consistency in elevation use and other metrics and the inconsistency in distance traveled can be explained by stable cattle grazing patterns and by differentiating “hill-climbers” and “bottom-dwellers” as they were coined by Bailey et al. (2004). Compared to other cattle grazing in the rangeland pasture, “hill-climber” cows in our study were using high elevation regardless of the watering site locations in year one, they just had to travel further from water to get access to the higher elevation areas. In year two, these cattle discovered the newly added water trough that did not exist in the previous year and likely used this higher trough to rest and drink rather than those at lower elevations. Between years, “hill-climbers” were still using higher elevation, hence the correlation, but now those specific individuals did not have to travel as far to achieve their preference for areas at higher elevation, and perhaps were now even traveling less far or the same as their “bottom-dweller” counterparts that preferred lower watering sites in year two. This explains the lack of a significant correlation between years for daily distance traveled. It should also be noted that distance traveled may not be as relevant or important for determining grazing distribution and classifying ‘hill-climbers’ and ‘bottom-dwellers' as other rangeland use metrics like elevation, slope, and distance to water especially on more rugged rangeland pastures (Bailey et al., 2004, 2015a). Cows use gradual terrain to travel to distant locations (Ganskopp et al., 2000; Rivero et al., 2021) and it may be that cows traveling longer distances on mountainous rangelands are also using more gradual terrain rather than those traveling on steeper slopes at higher elevation.

5.3 Cows that traveled higher and further from water were more variable in grazing patterns

Cattle differed in within-individual variation of average daily elevation and average daily distance traveled in both years, and average daily distance to water in year two. This indicates that some cattle may not have stable grazing patterns across each day in these metrics and are altering grazing patterns based more on environmental variability in temperature, vegetation, or social learning (i.e. behavioral plasticity; Chenard & Duckworth, 2021; Stamps & Biro, 2016). Cows that were more variable in elevation use across daily measures in year one and two were also using higher average daily elevation in that same year and between years, suggesting that "hill-climbing" cows were also fluctuating in their rangeland pasture utilization more-so than the "bottom-dwelling" cows. This fluctuation in elevation use was found even when the new water trough was added in year two. Accordingly, "hill-climbing" cows may be more flexible or plastic in their rangeland use than "bottom-dwellers" and may be reacting more to environmental or social factors to determine grazing bouts than their "bottom-dwelling" counterparts (Dingemanse et al., 2010; Hertel et al., 2020). Moreno García et al. (2020) proposed the idea of grazing personality plasticity that is the outcome of regulatory systems acting on gene expression, which could be considered a heritable behavior trait itself. Cows were also consistent in their within-cow variability in average daily elevation use between year one and two, pointing to a stable more or less variable or 'unpredictable' trait in these cows between years.

A larger distance from water in year one and year two were both correlated with more within-cow variability of distance to water in year two, which suggests that the "hill-climbing" cows that were farther from water in both years were more variable in distance to water in year two. This result may imply that there are even extreme "hill-climbing" individuals who remain far from water in both years despite the addition of a new water trough and the extreme climbers are more flexible in their behavior across days. This finding compliments the theory that "hill-climbing" cows may be more variable and plastic in their behavior than their "bottom-dwelling" counterparts that are closer to water in both years, lending more evidence that certain personality types in cows are also more plastic (Bailey et al., 2004; Moreno García et al., 2020).

The result that cows that were further from loafing sites in year two were also less variable in their distance to loafing sites in year two could provide weak evidence of spatial learning and memory retention after one year. Cows learn and remember where resting sites were in year one and cows that may prefer not to loaf at these sites determinedly avoid these sites altogether or choose other areas on the rangeland pasture to rest in year two. It is well documented that grazing animals rely on spatial memory to locate foraging and resting sites (Bailey et al., 1996; Gillingham & Bunnell, 1989; Howery et al., 1999; Launchbaugh & Howery, 2005) and this has also been directly studied in domestic livestock species like sheep and cattle (Bailey et al., 1989; Edwards et al., 1996; Laca, 1998).

5.4 Limitations

In year two, supplement sites were slightly shuffled (Figure 1), though most remained the same and all locations were the same supplement type. The supplements that were moved between years were in similar locations as the previous year and were mineral supplements, which cattle spend less time grazing by and do not alter grazing distribution as much as low moisture protein blocks or off-stream water (Bailey, 2004; Bailey & Welling, 2002). In general, as an exploratory field study implemented on a working ranch, there were certain factors we could not control, however we believe that this study provides important insight into understanding individual grazing personalities and may be more representative of how cattle grazing at working ranches is functioning.

5.5 Implications and conclusion

Management tools, such as the addition of a new water trough at higher elevation, are often implemented to achieve more optimal grazing distribution of cattle on expansive range landscapes (Bailey, 2004; Creamer et al., 2020; Delcurto et al., 2005). This study provides evidence that while cows may use marginally higher elevation overall with the addition of a higher elevation water site (Table 2.1), cattle still had consistent grazing styles or personalities that may or may not have incorporated the presence of the water trough. “Hill-climbing” cows that use higher elevation may remain longer at higher elevation provided a water trough at those sites, but “bottom-dweller” cows may still maintain their preference for lower elevation. Studies regarding the effectiveness of the combination of management tactics that rely on both environmental manipulation (i.e., a new water trough) and animal manipulation (i.e., individual animal selection) are lacking in grazing literature (Creamer et al., 2020). The current study provides a first step in exploring this combination, but studies in which animals are both selected based on their behavior traits (a direct manipulation) and a management tool is added are needed for causal inference about grazing distribution.

Cows that were more variable in elevation use were also those that were traveling higher in elevation, which might contain a benefit to range landscapes that are heterogeneous and patchy. Vegetation in patchy landscapes may be better maintained by cows that travel to higher points on the landscape, but also are more variable in grazing and may alter their patterns more based on social and spatial learning or environmental factors (Fuhlendorf & Engle, 2001; Fynn, 2012). Cattle were not consistent in their distance traveled between the two years, which might suggest that those cattle that found the new water trough were not expending the same amount of energy in year two to travel to higher forage locations. This insinuates that adding resources at higher elevations or in various parts of the landscape will distribute some cattle more optimally and may also reduce their necessity to expend energy especially during excessive heat, which may increase calf quality (Takahashi, 2012; Tao & Dahl, 2013).

If cattle are distributing more optimally on range, cows are utilizing forage more uniformly and more efficiently (Saul & Chapman, 2002), and stocking rates can be adjusted (increased) based on cattle willingness to graze what previous may have been classified as ‘ungrazeable’ (Castillo & Wallau, 2023; Millward et al., 2020). This study provides evidence for the slight alteration of herd grazing patterns between two years given the implementation of a new watering site, but also the stability of grazing styles and patterns within individuals. There could be value in shaping cattle herds based on individual behaviors, and adding management tools effective for those particular individuals, to achieve more sustainable grazing and higher continuous stocking rates in rangeland allotments.

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Chapter Three: Consistent Individual Differences in Cattle Behavior and How they Relate to Grazing Distribution on Extensive Rangelands

1. *Introduction*

While consistent individual differences in behavior (CIDs) among non-human animals is a topic growing in popularity, each disciple (i.e., ethology, ecology, animal science) employs different terminology to describe this phenomenon (i.e. coping styles, personality, temperament; Finkemeier et al., 2018; Laskowski et al., 2022; MacKay & Haskell, 2015). CIDs refer to relatively stable, behavioral traits in animals (Bell et al., 2009) where some behaviors may be consistent across time, yet are context-dependent (e.g., only exhibited when predators are present; Dhellemmes et al., 2021), while others span multiple contexts. Measuring behavior across contexts is therefore important because it allows researchers to distinguish 'behavior types' of animals rather than context-dependent traits (Sih et al., 2004a). Behavior types versus more plastic context-dependent behavior have different consequences and implications for individuals and relate to outcome measures differently as well (growth, fecundity, movement and space use; Sih et al., 2004b; Wolf & Weissing, 2010). Testing behaviors while animals are isolated versus in a social context is especially important for gregarious herding or flocking specie which are highly influenced by the behavior and presence of their conspecifics (Searle et al., 2010; García et al., 2020; Costa et al., 2016). It is an open question of how and whether behaviors exhibited in isolation predict behaviors in social contexts (Webster & Ward, 2011; empirical example: Atkinson et al., 2024). Contexts are a crucial consideration also because some contexts used to measure animal behavior may be based on convenience or are subjective and derived from what a researcher believes is relevant or important to an animal, but ultimately may not be.

Cattle (*Bos taurus*) are a herding species which have been reported to display CIDs in repeated temperament and personality assessments in mildly stressful environments and in isolation (Haskell et al., 2014; Finkemeier et al., 2018; Forkman et al., 2007). Determining whether these CIDs are only exhibited in specific contexts (i.e. in isolation) or are indicative of an underlying trait of the animal that is exhibited in other contexts and related to outcome measures may help to inform selective breeding practices or herd selection regimes. For example, cattle may be selected to remain in the herd based on their behavior towards humans during processing procedures or vet checks (i.e. aggressive or dangerous cows are often culled), however, because temperament is hereditary and coincides with other behaviors across contexts and relevant outcome measures, this selection could shape behavior and production traits over time (Haskell et al., 2014). Temperament of cattle, often described as docility or reactivity when humans are present, has been shown to relate to a variety of behaviors across contexts, such as maternal behavior (Phocas et al., 2006), breeding (Cooke et al., 2012), feeding behavior and weight gain (Black et al., 2013; Bruno et al., 2018; Burrow, 1997; Hoppe et al., 2010), social behavior (Bruno et al., 2018), and activity (Mackay et al., 2013; 2014). There are multiple reports in the literature that more reactive cattle have lower feed intake and graze less (Black et al., 2013; Café et al., 2011; Neave et al., 2022). Cows and sheep which are more reactive to isolation, restraint, and human interaction have been shown to be more socially cohesive, or more proximate to conspecifics, than less reactive individuals (Doyle et al., 2016; Fisher et al., 2000; Gibbons et al., 2010; Kilgour et al., 2006).

Contrarily, there are several studies that did not find an association between temperament/docility and other behaviors (maternal behavior: Aitken, 2011; Pérez-Torres et al., 2014; Turner et al., 2013; feeding behavior: Elzo et al., 2009; reviewed by Haskell et al., 2014).

Recent studies in cattle, have moved beyond only measuring docility, to also measuring other behaviors that can be described using the terms used in Réale et al. (2007): boldness, aggression, sociality, exploration, and activity measured in tests such as open field or novel object (reviewed by Forkman et al., 2007 and Finkemeier et al., 2018, empirical examples: Gibbons et al., 2009; Graunke et al., 2013; Hirata et al., 2016; Hirata & Arimoto, 2018; Kilgour et al., 2006; Neave et al., 2022). Primarily, these studies investigate relationships or correlations among these different behaviors, or to how these behaviors might relate to productivity and fertility traits, sex, and breed. However, another major component to consider for grazing beef cattle (and in some cases dairy cattle) is how CIDs in more confined or controlled contexts might relate to foraging patterns under more natural conditions. This can have important implications both for sustainability of the land allotted for them to graze, but also to understand their feeding efficiency.

Beef cattle are managed to produce quality beef for consumers of meat products, but they are also inextricably linked to conservation of grazing lands, especially in California (Delcurto et al., 2005; Svejcar et al., 2014). Beef cattle in California graze expansive landscapes called rangelands, that host a variety of ecosystem services (e.g. pollination, carbon sequestration, maintenance of native vegetation and habitats; Maczko et al. 2022). The ways in which cattle graze have implications for the sustainability and conservation of these rangelands and the ecosystem benefits they provide (Roche et al., 2015; Svejcar et al., 2014). Similar to temperament, cattle exhibit inter-individual variation in grazing patterns on rangeland, described as ‘grazing personalities’ (Bailey et al., 2004, 2006; 2015; García et al., 2020). If individual variation in temperament or personality observed in management contexts is related to how cattle graze on expansive landscapes, there is immense potential to identify and select specific cattle to achieve rangeland sustainability and conservation goals.

Two studies on rangeland beef cattle by Wesley et al. (2012) [and expanded upon by Goodman et al., (2016)], and Wyffels et al., (2021) examine grazing patterns on rangeland through the framework of behavioral syndromes. They found contradictory results that a faster supplement consumption rate did (Wesley et al., 2012) and did not (Wyffels et al., 2021) relate to more optimal, expansive grazing behavior. Although their studies lay the groundwork for relating cattle behavior across two contexts (confinement in feeding stalls and on range), they used supplement consumption rate only as a method of classifying cows into behavioral types rather than broader assessments measuring multiple behaviors that may better pinpoint underlying traits (along temperament or personality axes) that are predictive of rangeland behaviors or at least are more practically observed on ranches like chute score or exit velocity. Bailey et al. (2010) found no relationship between temperament (i.e. aggressiveness toward calf handlers) at calving and grazing distribution of rangeland beef cattle, however, temperament at calving was subjectively scored on a scale of 1 to 6, and did not involve standardized behavior assessments. Neave et al. (2022) conducted practical and standardized personality assessments and found that more calm and investigative dairy cattle had greater grazing time and milk production. Dairy cattle and rangeland beef cattle are distinct breeds and managed very differently, especially in the amount of land they are allotted to graze. Neave et al. (2022) measured grazing behaviors on 0.75 ha pastures, which is a small fraction of the thousands of hectares grazed by beef cattle. To our knowledge, no studies to date have used multidimensional, practical behavior assessments in beef cattle and related the results of these assessments to grazing behavior on rangeland.

The objective of this research was to determine whether behaviors from practical behavior assays were related to grazing patterns on rangeland. We administered three different repeated behavior assays across two years: (1) observations of behavior while cattle were handled into and traversed a chute (management assay), (2) a preference assay that featured a social-feed tradeoff, and (3) a preference assay that featured a novel item approach (see Chapter 1). The same cattle were tracked with GPS collars while they grazed on rangeland across two summers (see Chapter 2) and various rangeland use metrics were obtained from these data including home range area and social network information. If behaviors from the management assay and feeding behavior from the preference assays predict rangeland use metrics, we would expect that cattle that were (a) calmer in the management assay while handled and during isolation and (b) approached the supplement more quickly in both the social-feed tradeoff and novel approach assays will be those that travel farther, higher, cover more area to graze on rangeland, and have lower degree strength in the social network than cattle that are more active or excitable and/or that did not approach supplement quickly.

2. *Methods*

2.1 Animals and housing

Fifty Angus x Hereford cows were selected for this study if they were at least parity one heifers and were within the range of 80-100 days pregnant determined via ultrasound. Study cows ranged from 2-8 years old (mean = 4.96), weighed between 1009-1890 pounds (mean = 1340.55) and resided at the Sierra Foothill Research and Extension Center (SFREC) in Browns Valley, CA that is managed by University of California Agricultural and Natural Resources (UCANR). This research was approved by the Institutional Animal Care and Use Committee of

UC Davis, protocol #22672. This cattle herd represents typical age and breed composition of rangeland cattle herds in the Sierra foothills region.

2.2 GPS tracking and pasture

All fifty cows were collared with custom-built GPS collars (Knight Collars, Knight et al., 2018), which were leather collars with a PVC box that contained a GT-120 iGotU GPS tracker (Mobile Action, Taiwan), and a rechargeable Li-ion battery pack. The units were programmed to record location every 10 minutes. According to Morris & Conner (2017), these particular GT-120 iGotU trackers have a location error of less than 10m, a mean 50% circular error probable of less than 7m, and fix success rate is not significantly affected by cover.

Study cattle grazed a fenced 2.53 sq. kilometer (253 hectare), oak woodland rangeland pasture across two years (2021 and 2022) in months June-August. Cows were familiar with the climate and environment of SFREC and grazed at a stocking density of 0.26 AUM per acre (according to UC Rangelands Animal Unit Calculator, 2023), which as a low stocking rate is typical on California rangeland. This particular herd, however, might differ from other rangeland herds in that they are utilized for research, so may be more familiar to human presence and handling.

To collect minimum, maximum, and accurate average daily temperatures in the pasture, Onset HOBO data loggers^{TM} were placed in a solar radiation shield and set to collect temperature data every 30 minutes. In 2021, the average minimum temperature during the grazing period was 71°F, the average maximum daily temperature was 103°F, and the average mean daily recorded temperature was 84°F. In 2022, the minimum and average mean temperatures were slightly lower. The average minimum daily temperature was 68°F, the average maximum daily temperature was 103°F, and the average mean daily temperature was 82°F.

See Chapter 2 of this dissertation for a more detailed description of the study pasture. About 19% of this pasture was classified as open grassland versus 81% tree cover. Elevation in this pasture ranged from 201.4 to 618 meters (Figure 2.1) and slope ranged from 0 to 47 degrees, with an average slope of 16 degrees. Lower elevation areas of the pasture were fairly steep with rugged, rocky terrain and a few areas near the top of the pasture were also steep and rocky. Vegetation was diverse with representation from both native rangeland species and invasive rangeland species, and also palatable (e.g. wild oats and wheat grasses) and non-palatable (e.g. star thistle) species for cattle.

Loafing sites were identified by ranch managers and by observation in the first 4 weeks of data collection, and eleven of these sites were recorded for use in data analysis. Supplement sites were chosen by ranch managers to encourage grazing at higher elevation and on rugged terrain and were kept relatively consistent across years. The water sites were fixed pipe-fed troughs that had been established in the pasture for easy cattle access. A new water site, another pipe-fed trough, was added in year two at a higher elevation. Figure 2.1 shows study pasture characteristics including where loafing sites, supplement sites (both mineral supplement and low moisture protein blocks), and water sites can be found between both years.

2.3 Behavior and preference assays

Cattle behavior measures were obtained from a series of assessments that were administered in May-June in years 2021 and 2022 (Figure 1.1). A truncated description of assessments is provided below; see Chapter 1 of this dissertation for full details about the behavior assessments. To complete all testing of individuals in the morning before the daily temperature drastically increased (before noon), we split cattle into four groups of 12 or 13 cows balanced by age and pregnancy status; groups were kept consistent between years. Behavior tests commenced between 0730 and 1100 at a corral and chute which included a hydraulic squeeze chute. We began conducting behavior assessments one week after fence-line weaning and in year two of the study, we reversed the order of testing for subgroups to mitigate timing and post-weaning confounds.

The management assay was comprised of two situations: cattle were handled by an experienced, but previously unfamiliar handler (in the corral) and cattle were isolated in the chute (specifically in the cement chute, hydraulic squeeze, and exit; Figure 1.1). To begin behavior assessments, two subgroups of cows were herded into the holding pen by an experience, familiar, facility manager. The same familiar manager sorted the testing subgroup into the corral before the chute and other subgroup was randomly separated into a social group (n = 10 individuals) and a social buffer group (n = 2 or 3 individuals depending on the size of the subgroup being tested). At the beginning of testing, the study group and the social buffer group (n = 15) were in the corral that leads into the chute and hydraulic squeeze chute.

A different handler, previously unfamiliar to cows on the first day of assessment, but kept the same throughout all behavior assessments with all subgroups, herded cows into the chute one at a time. The handler, who also kept their appearance the same every day of testing, approached and moved cows following a standardized protocol (see Chapter 1). After the cow was herded individually into the chute and separated from the corral by a gate, each cow walked through the cement chute at their own pace and awaited at the closed doors of the hydraulic squeeze chute for 30s (seconds). After 30s had passed, a research assistant opened the squeeze chute doors at the same speed for each cow. Again at their own pace, cattle walked through and exited the hydraulic squeeze chute to a spray-painted line marking 2.5m from the exit doors of the squeeze chute. This management assay was repeated 4 times each year for 2 consecutive years.

Cattle exited the squeeze chute and after they crossed the 2.5m line, they participated in the preference assay (social-feed trade-off or novel approach) for a total of 5 minutes, which was set up as shown in Figure 1.1. The ‘social group’ of ten conspecifics from the other (non-test) subgroup were corralled in the alleyway on one side of the focal cow and were contained within 30m of the gate separating the focal cow from conspecifics (this distance was chosen because it is biologically relevant to herd cohesion according to Stephenson et al., 2016b). The separating gate allowed sensory contact (visual, olfactory, auditory) between the focal cow and conspecifics; it was used for physical separation only. Cattle chose to approach conspecifics on one side or to move towards a familiar bucket filled with supplement (~16 kg) to the opposite side that was 12m away from conspecifics. The social-feed tradeoff assessment was initially conducted with differing bucket distances to conspecifics, however at 12m, latency to supplement had the highest correlation coefficient across years, and thus deemed the most stable trait (see Chapter 1). The novel approach assay, which was conducted after a one-day rest from the last social-feed tradeoff assay was set up in the same T-maze configuration as the social-feed tradeoff assay, but the bucket was covered with an unfamiliar color and pattern that was novel to cows and the distance of the bucket was at 6m (Figure 1.1).

Each repetition of the management assay and the preference assays were recorded by camcorders (DCR SX85, Sony Corporation of America, New York, NY, USA) on tripods (4m high) that captured cattle positions clearly from above and to the sides of the chute and T-maze. Behaviors were coded from video with all-occurrence continuous sampling of states and events (Altmann, 1974) by trained and reliable observers (see Chapter 1) using The Observer XT software v.11 (Noldus Information Technology, Wageningen, The Netherlands).

We recorded six practical behavior measures from the management and tradeoff assays to represent CIDs (definitions provided in Table 3.1). From the management assay, we recorded (1) total time needed to handle cattle into the chute, (2) duration in the cement chute, (3) duration in the hydraulic squeeze without restraint, and (4) duration to exit the squeeze to 2.5m. From the trade-off tasks, (5) latency to familiar supplement while the bucket was at 12m and (6) latency to the novel bucket during the novel approach task (see Chapter 1). All behaviors recorded from videos for this analysis and definitions can be found in the behavioral ethogram (Table 3.1).

2.4 Data Cleaning

See Chapter 2 for a detailed description of how raw GPS data were handled to be used for models, a truncated description of cleaning is as follows. GPS data were imported from collars directly into ArcPro GIS software (GIS software by ESRI^{TM}, Version 2.5.0, Redlands, CA) along with the exact rangeland boundary (fence-line) obtained with Trimble GEO 7x handheld GNSS receiver. A methods study on iGotU 120 device error by Morris & Conner (2017) noted 27m was the 95% circular error probable with dense cover, thus locations outside of 27m of the pasture fence were deemed improbably correct and removed from the dataset. Outliers in the GPS data that indicated the cow was running at a speed greater than 3 m/s for the full fix interval (10 minutes) were removed based on biological evidence cattle running speeds (Café et al., 2011). Outliers were checked before and after this cleaning process with the R package ctmm (Calabrese et al., 2016), and removing these points was effective in eliminating all previously flagged outliers. GPS points that had zero satellite fixes were also removed from the data to reduce potential error.

We used ArcPro GIS tools and movement packages in R (R Core Team, 2023) to calculate rangeland metrics for data analysis. We computed distances to water sites, supplement sites, and loafing sites using the Near tool provided in ArcPro GIS software (GIS software by ESRI^{TM}, Version 2.5.0, Redlands, CA). We used a Digital Elevation Model with 1/3 arc second resolution of the study area and the ArcPro Extract Values to Point tool (GIS software by ESRI^{TM}, Version 2.5.0, Redlands, CA) to append elevation and slope data to each GPS data point. To calculate daily trajectories (distance traveled) by cattle from GPS points, we used the AdehabitatLT package (Calenge, 2011) in R (R Core Team, 2023). Daily values of elevation, slope use, and distances to water sites, supplement sites, and loafing sites were averaged across the week to evaluate broader, weekly changes in daily grazing patterns and to enhance model fit across years by aggregating the data to week (similar to Michelangeli et al., 2022). Before aggregating data to week, we filtered data to contain only days where there were at least a third of the total possible fixes for the day (threshold of greater than 48 GPS points per day, removed 1.7% of data).

Two rangeland use metric variables of interest were calculated with data from the full three months of data within year of grazing season. These were the 50% (core range) autocorrelated kernel density estimate of home range and the weighted degree strength of each individual in the social network. The ctmm package (Calabrese et al., 2016) in R, which uses the CTSD (continuous-time speed and distance) method of approximating speed and distance (Noonan et al., 2019), was used to calculate autocorrelated kernel density estimators for the area of each individual cow's 50% 'core range'. Autocorrelated kernel density estimators account for non-random missing data (possible due to cover), autocorrelation of GPS data, and can process large datasets (Fleming et al., 2018). Weighted degree strength is a centrality measure that is commonly used in animal social networks to reflect the social status of individuals and their influence on one another (Büttner et al., 2015; Krause et al., 2007; Newman, 2004). Undirected, weighted, degree centrality based on GPS proximity data with other collared cattle was calculated via the density of interactions with the spatsoc package in R (Barrat et al., 2004; Robitaille et al., 2018) such that interaction was defined as two cattle within 30m of each other in a window of 5 minutes. The 30m threshold was chosen based on previous literature indicating this distance captures appropriate subgroups of cattle and has undergone ground-truthing by visual observations (Harris et al., 2007; Stephenson et al., 2016b).

2.5 Datasets between years

In year one, 48 of the selected 50 study cattle participated in all behavior experiments (see Chapter 1) and all 50 cows were tracked by GPS collars with 20 cohorts on rangeland pasture for 70 days total (June 22, 2021 – Aug 30, 2021), although some collars failed before the end of the grazing season (mean days tracked = 66.6, SD = 7 days). In year two (2022), 48 of the same 50 cows participated in behavior experiments and 49 of the same 50 cows were tracked by GPS collars; one cow was added in year two to replace a culled cow (due to concerning calving issues) after year one and one cow that had not completed all repetitions of behavior experiments in year one did complete all repetitions in year two. Thus, in year two, 69 of the same cattle (with one replacement cow to make 70 total) grazed on rangeland pasture for 77 days total (June 15, 2022 – Aug 30, 2022; mean days tracked = 75.4, SD = 5.3 days). Due to a few collars failing very early in the season or falling off, there were 47 cows with analyzable GPS datasets within each year (mean age year one = 4.96, SD = 1.92; year two = 5.97, SD = 1.90), and 43 of the same cows with analyzable GPS datasets across both years.

2.6 Statistical Analysis

2.6.1 Repeatabilities and correlations of behavior variables

We calculated repeatabilities of behaviors from the management assay (also called the intra-class correlation coefficient and/or variance partitioning component; MacKay & Haskell, 2015; Nakagawa & Schielzeth, 2010) to ensure the first day of data could represent consistent individual variation in cattle behavior (i.e. a stable trait) in predictive models. We did not average behaviors for regression, as aggregation of repeated measures leads to information loss and can weaken important among individual differences (Estes, 1956; Leppink, 2019). Repeatability of behavior is calculated by dividing among individual variance σ_α^2 by the total variance, $\sigma_\alpha^2 + \sigma_\epsilon^2$

$$\frac{\sigma_\alpha^2}{\sigma_\alpha^2 + \sigma_\epsilon^2}$$

(Nakagawa & Schielzeth, 2010).

We used the brms package in R (Bürkner, 2017; R Core Team, 2022), an interface to Stan (Stan Development Team, 2022), to run Bayesian multilevel models to examine broad-sense repeatability (Biro & Stamps, 2015) of behaviors exhibited in repetitions of the management assay (see Chapter 1). We included year as a predictor variable in these models to account for latent differences in behavior between years (Biro & Stamps, 2015) and used relatively weak, uninformative priors for these data. Repeatability, which has the same calculation as intra-class correlation coefficients for grouping variables, was calculated for cow ID using the variance_decomposition function in the performance package (Lüdecke et al., 2021). This function is the recommended way to estimate ICC or repeatability for Bayesian models because it uses the posterior predictive distribution and can be used with a wider variety of data types (i.e. ‘families’; Lüdecke et al., 2021). Repeatabilities adjusted for year are reported in Table 3.2. Because repeatability must inherently be positive (it is a ratio), if the lower bound of the confidence interval of the repeatability estimate was not close to zero (>0.10), then the behavior was considered to be repeatable. Between-year correlations of latencies to the group and to supplement across bucket distances and novel approach were calculated with Spearman rank correlations in Chapter 1 of this dissertation. The Spearman rank correlation coefficient between years of the latency to supplement in the familiar and novel assays are presented also in Table 3.2.

2.6.2 Rangeland use models

We used the glmmTMB package in R (Brooks et al., 2017; R Core Team, 2023) to run mixed models for analysis of these data. We ran eight separate models for the six weekly-averaged rangeland use metrics and the two full-season metrics (average elevation, average daily distance traveled, average slope, average distance to water, average distance to loafing sites, average distance to supplement sites, adjusted kernel density 50% core range [one measure per year], social network strength [one measure per year]). Statistical models accounted for year, week (only for weekly averaged measures, not for the kernel density estimate nor social network strength), age of cows, and temperature (again only for average weekly measures) and included the four behavior measures from the first repetition per year of the management assay, latency to familiar supplement for each year, and latency to novel bucket for each year as fixed effects. We used a second-order polynomial term for week to account for temporal autocorrelation where weeks closer together in time are more similar to each other (Hertel et al., 2020; Michelangeli et al., 2022). Models contained a random effect of cow ID to account for repeated measures across weeks and years.

We centered and scaled predictor variables to standard deviations (i.e. standardized) to aid in the interpretation of relative effect of the predictor variables on the rangeland use metrics

(Schielzeth, 2010) except we did not scale year or week because they were temporal components in our models. We checked collinearity on a linear model of the same predictor variables with the vif function in the car package (Fox & Weisberg, 2018), all VIFs (variance inflation factor) were around 1, indicating no issues with collinearity between predictors.

We modified additional model parameters that improved model fit and the residuals versus predicted plots, like setting the dispersion parameter (dispformula) to year and transforming skewed variables to the log scale. These modifications are indicated in the results table (Table 3.3). We checked models via visualizing QQ plots from simulated residuals in the DHARMa package (Hartig, 2022) and residual versus predicted plots, which did not show any obvious patterns in the residuals.

3. *Results*

3.1 Effect of temporal, environmental, and animal variables on rangeland use metrics

In comparison to year one, cows were recorded to be at higher elevations ($p < 0.001$), traveled shorter distances ($p < 0.001$), were closer to water ($p = 0.002$), supplement ($p < 0.001$), and loafing sites ($p = 0.048$), and had smaller core home ranges in year two (statistical trend $p = 0.097$; Table 3.3). In addition, cows also had lower social network degree strengths in year two than in year one (statistical trend, $p = 0.051$; Table 3.3). This indicates that there was weak evidence that cows had lower cohesion (less proximity to conspecifics) while on rangeland in year two. For both years, cows expanded their location across the pasture over the weeks; being found at higher elevations ($p < 0.001$), on steeper slopes ($p < 0.001$), further from water ($p < 0.001$) and closer to supplement sites ($p < 0.001$; Table 3.3), and they traveled further distances ($p < 0.001$). Higher average temperature meant cows used more gradual slopes ($p < 0.001$), were closer to water ($p < 0.001$), and traveled shorter distances ($p < 0.001$), and there was weaker evidence they also used lower elevations (p=0.061; Table 3.3). Average temperature did not influence distance to supplement or loafing sites. In both years, older cows used areas closer to loafing sites (p = 0.022), and there was a trend for older cows to also use areas closer to supplement (p = 0.078; Table 3.3). Age of cattle did not affect other rangeland use metrics.

3.2 Effects of behavior variables on rangeland use metrics

The time it took humans to move cows into the chute, as well as the time the cow took to exit the hydraulic squeeze, did not predict any rangeland use metrics (Table 3.3). In contrast, the behavior of cows once inside the chute did relate to a few rangeland metrics; in general, more passive cows in the chute ranged higher and were more expansive in their rangeland use. For both years, cows that took longer to traverse the cement chute traveled higher in elevation on range (p = 0.017), were further from water (p = 0.043), and closer to supplement sites (p = 0.029), and also tended to use steeper slopes (p = 0.060) and travel wider areas (p = 0.067; Figure 3.1). The duration in the cement chute did not significantly predict distance traveled, distance to loafing sites, nor social network strength. Cows that took longer to traverse the hydraulic squeeze also tended to be closer to loafing sites (p = 0.076) and have lower social network strength (p = 0.095) for both years. Time to traverse the hydraulic squeeze did not significantly predict any rangeland use metrics. Cows that had higher latencies to supplement in the social-feed tradeoff assay (SFTA) traveled shorter daily distances on rangeland (p = 0.035; Table 3.3) for both years. Latency to supplement in the social-feed tradeoff assay did not predict other rangeland use metrics besides distance traveled. The latency to supplement in the novel approach assay did not significantly predict any rangeland use metrics (Table 3.3).

4. Discussion

This study was the first to relate consistent individual differences (CIDs) in beef cattle behavior measured in a management assay and feeding preferences in tradeoff assays to grazing patterns on extensive rangeland. The results of this research provide evidence that less active cows during isolation in a management assay traveled to higher elevations and further from water during two summer grazing seasons in the Sierra Nevada foothills. Feeding behavior in a social-feed tradeoff assay predicted distance traveled while cattle were on rangeland (a group setting with minimal human interference). There was no evidence that handling durations nor exit velocity related to grazing behavior while cows are on rangeland, but weak evidence that behavior while cows are in the squeeze predicted closer proximity to loafing sites and less social proximity while on rangeland.

4.1 Cows Become Specialized in Grazing Patterns Over Time

In year two, cows altered grazing patterns to utilize a new water source that was added at higher elevation, which explains their use of areas at higher elevation and closer to supplement (Figure 2.1). Walburger et al. (2009) concludes that water is one of the most influential factors shaping grazing distribution in herds of cattle, so it is not surprising that, overall, cattle altered grazing patterns in year two to accommodate a new water source. However, we have evidence that *individual* cattle grazing patterns were relatively consistent across years (see Chapter 2). Thus, cows likely traveled shorter distances and were closer to water and supplement at higher elevations in year two because they ‘specialized’ on being bottom dwellers or hill climbers and utilized their preferred higher or lower water source (Bailey et al., 2004); they relied on their past experience and memory (Bailey et al., 1996; Wyffels et al., 2020) with how the pasture was set up in year one to inform and update grazing patterns in year two (similar to findings by

Anderson & Urquhart, 1986; Howery et al., 1996). This specialization is also likely why we see evidence (although weaker) that they graze smaller core home ranges in year two.

Although it was not directly measured, this supports literature that suggests cattle use spatial memory for finding and remembering quality vegetation and other resources, like water, on grazing land (Howery et al., 1996; 1999; Hirata & Takeno, 2014). Spatial memory of cattle can be manipulated to create optimal grazing patterns and target areas of rangeland to graze by providing resources in these locations (Bailey, 2004; Delcurto et al., 2005). This specialization in bottom-dwelling or hill-climbing in year two may have also influenced their social interactions such that they were more insular in subgroups of cattle (Sowell et al., 1999; Stephenson & Bailey, 2017) that shared similar grazing patterns rather than belonging to a larger group of exploratory cattle in year one, hence the lower social network degree strength in year two than in year one.

Conversely cows expanded grazing patterns as weeks passed within the grazing season. Cows were using higher elevation on more rugged terrain, and further from water sites as weeks passed within the grazing season because preferred grazing areas were depleted of quality vegetation (Tobin et al., 2021), and cows had to travel further to graze where vegetation was readily available (Bailey et al., 1996; Barcella et al., 2016; Rivero et al., 2021). Cattle likely also explored to find resources when introduced to the pasture and establish preferred areas to graze in latter weeks of the season (Howery et al., 1996; Bailey et al., 2004). Providing diversified management tools and strategic placement of resources, and if feasible doing this dynamically throughout a season, could contribute to improving grazing distribution within and across seasons.

Hotter temperatures meant cows prioritized water and conserved their energy exertion by not traveling far from water sites, nor traveling as far, as high, or on rugged terrain which makes intuitive sense and has also been found in several studies (Larson-Praplan et al., 2015; Schoenbaum et al., 2017; reviewed by Rivero et al., 2021). Older cows used areas on rangeland closer to supplement and closer to loafing sites. Several other studies have also found older cows to consume more supplement (Sowell et al., 2003; Kincheloe et al., 2004), and remain closer to supplement during grazing (Parsons et al., 2021) than younger cows. Age has been found to be related to dominance and social rank in many studies of beef and dairy cattle (Hubbard et al., 2021; O'Connell et al., 1989; Šárová et al., 2013) and because resting sites are often selected by more dominant individuals (Sowell et al., 1999; Sato, 1982), it is possible that older cows are closer to loafing sites because they are the individuals that have established these sites among the herd.

4.2 Less active cows in the chute have more optimal grazing distribution

Cows that took longer to traverse the cement alley, showing a more passive response to the handling procedure and to isolation, also exhibited more optimal grazing behavior by traveling higher in elevation, further from water, closer to supplement (most placed at higher areas on range, Figure 2.1) and they tended to have larger core home ranges (Figure 3.1) and use more rugged terrain. Although we did not presume to measure coping styles, the duration it took cows to traverse areas of the chute (a stressful and isolated context) may have been a measure of stress coping in cows. Proactive and reactive coping styles are a way to classify animals, most commonly used with pigs (Finkemeier et al., 2018), wherein proactive individuals show a more active, routine response to stress and less HPA axis reactivity and reactive individuals show a more passive, cautious response to stress and have higher HPA axis reactivity (Koolhaas et al., 1999; Koolhaas & Van Reenen., 2016; Øverli et al., 2007). We did not measure physiological response to stress to validate our behavior assessments, but cows that took longer in the cement alley were also more stationary (see Chapter 1), thus may be exhibiting a "passive" or reactive coping style to a stressful environment (Koolhaas et al., 1999). More reactive individuals have been found to exhibit more behavioral flexibility in changing environments (social or physical; Brust et al., 2013; Coppens et al., 2010, Nogues et al., 2023; de Lourdes Ruiz-Gomez et al., 2011) than their proactive counterparts, which may explain why reactive coping individuals in the chute exhibit more optimal grazing patterns on a complex, rangeland environment where social groups and access to quality vegetation varies throughout the season. This would also explain why they demonstrate flexibility in traveling further from water, higher on range, and why they used upland supplement that they had to explore the range to discover. This finding would contrast preliminary results presented by Wesley et al. (2008); that reactive individuals graze closer to water and explore less average area per day as compared to proactive cattle.

Coping styles and temperament are often conflated (Finkemeier et al., 2018) and in our study, as well as others, it was difficult to distinguish 'calm' temperament from a passive response in cows (or reactive coping style). In a study conducted by Neave et al. (2022), they found that calmer and investigative dairy cattle also had greater grazing time while on pasture. Our study corroborates the findings by Neave et al. (2022) as seemingly 'calmer' or less active cattle in the cement chute appeared to forage higher, wider, and further from water on rangeland.

Some cows have larger, more sensitive, flight zones and react more actively to handling interventions, while others may show a more passive response (Grandin, 2021). If ranchers cull cattle that are 'stubborn' or less active upon moving or sorting, they may unintendedly be shaping a less optimal distribution of their animals on rangeland by culling those that graze higher elevations, are finding upland supplement, and are not clumping near water. Ranchers often cull cattle of the opposite extreme, those that are highly excitable and aggressive because they are a concern for animal welfare and human safety (Grandin, 2021). In our study, we did not find strong evidence indicating highly active cattle are displaying more optimal grazing patterns, so culling more excitable cows because of these concerns may be conducive to sustainable grazing. Given that more passive cattle in the chute exhibit more flexibility on rangeland and were closer to supplement sites and further from water, ranchers may be able to shape their environment to optimize distribution of a cow herd with these individuals by setting up targeted supplement distributed in far locations around the rangeland pasture (Stephenson et al., 2016a).

4.3 Less active cows in the hydraulic squeeze rest more and are less social on rangeland.

There was weak evidence that cows that were slower in the hydraulic squeeze, thought to be less excitable cows given literature on chute restraint behavior (Burrow, 1997; Hoppe et al., 2010; Tulloh, 1961), were closer to loafing sites and had lower social network degree strength. Cows that took longer in the hydraulic squeeze had a less active response toward potential restraint and to isolation from other social mates. Neave et al. (2022) found dairy cows less fearful of humans, not showing active or avoidant behavior responses, had longer lying times and Llonch et al., (2018) found beef cows housed at a feedlot that were less excitable determined by chute score and flight speed had less frequent standing bouts. Although our cattle did not have accelerometers, thus we cannot assess actual lying time, we can speculate that cows were resting or lying at loafing sites, which were the behaviors observed at loafing sites throughout the season. If squeeze duration is considered a measurement of excitability and a similar mechanism to fear of humans, then our study supports findings by Neave et al., (2022) and Llonche et al., (2018) that cattle with calmer temperaments in the squeeze perhaps lie and rest more. Cows that took longer to traverse the squeeze remained isolated for a longer period of time; anecdotally, cows that took longer in the squeeze nosed the walls, ground, and ceiling as they moved through, investigating their surroundings, dissimilar to other cows that would walk through as quickly as possible toward visual contact of conspecifics. These cows that took longer in the squeeze might indicate they are not only calmer or more passive, but also more exploratory and independent, and overall less reliant on social buffering than conspecifics or less 'socially active' (similar to findings of social separation tests of cattle: Müller & von Keyserlingk, 2006; Müller & Schrader, 2005). Hirata et al., (2016) also found that cows that were less reactive to handling approached conspecifics slower than other cows and Lansade et al., (2008) found horses more reactive in isolation were also more gregarious.

Cows with a more passive, slow response in the squeeze chute may also be considered to have a reactive stress coping response (Hoppe et al., 2010). Animals with reactive coping styles to stress also have been shown to be more tolerant of other individuals (non-aggressive), but also less 'synchronous' with the rest of the group in feeding behavior (Koolhaas & Van Reenen, 2016; Nogues et al., 2023; Zobel et al., 2011). This could be an alternative explanation to why more time to traverse the squeeze chute is weakly related to closer proximity to loafing sites (showing tolerance of other individuals), but lower social proximity and cohesion while on rangeland (showing lower group synchronicity in feeding behavior; Searle et al., 2010).

Social cohesion has benefits to cattle on rangeland including antipredator behavior and social learning of grazing sites (García et al., 2020; Searle et al., 2010), which can also benefit rangeland conservation if learning encourages cattle to use upland areas (Howery et al., 1998; Sowell et al., 1999). However, in deer, social cohesion of the group led to less foraging efficiency (Stutz et al., 2018) because the herd prioritized other benefits of sociality while foraging, which may also occur with cattle on rangeland. Cattle that form subgroups and are in close proximity with herd mates are more influential in group movements (Ramseyer et al., 2009; Searle et al., 2010; Sueur et al., 2018). Identifying influential cows by those with shorter squeeze durations that also have desirable grazing patterns (i.e. those with larger core home ranges or that use areas at higher elevation) and perhaps are more efficient foragers could allow ranchers to take advantage of social learning and train or herd influential cows to targeted areas on rangeland (Creamer et al., 2020; Sowell et al., 1999; Stepheson et al., 2016a). Retaining more socially cohesive cows in the herd could also be useful for the newest frontier in cattle management, virtual fencing (Goliński et al., 2022), because virtual fencing relies on social learning within groups of cattle (Keshavarzí et al., 2020).

4.4 Measuring latency to feed, chute, and squeeze behavior could improve grazing distribution.

Latency to supplement in the social-feed tradeoff task represented a consistent feeding behavior such that cows that were less feed-centric during the task, with longer latencies to the supplement, also traveled less on rangeland to forage (similar to findings by Wesley et al., 2012; Goodman et al., 2016 with supplement consumption rate). Cows with longer latencies to supplement were presumably less food-motivated or less willing to travel away from their social group to consume food or supplement (Sibbald et al., 2006; Hirata et al., 2013; Searle et al, 2010). Ranchers often want to retain cattle in the herd that travel further on rangeland and are more willing to separate from herd mates to do so because they are better maintaining vegetation and soil health, and not clumping in the same locations (Delcurto et al., 2005; Fuhlendorf & Engle, 2001; Stutz et al., 2018). Observing cow willingness to consume supplement at least 12 meters away from conspecifics could enable ranchers to predict how cattle will travel to forage on rangeland.

Neither handle duration, exit duration, nor the novel approach assay predicted behaviors on rangeland. It was perhaps not surprising that handle duration did not relate to rangeland use metrics because this relied on subjectivity of human handling and uncontrollable reactions from groupmates that were in the corral. Although the same handler was consistently used in this study, and they followed a standardized protocol for handling, stockpersons can inadvertently react to the arousal level of the animal (Hultgren et al., 2020), which can influence animal behavior. Additionally, the behavior of individual cows could have been biased by the social buffering effect (Grignard et al., 2000; Parham et al., 2022). It is, however, surprising the exit duration did not relate to any rangeland use metrics as this is a widely accepted measurement of temperament in cattle (Burrow, 1997; Forkman et al., 2007) and has been found to relate to a multitude of behaviors in cattle (like social behavior [Bruno et al., 2018], and feeding behavior [Café et al., 2011]).

We assumed this novel approach assessment would relate to grazing behavior because it involved a practical social versus novelty tradeoff that cattle are likely to face especially while on new pastures. However, novel object tests in cattle have been used in a variety of experiments and have not related to other behaviors in some studies (Hirata et al., 2016; Gibbons et al., 2009) including also in Chapter 1 of this dissertation. In this case of relating novel approach to rangeland metrics, it’s possible we did not find a relationship because this herd had been previously exposed to this specific pasture and are familiar with this landscape. Thus, this novel approach assessment did not translate to foraging behaviors in a non-novel environment. We also used novel color and visual patterns on the bucket that were species-specific in terms of cattle vision (Phillips & Lomas, 2001), but not in terms of what they might confront on rangeland. This assessment could be modified to include novel, but natural, stimuli like a novel vegetation species (carrots have been used in dairy cattle; Mainardes & DeVries, 2016) or a bucket surrounded with novel logs or rocks.

The two behavior measures that related to grazing, duration to traverse the cement chute and the time to traverse the hydraulic squeeze (although only statistical trends for hydraulic squeeze), did so in different ways and with different rangeland use metrics. This suggests that duration to traverse the chute and the squeeze are behaviors exhibited by different underlying mechanisms (which corroborates the fact that they loaded onto different principal components in Chapter 1). Duration to traverse the cement chute related to grazing behaviors that might be labeled more feed oriented and/or more exploratory, whereas squeeze behaviors related to resting and social behavior on rangeland. This information could be useful for determining breeding regimes and using chute and squeeze behaviors as predictors for divergent solutions to sustainable grazing on rangeland.

Studies that measure consistent individual differences across manipulated experiments and in field settings are rare and crucial (Archard & Braithwaite, 2010), and overcome methodological hurdles of validating representative behavior traits in animals. Although measuring individual cattle behavior while in a narrow chute without restraint may not be the most practical measure that ranchers can implement, most all ranches have working chute infrastructure. It has also been expressed in studies and surveys that allowing cattle to habituate to handling and move through chutes unrestrained (Parham et al., 2022) will promote more efficiency and better animal welfare in future processing procedures in cattle (breeding, health checks, vaccinations, etc.; Grandin, 2007; Ujita et al., 2021). If cattle managers can observe behavior of cattle during this situation of minimal interference in the narrow chute while habituating animals, they may be able to identify less active cows that are likely to exhibit more optimal foraging patterns. Our behavior measures were from the first day of data of each year because it is likely only one exposure to assessments would be used on working ranches to assess temperament (Mackay & Haskell, 2015; Neave et al., 2022). Identifying desirable grazing characteristics of cattle and understanding cattle social behaviors could allow ranchers to shape herds constituting certain individuals or strategically plan certain management tools like targeted supplement (Bailey et al., 2006; DelCurto et al., 2005; Stephenson et al., 2016a).

4.5 Limitations

We did not use accelerometers in this study; thus, we can only infer grazing and resting bouts based on rangeland metrics gleaned from GPS data. This is limiting when we are trying to make conclusions more specifically about feeding and lying behaviors and relate to previous studies in cattle with this type of behavior data (e.g. Neave et al. 2022; MacKay et al., 2013). We recognize that some of our reported results are statistical trends rather than below the threshold of statistical significance, but we are reporting all evidence of relationships in our data, rather than conforming to a more black and white 'binary' reporting of p-values as significant or not (Muff et al., 2022; Schumm et al., 2013). Because we were not hypothesis testing per se, but rather conducting an exploratory study on these data, we believe it is important to report weaker relationships and hope to encourage future researchers to replicate these techniques on more herds of cattle with similar experimental set-ups and larger sample sizes. Additionally, standardization of the predictors and response variables that are on the log scale to improve model fit make interpretation of the results difficult. Regardless, these results at least should inform researchers about potential relationships to investigate and caution ranchers about changes to grazing distribution that could occur given culling for certain behaviors in management contexts.

4.6 Conclusion and Implications

Cows that were less active in a narrow cement chute were found to have more optimal grazing distribution for rangeland conservation by using higher elevation, grazing further from water, and closer to upland supplement. Cows with higher latencies to a familiar supplement in an experimental social-feed tradeoff task did not travel as far on rangeland to forage. Optimal grazing on extensive rangeland provides a suite of direct benefits to humans, animals, and the environment (Svejcar et al., 2014). There is discernable potential for unmanaged or unchecked cattle grazing to negatively interfere with rangeland benefits and result in a host of issues ranging from diminished water quality to degradation of important habitats for a variety of ecosystems (Bailey et al., 1996; DelCurto et al., 2005). There is evidence that duration to traverse the chute and the hydraulic squeeze, and latency to a familiar supplement, are cross-contextual measures relating to behaviors on rangeland. Observable consistent individual differences (CIDs) in cattle during handling and management procedures that predict grazing patterns has potential to inform ranchers on shaping cattle distribution to achieve rangeland conservation goals and avoid the negative impacts of uneven grazing.

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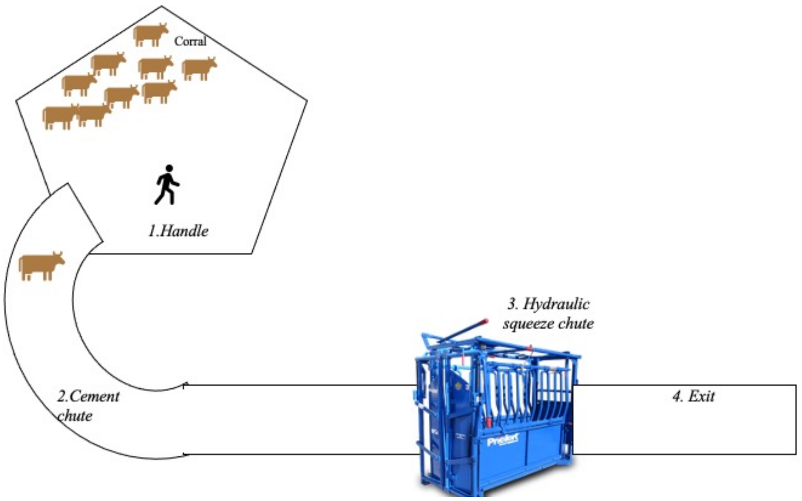
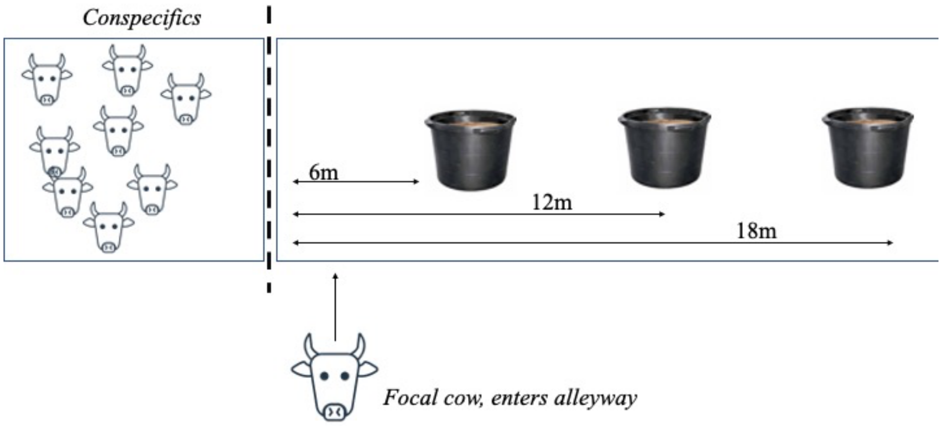
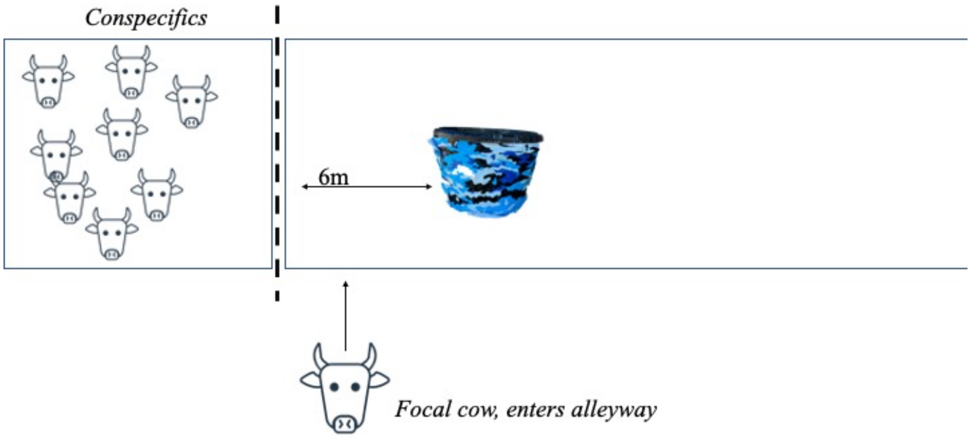
Tables and Figures

Figure 1.1







Set-ups of the management assay (top), denoting the two different situations (handle and chute) and four different areas where observations were taken (handling corral, cement chute, hydraulic squeeze, and exit), social-feed tradeoff assay (middle) and novel approach assay (bottom). The dotted line in the social-feed tradeoff assay and novel approach assay represents the gate separating conspecifics from the area where the assay took place. We conducted all-occurrence, continuous, behavior sampling from video recordings of assessments.

Table 1.1 Sample sizes of cows to participate in all repetitions of assessments (full data).

Behavior test	*Year*	*N cows (full reps)*
Management context	1	48
	2	49
Social-feed Tradeoff	1	48
	2	49
Novel approach	1	38
	2	49

Table 1.2 Ethogram of behaviors. All behaviors were continuously recorded from videos of behavior assessments using all-occurrence sampling. Some behaviors are durations of behavior as they occurred (start-stop) and some behaviors are indicated if they occur (frequencies).

Durations (start-stop, mutually exclusive)	
Squeeze$^{\Delta}$	Duration of time from when entire cow head (behind ears) crosses squeeze gate to when hindquarters (base of tail) cross squeeze exit gate.
Exit$^{\Delta}$	Duration of time from when cow hindquarters cross squeeze exit gate to when cow hindquarters cross orange exit line at 2.5m.
Chute $^{\Delta}$	Duration of time from when hindquarters (base of tail) crosses the cement chute gate to when hindquarters cross chute exit gate.
Enter squeeze $^{\Delta}$	Duration of time from when back squeeze door opens to when cow head (behind ears) crosses squeeze door threshold.
Handle time total$^{\blacklozenge}$	Duration of time from when handler is able to isolate the cow of interest (the cow that eventually goes through the chute) with one or two other herd mates (handler is between cow of interest and herd mates) to when cow's hindquarters cross through cement chute gate.
Frequency behaviors	
Change direction $^{\Delta}$	Cow transitions from forward to backward progress or vice versa.
Urge weighted$^{\Delta}$	Human interferes with forward progress of cow using flight zones to force forward progress, this occurred if cow did not traverse portions of the chute within 3 minutes. Escalating urge steps were used if cows were not responsive or did not make forward progress, thus the urges are weighted by the necessary escalation used (1-7).
Latencies (start-stop, not mutually exclusive) $^{+\pm}$	
Latency to supplement$^{+\pm}$	Duration of time from when hindquarters (base of tail) crosses exit line to when cow takes first bite of supplement.
Latency to group$^{+\pm}$	Duration of time from when hindquarters (base of tail) crosses exit line to when majority of cow's body (>50%) is within one cow's length of groupmate gate.
Activity behaviors (mutually exclusive, across situations of management assay):	
Stationary$^{\Delta+\pm\blacklozenge}$	Cow does not move forward or backward for minimum of 2 seconds; head is facing forward or not at perpendicular angle to plane of body.
Walk$^{\Delta+\pm\blacklozenge}$	Cow moves forward or backward at steady, slow pace (less than 3 steps per second).
Run$^{\Delta+\pm\blacklozenge}$	Cow moves forward or backward at rapid pace (3 steps per second).
Group location in tradeoff and novel approach assays (mutually exclusive) $^{+}$	
Near$^{+\pm}$	At least one cow is closer than a 10 m marker in the alley which contains the cows.
Far$^{+\pm}$	Cows are further than the 10 m marker in the alley which contains the cows

Symbols denote the different assays or situations for specific behaviors: ♦ Handle situation, Δ Chute situation, + Social-feed tradeoff assay, ± Novel approach assay. Running was too infrequent of a behavior to analyze further, thus only walking and stationary were used to assess repeatability and for component analyses.

Table 1.3 This table contains a) repeatability estimates of behaviors across repetitions with 95% confidence intervals (CI), b) correlation coefficients of behaviors between years with 95% confidence intervals (CI), and c) spearman rank correlations with p values between years of latencies in the social-feed tradeoff assay and novel approach assay. Behaviors considered to be repeatable and correlated for further component and regression analyses are bolded. All estimates of non-latency behaviors were calculated from Bayesian mixed models. Repeatabilities are broad-sense repeatabilities adjusted for year and correlations are among-individual correlations between years from multivariate models. The variance_decomposition() function in the performance package (Lüdecke et al., 2021) was used to calculate repeatability (or icc) estimates for Bayesian models. The variance decomposition function can be used for a wide variety of models with non-gaussian distributions, but the error in the estimate, especially if the error is large, is not always reflective of the constraint for repeatability to be positive (Lüdecke et al., 2021), hence why some lower bounds of confidence intervals below are negative. Spearman rank correlations between years was calculated with the cor.test() function in the stats package included in R (R Core Team, 2023).

Repeatability estimates and correlations for management assay behaviors and choice

	Repeatability (R)	CI Repeatability	Between Year Correlation	CI Between Year Correlation
Squeeze duration	**0.76**	**[0.47, 0.90]**	**0.85**	**[0.65, 0.98]**
Exit duration	**0.72**	**[0.37, 0.90]**	**0.66**	**[0.39, 0.86]**
Chute duration	**0.69**	**[0.42, 0.84]**	**0.67**	**[0.43, 0.84]**
Handle duration	**0.60**	**[0.30, 0.79]**	**0.39**	**[0.06, 0.66]**
Enter squeeze duration	**0.81**	**[0.16, 0.97]**	**0.82**	**[0.57, 0.98]**
Walk (chute)	**0.53**	**[0.41, 0.63]**	**0.74**	**[0.53, 0.89]**
Stationary (chute)	**0.55**	**[0.43, 0.64]**	**0.76**	**[0.55, 0.90]**
Walk (handle)	0.08	[-0.19,0.29]	0.36	[-0.40, 0.93]
Stationary (handle)	0.28	[-0.06, 0.54]	0.33	[-0.29, 0.88]
Change direction	0.48	[[0.04, 0.75]	**0.84**	**[0.48, 1.00]**
Urge weighted	0.25	[-0.23, 0.60]	-0.49	[-0.98,0.47]
Order	**0.26**	**[0.13, 0.37]**	**0.75**	**[0.45, 0.96]**
Choice	0.03	[-0.07, 0.21]	0.48	[-0.02,0.90]

Latency to groupmates and supplement correlations between years

	6m		12m		18m		Novel	
	rho	p	rho	p	rho	p	rho	p
Latency to group*	0.115	0.443	0.013	0.930	0.174	0.243	**0.448**	**0.007**
Latency to supplement*	**0.351**	**0.016**	**0.353**	**0.015**	0.170	0.253	**0.559**	**<0.001**

Table 1.4 This table shows behavior loadings onto the first three components of the principal component analysis. The strongest loadings for each variable onto the first three components are shown.

	PC1 'activity'	**PC2 'fearfulness'**	**PC3 'excitability'**
	Variance explained: 31.3% Eigenvalue: 2.506	Variance explained: 18.2% Eigenvalue: 1.453	Variance explained: 16.3% Eigenvalue: 1.300
Behaviors	*Loadings*		
Chute duration	0.417		
Stationary	0.608		
Walk	-0.602		
Enter squeeze duration		0.458	
Handle duration		0.474	
Order		-0.604	
Squeeze duration			0.494
Exit duration			0.569

Table 1.5 Results from models predicting the supplement versus social choice (betabinomial model) and latencies to supplement for both the social-feed tradeoff assay (SFTA) and novel approach assay (NAA; truncated negative binomial models with conditional model predicting latency and zero-inflated model for predicting a non-approach of supplement). Predictor variables included for both were year, age, position of social group (within 10m of assay), temperature, and component scores from the management assay. The predictor distance of supplement bucket to social mates was included for the choice and latency models for the social-feed tradeoff assay. Significant effects are bolded ($p < 0.05$), and trends are indicated with an asterisk * ($0.05 < p < 0.1$).

	Choice		Latency to Supplement SFTA (s)				Latency to Supplement NAA (s)			
			Conditional		Zero-Inflated		Conditional		Zero-inflated	
Random vars.	*Variance*		*Variance*		*Variance*		*Variance*		*Variance*	
Cow ID	1.236		0.418		1.386		0.412		44.17	
Group	0.520		0.000		0.000		0.303		10.70	
Predictor vars.	*Estimate*	*P*	*Estimate*	*P*	*Estimate*	*P*	*Estimate*	*P*	*Estimate*	*P*
(Intercept)	**4.338**	**0.027**	**3.19**	**<0.001**	**-5.037**	**0.012**	3.017	0.138	11.647	0.39
dist [12 m]	**-1.004**	**0.016**	**0.53**	**<0.001**	**1.238**	**0.010**	NA	NA	NA	NA
dist [18 m]	**-1.837**	**<0.001**	**1.11**	**<0.001**	**1.935**	**<0.001**	NA	NA	NA	NA
year [2]	**1.596**	**<0.001**	**-0.64**	**<0.001**	-0.055	0.886	**-1.207**	**<0.001**	1.665	0.33
Age	-0.025	0.855	0.046	0.509	0.019	0.893	0.180	0.084*	-1.404	0.24
Position (near)	-0.470	0.262	0.049	0.768	0.339	0.406	0.693	0.114	-0.052	0.98
Temperature	-0.041	0.067*	-0.001	0.942	0.026	0.243	-0.003	0.901	-0.104	0.50
PC1 (less active)	**0.406**	**0.010**	-0.070	0.344	-0.140	0.372	0.097	0.377	-1.342	0.35
PC2 (less fearful)	0.040	0.848	-0.037	0.721	0.147	0.497	0.062	0.647	0.699	0.62
PC3 (less excitable)	**0.477**	**0.039**	0.184	0.069*	-0.021	0.926	0.178	0.202	-4.335	0.18

Table 2.1 Mean and standard deviations of rangeland metrics in year one versus year two. According to paired sample T-tests, all differences are statistically significant, which is likely due to the large sample size.

	Year 1		**Year 2**	
Metric	*Mean*	*SD*	*Mean*	*SD*
Elevation (m)	393	55	410	69
Slope (degrees)	9.18	2.05	9.11	2.22
Distance traveled (m)	4284	845	3908	692
Near water (m)	337	157	311	159
Near supplement (m)	631	258	488	266
Near loafing site (m)	128	68	125	70

Table 2.2. Results of models for each rangeland metric: average daily elevation, average daily slope, daily distance traveled, average daily distance to water, average daily distance to supplement sites, average daily distance to loaf sites. All predictor variables were centered and standardized, thus effects on response variables represent relative effects across predictors. Models were run with the family specification lognormal() in the brms package, thus estimates in the table are of posterior means represented on the log scale and have not been back-transformed. Estimates represent changes on the log scale of the response variable for one unit change in standard deviation of the predictor variable. Results for model parameters which logged 95% confidence intervals do not cross 0 are indicated with bold font to differentiate a significant result. The subscript 1 means that predictors had different values within the given year and were used respectively in the model for their specific year. Ages all increased by one, pregnancy status was different across years and average daily temperature was also different across years.

Predictors	Estimates	CI (95%)	Estimates	CI (95%)
Elevation (m)	*Year 1*		*Year 2*	
Intercept	**5.97**	**5.95 – 5.99**	**6.04**	**6.00 – 6.07**
Smooth Terms (date)	**0.57**	**0.28 – 1.09**	**1.11**	**0.61 – 1.99**
Unpenalized Coeff (date)	1.08	-1.74 – -0.44	1.45	0.78 – 2.12
Age^1	0.00	-0.01 – 0.01	0.01	0.00 – 0.02
Pregstatus^1	0.00	-0.01 – 0.01	-0.01	-0.02 – 0.00
Temp^1	0.00	-0.01 – 0.01	**-0.02**	**-0.02 – -0.01**
Slope (degrees)	*Year 1*		*Year 2*	
Intercept	**2.20**	**2.17 – 2.23**	**2.21**	**2.15 – 2.26**
Smooth Terms (date)	**0.86**	**0.45 – 1.63**	**0.96**	**0.36 – 1.89**
Unpenalized Coeff (date)	1.07	-0.06 – 2.09	-2.13	-3.42 – -0.69
Age^1	-0.01	-0.02 – 0.01	0.02	0.00 – 0.04
Pregstatus^1	0.00	-0.02 – 0.01	-0.01	-0.02 – 0.00
Temp^1	**-0.02**	**-0.03 – -0.01**	0.00	-0.01 – 0.01
Distance Traveled (m)	*Year 1*		*Year 2*	
Intercept	**8.36**	**8.32 – 8.42**	**8.26**	**8.22 – 8.31**
Smooth Terms (date)	**0.66**	**0.35 – 1.24**	**0.59**	**0.28 – 1.13**
Unpenalized Coeff (date)	-1.82	-2.78 – -0.96	-1.39	-2.14 – -0.67

Age[1]	-0.01	-0.03 – 0.01	0.02	0.00 – 0.03
Pregstatus[1]	-0.01	-0.04 – 0.02	0.00	-0.01 – 0.01
Temp[1]	0.01	0.00 – 0.02	**-0.02**	**-0.03 – -0.01**
Distance to Water (m)	*Year 1*		*Year 2*	
Intercept	**5.76**	**5.68 – 5.86**	**5.75**	**5.65 – 5.86**
Smooth Terms (date)	**2.45**	**1.41 – 4.19**	**1.91**	**0.64 – 0.99**
Unpenalized Coeff (date)	-4.17	-6.74 – -1.67	-0.49	-2.68 – 1.72
Age[1]	0.00	-0.04 – 0.03	0.04	0.00 – 0.08
Pregstatus[1]	-0.02	-0.08 – 0.04	**-0.04**	**-0.06 – -0.01**
Temp[1]	-0.02	-0.05 – 0.00	**-0.06**	**-0.09 – -0.04**
Distance to Supplement (m)	*Year 1*		*Year 2*	
Intercept	6.94	6.66 – 7.20	6.05	5.77 – 6.34
Smooth Terms (date)	**5.33**	**2.86 – 9.27**	**9.23**	**5.72 – 15.09**
Unpenalized Coeff (date)	6.04	-0.91 – 13.18	-21.39	-27.30 – -15.76
Age[1]	-0.04	-0.14 – 0.06	-0.10	-0.22 – 0.00
Pregstatus[1]	0.05	-0.09 – 0.20	0.06	-0.01 – 0.12
Temp[1]	**0.16**	**0.09 – 0.23**	**0.19**	**0.13 – 0.25**
Distance to Loaf (m)	*Year 1*		*Year 2*	
Intercept	4.74	4.68 – 4.79	4.69	4.60 – 4.79
Smooth Terms (date)	**1.55**	**0.73 – 2.97**	**1.31**	**0.73 – 2.46**
Unpenalized Coeff (date)	4.30	1.90 – 7.18	0.14	-1.95 – 2.22
Age[1]	0.01	-0.01 – 0.04	-0.02	-0.05 – 0.02
Pregstatus[1]	0.00	-0.04 – 0.03	0.00	-0.03 – 0.02
Temp[1]	**-0.09**	**-0.12 – -0.06**	0.02	-0.01 – 0.04

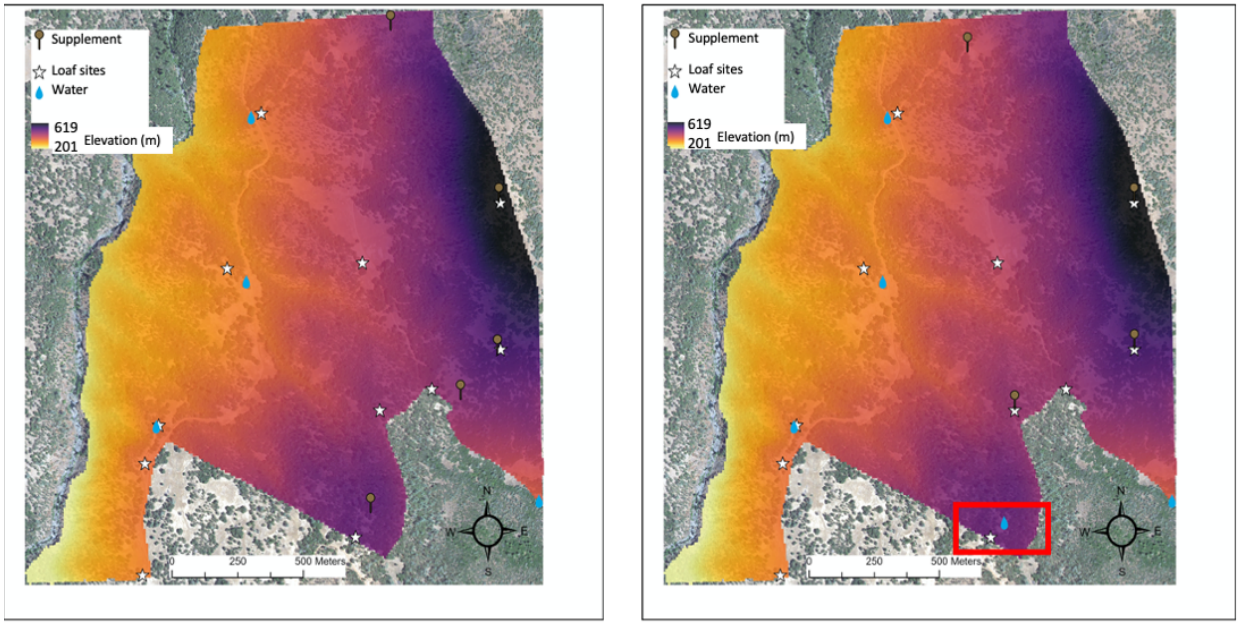
Table 2.3. The mean and range of the intra-individual variance back-transformed from posterior draws of predictions of sigma for individual cows is shown. Intra-individual variance is a measure of 'predictability' in the rangeland use metric (as described by Hertel et al., 2020), a higher IIV for an individual indicates more variability. Coefficient of within-animal variation (CV_p) and their confidence intervals are also shown. The CV_p is a standardized population-level measure of degree of variability among study animals.

Coefficient of Variations in Predictability

	Year 1				**Year 2**			
Metric	Mean IIV	Range IIV	CV_P	C.I.	Mean IIV	Range IIV	CV_P	C.I.
Elevation	3.11 (m)	2.07 – 5.72 (m)	0.12	0.08-0.16	3.16 (m)	1.95 – 6.44(m)	0.14	0.10-0.19
Slope	3.3°	2.34 – 5°	0.05	0.01-0.10	3.42°	2.54 – 5.57°	0.06	0.01-0.10
Distance traveled	3.4 (m)	2.07 – 16.77 (m)	0.20	0.15 – 0.26	3.22 (m)	2.18 – 9.95 (m)	0.12	0.08 – 0.16
Near water	4.27 (m)	3.36 – 6.04 (m)	0.02	0.00-0.07	4.53 (m)	2.75 – 14.44 (m)	0.15	0.10-0.20
Near supplement	5.93 (m)	4.14 – 12.02 (m)	0.04	0.00 – 0.11	5.62 (m)	3.66 – 12.17 (m)	0.09	0.02 – 0.16
Near loafing site	4.48 (m)	3.67 – 5.89 (m)	0.02	0.00-0.05	4.63 (m)	3.09 – 9.96 (m)	0.09	0.05 – 0.14

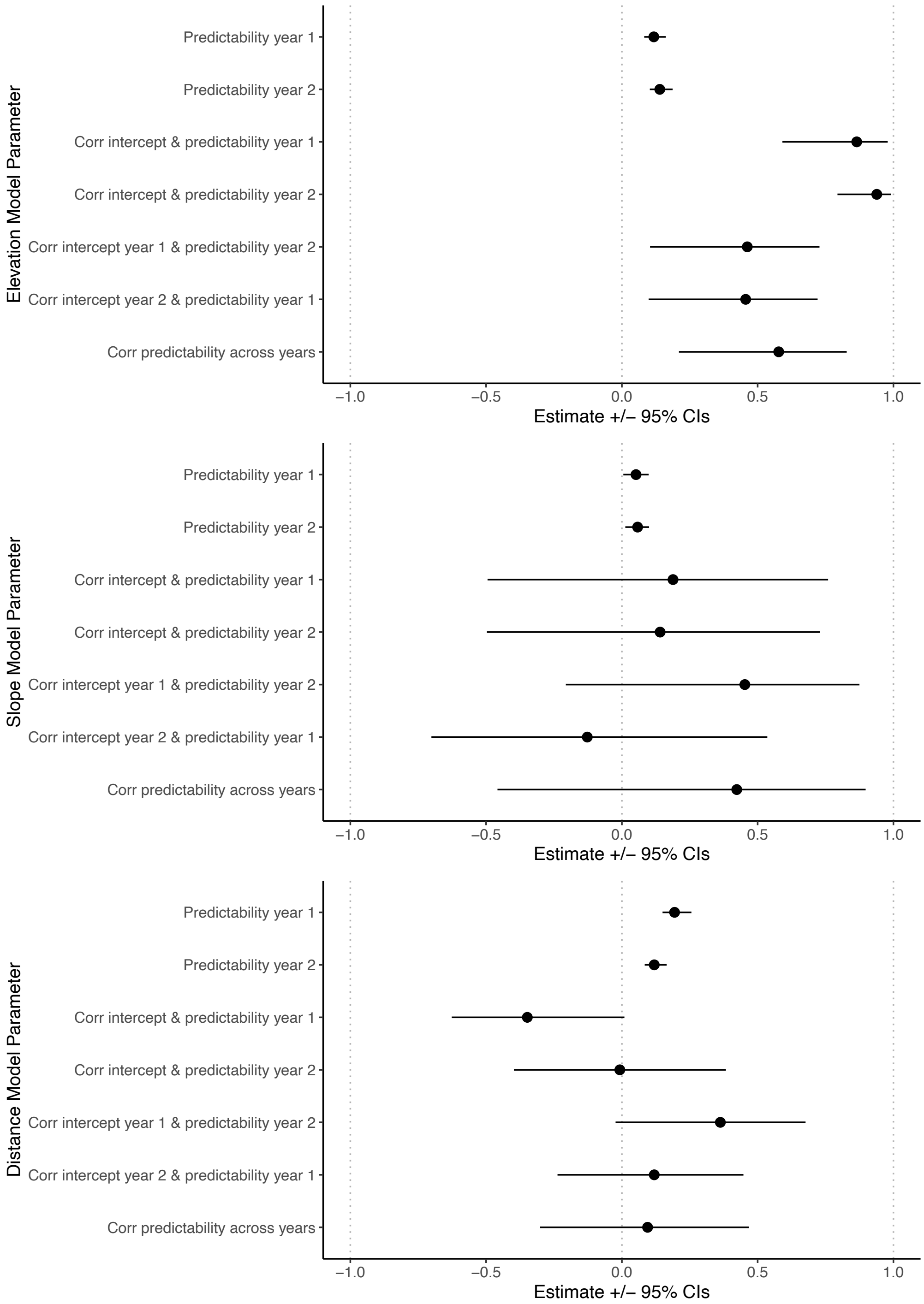
CV_p is calculated with the following equation: $CV_p = \sqrt{\exp(\omega^2_{ID}) - 1}$. Definition above and equation was provided by the guide by Hertel et al., (2020), who also recommend authors report CV_p so that it can be used across species, studies, and traits in future meta-analyses

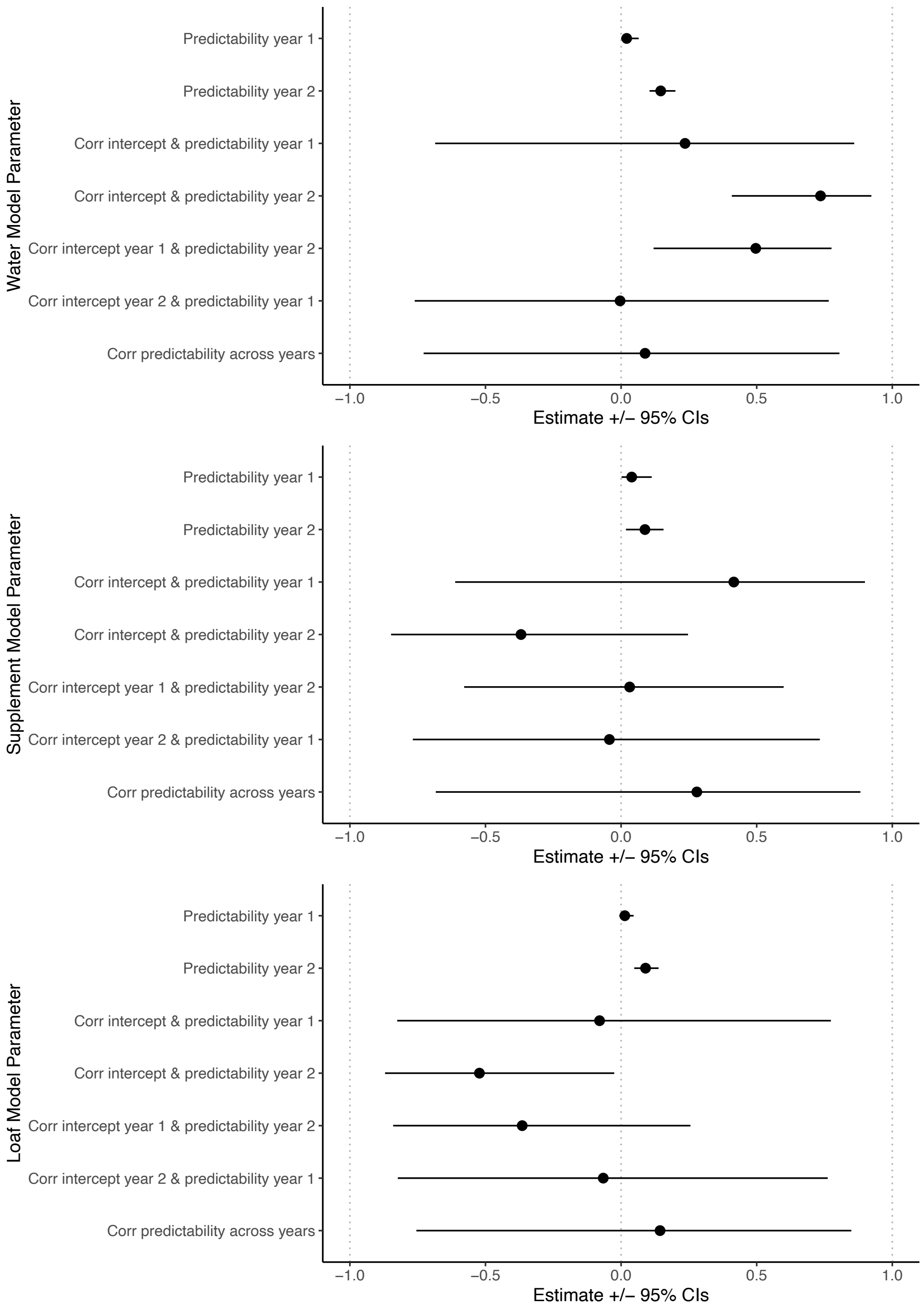
Figure 2.1.



Pasture topography in terms of elevation (meters) and size (meters) as well as where loaf sites, water sites, and supplement sites are placed in the pasture. The set up for year 1 (2021) is displayed on the left and the set up for year 2 (2022) is on the right. Between grazing seasons, a new pipe-fed water trough was added and is indicated by the red box on the right side of the figure.

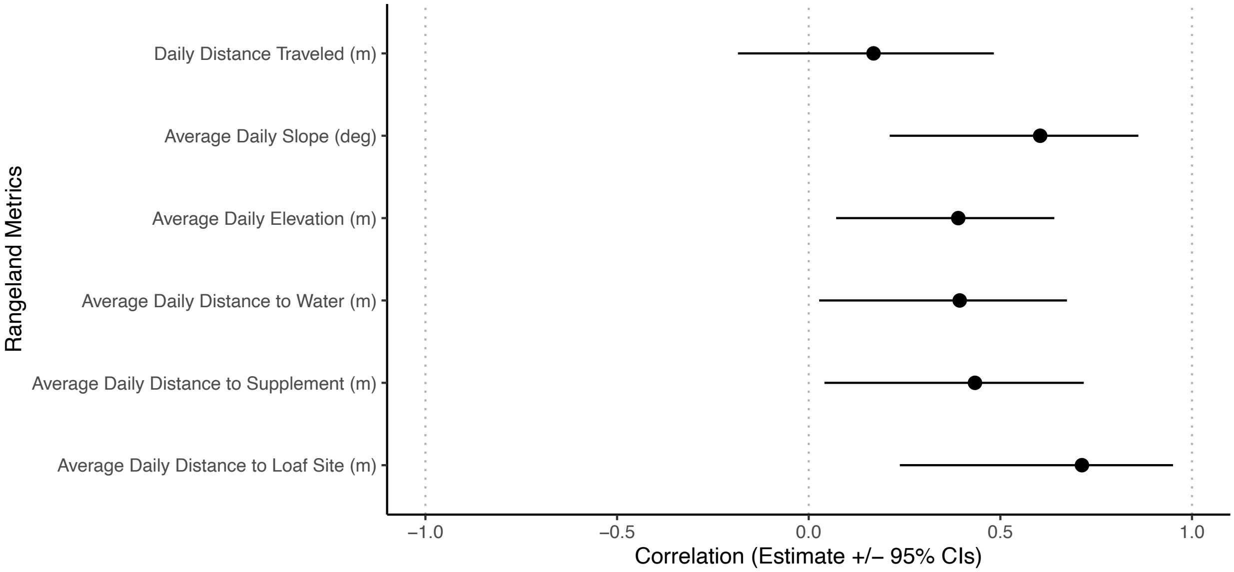
Figure 2.2 (a-f).


Elevation Model Parameter
Predictability year 1
Predictability year 2
Corr intercept & predictability year 1
Corr intercept & predictability year 2
Corr intercept year 1 & predictability year 2
Corr intercept year 2 & predictability year 1
Corr predictability across years
−1.0
−0.5
0.0
0.5
1.0
Estimate +/− 95% CIs
Slope Model Parameter
Predictability year 1
Predictability year 2
Corr intercept & predictability year 1
Corr intercept & predictability year 2
Corr intercept year 1 & predictability year 2
Corr intercept year 2 & predictability year 1
Corr predictability across years
−1.0
−0.5
0.0
0.5
1.0
Estimate +/− 95% CIs
Distance Model Parameter
Predictability year 1
Predictability year 2
Corr intercept & predictability year 1
Corr intercept & predictability year 2
Corr intercept year 1 & predictability year 2
Corr intercept year 2 & predictability year 1
Corr predictability across years
−1.0
−0.5
0.0
0.5
1.0
Estimate +/− 95% CIs



Estimates of within-cow variation of the six metrics of rangeland use and the correlations between within-cow variation and intercept estimates of the rangeland use metrics with corresponding 95% confidence intervals. Within-cow variability estimates are the standard deviations of sigma (error) values of the individual cows (as the random effect). Confidence intervals for correlations that do not cross the 0 line are considered significant correlations. Estimates and confidence intervals of standard deviations and correlations are obtained from samples of the posterior distribution.

Figure 2.3.



Correlation estimates of the among individual variation in cows between years and corresponding confidence intervals for the six rangeland metrics used to assess grazing distribution in this study. Correlations with confidence intervals that do not cross zero indicate consistency in individual cows between years of the corresponding rangeland use metric.

Table 3.1 Ethogram of behaviors that were continuously recorded using all-occurrence sampling.

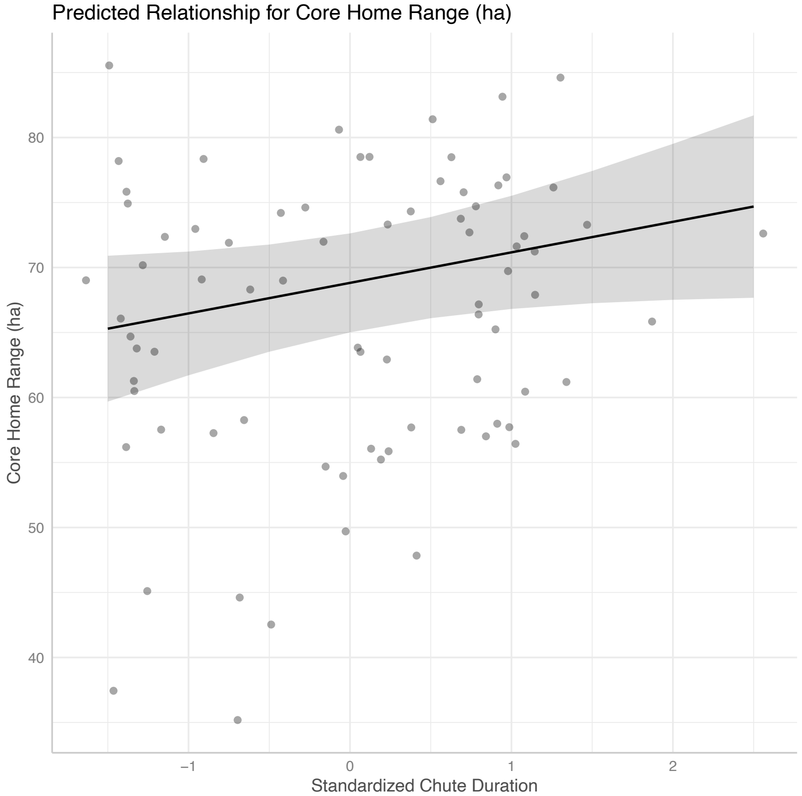
Durations (start-stop, mutually exclusive)	
Squeeze	Duration of time from when entire cow head (behind ears) crosses squeeze gate to when hindquarters (base of tail) cross squeeze exit gate.
Exit	Duration of time from when cow hindquarters cross squeeze exit gate to when cow hindquarters cross orange exit line at 2.5m.
Chute	Duration of time from when hindquarters (base of tail) crosses the cement chute gate to when hindquarters cross chute exit gate.
Handle time total	Duration of time from when handler is able to isolate the cow of interest (the cow that eventually goes through the chute) with one or two other herd mates (handler is between cow of interest and herd mates) to when cow's hindquarters cross through cement chute gate.
Latencies (start-stop, not mutually exclusive) [+±]	
Latency to supplement	Duration of time from when hindquarters (base of tail) crosses exit line to when cow takes first bite of supplement.

Table 3.2 This table displays both repeatability estimates of behaviors across repetitions of the management assay with 95% confidence intervals (CI), and spearman rank correlations with p values of latencies in the social-feed tradeoff assay and novel approach assay between years. Repeatability estimates were adjusted for year and calculated from Bayesian mixed models. We used the variance_decomposition() function in the performance package (Lüdecke et al., 2021) to calculate repeatability estimates for Bayesian models from posterior predictive distributions. Spearman rank correlations were calculated with the cor.test() function in the stats package included in R (R Core Team, 2023).

<table>
<tr><td colspan="5">Repeatability estimates and correlations for management assay behaviors and choice</td></tr>
<tr><td></td><td>Repeatability (R)</td><td colspan="3">CI Repeatability</td></tr>
<tr><td>Squeeze duration</td><td>0.76</td><td colspan="3">[0.47, 0.90]</td></tr>
<tr><td>Exit duration</td><td>0.72</td><td colspan="3">[0.37, 0.90]</td></tr>
<tr><td>Chute duration</td><td>0.69</td><td colspan="3">[0.42, 0.84]</td></tr>
<tr><td>Handle duration</td><td>0.60</td><td colspan="3">[0.30, 0.79]</td></tr>
<tr><td colspan="5">Latency to groupmates and supplement correlations between years</td></tr>
<tr><td rowspan="2"></td><td colspan="2">Social-Feed Tradeoff</td><td colspan="2">Novel</td></tr>
<tr><td>rho</td><td>p</td><td>rho</td><td>p</td></tr>
<tr><td>Latency to supplement*</td><td>0.353</td><td>0.015</td><td>0.559</td><td><0.001</td></tr>
</table>

*Spearman rank correlations and corresponding p values.

Figure 3.1



This figure shows the relationship between chute duration (standardized as it was in the model) and core 50% home range area (in hectares) for both years. This was a statistical trend in the data ($p = 0.067$), thus there is weak evidence that chute duration is related to core rangeland use area over two summer grazing seasons. The plot shows raw data points with the predicted regression line from the glmmTMB model (plotted using the ggpredict() function in the ggeffects package; Lüdecke, 2018)

Table 3.3 Results of models for each rangeland metric: elevation, slope, distance traveled, distance to water, distance to supplement sites, distance to loaf sites, adjusted kernel density estimate of 50% home range, and social network degree strength. All predictor variables except year and week were centered and standardized, thus effects on response variables represent relative effects across predictors. Models that were run with log transformed versus gaussian response variables are specified as such in the table. Estimates of log-transformed response variables in the table are on the log scale and have not been back-transformed. Results for model parameters which p<0.05 are bolded, tendencies (0.05<p<0.10) are indicated with an asterisk *.

Elevation^y				
		Elevation (log, meters)		
Predictors	*Estimates*	*std. Error*	*Statistic*	*p*
Intercept	5.691	0.031	184.740	**<0.001**
Year (2)	0.045	0.009	5.234	**<0.001**
Week	0.009	0.001	9.037	**<0.001**
Avg temp (F)*	-0.006	0.003	-1.874	0.061*
Age	0.011	0.008	1.417	0.157
Handle duration	-0.002	0.004	-0.462	0.644
Chute duration	0.014	0.006	2.392	**0.017**
Squeeze duration	-0.003	0.005	-0.675	0.500
Exit duration	-0.001	0.005	-0.233	0.816
Latency to familiar supplement	-0.006	0.005	-1.144	0.252
Latency to novel supplement	-0.005	0.006	-0.771	0.441
Slope^y				
		Slope (log, degrees)		
Predictors	*Estimates*	*std. Error*	*Statistic*	*p*
Intercept	1.878	0.041	46.245	**<0.001**
Year (2)	-0.013	0.011	-1.215	0.225
Week	0.011	0.001	8.522	**<0.001**
Avg temp (F)	-0.018	0.004	-4.166	**<0.001**
Age	-0.002	0.007	-0.339	0.735
Handle duration	-0.001	0.005	-0.262	0.793
Chute duration*	0.013	0.007	1.878	0.060*

Squeeze duration	-0.004	0.005	-0.762	0.446
Exit duration	-0.009	0.006	-1.607	0.108
Latency to familiar supplement	0.004	0.006	0.594	0.552
Latency to novel supplement	0.002	0.006	0.272	0.786

Distance Traveled

	Distance Traveled (log, meters)			
Predictors	*Estimates*	*std. Error*	*Statistic*	*p*
Intercept	8.242	0.033	253.136	**<0.001**
Year (2)	-0.110	0.009	-12.080	**<0.001**
Week	0.004	0.001	4.201	**<0.001**
Avg temp (F)	-0.028	0.004	-8.040	**<0.001**
Age	0.005	0.007	0.645	0.519
Handle duration	0.000	0.004	0.004	0.997
Chute duration	-0.003	0.006	-0.439	0.660
Squeeze duration	-0.000	0.005	-0.084	0.933
Exit duration	0.003	0.005	0.709	0.478
Latency to familiar supplement	-0.011	0.005	-2.105	**0.035**
Latency to novel supplement	0.004	0.006	0.707	0.479

Distance to Supplement[y]

	Distance to Supplement (gaussian, meters)			
Predictors	*Estimates*	*std. Error*	*Statistic*	*p*
Intercept	1070.951	54.981	19.478	**<0.001**
Year (2)	-150.948	14.728	-10.249	**<0.001**
Week	-14.178	1.806	-7.849	**<0.001**
Avg temp (F)	2.006	6.074	0.330	0.741
Age*	-19.110	10.853	-1.761	0.078*
Handle duration	2.982	7.049	0.423	0.672
Chute duration	-20.059	9.202	-2.180	**0.029**
Squeeze duration	8.888	7.985	1.113	0.266

Exit duration	0.258	7.635	0.034	0.973
Latency to familiar supplement	4.619	8.229	0.561	0.575
Latency to novel supplement	7.275	9.369	0.776	0.437
Distance to Water				
		Distance to Water (log, meters)		
Predictors	*Estimates*	*std. Error*	*Statistic*	*p*
Intercept	4.843	0.080	60.465	**<0.001**
Year (2)	-0.070	0.022	-3.120	**0.002**
Week	0.031	0.003	11.981	**<0.001**
Avg temp (F)	-0.066	0.009	-7.664	**<0.001**
Age	0.029	0.020	1.439	0.150
Handle duration	-0.002	0.011	-0.171	0.864
Chute duration	0.030	0.015	2.024	**0.043**
Squeeze duration	0.002	0.012	0.139	0.889
Exit duration	-0.017	0.011	-1.507	0.132
Latency to familiar supplement	-0.007	0.013	-0.547	0.585
Latency to novel supplement	-0.007	0.016	-0.433	0.665
Distance to Loaf				
		Distance to Loaf (gaussian, meters)		
Predictors	*Estimates*	*std. Error*	*Statistic*	*p*
Intercept	130.268	11.452	11.376	**<0.001**
Year (2)	-5.800	2.931	-1.979	**0.048**
Week	0.005	0.379	0.012	0.990
Avg temp (F)	0.060	1.259	0.047	0.962
Age	-3.958	1.727	-2.291	**0.022**
Handle duration	-0.798	1.385	-0.576	0.565
Chute duration	0.016	1.623	0.010	0.992
Squeeze duration*	-2.691	1.514	-1.777	0.076*

Exit duration	-1.002	1.418	-0.707	0.480
Latency to familiar supplement	0.101	1.554	0.065	0.948
Latency to novel supplement	-1.541	1.600	-0.963	0.336
AKDE50				
	Area of 50% home range (gaussian, hectares)			
Predictors	*Estimates*	*std. Error*	*Statistic*	*p*
Intercept	73.213	4.368	16.760	**<0.001**
Year (2)*	-4.402	2.651	-1.660	0.097*
Age	-0.278	1.235	-0.225	0.822
Handle duration	-0.555	1.106	-0.502	0.616
Chute duration*	2.349	1.281	1.833	0.067*
Squeeze duration	-1.924	1.227	-1.568	0.117
Exit duration	0.870	1.191	0.730	0.465
Latency to familiar supplement	-0.137	1.257	-0.109	0.913
Latency to novel supplement	1.361	1.228	1.108	0.268
Social Network Strength				
	SN Strength (gaussian)			
Predictors	*Estimates*	*std. Error*	*Statistic*	*p*
Intercept	1.591	0.091	17.480	**<0.001**
Year (2)*	-0.106	0.054	-1.948	0.051*
Age	-0.025	0.029	-0.886	0.376
Handle duration	-0.013	0.024	-0.552	0.581
Chute duration	0.006	0.029	0.200	0.842
Squeeze duration*	-0.046	0.027	-1.671	0.095*
Exit duration	0.006	0.026	0.212	0.832
Latency to familiar supplement	-0.012	0.027	-0.450	0.653
Latency to novel supplement	0.040	0.027	1.476	0.140

[y] Models were run with dispformula = ~ year to account for heteroscedasticity in residuals.