

DOMINANCE AND COMPETITION: A GIVING-UP DENSITY ANALYSIS OF
RANK-BASED FORAGING DECISIONS OF SMALL GROUPS OF CONFINED
BISON (*BISON BISON*)

By
Marin Loncar

A thesis submitted in partial fulfillment of the degree of Master of Science in Forestry at
Lakehead University.

January 4, 2023

ABSTRACT

Socially foraging animals such as bison (*Bison bison*) modify their foraging behaviour based on social status and food availability to maximize individual fitness. Winter feeding trials were performed on juvenile bison at Stanley Hill Bison Farm in Kakabeka Falls, ON, using a giving-up density (GUD) framework to record the densities of a resource at which bison of various rank would cease foraging. Bison were provided with two food sources, abundant lower-quality hay and limited higher-quality oats mixed with blocks of wood in feeding trays. Time spent foraging from the high-quality trays by each bison, as well as all instances of voluntary quitting and involuntary abandonments of patches, were recorded and compared to the density of food remaining in the trays at the end of the trials. Rank was negatively related to GUDs, with high-ranked bison ceasing foraging at the lowest GUDs. Dominants prematurely abandon their own trays in favour of subordinates. However, lower-ranked bison forage for a shorter time from the oats and cease foraging altogether at higher GUDs to exploit lower-quality hay, likely to escape competition as the costs of foraging from the oats increased. Males may also have a lower GUD than females. That high- and low-ranked captive bison use different strategies of foraging in confined environments supports the widely acknowledged theory that social rank has a large effect on foraging behaviour and energetic intake, and the results of the trials quantify this through difference. This study highlights the existence of two feedback loops: (1) a positive loop where increased foraging efficiency reinforces rank for high-ranked bison, and (2) a negative loop whereby low-ranked bison are forced to forage inefficiently and are thus ever more disadvantaged against competition from higher-ranked bison.

CONTENTS

ABSTRACT	ii
CONTENTS	iii
TABLES	v
FIGURES	vi
ACKNOWLEDGEMENTS	vii
CHAPTER 1: A REVIEW OF BISON FORAGING BEHAVIOUR AND SOCIAL STRUCTURE	1
Bison foraging ecology	1
The time-minimizing foraging strategy	3
Social hierarchies in bison	4
A bison's rank and foraging behaviour	6
This study	8
LITERATURE CITED	10
CHAPTER 2: A GIVING-UP DENSITY ANALYSIS OF THE EFFECT OF SOCIAL RANK ON FORAGING BY CONFINED BISON	13
METHODS	16
Study Area	16
Feeding Trials	16
Data Collection	18
Data Analysis	19
RESULTS	21
DISCUSSION	27
Social rank, GUDs, time spent foraging and the perception of missed opportunity costs	27
The effect of sex	29
Feedback loops associated with dominance	33
Predicted GUDs compared to directly measured GUDs	34
The costs of competition	36
LITERATURE CITED	39
CHAPTER 3: A GAME-THEORETICAL ANALYSIS OF FORAGING DECISIONS BY CONFINED BISON	43
MODEL	46

RESULTS	49
DISCUSSION	53
LITERATURE CITED	55
CHAPTER 4: APPLICATIONS AND CONCLUSIONS	56
LITERATURE CITED	61

TABLES

Table	Page
1. Model comparisons of log transformed GUD for instances of voluntary quitting and involuntary displacements.	20
2. Results for model comparisons of log transformed GUD for instances of voluntary quitting and involuntary displacements.	23
3. Payoff matrix for interactions between bison during feeding trials.	49
4. Payoff matrix for interactions between bison during feeding trials at GUD=1000.	50

FIGURES

Figure	Page
1. Study design of the feeding trial.	18
2. Amount of oats remaining in a tray (GUD) plotted against patch occupancy time for individuals (N = 49) in enclosures separated by sex.	22
3. Mean predicted GUD (g) for high-, mid-, and low-ranked male and female bison.	24
4. Instances of patch abandonments for A) high-, B) mid-, C) low-ranking males and females, represented as the predicted GUD versus the proportion of the feeding trial length.	25
5. Average proportion of time spent foraging from feeding trays by males and female of high, medium and low rank versus total length of feeding trial.	26
6. Predicted average intake rates of oats by sex and rank class across feeding time among all feeding trials.	33
7. Average curve of GUDs (both voluntary quitting and involuntary displacements) for individuals of high, medium and low rank against the proportion of a feeding trial.	37
8. Potential payoffs for a dominant ($i = 1$) and submissive ($i = 2$) in a 2-player game as oat trays are depleted and GUDs are reduced.	51
9. Payoffs for the ESS as a function of GUD in a 3-player game among bison of high ($i = 1$), medium ($i = 2$) and low rank ($i = 3$).	53

ACKNOWLEDGEMENTS

I thank Tim and Ashley Janssens, owners of Stanley Hill Bison farm in Kakabeka Falls, ON for allowing me generous use of their animals and property and continued support for my research from my undergraduate thesis until now. I also thank Lakehead University and the Natural Science and Engineering Research Council (NSERC) for providing the funding necessary to complete my work through a teaching assistantship and the Alexander Graham Bell Canada Graduate Scholarship.

Acknowledgements are due as well to members of my committee, Dr. Adam Algar of Lakehead University, and Christine O'Reilly of the Ontario Ministry of Agriculture, Food, and Rural Affairs (OMAFRA), whose helpful comments and feedback contributed very much to this thesis. I also thank Dr. Quinn Webber of the University of Guelph who served as external examiner for contributing greatly to the final quality of the thesis. Great thanks are also due to my supervisor, Dr. Brian McLaren, who not only provided me a very interesting topic, but supported every step of the journey and was always happy to help. Finally, I thank my friends and family for their continuous support.

CHAPTER 1: A REVIEW OF BISON FORAGING BEHAVIOUR AND SOCIAL STRUCTURE

Bison foraging ecology

Bison (*Bison bison*) were once widespread across North America, with population estimates as high as 60 million at the beginning of the 19th century (Shaw 1995). By 1889, only 456 individuals remained, following a sharp decline of millions of bison over just a few years (Hornaday 1899). Bison still occur predominantly in small, geographically isolated populations in parks and preserves, on lands reserved for Indigenous people, or in captive herds on private property managed for commercial slaughter (Meagher 1986). Ninety-five percent of North America's estimated 500,000 bison are managed on private lands (Freese et al. 2007). Ironically, most research on the foraging behaviour of bison has been done on free-ranging herds, though the conditions under which members of a captive herd compete differ from those in the wild. The generally more limited availability of high-quality food and its higher degree of patchiness in a zoo, farm or ranch setting affect the distribution of resources among members of a captive bison herd (Robitaille and Prescott 1993). In contrast, natural forage conditions are more uniform over larger areas, such that all members of a free-ranging herd forage from a seemingly unlimited source. In the latter case, the result is an ability of bison to separate into distanced, small groups in a fission-fusion dynamic that reduces intraspecific competition, social stresses, and the risk of predation (Fortin et al. 2009). In an enclosed farm setting, less separation between individuals should result in higher competition. This statement sets the context for this thesis.

Socially foraging animals modify their behaviour based on their position in a social hierarchy to optimize foraging costs and energetic intake (Rands et al. 2006). Ungulates use information on social rank to modify their movements and maximize access to higher-quality patches (Webber et al. 2020). Patches of high quality always co-occur with low-quality patches, i.e., those with lower energetic return per time invested foraging (Wallis De Vries 1996). Bison are distinct from other ungulates in that they exhibit a ‘time-minimizing’ foraging strategy, favouring strategies of plant selection and interpatch movement that maximize short-term energy intake and minimize foraging time (Fortin et al. 2002). In the social herd context, then, a bison must allocate its time between high- and low-quality patches, as well as move between them, in a manner that maximizes energetic intake, as modelled for the general case by Olsson (2006); the same individual must also minimize not only costs of interpatch movement, but also interference competition for the patches, related to missed opportunity costs, and the costs of managing predation risk.

Aggregation (herd behaviour) during feeding occurs in many free-ranging animals, including the gregarious bison (Fryxell 1991). A theory for the occurrence of aggregation describes the benefit of reduced risk predation risk, achieved by increased vigilance (‘many eyes’) and individual risk dilution (Krause and Ruxton 2002). Predation risk should pose a lesser cost for bison (therefore a lesser effect on their foraging decisions) than for other large ungulate species, as bison experience a relatively lower predation risk. Their primary predator, the wolf (*Canis lupus*), prefers other prey species, including white-tailed deer (*Odocoileus virginianus*), elk (*Cervus canadensis*), and moose (*Alces alces*), partly because these species are easier to kill (Smith et al.

2000). Due to the size and fighting ability of an adult bison, predator kills are predominantly on vulnerable individuals, either young calves or older individuals in poorer condition. Nevertheless, Fortin et al. (2009) described managing predation risk as the strongest driver of habitat selection in free-ranging bison in Prince Albert National Park, Saskatchewan, where smaller groups of bison preferred areas with higher cover and lower predation risk. Smaller group sizes in farmed elk (40-50% lower mass compared to bison) were also hypothesized to experience higher perceived predation costs and consequently lower foraging effort, despite the absence of predators on the farm (Moreira and McLaren 2019). However, in captive herds of the larger bison, relatively free from predation risk, individuals choosing patches based on security should find relatively few gains.

The time-minimizing foraging strategy

While an energy maximizing species will attempt to maximize total energy input, a time minimizer will stop foraging once its energy requirements have been met (Hixon 1982). A major downside of this strategy is that, with competition, foraging effort is expected to increase, reducing the marginal value of feeding more so than if foraging effort remained constant (Mitchell 1990). A second downside of the time-minimizing strategy is that when viewed in a larger time frame, foraging decisions that maximize short-term gains may suffer the consequence of reduced long-term gains if bison focus on forage with higher instantaneous gains as opposed to total gains (Courant and Fortin 2010). Benefits promoting the time-minimizing strategy observed in bison must thus be hypothesized. Ideas have included that shorter foraging times allow for more (1) relief from insects during the summer, (2) more time to thermoregulate during temperature

extremes (Melton et al. 1989), (3) reduced predation risk, and (4) more time to obtain and maintain social rank, which has a direct positive impact on fitness (Bergman et al. 2001), and (5) more time for rumination (Debeffe et al. 2017). The fourth idea is of particular interest because predation risk for bison is relatively low, and because the time-minimizing strategy is exhibited by bison year-round, while relief from insects and extreme heat should not be factors in winter. Since most instances of aggression outside of the rut occur during foraging (McHugh 1958), a time-minimizing strategy may allow not only higher energetic intake, but also reinforcement of social rank while feeding.

Social hierarchies in bison

A significant factor in foraging decisions made by an individual bison related to how it will maximize its energy intake per unit of time is its position within the dominance hierarchy of the herd. Social ungulates are known to have well-defined, stable dominance hierarchies and bison are no exception (mountain goats: Côté 2000, Alpine ibex: Willis and Neuhaus 2010, guanaco: Correa et al. 2013, cows: Sarova et al. 2013, giraffes: Horova et al. 2015). Social status correlates with differences in use of time and space, particularly when resources are limited (Robitaille and Prescott 1993, Ungerfeld et al. 2014). Individual bison of higher rank benefit by gaining first access to high-quality food, making it possible to meet their energy demands in less time than lower-ranking individuals that may have to forage less efficiently from lower-quality food sources. The dominance hierarchy in both females and males is linear, with high directional consistency and defined, unidirectional relationships (Rutberg 1983, Roden et al. 2005). Ranks are established early on and rarely challenged successfully. In males, rank is correlated with age and weight, heavier and older individuals occupying higher

social positions (Roden et al. 2005), with dominance largely determined by fighting ability that generally increases with size and experience (Wolff 1998). Male bison frequently confront each other with physical combat and other displays to establish and maintain their ranks (Roden et al. 2005). Polygynous dominant males are rewarded by more choice in mates and higher ability to defend them, assisted by their increased fat reserves, also associated with rank, which serve to increase reproductive output, as well as fighting ability. In females, rank is based mostly on age, older individuals occupying higher social positions. Females experience fewer challenges and rank reversals because fitness is less affected by rank than is the case for males. A female is likely to reproduce regardless of rank, whereas rank is related to mating success in males (King et al. 2019).

Thus, the primary advantage of maintaining a higher rank is increased fitness (Rutberg 1986). What are the costs? For male bison, it is stress owing to maintaining higher levels of aggression than subordinates ('stress of domination'); those of higher rank are forced to defend their social position and breeding advantage against lower-ranked challengers, while for the most part only the very highest-ranking males find and defend a mate (King et al. 2019). For female bison, the cost is stress related to risk of subordination ('stress of subordination'), where lower-ranked females experience lower foraging efficiency, leading to lower body condition and fat reserves (Vervaecke et al. 2005), which may negatively impact reproductive rates and offspring (King et al. 2019). These sex differences in fitness payoffs leads to major differences in frequency of aggression and challenges to status. What is less understood for males is what happens outside the breeding season. If males suffer the same stress of subordination as females throughout the year, then costs associated with foraging should be equal, as both sexes

would suppress the lowest ranks through interference competition manifested by acts of aggression (King et al. 2019). However, if males suffer the same stress of domination outside the breeding season, then foraging costs should be higher and aggression more frequent than in females throughout the year.

A bison's rank and foraging behaviour

Competition for resources is a major driver of foraging choices, including habitat and patch selection, and movement between habitats and patches. As a bison forages, it is under the pressure of exploitative and interference competition. Exploitative competition occurs when individuals compete for a diminishing resource, beginning when each individual attempts to maximize its own share of the resource; exploitative competition increases foraging performance over all individuals but negatively ultimately affects a population through the removal of shared resources (Berger-Tal et al. 2015). Interference competition occurs when individuals directly interfere with each other's foraging through acts of aggression (Rands et al 2006). Yet, each individual must adapt its behaviour based on its position within a dominance hierarchy as part of maximizing its fitness by foraging at the maximum instantaneous rate (Makin and Kotler 2019, Maynard Smith and Parker 1976). As any individual forages, it will encounter neighbours and be faced with a choice of whether to compete (contest a resource) or cooperate by means of group foraging. Contests over resources are always asymmetrical, and payoff asymmetry means that one individual may have more to gain in a competition. A subordinate individual will suffer greater costs if it chooses to challenge a dominant and loses than if it simply accepts defeat and moves on to a less productive patch (Parker 1974). Payoff asymmetry also occurs in the absence of asymmetry in

social rank when patches differ in the quality or quantity of a food. When one individual is foraging from a highly productive patch and another from a patch of lower quality, the net cost of contesting the higher-quality patch may be recognized as less than the potential gains of foraging from the higher-quality patch depending on the cost-benefit trade-off.

Thus, interference competition for a resource is more likely when a smaller difference in resource holding potential exists, i.e., fighting exists because larger differences are more easily recognized (Enquist and Leimer 1983). A subordinate individual is more likely to avoid confrontation when large differences are recognized. In addition, greater differences in rank may correspond with decreased interactions because the subordinate may avoid interacting with dominant individuals in favour of interacting with those nearer to them on a social hierarchy. Thus, an individual must analyze not only the value of a food patch, but also the potential risk (cost) of competing with another individual for that patch. An individual should choose to compete if they perceive the risk is worth the benefit. However, it is not wise for an individual with a significantly lower resource holding potential than a neighbour to compete, particularly for patches of lower quality where gains are reduced.

Therefore, an individual's position within the dominance hierarchy is a significant factor in determining how it interacts with the pasture and its conspecifics. For example, social status has recently been shown to impact the behaviour of male bison and the strategies they use to maximize fitness in relation to breeding success. Individuals, depending on their position within the herd, will engage in the most effective mating tactic through trade-offs between time and energy invested in

dominance interactions (Wyman et al. 2021). Dominant individuals are better adapted to compete for the most desirable females, and thus invest heavily in competing early for first pick in mates. For less competitive subordinates, engaging in a fight for females is risky in terms of serious injury or risk of injury. The emergence of separate strategies of competing for high-quality patches versus accepting lower-quality patches logically occurs, where individuals, based on their fighting abilities have better strategies for maximizing fitness and breeding success.

This study

In forage-limited environments, individuals must make trade-offs between time and energy invested in competing for food patches based on their competitive ability. The strength of dominance effects on different strategies of foraging in a small farm environment has not yet been quantified and will be the focal point of my thesis. This study was conducted in winter, when confined bison in their second year were provided mostly hay (lower energetic return) with small amounts of oats as a food supplement (much higher energetic return), a simplified representation of interpatch quality differences encountered in more natural settings. Dominant individuals are expected to invest more energy into competing for the high-quality food (oats provided in trays), as opposed to lower-ranked individuals that will avoid conflict and instead choose among the lower-quality sites (areas in the enclosure with hay). However, the degree to which the lower ranks choose lower-quality sites will not be equal throughout proposed feeding trials. When resources are plentiful and energy returns are high, individuals are expected to compete to a greater degree because the energy return is higher relative to the costs. Feeding behaviour is likely to change based on the difference in return between the

high- and low-quality patches as food is consumed, and the lowest-ranked individuals should be the first to cease competing due to their lower competitive ability. A sex difference is also proposed, where larger males that will compete for mating when they leave the subadult stage will have likely gained their advantage in part through expressing dominance in foraging.

In summary, it is hypothesized that small-scale forage patch heterogeneity should be a strong driver of movement and patch selection in confined bison herds. It is also hypothesized that individual differences such as rank and sex will affect how individuals interact with patches of various quality. In chapter 2, how feeding behaviour differs for individuals of high, medium, and low ranks will be investigated using artificial feeding trials and a 'giving-up density' (GUD) framework to quantify and compare an individual's social rank against the point at which it ceases foraging. Whether an individual ceases foraging voluntarily (quits feeding) or involuntarily (is displaced by a competitor) will be recorded, and how much time it invests in foraging from high-quality patches. Quitting rates and displacements will be compared for males and females. In chapter 3, bison decision-making will be described in the context of game theory to explore why the observed solutions occur. The significance of this approach is that it can describe differences in feeding tray utilization and quitting rates to quantify how foraging decisions differ among social ranks and sexes when a small group of competing bison is provided high- and low-quality patches.

LITERATURE CITED

- Bergman, C.M., Fryxell, J.M., Gates, C.C. and Fortin, D. 2001. Ungulate foraging strategies: energy maximizing or time minimizing? *Journal of Animal Ecology* 70:289-300.
- Berger-Tal, O., Embar, K., Kotler, B.P. and Saltz, D. 2015. Everybody loses: intraspecific competition induces tragedy of the commons in Allenby's gerbils. *Ecology* 96(1):54-61.
- Correa, L.A., Zapata, B., Samaniego, H. and Soto-Gamboa, M. 2013. Social structure in a family group of Guanaco (*Lama guanicoe*, Ungulate): is female hierarchy based on 'prior attributes' or 'social dynamics'? *Behavioural Processes* 98:92-97.
- Côté, S.D. 2000. Dominance hierarchies in female mountain goats: stability, aggressiveness and determinants of rank. *Behaviour* 137:1541-1566.
- Courant, S. and Fortin, D. 2010. Foraging decisions of bison for rapid gains can explain the relative risk to neighbouring plants in complex swards. *Ecology* 91(6):1841-1849.
- Debeffe, L., Rivrud, I.M., Brekkum, O., Meisingset, E.L. and Mysterud, A. 2017. Implications of the forage maturation hypothesis for activity of partially migratory male and female deer. *Ecosphere* 8(12):e02050.
- Enquist, M. and Leimer, O. 1983. Evolution of fighting behaviour: decision rules and assessment of relative strength. *Journal of Theoretical Biology* 102:387-410
- Fortin, D., Fryxell, J.M. and Pilote, R. 2002. The temporal scale of foraging decisions in bison. *Ecology* 83(4):970-982.
- Fortin, D., Fortin, M.E., Beyer, H.L., Duchesne, T., Courant, S. and Dancose, K. 2009. Group-size-mediated habitat selection and group fusion-fission dynamics of bison under predation risk. *Ecology* 90:2480-2490.
- Freese, C.H., Aune, K.E., Boyd, D.P., Derr, S.C.F., Gates, C.C., Gogan, P.J.P., Grassel, S.M., Halbert, N.D., Kunkel, K. and Redford, K.H. 2007. Second chance for the plains bison. *Biological Conservation* 136(2):175-184.
- Fryxell, J.M. 1991. Forage quality and aggregation by large herbivores. *American Naturalist* 138(2):478-498.
- Hixon, M.A. 1982. Energy maximizers and time minimizers: theory and reality. *American Naturalist* 119(4):596-599.
- Hornaday, W.T. 1889. The extermination of the American Bison. Report of the National Museum 1886-1987: 366-548.

- Horova, E., Brandlova, K. and Glonekova, M. 2015. The first description of dominance hierarchy in captive giraffe: not loose and egalitarian, but clear and linear. *PLoS ONE* 10(5):e0124570.
- King, K.C., Caven, A.J., Leung, K.G., Ranglack, D.H. and Arcilla, N. 2019. High society: behavioral patterns as a feedback loop to social structure in plains bison (*Bison bison bison*). *Mammal Research* 64:365-376.
- Krause, J. and Ruxton, G.D. 2002. *Living in groups*. Oxford University Press, New York. 210 pp.
- Makin, D.F. and Kotler, B.P. 2019. Does intraspecific competition among Allenby's gerbils lead to an ideal free distribution across foraging patches? *Behavioural Processes* 167:1-8.
- Maynard Smith, J. and Parker, G.A. 1976. The logic of asymmetrical contests. *Animal Behaviour* 24:159-175.
- McHugh, T. 1958. Social behaviour of the American buffalo (*Bison bison bison*). *Scientific Contributions of the New York Zoological Society* 43(1):1-40.
- Meagher, M. 1986. *Bison bison*. *Mammalian Species* 266:1-8.
- Melton, D.A., Larter, N.C., Gates, C.C. and Virgl, J.A. 1989. The influence of rut and environmental factors on the behaviour of wood bison. *Acta Theriologica* 24(12):179-193.
- Mitchell, W.A., Abramsky, Z.A., Kotler, B.P., Pinshow, B. and Brown, J. 1990. The effect of competition on foraging activity in desert rodents: theory and experiments. *Ecology* 71(3):844-854.
- Moreira, A. and McLaren, B. 2019. Monitoring the effects of feeding in groups: behavioural trials of farmed elk in winter. *Applied Animal Behaviour Science* 212:66-73.
- Olsson, O. 2006. Bayesian foraging with only two patch types. *Oikos* 112(2):285-297.
- Parker, G.A. 1974. Assessment strategy and evolution of fighting behaviour. *Journal of Theoretical Biology* 47:223-243.
- Rands, S.A., Pettifor, R.A., Rowcliffe, J.M. and Cowlshaw, G. 2006. Social foraging and dominance relationships: the effect of socially mediated interference. *Behavioral Ecology and Sociobiology* 60:572-581.
- Robitaille, J.F. and Prescott, J. 1993. Use of space and activity budgets in relation to age and social status in a captive herd of American bison, *Bison bison*. *Zoo Biology* 12:367-379.

- Roden, C., Vervaecke, H. and Elsacker, L.V. 2005. Dominance, age, and weight in American bison males (*Bison bison*) during non-rut in semi-natural conditions. *Applied Animal Behavior Science* 92:169-177.
- Rutberg, A.T. 1983. Factors influencing dominance status in American bison cows (*Bison bison*). *Zeitschrift für Tierpsychologie* 63:206-212
- Rutberg, A.T. 1986. Dominance and its fitness consequences in American bison cows. *Behaviour* 96(1):62-91.
- Sarova, R., Spinka, M., Stehulova, I., Caecero, F., Simeckova, M. and Kotrba, R. 2013. Pay respect to the elders: age, more than body mass, determines dominance in female beef cattle. *Animal Behaviour* 86:1315:1323.
- Shaw, J.H. 1995. How many bison originally populated western rangelands? *Rangelands* 17(5):148-150.
- Smith, D.W., Mech, L.D., Meagher, M., Clark, W.E., Jaffe, R., Philips, M.K. and Mack, J.A. 2000. Wolf-bison interactions in Yellowstone National Park. *Journal of Mammalogy* 81(4):1128-1135.
- Ungerfeld, R., Cajarville, C., Rosas, M.I. and Repetto, J.L. 2014. Time budget differences of high- and low-social rank grazing dairy cows. *New Zealand Journal of Agricultural Research* 57(2):122-127.
- Vervaecke, H., Roden, C. and De Vries, H. 2005. Dominance, fatness, and fitness in female American bison, *Bison bison*. *Animal Behaviour* 70:763-770.
- Wallis De Vries, M.F. 1996. Effects of resource distribution patterns on ungulate foraging behaviour: a modelling approach. *Forest Ecology and Management* 88:166-167.
- Webber, Q.M.R., Laforge, M.P., Bonar, M., Robitaille, A.L., Hart, C., Zabihi-Seissan, S. and Vander Wal, E. 2020. The ecology of individual differences empirically applied to space-use and movement tactics. *The American Naturalist* 196(1):1-15.
- Willisch, C.S. and Neuhaus, P. 2010. Social dominance and conflict reduction in rutting male Alpine ibex, *Capra ibex*. *Behavioral Ecology* 21:372-380.
- Wolff, J.O. 1998. Breeding strategy, mate choice, and reproductive success in American bison. *Oikos* 83(3):529-544.
- Wyman, M.T., Pinter-Wollman, N. and Mooring, M.S. 2021. Trade-offs between fighting and breeding: a social network analysis of bison male interactions. *Journal of Mammalogy* 102(2):502-519.

CHAPTER 2: A GIVING-UP DENSITY ANALYSIS OF THE EFFECT OF SOCIAL RANK ON FORAGING BY CONFINED BISON

Optimal foraging theory is used to predict the behaviour of animals while they forage. Individuals optimally utilizing time or energy engage in feeding activities for as long as the resulting gain in energy spent per unit food exceeds the loss (MacArthur & Pianka 1966). Any further continuation of the activity would result in a greater loss than if that activity was halted. Because food is often found in unequal amounts in different patches, an individual must decide how much time or effort to devote to each patch (Charnov 1976). This framework views patches as depletable food sources that foragers exploit differentially in order to maximize fitness. Thus, each individual must decide which patch will be visited when, and at what point the current patch should be abandoned (Davis et al. 2022). Experimental food giving-up densities (GUDs), a method that measures the food remaining in a patch after a forager leaves it, make for an attractive exploration of foraging ecology because GUDs make it possible to predict and quantitatively assess the foraging decisions made by individual animals (Bedoya-Perez et al. 2013). A forager behaving optimally should have a GUD that corresponds to a harvest rate that balances metabolic costs, predation costs, and missed opportunity costs, i.e., costs of not engaging in alternative activities (Brown 1988). When the harvest rate decreases in a patch as food is consumed, the forager should quit the patch when the benefits of harvest no longer outweigh the costs. The following equation is used to describe this phenomenon:

$$\text{GUD} = C + P + \text{MOC} \quad (\text{Equation 1})$$

Where GUD is the rate at which an individual quits harvesting, C is the metabolic cost of foraging, P is the cost of managing predation risk, and MOC represents the missed opportunity cost incurred by the forager when it chooses to feed in a particular patch. Each of these variables represents units of energy. The intensity of interference behaviour, I, incurs additional costs dependent on social rank if dominant individuals interfere with subordinates access to patches (Kotler & Brown 1988). The equation to describe social foragers in herds thus becomes:

$$\text{GUD} = C(I) + P + \text{MOC} \quad (\text{Equation 2})$$

An assumption in GUD experiments is that a forager depletes its resource as feeding time increases, therein increasing the instantaneous costs associated with continuing feeding. It is important that diminishing return be incorporated into the experimental framework for GUDs, and this is usually done by mixing an inert substrate with the food. As animals feed, the ratio of substrate to food increases, making it more costly to find and consume the remaining food. Individual feeding behaviour depends on the density of the resource and the amount of competition for the resource (Mitchell et al. 1990). The GUD will reflect how individuals perceive total costs of foraging in a particular patch, with a higher GUD indicating that individuals experience higher total costs. In uniformly risky habitats, e.g., on a farm where the environment is controlled in terms of predation risk, food patch quality directly influences GUDs, while missed opportunity costs relate indirectly to the cost of not foraging from higher-quality patches. MOC's encompass other activities as well that may increase fitness such as grooming, maintaining social rank, and seeking thermal cover (Eccard & Liesenjohann 2014).

In this study, GUDs will be calculated in small groups of captive bison to test hypotheses associated with optimal foraging theory that differences in sex and rank between individual bison will impact the point at which it is optimal for an individual to cease foraging. GUDs will be indirectly calculated from feeding trays that emulate natural high-quality patches to quantify how social structure in two small groups of subadult bison, separated by sex, affects individual foraging behaviour. The aim is to investigate how social rank influences individual bison foraging behaviour in a captive setting when individuals are provided with two food sources of different quality using a novel approach to GUD methodology wherein GUDs are predicted from established curves of quitting rates over time. Winter feeding trials were performed on two cohorts of juvenile bison separated by sex at Stanley Hill Bison farm in Kakabeka Falls, Ontario using artificial feeding trays that mimicked natural high-quality patches and allowed the density of food within a patch at any time to be quantified and compared to foraging decisions. The objectives were to 1) quantify how social rank affects GUDs and perception of missed opportunity costs in bison, 2) define how social rank influences time spent foraging as food resources are depleted, 3) compare how GUD and time spent foraging differs between sexes, and 4) present the application of the novel approach to recording and comparing GUDs.

The predictions are as follows: that 1) higher-ranked bison will have higher GUDs overall, because they perceive lower foraging costs in the trays of subordinates, abandoning trays earlier in favour of moving to the trays of subordinates; 2) higher-ranked individuals will forage longer from the high-quality patches than their subordinate counterparts; and 3) effects of rank on GUDs and displacement from

feeding trays will be stronger in males than in females. As costs of foraging increase, it will be the most dominant and best adapted individuals that can continue to compete for the shrinking benefits of the remaining food.

METHODS

Study Area

Stanley Hill Bison is located 20 km west of Thunder Bay, Ontario. The 40-hectare property comprises of field and mixed forest in various-sized paddocks with a small stream running through the south end of the property. It is bordered to the south by Trans-Canada Highway 11/17, and secondary roads to the west, north, and east. The area is divided into six paddocks, with subadult bison (20-22 months old) separated by sex and housed in two enclosures on the east side of the property, each 150 m by 200 m in size. During winter 2021, the western paddock contained six males and the eastern seven females. Each paddock had an artificial water source to the north and hay bales randomly placed throughout. Feeding trials occurred from January 18, 2021, to March 22, 2021.

Feeding Trials

An artificial feeding method derived from an elk study by Moreira and McLaren (2019) allows for individual GUD differences in patch to be measured by providing one feeding tray per individual. A shortcoming of the GUD methodology is that it only directly quantifies the cost for the last individual to forage from each tray, while social interactions include multiple individuals competing to spend time at each tray. This issue is addressed by estimating GUDs indirectly using video recordings to estimate foraging

time for each individual and converting time to food density at the time of abandoning a tray with an estimated depletion curve. Because abandonments occur along a curve of diminishing return, more time spent by all individuals foraging from a feeding tray implies a greater amount of food harvested from it.

Two sets of feeding trials were performed consecutively on the male and female herds on every sampling day. Feeding trays, one per bison, were placed along a fence, 5 m apart and secured to a post with wire (Figure 1). Each trial was considered complete when all bison ceased foraging and all trays were removed. Feeding trays were square boxes, 45 cm in length by 45 cm in width and 33 cm tall, composed of 5 cm by 10 cm softwood lumber. A square piece of plywood on the bottom of each box was used to keep contents inside while the top was open to allow the bison access. The trays were filled with 1000 g of dry rolled oats and 20 pieces of softwood lumber (5 cm by 10 cm by 15 cm) that constituted the inert substrate. Bison were freely allowed to forage from the feeding trays, and they would frequently move between trays either after voluntarily quitting a tray or being displaced by a higher-ranked bison. If an individual left the area with the feeding trays, it was to (1) feed from lower-quality hay patches, (2) rest, or (3) interact with conspecifics that had also ceased foraging. In all cases of abandonment, to maintain a 1:1 ratio of bison in the feeding area to trays, the tray was removed from the feeding area by pulling it through a gap in the fence.



Figure 1: Study design of the feeding trial. Note the patches of hay, lower-quality forage, in the background. The feeding trays, higher-quality food source with diminishing returns for continued feeding, are filled with oats in a mixture of small blocks of wood.

Data Collection

A camera (iPhone 11) was set up on a tripod 15 m away from the feeding area and the same nearby observer verbally noted the identity and spatial position of each bison at the commencement of each trial such that the movement and activity of each individual could be tracked by video playback. Video analysis was used to measure the amount of time spent foraging at each tray by each bison, the total time spent foraging by each bison, the amount of time each tray was occupied in total, and, for each bison, a tally of all instances of quitting or displacing trays. The food remaining in all trays at the end of a trial was oven-dried at 100 °C for three hours to remove moisture from saliva and snow. Dried samples were weighed to determine the GUD for each tray at final abandonment.

Cases of aggression were noted in the video recordings. Classifying winners and losers of contests defined the dominance hierarchy, which categorized each bison into rank classes of high (top 1/3), medium (middle 1/3), or low (bottom 1/3). Winning a contest was based on Reinhardt's (1985) four categories: (1) passive withdrawal, where the loser spontaneously withdrew without interaction and the dominant individual did not further acknowledge the presence of the subordinate, (2) threatening behaviour, where the winner expressed a gesture that encouraged withdrawal, typically pointing its horns, shaking its head, or undertaking short rushes, (3) the winner physically forcing a subordinate to move away, either by butting its head or pushing against the loser with the side of its body, and (4) the winner charging and pursuing the loser past the contested feeding tray in an apparent effort to make physical contact. The individual that won all contests was deemed to have the highest rank, with the rank hierarchy followed individuals that won contests against increasingly fewer individuals, until assignment of the lowest-ranked bison, which was not victorious in any contests (Chase and Seitz 2011).

Data Analysis

GUDs were recorded across 12 feeding days and both sexes. An exponential curve of best fit was defined to predict the amount of feed (dry weight) in a feeding tray at any point based on how long the feeding tray was foraged by any individual. The curve was used to predict the GUD at any instance of patch abandonment from the patch occupancy time for each bison prior to its abandonment of the feeding area. Predicted GUD values were plotted against the proportion of the feeding trial length, defined as the relative time between the beginning and the end of the trial. Relative time, the time

spent feeding by each individual divided by the duration of each trial, was used to remove bias caused by different feeding trial length from day to day. Variation is hypothesized to arise from uncontrolled factors such as differences in time of day (ie., how long before the trial did the bison eat), weather, and snow cover.

A set of generalized linear mixed models (GLMMs) was established to best predict individual, log transformed GUDs (Table 1). Each model was run for voluntary acts of quitting and for involuntary displacements. Akaike's Information Criterion for small samples (AICc) was used to compare models with independent variables including sex (a fixed factor), rank class (a fixed factor because no changes in rank occurred through the course of the study), individual (a random factor identifying behavioural differences unique to each bison) and day (a random variable) represented potential differences in the outcome of trials over the season or by day according to weather. Statistical analysis was done using IBM SPSS.

Table 1. Model comparisons of log transformed GUD for instances of voluntary quitting and involuntary displacements.

Model	Variables
1	Rank class, day, individual
2	Sex, day, individual
3	Rank class, sex, day, individual
4	Rank class
5	Sex
6	Rank class, Sex

Rank class and sex were compared to the time spent utilizing oat trays. Total time spent foraging from oat trays by each bison was divided by the total length of each respective feeding trial to calculate the proportion of time spent foraging. Proportion of feeding trial was used as opposed to simply time to remove bias from feeding trials

varying in length from day to day. A univariate general linear model was created in IBM SPSS with proportion of time spent foraging as the dependant variable and rank class as the independent variable.

RESULTS

The curve defining the relationship between GUD and patch occupancy time for all individuals measured across the 12 trials was best fit to an exponential with the equation $y = 1000 e^{-0.127x}$ (Figure 2). Cases of displacement of subordinates ($N = 550$) led more often to premature patch abandonment than voluntary quitting ($N = 430$). For instances of voluntary quitting models including rank class and sex are equivocal, indicating that there may be effects, but the evidence is not conclusive. For GUD's associated with involuntary displacements there is equivocal support for a model that distinguishes displacement by sex and rank class ($w = 0.514$) and one that predicts GUDs only by rank class ($w = 0.474$). In all cases, high- and medium-ranked bison are displaced at lower GUDs than low-ranked bison. There is support for the effect being stronger in males with lower GUD displacements occurring than for females. The random effects of day and individual were present in all top models, indicating that random variables had some effect on the GUD. For both voluntary and involuntary quitting, rank has a negative relationship with GUD, i.e., high-ranked bison had the lowest GUDs and low-ranked bison had higher GUDs.

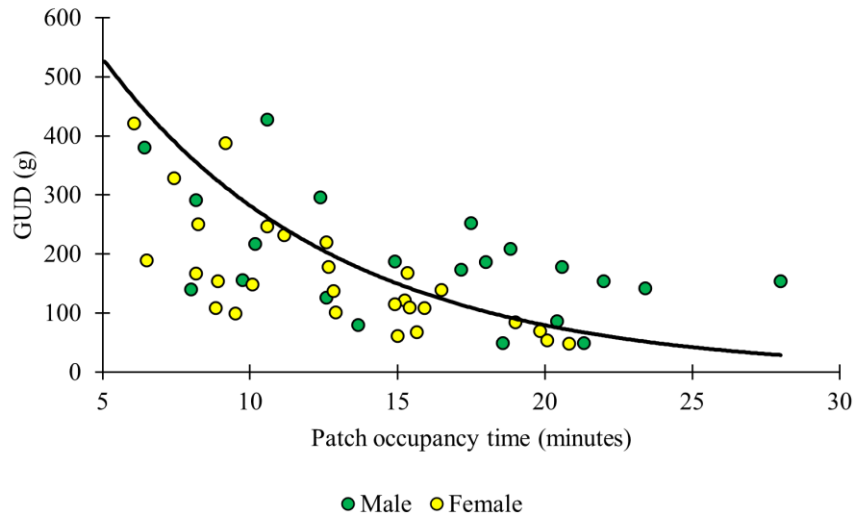


Figure 2: Giving-up density (GUD) plotted against patch occupancy time for individuals ($N = 49$) in enclosures separated by sex. Curve of best fit ($y = 1000 e^{-0.127x}$) represents rate of patch depletion and predicts the average GUD at any patch occupancy time. $R^2 = .3516$.

Table 2. Results for model comparisons of log transformed GUD for instances of voluntary quitting and involuntary displacements. AIC refers to Akaike's Information Selection Criterion for small selections, w is the Akaike weight. Parameter estimates show the direction of the effect.

Reason for abandonment	Model	Diagnostics			Parameter estimates (95% confidence interval)		
		AICc	Δ AICc	w	High rank	Medium rank	Male
Quitting	Sex, day, individual	887.805	0.000	0.457			-0.495, 0.233
	Rank class, day, individual	888.348	0.543	0.348	-0.527, 0.053	-0.366, 0.221	
	Rank class, sex, day, individual	889.501	1.696	0.196	-0.530, 0.056	-0.379, 0.216	-0.471, 0.226
	Rank	914.920	27.115	0.000	-0.542, -0.094	-0.367, -0.116	
	Rank, sex	915.451	27.646	0.000	-0.564, -0.114	-0.424, 0.072	-0.260, 0.018
	Sex	920.879	33.074	0.000			-0.261, 0.010
Displacement	Rank class, sex, day, individual	1001.953	0.000	0.514	-0.739, -0.147	-0.543, -0.147	-0.485, 0.062
	Rank class, day, individual	1002.117	0.164	0.474	-0.732, -0.111	-0.530, -0.130	
	Sex, day, individual	1009.531	7.578	0.012			-0.514, -0.168
	Rank, sex	1022.123	20.170	0.000	-0.588, -0.224	-0.444, -0.223	-0.273, -0.055
	Rank	1026.889	24.936	0.000	-0.557, -0.193	-0.415, -0.196	
	Sex	1054.665	52.712	0.000			-0.214, 0.009

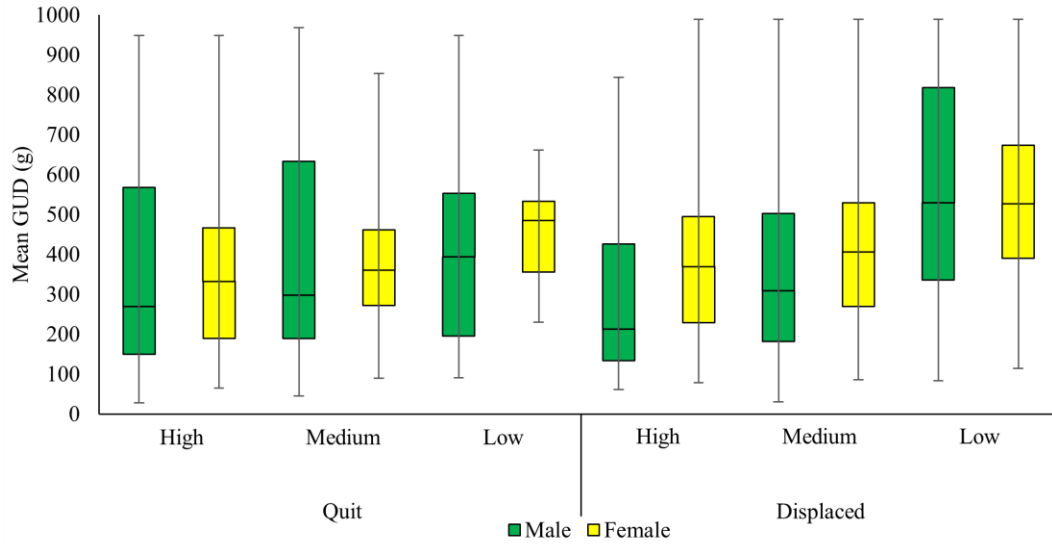


Figure 3: Mean predicted GUD (g) for high-, mid-, and low-ranked male and female bison. Mean is shown by sex, rank, and reason for abandoning a patch.

High-ranked bison of both sexes mostly quit voluntarily, in 88% of patch abandonments for males and 78% for females, while lower-ranked bison were mostly displaced, quitting in only 10% of cases for males and 23% for females; the pattern for mid-ranked bison was intermediary (Figure 4). Lower-ranked individuals were more likely to be displaced early in the feeding trial, while higher-ranked individuals quit throughout the trial.

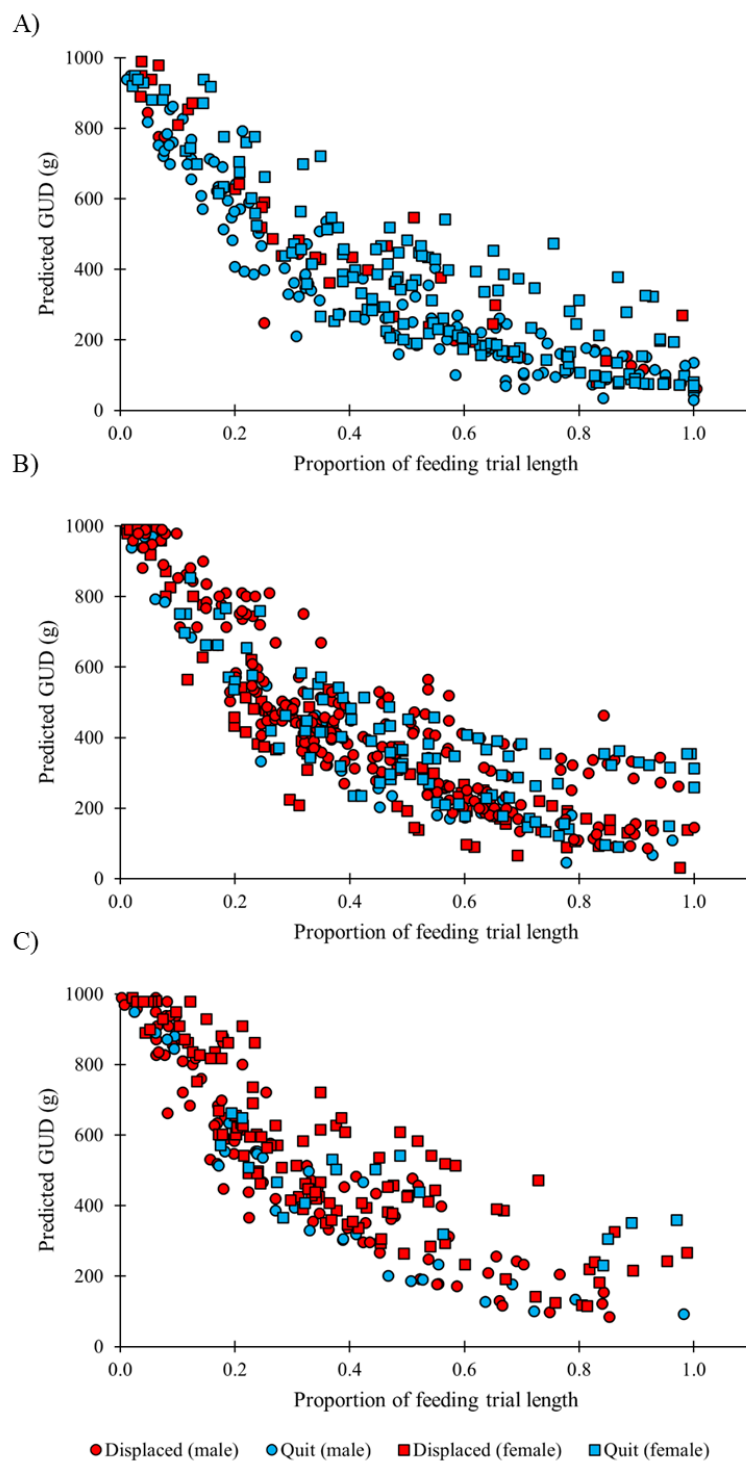


Figure 4: Instances of patch abandonments for A) high-, B) mid-, C) low-ranking males and females, represented as the predicted GUD versus the proportion of the feeding trial length.

Rank was significantly correlated with time spent foraging from the high-quality food patches (Figure 5; $F_{2,63} = 91.3, p = < 0.001$). No significant difference was observed between sexes ($F_{1,63} = 0.52, p = \text{ns}$). Higher-ranked individuals (average 84% of the trial length for males, 73% for females) spent significantly more time foraging from the high-quality patches compared to their lower-ranked counterparts (medium rank = 56% males, 55% females, low rank = 27% males, 32% females of trial length). Lower-ranked individuals spent a relatively small amount of time foraging from the high-quality patches and compensated by foraging more from the lower-quality hay patches.

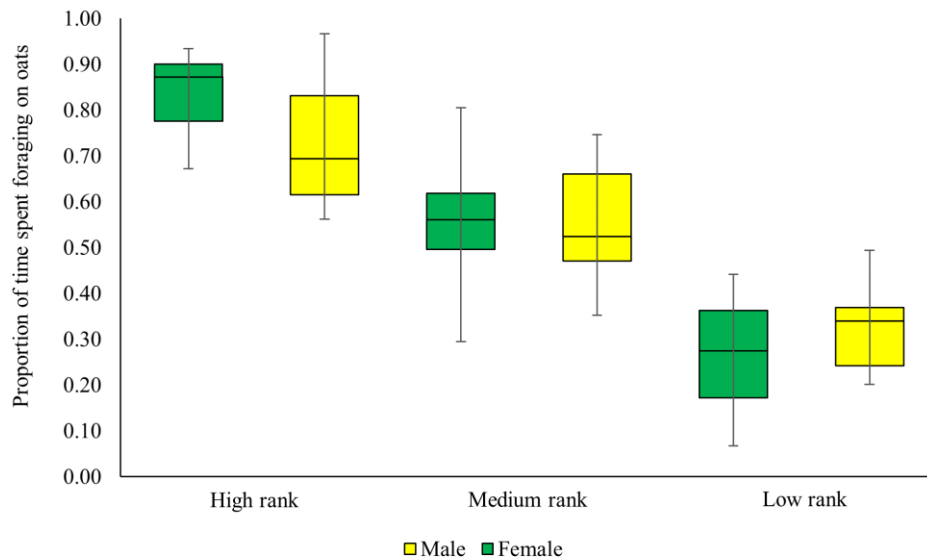


Figure 5: Average proportion of time spent foraging from feeding trays by males and female of high, medium and low rank versus total length of feeding trial. Proportion of time spent foraging by each bison (T_{fbison}) was determined by dividing by the total length of the feeding trial (T_{total}) using $T_{\text{fbison}} / T_{\text{total}}$. Standard error = 0.027.

DISCUSSION

Social rank, GUDs, time spent foraging and the perception of missed opportunity costs

Differences in GUD between individuals of divergent rank are indicative of (1) perception of foraging costs, and (2) differences in competitive ability. A bison's perception of between-patch food quality, which is influenced by short-term information sampling, varies during foraging bouts (Fortin 2002). By basing foraging decisions on local availability, a bison may choose to forage from a patch that yields high returns and abandon that patch when it perceives that another patch may yield higher returns. Here, higher-ranked individuals perceived higher missed opportunity costs due to their tendency to voluntarily quit foraging in a vast majority of the cases (88% of patch abandonments for males, 77% for females). Dominant bison abandon their feeding trays early and at higher GUDs to maximize perceived energy gain by foraging from trays first occupied by subordinate bison. This observation matches an earlier observation by McHugh (1958) that dominant bison prematurely abandon patches and cause frequent movement among an entire herd by displacing subordinates, even though abundant available foraging patches imply no visible difference in energy return between patches. McHugh's study is particularly interesting because the patches were spaced at much larger distances (30 m) than this study, indicating that the observed behaviours may occur at larger spatial scales. The GUDs measured in this study show that throughout the entire feeding trial, dominant individuals forage from higher-quality patches longer and at lower food densities.

This study similarly shows that lower-ranking bison may cease foraging at higher GUDs. It may appear to an observer of the experiment that higher ranks have lower GUDs because they are responsible for early abandonments. Had the experiment occurred on a much shorter scale, such that all trays were prematurely removed early in the trial, such would be the conclusion. This is not the case on a larger scale, such as that of the entire feeding trial, because high ranks continue to forage from subordinate trays after early abandonments, whereas lower ranks choose not to forage at lower GUDs. As a bison forages, it is under the pressure of exploitative and interference competition. Initially, as increased exploitative competition reduces the overall cost of foraging, it also reduces the GUD for all individuals because they will find value in obtaining energy and continue foraging (Davidson and Morris 2001). Individuals attempt to maximize their own gains and reduce the success of their neighbours through interference by quitting their own patches early in favour of exploiting patches occupied by subordinates. Interference competition is responsible for observed differences in GUDs and occurs between foraging individuals when competition for the diminishing resource leads to aggression (Rands et al. 2006). Because rank is related to competitive ability, it is the bison that are best equipped for competition, in this case those of the highest rank and usually larger that can continue to forage in and compete for lower-quality patches. In addition to estimating this effect by matching higher foraging times to lower GUDs in dominant bison, this study confirms that bison increase foraging activity under increased competition, as is expected by an animal employing a time minimizing strategy (Mitchell et al. 1990). Lower-ranked bison did not compete for higher-quality patches as the costs to do so increased; they instead favoured lower-quality patches by moving sooner to the area of the hay bales, where they experienced

less competition. Behavioral adaptations to foraging are an example of niche partitioning to avoid the costs incurred by competition and are not unique to bison (Smith et al. 2017). In fact, niche partitioning leading to differences in time and space use occurs between both sexes and social ranks of many species (Alanara et al. 2001, Donald et al. 2007, Sheppard et al. 2018). The benefit of using lower-quality patches to escape competition costs should still be increased foraging efficiency as opposed to continuing to compete for the high-quality patches, although the foraging efficiency between individuals using oat-heavy, as opposed to hay-heavy patches was not measured in this study. The observations in this study also support the notion that dominant bison may forage more efficiently than subordinates. Such theory is not new, as the relationship between dominance and improved foraging efficiency due to priority access to high-quality food has already been observed in ungulates (Haskell et al. 2019).

The effect of sex

As predicted, the models suggested that behaviour differed between the male and female cohorts. Males were more likely to prioritize missed opportunity costs, especially in displacing neighbours at lower GUDs than females. Normally, the relationship between sex and GUD is not significant, e.g., the Arctic ground squirrel (*Urocitellus parryi*, Wheeler & Hik 2014), brushtail possum (*Trichosurus vulpecula*, Mella et al. 2015), and lesser spotted woodpecker (*Dendrocopos minor*, Olsson et al. 1999). Differences in social structure and aggressive behaviour that distinguish the sexes suggested that a male bison might abandon their patches at a higher GUD due to increased costs of maintaining status (Mooring & Penedo 2014). Females were expected to abandon their patches at lower GUDs, as the benefits that come from early quitting

and displacement of subordinates are less. Thus, the cost of continuing to forage was lower and translated to a lower GUD.

An individual's sex, although weaker than its rank, may have had an effect on GUDs because of higher rates of male-male displacement, and interference as suggested by differences in predicted oat consumption rates (Figure 6). It is hypothesized this discrepancy between sexes is a result of the fitness differences that come with being a dominant of either sex but acting in a direction different to my prediction. A classic model of GUDs proposed by Brown (1988) views the cost of competition as simply increasing the GUD with the assumption that an individual is foraging optimally, the case in female bison who primarily compete for access to feed. In male bison, foraging behaviour must balance access to feed with the costs and benefits of maintenance of status, leading to decreased GUDs. Because only a few high-ranking bison reproduce with a majority of females (Roden et al. 2003), the cost-benefit ratio of continuing to compete for oats should vary with rank.

Thus, outside of the breeding season, males might still primarily suffer a stress of domination where high-ranked individuals are forced to defend their status against subordinate challengers. Although most aggressive contests occur during the breeding season as direct competition for mates (Wyman et al. 2021), most aggressive interactions outside of breeding occur during foraging (McHugh 1958). These acts of aggression serve not only to increase a dominant's fitness through foraging but reinforce rank for the breeding season. Thus, dominants not only benefit from reinforcing their status but also from access to primary forage, aiding in the maintenance of status for the

coming breeding season when competition and aggression shifts from foraging to mating.

Because females suffer primarily a stress of subordination where dominants suppress subordinates and challenges to status are less frequent than males (King et al. 2019), it was assumed that females will displace subordinates at lower GUDs than males. This difference explains why displacement GUDs are higher for females, and that although the costs of competition are reduced, which should reduce GUD, so are the benefits of a subordinate continuing to attempt to compete, not giving dominants the opportunity to continue displacing at lower GUDs. An analysis of the average oats consumed per time by each sex (shown here in Figure 6) suggests that males are affected to a greater degree. Higher-ranked males gain more than their higher-ranked female counterparts, while lower-ranked males lose more than their lower-ranked female counterparts, at least in terms of displacement GUDs and foraging efficiency. It is proposed that the fitness benefit to males causes dominant males to forage at a higher rate than their female counterparts. On the other hand, the increased interference by dominant males causes subordinate males to forage less efficiently than their female equivalents. Males on average also tended to forage for longer durations, an observation indicative of the higher importance of competing to forage due to the fitness associated with dominance. As displacements force individuals to travel between patches, thus incurring higher travel costs, individuals will leave lower GUDs as they are more likely to avoid prematurely quitting a patch and thus deplete patches to a greater degree (Ziv & Kotler 2003). Because male bison are more aggressive, thus displacing subordinates more often, travel costs are increased and males are more likely to try and forage at

lower densities, causing high ranked males to displace at lower GUDs. A second potential explanation could be that the increased GUDs from increased foraging costs in males could be offset by the increased nutritional requirements of the larger bulls. The six males in the study weighed an average of 441 kg and were larger than the seven females that averaged 379 kg. This may have reduced the GUD at which they competed for oats because they were experiencing a more limit-feed situation. In this situation, any additional costs incurred from the maintenance of status for breeding success would not be apparent through an increased GUD. An analysis of the predicted average oats consumed per time by each sex (shown here in Figure 6) suggests that males are affected to a greater degree by rank despite no significant difference in GUD. Higher-ranked males gain more than their higher-ranked female counterparts, while lower-ranked males lose more than their lower-ranked female counterparts, at least in terms of foraging efficiency, supporting this theory.

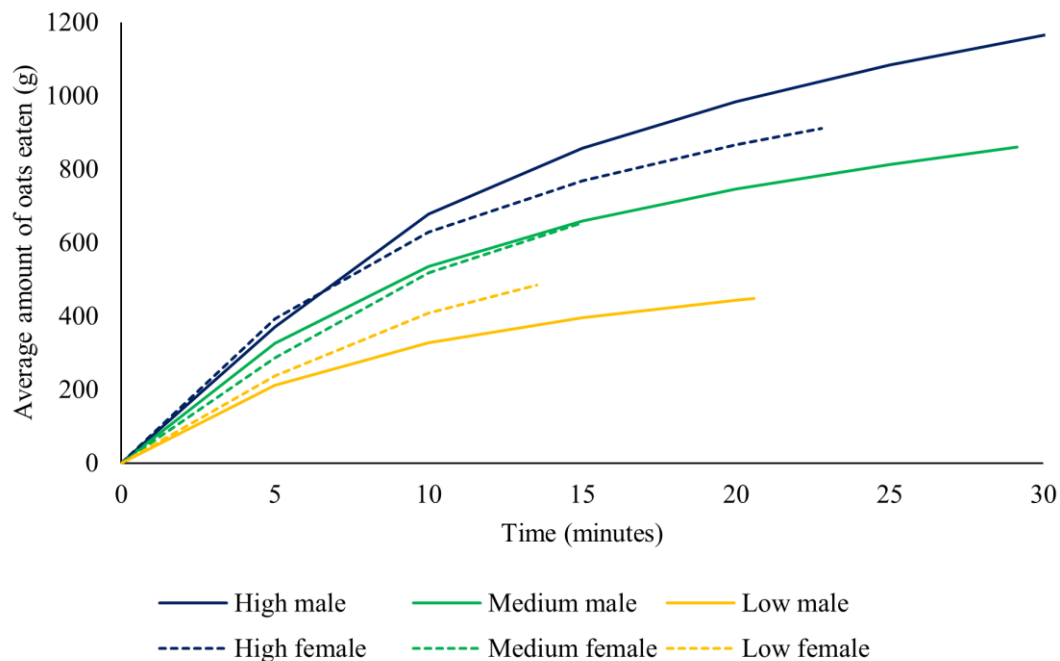


Figure 6: Predicted average intake rates of oats by sex and rank class across feeding time among all feeding trials. Average intake is a function of the estimated total food consumed at each instance of patch abandonment for bison of each rank class (high, medium, low).

Feedback loops associated with dominance

Intrasexual selection sets up an advantage to being dominant from a fitness standpoint in males of many species (Schuster and Wade 2003). But if dominance inadvertently leads to a set of established ranks, perhaps inevitable for very large organisms for which size differences among males can become exaggerated, then a sort of 'forage patch domino effect' occurs to reinforce the hierarchy. Such a pattern suggests that the dominance hierarchy is reinforced by inadvertent gain. The result is that when as soon as the highest-ranked bison begin to challenge a tray, it sets up a chain reaction of individuals displacing those of lower rank and inherently competitive ability. Intrinsic attributes leading to differences in competitive ability are dynamic (Dehnen et al. 2022).

In this case, body size, which flags probable differences in fighting ability, is a function of an individual's social status, leaving low-ranked individuals deprived of the ability to work (eat) their way up the social ladder. Lower-ranked bison of both sexes are consistently losers in the game of displacements while higher-ranked males have the most to gain through displacement.

It is widely accepted that the outcomes of dominance interactions impact the factors that determine them (Dehnen et al. 2022). Feedback loops interconnect interaction outcomes and their determinant factors. This study hypothesizes the existence of two feedback loops based on differing strategies for bison of high versus low rank. The first, a positive feedback loop, occurs when higher-ranked bison forage more efficiently and access higher-quality patches, reinforcing size and the ability to maintain status. The second, also a positive feedback loop, is about subordinates that wish to challenge status; they are disadvantaged as they are forced to forage less efficiently from lower-quality food sources and receive less energy returns per time invested. The result is a self-reinforcing feedback system that does not favour status changes. Instead, the dominants continue to get bigger, while subordinate bison continue to remain smaller in body size. These proposed feedback loops support observations by King et al. (2019) that social hierarchies in bison may be stabilized by intrinsic distinctions between high- and low-ranking individuals.

Predicted GUDs compared to directly measured GUDs

The ability to predict GUDs with the approach used in this study offers a unique benefit in that it can quantify the GUDs of all foraging individuals and not just the final individual to forage from a patch. The approach is beneficial in allowing a comparison

of individual differences in a herd setting where the decision of the final forager is not representative of the entire herd. A downside of this method is the inherent lack of accuracy compared to traditional measures of GUD which directly compare densities of food patches after a forager quits (fox squirrel: Kotler et al. 1999, voles: Morris 2009, white-tailed deer: Vickery et al. 2010, dabbling duck: Hagy et al. 2016). As opposed to a traditional GUD with a discrete final value, predicted GUDs depend on interpolated data derived from comparing the GUD to the total time spent in a foraging patch. However, substituting artificial feeding trays, depleted at an imperfect but predictable rate, the decisions of different foragers within the same group are easily measurable. A second, more readily addressable drawback is in attaining the data points necessary to define the predicted curve along the entire length of the feeding trial. Collecting data points at the end of the trial when all individuals have ceased foraging yields little insight to variation within the group and is more appropriate for situations where an external variable is being compared (i.e., predation cost, Moreira and McLaren 2019). In this study, this shortcoming was addressed by removing trays through gaps in the fence continuously throughout the trial, such that actual GUD values could be recorded at both early and late stages of the trial to create a more accurate predicted curve. Here, a ten-day acclimatization period assisted in allowing bison to be conditioned to the presence of the feeders and experimenter, such that they did not prematurely abandon foraging. Before this conditioning period, GUDs appeared to be related to an individual's boldness of personality, i.e., which bison was more willing to pay for the risk of foraging in a novel environment. The acclimatization period lasted until GUDs did not decrease each day, when the perceived predation risk became constant, at which point usable data could be collected.

The costs of competition

While the primary focus of this study is to compare foraging behaviour at the individual scale, it indirectly allowed the cost of competition to be observed at the herd level. An involuntary effect of competition in social ungulates is the reduced foraging efficiency across all individuals (Stutz et al. 2018). This is due to (1) reduced searching effort because of herding behaviour, and (2) a reduction in feeding time, where time gains are used for competitive behaviours (Molvar and Bowyer 1994). The intake rate of foraging animals is often negatively related to the density of foragers due to exploitative and interference competition (Vahl et al. 2007). This is particularly of concern for farmed bison, where competition is increased under the constraints of captivity. Under such conditions, to what degree does the aggressive behaviour observed have a net negative effect on the overall costs of foraging as a function of the rate of depletion of the oat patches? Interference competition may shift the depletion rate negatively if individuals spend time competing for patches as opposed to foraging uninterrupted. However, if the foraging rate is increased through exploitative competition as each bison attempts to maximize their share of an ever-depleting resource through increased intake, this effect may be negated.

Differences between the ideal patch depletion rate and the observed patch depletion rate notes that competition had a negative impact on the energy intake rate and patch depletion rate of all individuals as noted by the difference between the ideal patch depletion rate and average GUD curves, shown in Figure 7. The ideal patch depletion rate, also known as the predicted GUD curve (Figure 2), represents a patch depletion rate uninhibited by interference competition, as it does not account for any time spent

competing for the patch, interpatch movement, or the time a patch sat uninhabited. It represents a scenario where each bison only foraged from one patch without premature quitting, displacements, or alternative activities.

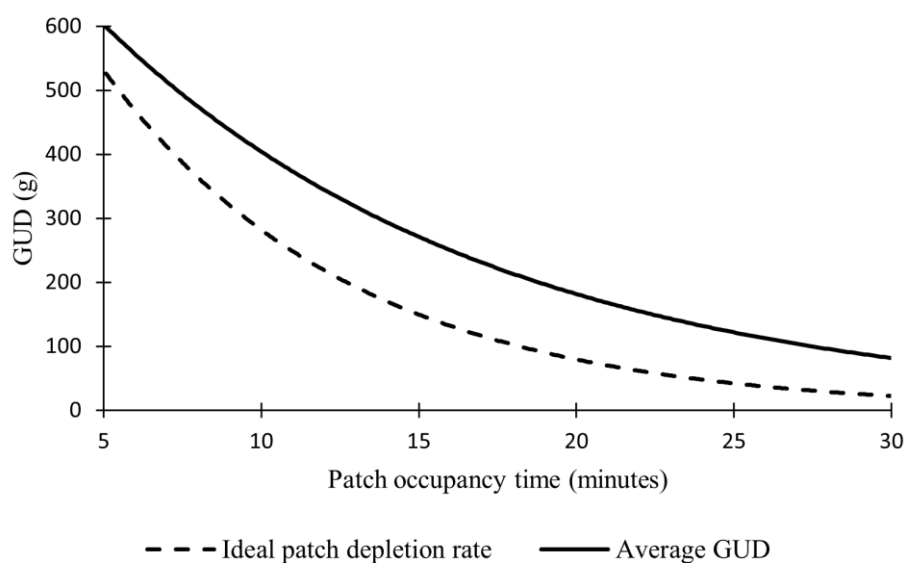


Figure 7: Average curve of GUDs (both voluntary quitting and involuntary displacements) for individuals of all ranks against the proportion of a feeding trial.

Early patch abandonments by dominants and subsequent displacements of subordinates causes patches to be used less continuously, thus decreasing the energy intake rate of the bison who would otherwise be foraging from them uninterrupted. Bison of all social ranks are similarly and negatively impacted by interference competition, which is manifested as an increased foraging cost applicable to all bison. Within-group competition for resources reduces the foraging efficiency of all individuals in a group (Halliday and Morris 2013). This phenomenon, although previously not measured in bison, correlates with observations of other species such as the oystercatcher (*Haematopus ostralegus*, Rutten et al. 2010) and southern red-backed vole (*Myodes gapperi*, Halliday and Morris 2013). Although the foraging strategy adopted by

different individuals is related to dominance, the food intake rate of individuals may be constant regardless of social rank or foraging method (Liker and Barta 2002). Each time a subordinate loses energy efficiency by being forced to cease foraging, the dominant also loses efficiency while they cease foraging temporarily to move between patches. Interference competition reduces foraging success of both individuals in a competitive interaction as a result of reduced intake rates and the additional energy and time required to displace or to protect the patch from another individual. It is important to note, however, that this study omits any positive effects of competition, which in ungulates has been observed as increases in the rate of food intake (Olofsson 1999). When an animal is in the presence of neighbours that also wish to exploit a patch (exploitative competition), it will forage at a higher rate than if it were alone such that neighbours cannot acquire the contested resource. However, this increase in foraging speed is not enough to offset the additional costs of displacement, aggression, and premature quitting, which arise from greater competition.

LITERATURE CITED

- Alanara, A., Burns, M.D. and Metcalfe, N.B. 2001. Intraspecific resource partitioning in brown trout: the temporal distribution of foraging is determined by social rank. *Journal of Animal Ecology* 70:980-986.
- Bedoya-Perez, M.A., Carthey, A.J.R., Mella, V.S.A. and McArthur, C. 2013. A practical guide to avoid giving up on giving-up densities. *Behavioral Ecology and Sociobiology* 67(10):1-13.
- Brown, J.S. 1988. Patch use as an indicator of habitat preference, predation risk, and competition. *Behavioral Ecology and Sociobiology* 22:37-47.
- Charnov, E.L. 1974. Optimal foraging, the marginal value theorem. *Theoretical Population Biology* 9:129-136.
- Chase, I.D. and Seitz, K. 2011. Self-structuring properties of dominance hierarchies: a new prospective. *Advanced in Genetics* 75:51-81.
- Davis, G.H., Crofoot, M.C. and Farine, D.R. 2022. Using optimal foraging theory to infer how groups make collective decision. *Trends in Ecology and Evolution* 37(11):942-952.
- Davidson, D.L. and Morris, D.W. 2001. Density-dependent foraging effort of deer mice (*Peromyscus maniculatus*). *Functional Ecology* 15:575:584.
- Dehnen, T., Arbon, J.J., Farine, D.R. and Boogert, N.J. 2022. How feedback and feed-forward mechanisms link determinants of social dominance. *Biological Reviews* 97:1210-1230.
- Donald, P.F., Hille, S., Brooke, M.L., Taylor, R., Wells, C.E., Bolton, M. and Marlow, T. 2007. Sexual dimorphism, niche partitioning and social dominance in the feeding ecology of the critically endangered Raso Lark *Alauda razae*. *Ibis* 149:848-852.
- Eccard, J.A. and Liesenjohann, T. 2014. The importance of predation risk and missed opportunity costs for context-dependant foraging patterns. *PLoS ONE* 9(5): e94107.
- Fortin, D. 2002. Searching behavior and use of sampling information by free-ranging bison. *Behavioral Ecology and Sociobiology* 54:194-203.
- Hagy, H.M., Stafford, J.D., Smith, R.V., Yetter, A.P., Hine, C.S., Horath, M.M. and Whelan, C.J. 2016. Opportunity costs influence food selection and giving-up density of dabbling ducks. *Journal of Avian Biology* 48:804-814.

- Halliday, W.D. and Morris, D.W. 2013. Safety from predators or competitors? Interference competition leads to apparent predation risk. *Journal of Mammalogy* 94(6):1380-1392.
- Haskell, M.J., Rooke, J.A., Roehle, R., Turner, S.P., Hyslop, J.J., Waterhouse, A. and Duthie, C-A. 2019. Relationships between feeding behaviour, activity, dominance and feed efficiency in finishing beef steers. *Applied Animal Behaviour Science* 210:9-15.
- King, K.C., Caven, A.J., Leung, K.G., Ranglack, D.H. and Arcilla, N. 2019. High society: behavioral patterns as a feedback loop to social structure in plains bison (*Bison bison bison*). *Mammal Research* 64:365-376.
- Kotler, B.P. and Brown, J.S. 1988. Environmental heterogeneity and the coexistence of desert rodents. *Annual Review of Ecology and Systematics* 19:281-307.
- Kotler, B.P., Brown, J.S. and Hickey, M. 1999. Food storability and the foraging behavior of fox squirrels (*Sciurus niger*). *American Midland Naturalist* 142(1):77-86.
- Liker, A. and Barta, Z. 2002. The effects of dominance on social foraging tactic use in house sparrows. *Behaviour* 139:1061-1076.
- MacArthur, R.H. and Pianka, E.R. 1966. On optimal use of a patchy environment. *American Naturalist* 100(916):603-609.
- McHugh, T. 1958. Social behaviour of the American buffalo (*Bison bison bison*). *Scientific Contributions of the New York Zoological Society* 43(1):1-40.
- Mella, V.S.A., Ward, A.J.W., Banks, P.B. and McArthur, C. 2015. Personality affects the foraging response of a mammalian herbivore to the dual costs of food and fear. *Oecologia* 177:293-303.
- Mitchell, W.A., Abramsky, Z.A., Kotler, B.P., Pinshow, B. and Brown, J. 1990. The effect of competition on foraging activity in desert rodents: theory and experiments. *Ecology* 71(3):844-854.
- Molvar, E.M. and Bowyer, R.T. 1994. Costs and benefits of group living in a recently social ungulate: the Alaskan moose. *Journal of Mammalogy* 75(3):621-630.
- Mooring, M.S. and Penedo, M.C.T. 2014. Behavioral versus genetic measures of fitness in bison bulls (*Bison bison*). *Journal of Mammalogy* 95(5):913-924.
- Moreira, A. and McLaren, B. 2019. Monitoring the effects of feeding in groups: behavioural trials of farmed elk in winter. *Applied Animal Behaviour Science* 212:66-73.

- Morris, D.W. 2009. Apparent predation risk: tests of habitat selection theory reveal unexpected effects of competition. *Evolutionary Ecology Research* 11:209-225.
- Olofsson J. 1999. Competition for total mixed diets fed for ad libitum intake using one or four cows per feeding station. *Journal of Dairy Science* 82:69–79
- Olsson, O., Wiklander, Ul., Holmgren, N.M.A. and Nilsson, S.G. 1999. Gaining ecological information about Bayesian foragers through their behaviour. II. A field test with woodpeckers. *OIKOS* 87:264-276.
- Rands, S.A., Pettifor, R.A., Rowcliffe, J.M. and Cowlshaw, G. 2006. Social foraging and dominance relationships: the effects of socially mediated interference. *Behavioural Ecology and Sociobiology* 60:572-581.
- Reinhardt, V. 1985. Social behaviour in a confined bison herd. *Behaviour* 92(3):209-226.
- Rutten, A.L., Oosterbeek, K., Verhulst, S. Dingemanse, N.J. and Ens, B.J. 2010. Experimental evidence for interference competition in oystercatchers, *Haematopus ostralegus*. II. Free-living birds. *Behavioral Ecology* 21:1261-1270.
- Roden, C., Vervaecke, H., Guy, M. and Linda, V.E. 2003. Reproductive success of bison bulls (*Bison bison bison*) in semi-natural conditions. *Animal Reproduction Science* 70(1-2):33-43.
- Sheppard, C.E., Inger, R., McDonald, R.A., Barker, S., Jackson, A.L., Thompson, F.J., Vitikainen, E.I.K., Cant, M.A. and Marshall, H.H. 2018. Intragroup competition predicts individual foraging specialisation in a group-living mammal. *Ecology Letters* 21:665-673.
- Shuster, S.M. and Wade, M.J. 2003. *Mating Systems and Strategies* (Vol. 61). Princeton University Press, Princeton. 533 pp.
- Smith, A.R., Kitchen, S.M., Toney, R.M. and Ziegler, C. 2017. Is nocturnal foraging in a tropical bee an escape from interference competition? *Journal of Insect Science* 17(2):62;1-7.
- Stutz, R.S., Bergvall, U.A., Leimar, O., Tuomi, J. and Rautio, P. 2018. Cohesiveness reduces foraging efficiency in a social herbivore. *Animal Behaviour* 135:57-68.
- Vahl, W.K., Van Der Meer, J., Meijer, K., Piersma, T. and Wessing, F.J. 2007. Interference competition, the spatial distribution of food and free-living foragers. *Animal Behaviour* 74:1493-1503.
- Vickery, W.L., Guillaume, R. and Doucet, G.J. 2010. Comparing habitat quality within and between environments using giving up densities: an example based on the

winter habitat of white-tailed deer *Odocoileus virginianus*. *Oikos* 120(7):999-1004.

Wheeler, H.C. and Hik, D.S. 2014. Giving-up densities and foraging behaviour indicate possible effects of shrub encroachment on Arctic ground squirrels. *Animal Behaviour* 95:1-8.

Wyman, M.T., Pinter-Wollman, N. and Mooring, M.S. 2021. Trade-offs between fighting and breeding: a social network analysis of bison male interactions. *Journal of Mammalogy* 102(2):502-519.

Ziv, Y. and Kotler, B.P. 2003. Giving-up densities of foraging gerbils: the effect of interspecific competition on patch use. *Evolutionary Ecology* 17:333-347.

CHAPTER 3: A GAME-THEORETICAL ANALYSIS OF FORAGING DECISIONS BY CONFINED BISON

The feeding trials described in chapter 2 demonstrated that higher-ranked bison may be afforded better foraging opportunities by displacing nearby competitors, in many cases the next lowest-ranked individual. This starts a chain reaction, as described by McHugh (1958), of bison displacing lower-ranked competitors until the last bison finds itself without a food patch and with a choice of whether to continue competing for an empty patch or to leave in favour of another activity, such as foraging from lower-quality patches elsewhere. During the same feeding trials, a comparison between the oat intake rate observed and the ideal rate of intake expected to occur in the absence of competition (purely cooperation) demonstrated that competition for trays resulted in inefficient foraging. What leads to bison abandoning more efficient cooperation in favour of a competitive strategy involving frequent displacements?

Defection from cooperation occurs for males because the social hierarchy evolved as a function of competition for mates (Kuijper et al. 2012). What we observe outside the bison breeding season starts as a legacy of intrasexual selection, whereby males compete not just to eat, but also to maintain status by displacing subordinates in the prime foraging area (Mooring and Penedo 2014, Wyman et al. 2021). Prime access to forage also allows high-ranking males to increase their competitive ability via the forementioned positive feedback loops. Thus, there is a benefit to competition among males despite a loss in foraging efficiency. For females, a defection from cooperation is not a product of sexual selection but rather competition for forage (Vervaecke et al. 2005). Therefore, defecting from cooperation is also evolutionarily stable for females

since high-ranking individuals can slightly increase their intake from high-quality patches by engaging in a competitive strategy and excluding subordinates from the oats. This chapter will apply game theory to explain the rationale that causes each bison to decide whether to compete, cooperate, or abandon foraging altogether.

The previously described phenomenon is easily envisioned using an analogy of many cribbage players in a room with tables in a straight line, known to some as a cribbage tournament. All are ordered from the best player on one end chronologically to the worst player at the other end. Each player can choose to play a better (higher-ranked) player, a worse (lower-ranked) player or quit and go home. If a player defeats a better player, they assume a higher rank; likewise, if a player loses to a worse player, their rank is lowered. Now, assume that each player is playing to have the highest score, also referred to as payoff, with wins adding 1 point and losses costing -1 point. Each player's skill level, i.e., their ability to play the game, which they will learn by trial, will dictate the strategy they use to maximize their payoffs or minimize their losses. The optimal strategy for the better players is to continue playing as long as there are worse opponents to challenge and beat. The optimal strategy for the worst player is to minimize losses, and this player will soon learn that they cannot compete with any other player and will go home first. When the worst player abandons the room, the player who could previously win by challenging and beating the lowest player can no longer win the tournament. Thus, their best strategy is to "cut losses" and they also leave the room, and so on. If any player in between the groups of best and worst players (a mid-ranked player) loses to a better player, it is wiser for them to challenge a worse player than a better one because each player learns that they have an advantage against those of lower

rank. It is unwise for any player to challenge a better player because the risk of losing is high. Therefore, in this tournament, the best player is always the likeliest winner, but any player other than the worst player also has the possibility to be a winner by always beating lower-ranked players. However, the likelihood of winning the tournament is low, so challenges in both the high- and the mid-ranked group are best made to the nearest-ranked.

A similar scenario to the cribbage tournament occurs during the feeding trials described in chapter 2. Bison are playing a similar game to maximize oat intake with a key difference from the cribbage scenario being that the payoff decreases as the game continues due to the diminishing return in feeding on the oats mixed with wooden blocks. Thus, each bison must evaluate the payoff, making a decision about GUD not only on diminishing returns, but also on their ability to compete for a new payoff by using the winner's strategy to maximize gains by moving to a competitor's tray. Thus, a bison's optimal strategy does not depend only on the GUD and rank, but also on the decisions of higher-ranked competitors whose strategies affect the ideal strategies of subordinates. The game is randomized only to the extent that feeding trays are approached quickly and neighbours are not always close in rank.

Game theory explains conflicts in terms of costs and benefits to all players (Riechert 1998). Here, it can be employed to model foraging decisions as a game of pairwise interactions between bison differing in rank and competitive ability where each individual attempts to maximize its own fitness, referred to from this point only as payoff. Because players always differ in competitive ability, in this case fighting ability, an asymmetrical game exists with one individual favoured to win due to some

advantage, which may be size or experience (Maynard Smith & Parker 1976).

Asymmetries allow contests to be settled without escalation of aggression because an individual of lower ability risks greater costs to escalation. Thus, the payoffs for certain strategies may differ depending on whether the individual is dominant or submissive within any interaction (McAvoy and Hauert 2015).

The objective of this chapter is to model the feeding trials from chapter 2 in the context of game theory, firstly to illustrate how bison evaluate their own individual GUDs not only to quit feeding, but also to challenge a nearby tray based on the neighbour's rank relative to their own. Secondly, I will build the model such that bison have an advantage to bump individuals of lower rank and by doing so, the competitive individual may begin to win the game. As this behaviour is repeated down the ranks, every bison but the lowest ranked is winning the game of displacement. Bimatrix models can be created to define the evolutionary stable strategy (ESS) in asymmetrical games (Tuyls et al. 2018). The first game will involve two bison differing in rank. while the second will involve two games between three bison differing in rank where a bimatrix is used twice, the first time to define the strategies of the high- and medium-ranked bison, the second to define the strategies between the mid- and low-ranking bison.

MODEL

We derive the model from the classical Hawk and Dove game modelled by Maynard Smith and Price (1973), which considers a game between two strategies where the hawk (equivalent to competitive) strategy always beats the dove (equivalent to cooperative) strategy, and payoffs and costs are shared equally between plays if both choose the same strategy. A downside of this model is that it does not address

differences between players that may give one an advantage when utilizing a particular strategy, as often occurs in nature. Thus, the matrix must identify the different payoffs of each strategy for each individual, as opposed to just one payoff per strategy (Krivan and Cressman 2022). I expand on these models by adding another strategy to the two-strategy Hawk and Dove game. At any point along the feeding bout, individuals choose any of three foraging strategies: 1) compete, 2) cooperate, and 3) quit. Individuals that compete will exhibit aggressive behaviour to compete for a patch. Individuals that cooperate will remain in a patch until they are displaced without a fight by competitors. The final set of individuals quit foraging from the best patches in favor of alternative fitness increasing activities, including to begin foraging from lower-quality patches. Because a linear hierarchy exists, a unique rank is assigned to each individual, $i = 1$ refers to the highest rank, $i = 2$ refers to next highest, and so on down to the lowest-ranked bison.

Payoff is determined as a function of the GUD, a measure of the remaining energy returns available in a patch, plus the benefits of maintaining rank, minus the costs of being displaced. The model assumes all patches are depleted throughout foraging time at similar and constant rate. If competition occurs, any bison will incur a slight time cost due to travel time between patches, defined as a payoff decrease of $(T)GUD$. The winner of the competition will accept a long-term payoff from reinforcing rank, R , that is equal to a hypothetical value of the long-term benefit of rank reinforcement multiplied by the difference in rank (competitive ability) between the winner and loser, Δi . The loser of competition will incur a cost of competition, C , equal to a hypothetical value of losing

an aggressive challenge multiplied by the difference in rank between the winner and loser, Δi .

To cooperate yields a payoff equivalent to GUD unless the neighbouring individual chooses competition, at which point the cooperating individual will suffer an interference cost and be forced to move to a patch of presumably lesser quality, a loss equivalent to (I)GUD, where I is the value of the lesser quality patch relative to GUD. An individual that chooses to quit can receive a payoff equal to A, the alternative fitness that comes from foraging from the unlimited but lower-quality hay. Because of the lower energy return from foraging on hay, the value of A is set significantly lower than the starting GUD for the oats. It is assumed because of the high number of previous interactions and stability of the dominance hierarchy that bison have perfect information on their own competitive ability and that of their competitors. The model is based on the feeding trials described in chapter 2, where there is one high-quality oat patch (feeding tray) per bison playing the game and an unlimited amount of lower-quality hay. An asymmetric bimatrix game is used to define the payoffs for each player (Table 3). GUD estimates come from the results of chapter 2.

Table 3. Payoff matrix for interactions between male bison during feeding trials. For each combination of behaviours, the top formula refers to the payoff of the higher-ranked, lower formula refers to the payoff of the lower-ranked.

Strategy		Lower-ranked		
		Compete	Cooperate	Quit
Higher-ranked	Compete	$GUD - T(GUD) + R_{\Delta i}$ $GUD - T(GUD) - C_{\Delta i}$	$GUD - T(GUD) + R_{\Delta i}$ $(I)GUD - (T)GUD$	$GUD - (T)GUD + R_{\Delta i}$ A
	Cooperate	$I(GUD) - T(GUD) - R_{\Delta i}$ $GUD - T(GUD) + R_{\Delta i}$	GUD	GUD A
	Quit	$A - R_{\Delta i}$ $GUD - T(GUD) + R_{\Delta i}$	A GUD	A

The model was run in Excel from $GUD = 1000$ to $GUD = 100$ in increments of 50 to analyze how strategies change as the oat trays were depleted in the experiment. R values were run between 50 and 250, C between 50 and 250, and A between 200 and 700 to test the best fit. The first model involved a 2-player game between a dominant ($i = 1$) and submissive ($i = 2$). A second model used a 3-player game, where each individual's optimal strategy is dependant on the decisions of dominant and subordinate players. This model used two separate matrices, the first between $i = 1$ and $i = 2$, and the second between $i = 2$ and a third less dominant player $i = 3$. In the second matrix all GUD values were set equivalent to $(I)GUD$ to recognize a presumed loss arising from earlier displacement in the first matrix.

RESULTS

The best fit to the observations in the feeding trials in chapter 2 occurred when $I = 0.95$, signifying a 5% decrease in GUD when moving to a tray previously occupied by a subordinate (Table 4). $T = 0.01$ was used to represent a 1% loss in payoff due to travel

time between patches, which was on average about 5 seconds. $R = 155$ was a relative value to denote the fixed benefit of rank reinforcement arising with competition, while $C = 200$ reduced the payoff by 200 to signify the cost to fitness of the subordinate bison choosing to compete with the dominant. $A = 500$ was set as the payoff in opting for alternative activities and was based on a proposed value of foraging from hay of 50% of the same value for the oats in the feed trays at the outset of the trials. An example of the payoff matrix at the beginning of each feeding trial in a simplified 2-bison game, $GUD = 1000$, demonstrates that payoff is at the outset maximized when the higher individual competes, and the lower rank cooperates.

Table 4. Payoff matrix for interactions between bison during feeding trials at $GUD = 1000$. For each combination of behaviours, the top formula refers to the payoff of the higher-ranked, lower formula refers to the payoff of the lower-ranked. Bold indicates the highest payoff strategies. $I = 0.95$, $T = 0.01$, $R = 155$, $C = 200$, $A = 500$.

Strategy		Lower-ranked		
		Compete	Cooperate	Quit
Higher-ranked	Compete	1145 790	1145 940	1145 500
	Cooperate	477 1145	1000 500	1000 500
	Quit	190 1145	500 1000	500 500

For the higher-ranking bison, competition will yield the greatest payoff until it falls below the payoff of A , at which point quitting the foraging area will yield a higher payoff (Figure 8). Because it is assumed that any bison will forage optimally, $i = 1$ (the dominant) should choose competition whenever the GUD of its tray exceeds ~ 350 g

(Figure 8) because the payoff from competition yields an additional benefit to rank reinforcement. This value of 350 g matches the observed average GUD of high-ranking bison in the feeding trials (chapter 2). The dominant does not choose to cooperate and remain at its tray because, although this may yield a higher energy intake per time of food, it does not yield the maximum payoff. By displacing the subordinate, the dominant can forage below the point at which the value at GUD makes foraging from the oats less efficient than foraging from the lower-quality hay. For $i = 2$ (the subordinate), competition is costly and engaging in it will decrease its payoff. Thus, the greatest payoff for $i = 2$ will be to cooperate until reaching A. However, because the payoffs to cooperate for $i = 2$ are less than to compete for $i = 1$, the subordinate will reach an A threshold at the higher GUD of ~ 550 g.

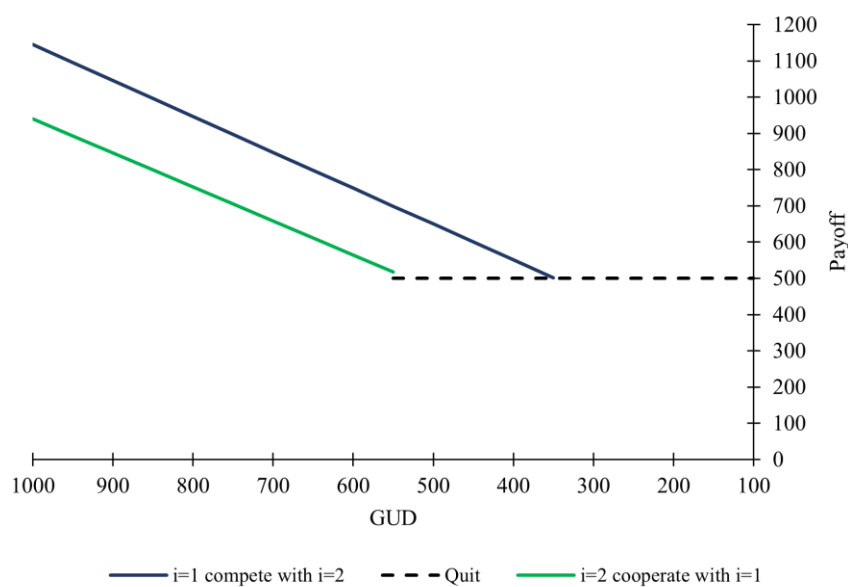


Figure 8: Potential payoffs for a dominant ($i = 1$) and submissive ($i = 2$) in a 2-player game as oat trays are depleted and GUDs are reduced. $I = 0.95$, $T = 0.01$, $R = 155$, $C = 200$, $A = 500$.

In a 2-player game, the optimal payoff of $i = 2$ is dependent largely on the decision of $i = 1$. However, in an n -player game, the decision of $i = 2$ is not only dependent on $i = 1$, but also on the presence of at least one other subordinate. Considering the case of one subordinate, $i = 3$, if $i = 1$ chooses to compete and displace $i = 2$, the newly displaced $i = 2$ confronts a choice of whether to compete or cooperate with its subordinate. By choosing to cooperate with $i = 1$ and compete with $i = 3$, the mid-ranked $i = 2$ now receives an additional payoff from rank reinforcement, where at any payoff above A it is winning by competing with its subordinate. Now, $i = 3$ becomes a loser in the game of displacement and, as Figure 9 depicts, the ideal GUD for $i = 2$ has shifted to a lower GUD, from 550 g when it was the only subordinate in the 2-player game, to 400 g when it became a mid-ranked bison in a 3-player game. This model matches the observations for average GUDs separated by rank class. Combined, high-ranked bison (B_H) had an average combined GUD of 372 g, medium-ranked (B_M), 417 g, low-ranked (B_L), 536 g.

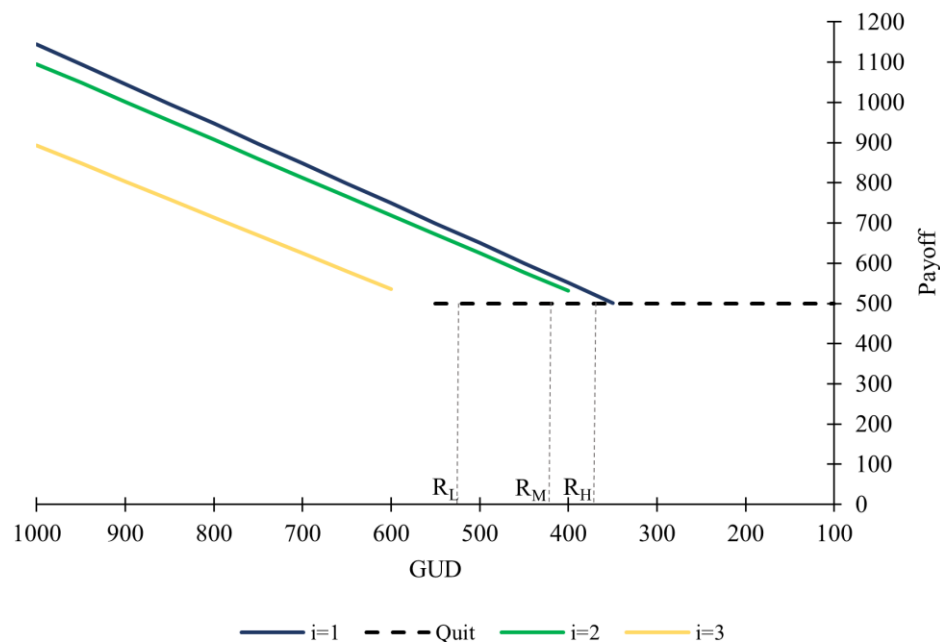


Figure 9: Payoffs for the ESS as a function of GUD in a 3-player game among bison of high ($i = 1$), medium ($i = 2$) and low rank ($i = 3$). Vertical lines represent average combined GUDS (both instances of quitting and displacement) for low- (R_L), medium- (R_M), and high-ranked (R_H) bison. $I = 0.95$, $T = 0.01$, $R = 155$, $C = 200$, $A = 500$.

DISCUSSION

The models show that the ESS is one where a dominant bison benefits from competing with and displacing subordinates so long as the payoffs of competing exceed the potential payoffs of alternative activities. The observed cooperation to dominants by subordinates is quite common in animals when the cost to benefit ratio favours the dominant individual in an interaction (Yasukawa and Bick 1983). The dominance of a single stable strategy in this situation is unsurprising considering asymmetries in competitive ability often yield pure strategies (Maynard Smith and Parker 1976). Competition is favoured over cooperation by all individuals except the lowest ranked

because competing with subordinates can still increase payoff over quitting. (Oprea et al. 2010). A purely cooperative strategy would experience a lack of aggression, early patch abandonments, and contests for subordinate patches. High-ranked bison are winners by default because they can always win. Mid-ranked individuals may also be considered winners by displacement because they are winning against their subordinates. This model helps form two predictions. Firstly, that asymmetries in competitive ability cause bison to individually recognize their own payoffs. GUDs differ for each individual due both to differences in interference costs from dominants and to benefits from displacing subordinates. That rank is related to the average GUD at which a bison will choose to cease playing the game (i.e., abandon the competing strategy) may be indicative of a system where each bison understands that once it is the lowest ranked and can no longer displace subordinates, it is optimal to quit foraging. This notion may be considered novel in the GUD framework as classical interpretations of GUDs only analyze the decisions of the last forager and cannot perceive the costs of any previously foraging individuals (Bedoya-Perez et al., 2013). Secondly, it has demonstrated that bison have an advantage to bump individuals of lower rank. By doing so, they can increase their own payoffs by continuing to forage in a game that includes direct competition. It would be intuitive to assume from Figure 7 that maximizing instantaneous intake rate through a purely cooperative strategy would be evolutionarily stable, as this would yield the highest payoff per time invested in terms of energy intake to all herd members. Bison must have evolved such that by displacing subordinates at the cost of slightly reduced energy intake, they are reinforcing rank and receiving other benefits. Therefore, so long as bison remain dominant through the competitive strategy, the observed strategy is evolutionarily stable.

LITERATURE CITED

- Bedoya-Perez, M.A., Carthey, A.J.R., Mella, V.S.A. and McArthur, C. 2013. A practical guide to avoid giving up on giving-up densities. *Behavioral Ecology and Sociobiology* 67(10):1-13.
- Kuijper, B., Pen, I. and Weissing, F.J. 2012. A guide to sexual selection theory. *Annual Review of Ecology, Evolution, and Systematics* 43:287-311.
- Krivan, V. and Cressman, R. 2022. The asymmetric Hawk-Dove game with costs measured as time lost. *Journal of Theoretical Biology* 547:111162.
- Maynard Smith, J. and Parker, G.A. 1976. The logic of asymmetric contests. *Animal Behaviour* 24:159-175.
- Maynard Smith, J. and Price, G.R. 1973. The logic of animal conflict. *Nature* 246:15-18.
- McAvoy, A. and Hauert, C. 2015. Asymmetric evolutionary games. *PLoS Computational Biology* 11(8):e1004349.
- McHugh, T. 1958. Social behaviour of the American buffalo (*Bison bison bison*). *Scientific Contributions of the New York Zoological Society* 43(1):1-40.
- Mooring, M.S. and Penedo, M.C.T. 2014. Behavioral versus genetic measures of fitness in bison bulls (*Bison bison*). *Journal of Mammalogy* 95(5):913-924.
- Oprea, R., Henwood, K. and Friedman, D. 2010. Separating the hawks from the doves: evidence from continuous time laboratory games. CESifo Working Paper 3129.
- Riechert, S.E. 1998. Game theory and animal contests pp. 64-93 in Dugatkin, L.A. & Reeve, H.K. *Game theory and animal behavior*. Oxford University Press, New York. 320pp.
- Tuyls, K., Pérolat, J., Lanctot, M., Ostrovski, G., Savani, R., Leibo, J.Z., Ord, T., Grapel, T. and Legg, S. 2018. Symmetric decomposition of asymmetric games. *Scientific Reports* 8:1015.
- Vervaecke, H., Roden, C. and de Vries, H. 2005. Dominance, fatness and fitness in female American bison, *Bison bison*. *Animal Behaviour* 70(4):763-770.
- Wyman, M.T., Pinter-Wollman, N. and Mooring, M.S. 2021. Trade-offs between fighting and breeding: a social network analysis of bison male interactions. *Journal of Mammalogy* 102(2):502-519.
- Yasukawa, K. and Bick, E.I. 1983. Dominance hierarchies in dark-eyed juncos (*Junco hyemalis*): a test of a game-theory model. *Animal Behaviour* 31:439-448.

CHAPTER 4: APPLICATIONS AND CONCLUSIONS

The results of this study suggest that rank influences GUDs at an individual level for confined socially foraging bison. Rank may be negatively related to GUDs in both male and female bison, with a stronger effect suggested in males. Dominant individuals are better suited to compete for high-quality food sources, as energy returns are diminished and costs to continue foraging are increased over feeding bouts. High- and mid-ranked males may exhibit lower GUDs in comparison to females of similar ranks, due largely to their propensity to displace competitors by passive or active aggression. However, a more comprehensive understanding of factors attributing to individual differences in GUD requires not only an understanding of the effect of dominance and sex through more observations but the study of additional variables. These are predation risk manifested through group size (Krause and Ruxton 2002), habitat type (Hayward et al. 2015), and individual differences such as size (weight) and personality (Mella et al. 2015).

This study reinforces the idea of the existence of two feedback loops; a positive loop that aids dominant individuals in continuing to reinforce their status, and a negative loop that reinforces a subordinate's low rank and keeps them at a competitive disadvantage. It is understood that, in bison, differences in rank are well established early in life and remain largely consistent in the absence of extraneous circumstances (Rutberg 1983). What is less understood is the factors that set up these feedback loops that may persist for much of a bison's life. Calves begin developing social hierarchies at four months, and these hierarchies remain largely stable throughout life and dictate how each bison interacts with its environment and conspecifics (McHugh 1958). Yet, little is

known about the factors that cause bison calves to adopt varied degrees of dominance. Several factors are believed to affect dominance in ungulate calves, such as dominance of the mother (Veiberg et al. 2004), timing of birth (Green and Rothstein 1993), initial interactions through the winner-loser effect (Odlham et al. 2020), weight of the mother (Vervaecke et al. 2005), and temperament (Neave et al. 2020). A comprehensive understanding of feedback loops in bison requires studies of the factors that lead to the dominance hierarchy and directly the feedback loops observed.

The primary impact of this study is in relation to captive managed herds where the level of competition may be artificially regulated. Bison naturally form fusion-fission societies where members of the herd tend to separate into smaller subgroups and frequently leave and join new groups (Ramos et al. 2015). However, it may be possible to manage the size and composition of subgroups if multiple enclosures are present in an environment. The ability for a limited environment to sustain a species increases with a rotational grazing system, which involves the frequent movement of animals between separate paddocks to ensure overgrazing is minimized (Teague & Dowhower 2003). Pastures show enhanced carrying capacities when bison numbers are adjusted to match available forage biomass and short periods of grazing occur followed by adequate recovery periods (Hillenbrand et al. 2019).

Cohesive foraging benefits the implementation of rotational grazing systems through the maintenance of short-term intensive foraging of small areas (Billman et al., 2020). Thus, cooperation between individuals is favoured because individuals that cooperate can forage closer together, thus foraging in smaller areas and more intensely. Spatially uneven distributions of grazing as a result of individual dispersion and niche

partitioning may lead to inefficient uses of resources (Ganskopp and Bohnert 2009). Secondly, cooperative foraging reduces predation costs, allowing individuals to forage with less fear and time lost to predator observance and avoidance (Kraai and Shrader 2018). Downsides of cohesive foraging may include increased interference competition and inefficient foraging, as bison may congregate in areas that are not of the highest quality, as opposed to spreading out and searching for new areas that may be of better quality.

One hypothesized technique to improve rotational grazing in captive bison may be to separate the herd into smaller groups that maximize cooperation and cohesion. Because all bison foraged in the limited high-quality patches, it can be argued that cohesion is also a factor of patch quality, as is apparent by all ranks foraging at high GUDs (high patch quality), and lower ranks abandoning patches first as they are depleted. Thus, cohesive foraging requires areas of high-quality resources abundant for all bison to simultaneously feed. Based on this study, a prediction can be made that separating the herd into equal subgroups based on relative rank, where all low-ranked individuals are together, all mid-ranked are together, and high-ranked are together may yield the most cohesive foraging. Although in each group individuals will inevitably assume new ranks of high-low dominance relative to those around them, the net difference in competitive ability will be lesser than if high-ranking individuals were placed in the same enclosure as those with medium or low ranks. The same can be said about grouping mid-ranking with low-rank individuals. If differences in competitive ability are lesser from one bison to the next in each group, it is possible that subordinates will forage from the high-quality patches longer than if they recognized that they are

highly disadvantaged due to the presence of a dominant with a large competitive advantage. This prediction is supported by observations in horses that groups with less variation between individuals experience more displacement encounters and interactions between individuals, suggesting that less variation in traits may increase cohesion (Giles et al. 2015). However, this idea has not been tested in bison and further experimentation beyond the scope of this thesis is required to test this hypothesis.

Unlike captive bison, in less area-constrained free-ranging bison the formation of fission-fusion subgroups occurs naturally to reduce competition for resources (Ramos et al. 2015). Because ranks in this study were associated with different strategies of niche partitioning, i.e., lower-ranked individuals adapted behaviour to initiate movement away from the oat patches, it is possible that the formation of fission-fusion subgroups may occur with lower-ranks initiating fusion. This is supported by previous observations that subgroups tend to be comprised of individuals similar in sex and rank (Ramos et al. 2015), both factors that may relate to dominance status (Rutberg 1983, Roden et al. 2005). Merkle et al. (2015) describe the processes to explain fission-fusion as (1) animals learn new sites by joining those with dissimilar information, (2) the amplification of information will increase frequency of favourable behaviour such as foraging from the best sites, and (3) that knowledge transfer will cause conspecific attraction which will increase crowding and competition. It is predicted that the resulting crowding and competition may cause lower ranks to inevitably initiate new fission processes.

In conclusion, this study highlights three areas where future research should focus. Firstly, studying the effects of additional factors on GUD such as group size,

habitat type, size, and personality, such that management decisions can be made that improve cohesions. Managing factors and maximizing GUDs can promote healthier herds and more effective use of foraging areas. Secondly, effort should be made to further understand the relative impacts of factors on the development of dominance hierarchy in bison calves because of the effect this has on feedback loops that follow bison throughout their lives. Finally, research should also strive to improve the understanding of the relationship between rank differences and cohesion using field studies in open pastures, with the aim of understanding if certain ranks tend to forage more cohesively with one another in a captive environment. Further work on artificial subgroups that are comprised of these cohesively foraging individuals may aid in the implementation of rotational grazing systems for captive bison. With most bison today residing in captivity, maximizing bison occurrence and pasture productivity, i.e., carrying capacity, is a focal concern for farmers and managers. The artificial management of behaviour through selective group composition may offer to aid the implementation of rotational grazing systems and maximize the carrying capacity of area-constrained pastures.

LITERATURE CITED

- Billman, E.D., Williamson, J.A., Soder, K.J., Andreen, D.M. and Skinner, R.H. 2020. Mob and rotational grazing influence pasture biomass, nutritive value, and species composition. *Agronomy Journal* 112:2866-2878.
- Ganskopp D.C. and Bohnert, D.W. 2009. Landscape nutritional patterns and cattle distribution in rangeland pastures. *Applied Animal Behaviour Science* 116:110–119.
- Giles, S.L., Nicol, C.J., Harris, P.A. and Rands, S.A. 2015. Dominance rank is associated with body condition in outdoor-living domestic horses (*Equus caballus*). *Applied Animal Behaviour Science* 166:71-79.
- Green, W.C.H. and Rothstein, A. 1993. Persistent influences of birth date on dominance, growth and reproductive success in bison. *Journal of Zoology* 230:177-186.
- Hayward, M.W., Ortmann, S. and Kowalczyk, R. 2015. Risk perception by endangered bison (*Bison bonasus*) is context (condition) dependant. *Landscape Ecology* 30:2079-2093.
- Hillenbrand, M., Thompson, R., Wang, F., Apfelbaum, S. and Teague, R. 2019. Impacts of holistic planned grazing with bison compared to continuous grazing with cattle in South Dakota shortgrass prairie. *Agriculture, Ecosystems and Environment* 279:156-168.
- Kraai, M. and Shrader, A.M. 2018. How do free-ranging domestic herbivores reduce competition within owner determined herds? *Applied Animal Behaviour Science* 205:8-13.
- Krause, J. and Ruxton, G.D. 2002. *Living in groups*. Oxford University Press, New York. 210 pp.
- McHugh, T. 1958. Social behaviour of the American buffalo (*Bison bison bison*). *Scientific Contributions of the New York Zoological Society* 43(1):1-40.
- Mella, V.S.A., Ward, A.J.W., Banks, P.B. and McArthur, C. 2015. Personality affects the foraging response of a mammalian herbivore to the dual costs of food and fear. *Oecologia* 177:293-303.
- Merkle, J.A., Sigaud, M. and Fortin, D. 2015. To follow or not? How animals in fusion-fission societies handle conflicting information during group-decision making. *Ecology Letters* 18:799-806.
- Neave, H.W., Costa, J.H.C., Weary, D.M. and von Keyserlingk, M.A.G. 2020. Long-term consistency of personality traits of cattle. *Royal Society Open Science* 7:191849.

- Oldham, L., Camerlink, I., Arnott, G., Doeschl-Wilson, A. Farish, M. and Turner, P. 2020. Winner–loser effects overrule aggressiveness during the early stages of contests between pigs. *Scientific Reports* 10:13338.
- Ramos, A., Petit, O., Longour, P., Pasquaretta, C. and Sueur, C. 2015. Collective decision making during group movements in European bison, *Bison bonasus*. *Animal Behaviour* 109:149-160.
- Roden, C., Vervaecke, H. and Elsacker, L.V. 2005. Dominance, age, and weight in American bison males (*Bison bison*) during non-rut in semi-natural conditions. *Applied Animal Behavior Science* 92:169-177.
- Rutberg, A.T. 1983. Factors influencing dominance status in American bison cows (*Bison bison*). *Zeitschrift für Tierpsychologie* 63:206-212.
- Teague, W.R. and Dowhower, S.L. 2003. Patch dynamics under rotational and continuous grazing management in large, heterogeneous paddocks. *Journal of Arid Environments* 53:211-229.
- Veiberg, V., Loe, L.E., Mysterud, A., Langvatn, R. and Stenseth, N.S. 2004. Social rank, feeding and winter weight loss in red deer: any evidence of interference competition? *Oecologia* 138:135-142.
- Vervaecke, H., Roden, C. and De Vries, H. 2005. Dominance, fatness, and fitness in female American bison, *Bison bison*. *Animal Behaviour* 70:763-770.