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Gregarious Behavior in Large Mammals: Modeling, Methodology, and Application

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GREGARIOUS BEHAVIOR IN LARGE MAMMALS:

MODELING, METHODOLOGY, AND APPLICATION

by

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CONTENTS

LIST OF TABLES

vii

LIST OF FIGURES

Figure

Page

ABSTRACT

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by

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Gregarious behavior of ungulates was considered in four ways. The first concern was W. D. Hamilton's hypothesis that a simple movement rule could reduce predation risk and encourage grouping behavior. Simulations showed little effect of this nearest-neighbor rule on predation risk. Similar, more complicated rules reduced predation risk by up to two thirds.

The second focus was on the accuracy of ground observers in diagramming individual animal locations in small herds of elk. A remotely controlled airplane was used to photograph the herds from above. A substantial distance discrepancy was found between "true" and "observed" animal locations. This discrepancy increased with group size and was

different between observers but not between herds. Observers were better at predicting relative animal locations than absolute animal locations.

The third consideration was interanimal spacing in bison herds photographed from an airplane during a three-month period. At later dates photographed herds were located, and cover-sampling methods were adapted to estimate bison visibility in each area. These data were used in linear regression models which explained over two-thirds of the variance in nearest-neighbor distance. Important indicator variables were the number of animals in the herd, a cover measurement, the north and east location of herds, the time photographed, and the fraction of the animals standing.

The fourth focus was the development of simulations of simple movement rules used to mimic grouping behavior. Individuals moved according to two simple first nearest-neighbor rules: if within a minimum distance, move directly away, and if outside a maximum distance, move directly toward. Four other rules were used to determine individual states. Two different measurements were made for each simulation run: the overall mean nearest-neighbor distance and the overall mean subgroup size. Results showed that the means and variances of near-neighbor distances decreased as the number of individuals in the simulation increased. Different near-neighbor rules had little effect on mean nearest-neighbor distance. All rules produced results similar to each other and different from bison data. A random model was more similar to the bison data. (132 pages)

CHAPTER I

INTRODUCTION

Gregariousness is a conspicuous behavior in the animal kingdom. Familiar examples are herds of large, grazing ungulates in east Africa or the formerly prominent bison on the Great Plains of North America. Social ungulates are quite adaptive, occurring from tropical and temperate areas to the polar regions; they form a conspicuous resource and have historically captured man's interest. That interest is currently reflected in the enormous quantity of research these species inspire. Yet, despite much investigation, the mechanisms underlying gregariousness in ungulates are poorly understood. Aggregation may be the result of chance, resources, predation, or a combination of factors, the relative importance of each depending upon the species and location.

In ungulate research little attention has been given to the interaction between individual behaviors and the internal dynamics of herds. Many researchers have addressed the question of why a herd forms, but few have actually collected sufficient data on herd structure to address the questions of how a herd forms and how its members coordinate their movements. In other words few people have considered how the interactions of individuals operate to produce the behavior of the herd.

Two prominent hypotheses concern the mechanisms of gregariousness in ungulates. The first is that animals aggregate in

response to predation; the second is that animals aggregate in response to resources (Alexander 1971; Bertram 1978; Sinclair 1985; Wrangham & Rubenstein 1986). The majority of the theoretical arguments have invoked predation as the overriding cause of gregariousness (e.g., Brock & Riffenburgh 1960; Treisman 1975). As a result, only in recent years have sound resource-based arguments surfaced, these supported from observations of African ungulates (Jarman 1974; McNaughton 1984). I will review the literature concerning the effects of predation and of resources on ungulate grouping behavior.

The theoretical arguments for the importance of predation revolve around the influence of grouping on detectability of prey, detectability of predators, and the vulnerability of prey to capture. Early work on prey clumping and detection by predators was performed by Brock and Riffenburgh (1960), who argued for the benefits of schooling in fish via the decreased probability of visual detection. Their deduction followed from three relatively inconspicuous assumptions: that predators have a low satiation level compared to the number of prey per group, that groups are no more detectable than individuals, and that predators continue to search at random even after initial contact with prey. Taylor (1976, 1984:105) argued that such assumptions are only valid for ambush predators, those exhibiting no complicated group-following behaviors but simply attacking prey within range. In such a case uncaptured prey flee after an initial attack and break contact with the predator. Taylor's model verified that

prey always benefit from aggregating when faced with ambush predation. These studies suggest that detection of prey is reduced by grouping, although the specifics of predatory behavior are important considerations.

A good deal of theoretical work has also been done on the detection of predators by prey, or vigilance behavior. An early paper by Treisman (1975) presented a formal model based on signal detection theory. He modeled a contest of detection between predator and prey, predicting that the likelihood of detection is inversely related to the number of neighbors and that grouped animals do better than dispersed ones. A more recent theoretical paper constructed a model based upon the risks of starvation and predation with various environmental and behavioral considerations (Lima 1987a). His results addressed the change in scanning rate in relation to group size, resources, and distance to cover. An empirical test of the model demonstrated that individual vigilance (i.e. scanning) decreased with increased group size and distance to cover, although sparrows preferred to forage close to protective cover (Lima 1987b). This supports previous studies reporting a decrease in individual vigilance with group size but questions findings that vigilance increases with distance to cover. Lima discusses these contradictory data in light of two opposing functions of cover, either as a haven for prey or a harbor for predators. In the first, prey increase their vigilance up to some threshold distance, then abandon vigilance in an effort to minimize time away from protective cover (Barnard 1980; Caraco *et al.* 1980; Caraco & Bayham 1982; Lima 1987a,

1987b). In the second, cover serves as a visual obstruction to prey, allowing predators the concealment for stalking and ambush. In this case prey appear to minimize vigilance close to cover in an effort to minimize the time in a dangerous area (Metcalfe 1984; Lima 1987b). These studies suggest that the interrelations of group size, resources, and distance to cover are complex and sometimes nonintuitive. (See Elgar [1989] for a review of vigilance behavior.)

The benefits of grouping may also lie in decreased individual vulnerability to attack and capture. An idea verbalized by many (e.g., Williams 1964) but first formalized by Hamilton (1971) and Vine (1971) is that in the absence of protective cover individual animals should seek shelter behind conspecifics; that gregariousness originates from selfish cover-seeking behaviors. Hamilton's selfish-herd concept assumes that individuals attempt to minimize the probability of being closest to an ambush predator. This is accomplished by placing protective cover (i.e., neighbors) between oneself and the predator to reduce one's domain of danger, the probability of being the individual attacked. Given this assumption, Hamilton demonstrated mathematically that the selfish avoidance of a predator could lead to aggregation. This model was further developed by Vine (1971) to include two dimensions and a predator searching from outside the immediate environment of the prey. Vine predicted that the greatest individual security is achieved by a circular flock and is maximized by prey locating inside the periphery of this flock.

Logical implications of this selfish-herd idea are that individuals should favor central positions within a group and that, once initiated, grouping should persist, even in the immediate absence of the predator.

The selfish-herd idea was proposed over twenty years ago, and since then has been cited heavily as a mechanism of gregariousness in ungulates (e.g., Eisenberg 1981; Sinclair 1985). Such citations are not surprising, for Hamilton specifically mentioned African cattle as an example of his model, yet little empirical work has been done to test the predictions. Recent studies on vigilance provided indirect supportive evidence for the selfish-herd idea. It has been shown that peripheral animals are more vigilant than their central counterparts for various birds and ungulates (Berger 1978; Jennings & Evans 1980; Lipetz & Bekoff 1982; Alados 1985; Petit & Bildstein 1987; Berger & Cunningham 1988).

The effects of resource distribution on the social behavior of ungulates has seen much less theoretical development. Jarman (1974) was one of the first to seriously discuss resources as a major influence on gregariousness. He proposed that the physiological constraints of foraging define an upper limit on group size, while predation pressure defines a lower limit. Using African antelope as an example, he reasoned that small ungulates with high energy demands should be selective feeders, extremely particular in their choice of vegetation and plant parts. Because of these special foraging needs, which make resources limited, small ungulates should be solitary or found in small bands with other kin. In contrast,

larger ungulates, whose energy requirements demand a higher volume of food, should be generalists in their selection of plant parts. Their resources, which are relatively abundant in a local, short-term sense, facilitate larger groups. These groups, however, quickly deplete local resources and need to migrate constantly. In large species, maximum group size should be constrained by limits on coordination of members.

Jarman explained grouping behavior by claiming predation as the primary driving force, and resources as the secondary driving force. Although his arguments are based on interspecific comparisons of ungulates, they should hold intraspecifically as well. Ungulate behavior is quite plastic. Eisenberg (1981:208) stated that "variation in group size and group composition can be shown within a species over a geographic range." Leuthold and Leuthold's (1975) observations of African ungulates have supported the idea of intraspecific variation within aggregating species; they found significantly larger groups in more open vegetation types. Similar data have been presented by Jungius (1971), Walther (1972), and Franklin *et al.* (1975).

Since the publications of Hamilton (1971), Vine (1971), and Jarman (1974) only a few studies have attempted to distinguish between the effects of predation, cover, and resources on ungulate grouping behavior. Hirth (1977) compared group sizes of white-tailed deer in a deciduous woodland habitat in Michigan to those in a brush-savanna habitat in Texas. His study concentrated on gregariousness as an antipredatory response and

supported predictions that group size is inversely related to the amount of cover. His results, however, may be confounded by differences in both the distribution of food and the hunting pressure between the two areas; consequently, they do not distinguish unambiguously between the effects of resources and predation.

A similar study by LaGory (1986) addressed the influence of cover on group size in white-tailed deer. Within each of three different habitat types (forest, woodland, and grassland), deer were observed for group size, nearest-neighbor distances, intraspecific interactions, and individual time budgets. LaGory demonstrated that individual vigilance increased while group size and nearest-neighbor distances decreased from open pastures to forested areas. This supports predictions of an antipredatory mechanism for grouping: groups become more tightly packed and individuals become more wary as cover (i.e., risk of ambush) increases.

In spite of these results, LaGory concluded that his "time budget data did not support the hypothesis that habitat differences in group size reflect different anti-predator strategies" (LaGory 1986:176). He argued that if cover-seeking behavior occurs, then individuals moving from coverless to covering environments should be less wary. His data demonstrate the opposite, that individuals become more wary as cover increases. There appears to be confusion between Hamilton's use of cover (i.e., a target prey between one's self and the predator) and Lagory's definition (i.e., vegetation or any visual obstruction). In the first case, an

animal can use "cover" as protection from predation and maintain his visibility and vigilance. In the second case, "cover" hinders an animal's ability to detect approaching predators and to communicate with other vigilant conspecifics. It follows then that vigilance may increase with cover that hinders visibility. Metcalfe's (1984) results with shorebirds support this conclusion, as well as do observational data on African antelope (Underwood 1982). In both cases, as with LaGory (1986), vigilance increased with cover and decreased visibility.

A third study was performed by Berger *et al.* (1983) on pronghorn in southern Utah. They observed animals for group size, vigilance, escape effort, and foraging efficiency in two areas with (assumed) equal predation pressure but unequal resource and disturbance levels. They demonstrated that mean group size was larger for disturbed animals and larger than predicted for optimal foraging. They concluded that pronghorn subjected to human disturbance, as opposed to coyote predation, form larger groups, are more vigilant, and have a greater flight distance than undisturbed pronghorn. Their data support antipredator predictions if one considers human disturbance (e.g., hunting) as predation.

This brief discussion of spatial resource patterns and ungulate grouping reveals how little empirical work has been done on the subject and how much confusion exists between "cover" in the sense of density and distribution of resources, "cover" in the sense of protection from predators, and "cover" as a physical block to visibility and visual communications.

The purpose of the present work is to consider spacing behavior in American bison *(Bison bison)*, once a prominent member of the North American plains ecosystem (Yoakum 1978). Bison are quite gregarious and probably evolved under pressure from Pleistocene predators such as cursorial bears, large felids, and large canids. In some areas modern predators still exist such as bears, bobcats, coyotes, wolves, and native Americans.

The discussion of gregarious behavior in large ungulates consists of five parts. The first simulates simple nearest-neighbor rules and grouping behaviors according to Hamilton's (1971) selfish-herd concept (Chapter II). The second assesses the accuracy of human observers in determining spacial location data on grouping ungulates (Chapter III). The third analysis addresses bison data and a variety of indicator variables of spacing (Chapter IV). Modeling is the topic of Chapter V, where simple movement rules are analyzed in another context. Finally, a synopsis of the study is delivered in Chapter VI.

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CHAPTER II

THE SELFISH HERD REVISITED: DO SIMPLE MOVEMENT

RULES REDUCE RELATIVE PREDATION RISK?

ABSTRACT

Over two decades ago W.D. Hamilton argued that animal grouping behavior could evolve if individuals selfishly avoided predation by reducing their domains of danger (Voronoi polygons). I examined this hypothesis through dynamic simulations of individual movement directed by a nearest-neighbor and other simple rules. Results from 500 simulations of 100 individuals moving towards their nearest neighbors for 100 moves (time steps) showed a 20% increase in relative predation risk and a 1.2% decrease when adjusted for edge effects. This increase was 16% less than that of a random movement rule. When the two rules competed in a two-strategy game simulation, the nearest-neighbor rule always performed better than the random-movement rule with up to 41% differences in relative predation risk. The use of more complicated rules, based on consideration of multiple neighbors, decreased relative predation risk as much as 67%. These slightly more complicated movement rules are adequate to explain the evolution of grouping behavior.

INTRODUCTION

Two reasonable explanations why animals aggregate are to increase
resource acquisition and to reduce predation risk (Alexander 1974; Jarman
1974; Bertram 1978; Sinclair 1985; Folt 1987; Fryxell 1991). One
mechanism by which an individual might reduce predation risk is to
aggregate with other individuals, thereby reducing the probability of
consumption by a satiable predator. Hamilton (1971) argued that a simple
movement rule for selfish individuals can generate and maintain
aggregation by reducing predation risk. Hamilton's hypothesis countered a
group-selection explanation for gregarious behavior (Wynne-Edwards 1962)
and is currently a popular explanation for animal aggregation, receiving
over 600 citations in reference to the antipredatory function of prey
grouping. I explored the logic of Hamilton's argument through simulation
models and assessed the ability of simple movement rules to reduce
exposure to predation, thereby encouraging gregarious behavior.

METHODS

Hamilton's model began with prey randomly positioned on a two-
dimensional plane. At any time and position within the nonaggregated
field of prey a predator could appear and capture the closest prey. This
idealized predator was free from other constraints such as prey detection
distance, predator pursuit, or prey evasion. Thus, the probability of a prey

being captured depended upon the area of a Voronoi polygon surrounding each prey (see Rogers 1964; Cruz Orive 1979; Aurenhammer 1991). This area, labeled the domain of danger (or DOD) by Hamilton (1971:301), contains "all points nearer to the owner of the domain than to any other individual." He asserted that under these conditions a prey individual benefits by moving towards its nearest neighbor, thereby reducing its DOD and predation risk. He suggested this nearest-neighbor rule as a simple yet effective way to avoid predation. (For theoretical support of this idea see Cannings & Cruz Orive 1975.) Although this model is much simpler than others (e.g., Brock & Riffenburgh 1960; Turner & Pitcher 1986), plausible examples of this situation do exist, for example a group of surface-dwelling aquatic insects preyed upon from below (e.g., whirligig beetles) or a herd of grazing ungulates (e.g., zebras) unknowingly surrounding a hidden lioness.

I investigated nearest-neighbor and other simple rules by simulating the movement of individuals. (Hereafter, movement behavior rules are designated by the letter 'N' and a value representing the number of closest neighbors used in determining an average location, e.g., nearest neighbor = N1.) Voronoi polygons were calculated at time-steps 0 and 99 for 100 individuals in each of 500 simulations. Individuals began at random locations in an area of 500 x 500 units and, thereafter, were not restricted by boundaries. An individual's next position was determined by the angle to the average location of its n-closest neighbors and an arbitrary move

distance of 8 units, or one-half a bodylength (BL=16 units). All individuals were moved and the process repeated for a total of 100 time steps. This procedure differs from Hamilton (1971) where animals jumped to their nearest neighbor in one time step. However, this difference had little effect on the results. Simulations were stopped after 100 iterations because preliminary results showed that most individuals had reached subgroups from which they did not exit in that time. For consistency with a simulation of random movement (N0), individuals were not stopped after reaching a subgroup.

My analysis differs from Hamilton in another important way; his example detailed the movement of only one individual while I based my results on the behavior of many individuals. Hamilton extrapolated his results from single to groups of individuals but failed to mention the potential statistical problems of considering herds with multiple interactions among finite numbers of animals. My analysis used all individuals when possible or only individuals with closed (finite) polygons when necessary to avoid meaningless calculations with open polygons. I also analyzed central individuals, those fifty whose most distant polygon vertices are closest to the group center, in an attempt to eliminate edge bias (see Donnelly 1978; Haefner *et al.* 1991). I consider the analysis of all individuals to be a literal interpretation of Hamilton (1971), the analysis of finite individuals to be a realistic interpretation, and the analysis of central individuals to be a liberal interpretation.

Hamilton (1971) predicted that an individual's DOD would decrease with movement to its nearest neighbor and suggested that similar behavior would be profitable for all individuals. To test this prediction, I calculated each individual's change in DOD from start to finish. These values from all 100 individuals in a simulation produced skewed distributions. Therefore, the median, rather than the mean, of each distribution was selected as a best average measure of change in DOD. This median value is reported in two ways: as an area (BL^2) and as a percent. The latter, referred to as relative predation risk, is the change in DOD divided by the median DOD of evenly distributed individuals over the same initial area (i.e., 9.76 BL^2).

Hamilton (1971) also asserted that DOD is more likely to increase if individuals move toward isolated members of the group and decrease if individuals are surrounded by many neighbors. I interpreted an "isolated nearest neighbor" (Hamilton 1971:303) to be a nearest neighbor who in turn has a large nearest-neighbor distance. Therefore, to test the former assertion the nearest-neighbor-distance of an individual's nearest neighbor was regressed on change in DOD for individuals of 500 simulations. To test the latter assertion, the number of sides of an individual's DOD was considered equal to the number of neighbors. I then regressed the number of polygon sides on change in DOD for relevant individuals of 500 simulations. I report the number of regressions with significant slope and R^2 values.

Although Hamilton (1971) did not mention this, I suggest that if N1 is an evolutionarily beneficial rule, then the majority of the individuals using N1 should decrease their DOD. To evaluate this prediction about N1, I calculated the percentage of 100 individuals whose DOD decreased between time-steps 0 and 99 for each simulation. I considered the change from an infinite to a finite DOD as a decrease, and similarly a change from a finite to an infinite DOD as an increase, in DOD. Individuals beginning and ending with an infinite DOD were not included in the calculations.

My second analysis compared N1 to a random movement model, N0. The random movement algorithm selected random angles for each individual at each time step. Otherwise, the simulations and analysis were identical to N1.

I increased the realism of Hamilton's model by simulating rules which produced larger average group sizes. (For examples of larger naturally occurring groups see Breder 1967; Treherne & Foster 1982; Petit & Bildstein 1987; Berger & Cunningham 1988.) Hamilton (1971) argued that large groups will form because individuals in small groups will see a common advantage for their group to consolidate with other groups. Without debating whether this concept violates the hypothesis of individual selection, I have not tried to simulate such a complex rule. However, I did hypothesize that individuals decrease their DOD by moving towards multiple neighbors, rather than single individuals. Two types of rules were simulated. In the first type, individuals moved toward the

average location of their n-closest neighbors. For example, using N2 a prey determines its nearest neighbor and its second closest neighbor. The prey then moves toward the average location of the two neighbors. I report results using 2, 3, 5, and 9 near neighbors.

The second type of rule, the Quadrant Rule, approximated a high-order rule in which individuals moved towards an area with a high density of neighbors. To accomplish this, an individual uses itself as the origin of a fixed coordinate system and counts the numbers of individuals in each of the four quadrants. The individual then moves towards the middle of the quadrant with the greatest density of individuals. Density is calculated as the total number of individuals within a quadrant divided by the approximate area of that quadrant.

My final evaluation of Hamilton's model was also suggested by his methodology. Hamilton determined all initial individual DOD, moved a single individual, and assessed this individual's change in DOD in relation to others. This "evolutionary" approach suggests that individuals using one movement strategy may benefit when competing with others using different strategies. (For examples see Hines 1987; Axelrod & Hamilton 1981.) To implement a similar approach I simulated a herd in which a fraction of individuals used N1 and the remainder N0. Each simulation was conducted as before with the modification that only 10, 50, or 90 of the 100 individuals used the N1 rule. At the end of each simulation a comparison of the change in DOD from each strategy was made.

RESULTS

The plots of individuals' positions and their corresponding DOD are markedly different between random, nearest-neighbor, and nine-closest-neighbor movement rules (Fig. II-1). DOD distributions become more bimodal and group size increases as the order of the rule increases, i.e., the number of neighbors per individual calculation increases.

Hamilton (1971) predicted that DOD will decrease as an individual moves closer to its nearest neighbor. Simulations of N1 for 100 time steps did not support this prediction; the average DOD from start to finish using all individuals increased by 20%, or 2.00 BL^2, while using central individuals the average DOD decreased by 1.2%, or 0.12 BL^2 (Fig. II-2, A and B). Analyzing the data another way, 51% of the individuals decreased their DOD when using N1. This result held when analyzing all individuals and central ones (Fig. II-2, C and D).

Two other assertions by Hamilton (1971) were that DOD is more likely to increase if individuals move toward isolated members of the group and decrease if individuals are surrounded by many neighbors. First, I found no positive correlation between the degree of isolation of a nearest neighbor and change in DOD. Of the 500 regressions conducted, only 3% from the finite approach, and only 1% from the central approach resulted in significant positive slopes, but with poor fitting lines (R^2 values fall between 0.05-0.11 and 0.10-0.26, respectively). Second, I found that the

number of neighbors surrounding an individual was weakly correlated with decreases in DOD. Nine percent of the simulations using finite individuals and 59% of the simulations using central individuals had significant negative slopes (R^2 values range from 0.05-0.14 and 0.08-0.50, respectively).

Further analysis compared the random movement model N0 to N1. When using N0 and all individuals there was a mean median change in DOD of 36.4% (3.55 BL^2). This significant increase was 15.9% (1.55 BL^2) greater than that of individuals using N1 (two-sample t-test for unequal variances, df=975.1, P=0.0002; Fig. II-2, A and B). The central individuals showed a similar but much less pronounced pattern. For example, an analysis with N0 and central individuals produced a mean median increase in DOD of 4.4% (0.426 BL^2). This was significantly greater than the decrease using N1 (two-sample t-test for unequal variances, df=942.4, P<0.001).

The percentage of individuals with decreasing DOD also varied between rules N0 and N1. I found that for N0 only 43.6% of all individuals decreased their DOD. This was a significant 7.4% decrease from N1 (two-sample t-test for unequal variances, df=967.4, P<0.0001). Again, the differences were apparent but less pronounced for the central individuals. I found that only 46.8% of the central individuals decreased their DOD. This was a significant 3.5% decrease from N1 (two-sample t-test for unequal variances, df=950.7, P<0.0001).

Comparisons of N0, N1, and higher-order rules showed that the average individual DOD declined, and a greater percentage of individuals decreased their DOD, as rule complexity increased (Fig. II-3). The mean median DOD values for all individuals ranged from an increase of 36.4% to a decline of 48.2%. There was significant overall heterogeneity when main effects were rules (one-way ANOVA, df=3499, f=1260.8, P<0.0001) and all rules were significantly different (Duncan's Range test, α=0.05). The central approach produced similar results with more pronounced benefits as rule order increased. The mean median DOD values ranged from an increase of 4.6% to a decline of 67.2%. There was significant overall heterogeneity when main effects were rules (one-way ANOVA, df=3499, f=2062.4, P<0.0001) and all rules were significantly different (Duncan's Range test, α=0.05).

A similar trend was seen with the percentage of individuals decreasing their DOD; as rule complexity increased more individuals benefitted. The percentage of all individuals with decreasing DOD ranged from 38.2 to 77.2, showing significant overall heterogeneity when main effects are rules (one-way ANOVA, df=3499, f=2848.6, P<0.0001). All rules were significantly different (Duncan's Range test, α=0.05). The central approach produced slightly higher but similar results ranging from 46.9% to 82.4% and significant overall heterogeneity (one-way ANOVA, df=3499, f=1539.2, P<0.0001), although rules Quadrant and N5 were statistically indistinguishable (Duncan's Range test, α=0.05).

The results from simulations with individuals of various strategies (Fig. II-4) demonstrated that N1 produced significantly larger decreases in DOD than N0 in all cases, except when N1 was absent (MANOVA, using rules N0 and N1 as groups, Wilke's lambda = 0.3408, df = 3, 185.75 [F-ratio approximation], $P < 0.0001$). Analysis of central individuals (Fig. II-4, B) revealed that individuals using N1 always reduced DOD while those using N0 always increased DOD. Furthermore, N1 appeared to do best when relatively scarce. N1 produced significantly larger decreases in DOD than N0 in all cases (MANOVA, using rules N0 and N1 as groups, Wilke's lambda = 0.3345, df = 3, 195.75 [F-ratio approximation], $P < 0.0001$).

DISCUSSION

The effects of ecological factors on sociality in various animals are well documented and numerous examples abound (see Rubenstein & Wrangham 1986). Among the possible evolutionary advantages and disadvantages of sociality, especially gregariousness, are a reduction in the effects of predation, an increase in resource exploitation distribution, and increased intraspecific competition (Wrangham & Rubenstein 1986). The focus of Hamilton (1971), and this paper, was a theoretical yet specific example of how gregariousness might evolve from selfish behavior, i.e., the reduction of predation risk through simply moving towards the nearest neighbor.

Overall, my results do not support Hamilton's model. My simulations demonstrated that using the simple nearest-neighbor movement rule has little effect on relative predation risk. Hamilton's rule taken literally resulted in an increase in relative predation risk and, when adjusted for edge effects, produced only small relative predation risk reductions. Furthermore, slightly more than one-half (i.e., 51%) of the individuals decreased their relative predation risk from start to finish. These mild reductions were surely not the strong evolutionary consequences of selfish behavior envisioned by Hamilton (1971). However, individuals using the nearest-neighbor rule did perform better than individuals using the random rule. This was true when comparing the rules from independent simulations and from the two-strategy game. N1 always performed better than N0 and demonstrated a reduction in relative predation risk when adjusted for edge effects.

My simulation emphasizes two points about Hamilton's model; it is a reasonable and detailed hypothesis for the evolution of gregariousness in some individuals but is ambiguous about how the details apply to all individuals. The former allowed me to simulate the model while the latter forced me to interpret and modify it. The most pronounced modification was in terms of which individuals to include in calculating relative predation risk. This is a question of scale. Individuals with open polygons or infinite DOD could not be used in calculations of change in relative predation risk. This forced me to focus on individuals with closed polygons

or finite DOD at the beginning and end of the simulations. In an effort to test the spirit of Hamilton's model, I also concentrated on the central most individuals which I considered free of edge effects. In all cases my results produced questionable support for Hamilton's model.

Improvements on Hamilton's model might come from two sources. The first would be the use of similar but more complicated rules in the model. I accomplished this by creating higher-order rules where individuals moved towards multiple, rather than single, neighbors. This resulted in a decrease in relative predation risk as the number of neighbors being considered increased. This decrease corresponded to an increase in the percentage of individuals decreasing their relative predation risk. The implication is that moving towards neighbors reduces one's relative predation risk much better than moving towards a nearest neighbor. There is independent confirmation of these findings. A recent model of school formation has shown that individuals averaging their decisions over multiple neighbors rather than a single one demonstrate schooling behavior similar to that of real fish schools (Huth & Wissel 1992).

Complicated rules, although producing more realistic group behavior, may be difficult for individuals to perform. Moving towards one's nearest neighbor is an easy task and one which could probably evolve (Hamilton 1971). It is conceivable that computing the average position of one's first through third near neighbor is possible for large ungulates.

There may be "rules-of-thumb" that make this easy (e.g., based on the percentage of the visual field occupied by a neighbor). However, evaluating the average position of nine near neighbors is clearly a difficult computation. I doubt that real organisms use such a rule, even though it might be to their advantage. For this reason, I analyzed the Quadrant Rule. I conjectured that visually ascertaining which of a few coarse divisions of space (quadrants) contained the greatest density of neighbors was feasible for primitive brains. Such a rule would not require counting, averaging or sophisticated memory, but simply the ability to determine the segment of the horizon that has the most neighbors (e.g., dark objects). The vertebrate visual system seems adapted for the task.

Second, Hamilton's model might be improved with the addition of more realistic constraints. The most apparent is the addition of detection distances. Limits on the predator detection distance were employed by Brock & Riffenburgh (1964) and also for the prey by Vine (1971). The latter was an extension of Hamilton's model where a predator attacked from outside the group of prey. Turner & Pitcher (1986) have used risk of capture in an evolutionary approach model. Others have modeled animal movement on two-dimensional surfaces and considered feeding (Murai *et al*. 1979) and mating behavior (Gibson *et al*. 1990). I have not modified Hamilton's model because my intention was to test its validity and not to build realism.

In conclusion, I agree with Hamilton and others that aggregation can lower individual predation rates, but I do not agree that simply moving towards the nearest neighbor is an effective mechanism. My simulations suggest that the natural selection of selfish individuals using simple movement rules to produce aggregations can occur, especially if individuals consider more than one neighbor at a time.

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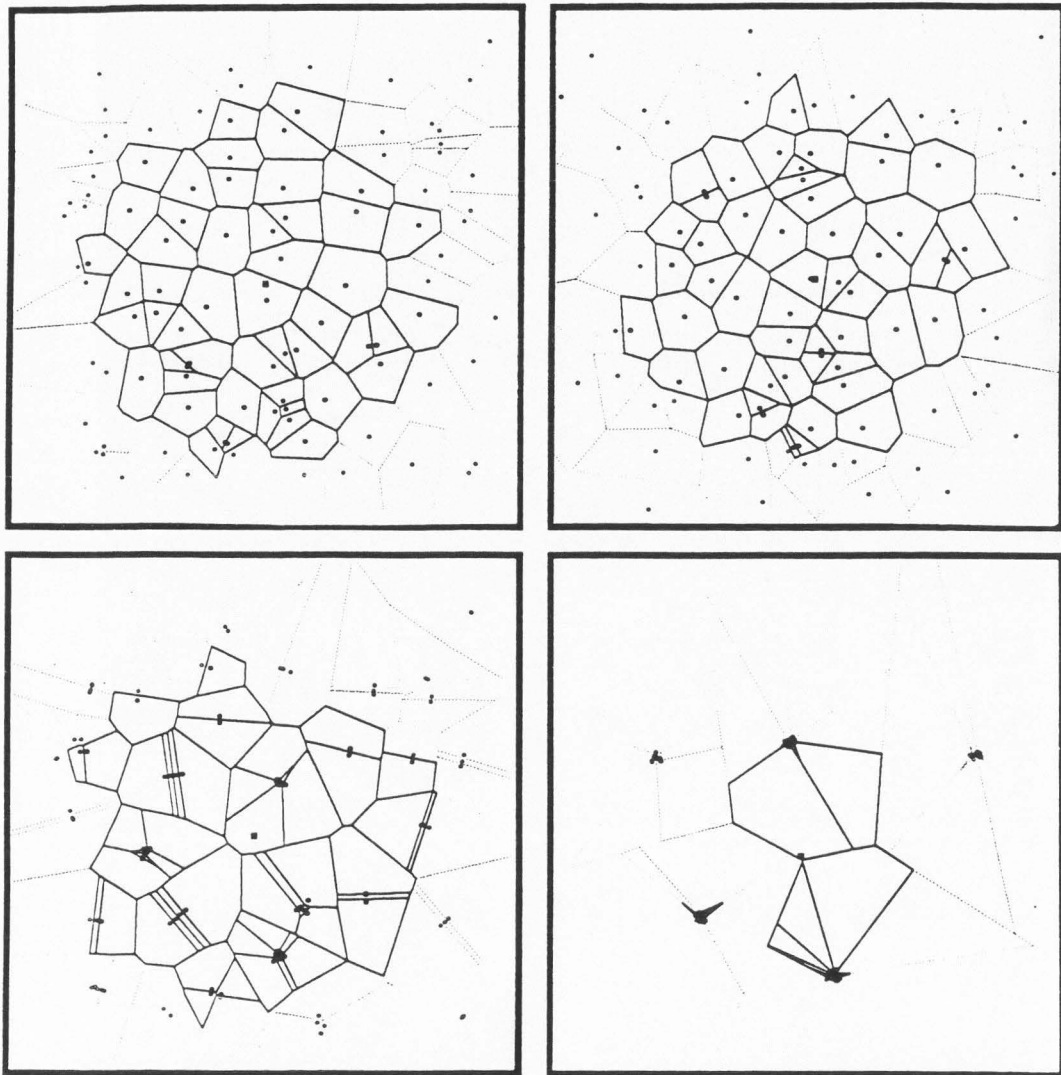
Figure II-1. Voronoi polygons, Hamilton's (1971) domain of danger, calculated from a computer simulation of 100 animals (circles) randomly distributed on a two-dimensional plane at time-step 0 (A). Polygons represent central (solid) and peripheral (dashed) individuals' domains of danger from predator attack. Results after 99 iterations are shown for individuals moving randomly, N0 (B), towards their nearest neighbor, N1 (C), and towards the average location of nine-closest neighbors, N9 (D).
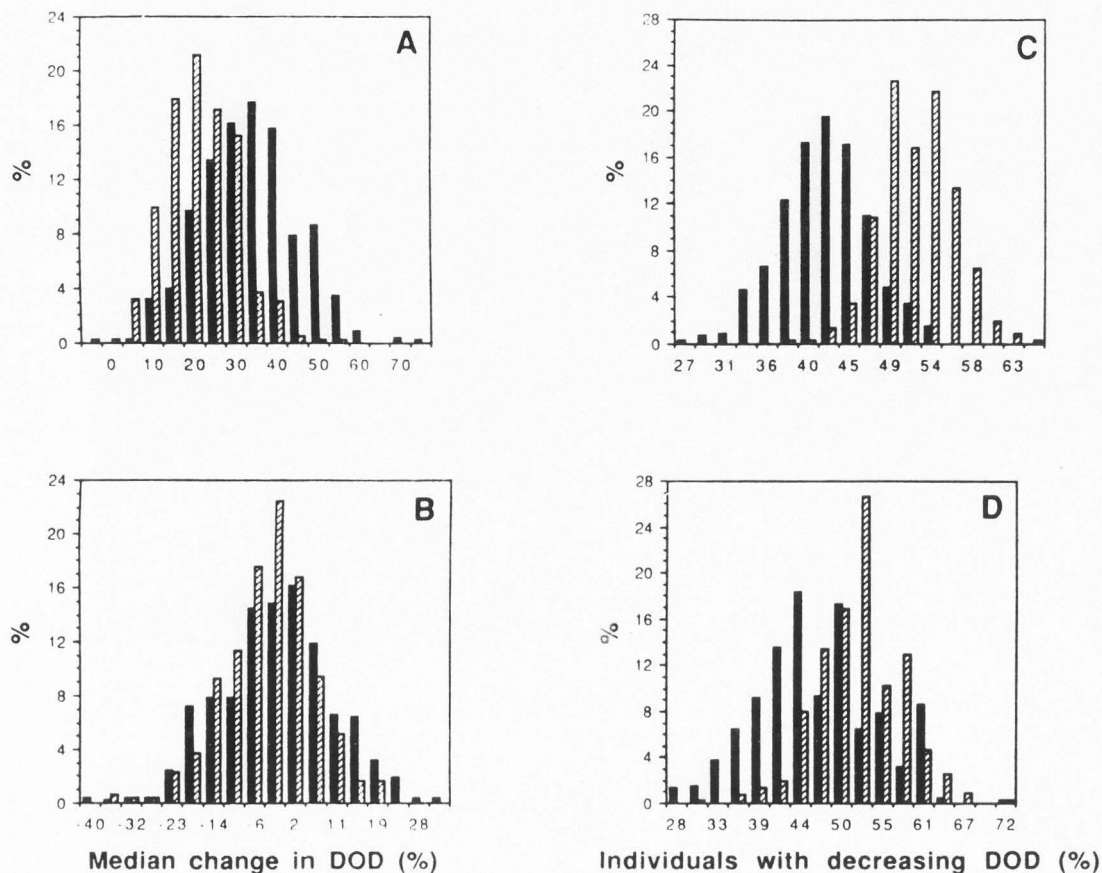
Figure II-2. Comparisons of changes in domain of danger (DOD) for frequency distributions of 500 simulations of N0 (closed bars) and N1 (hatched bars). The median change in DOD is given for all individuals (A) and for central individuals (B). Likewise, the mean percentage of the herd with decreasing DOD is given using all individuals (C) and only central individuals (D). For C and D, proportions are transformed using the arc-sin of the square root of the frequencies.
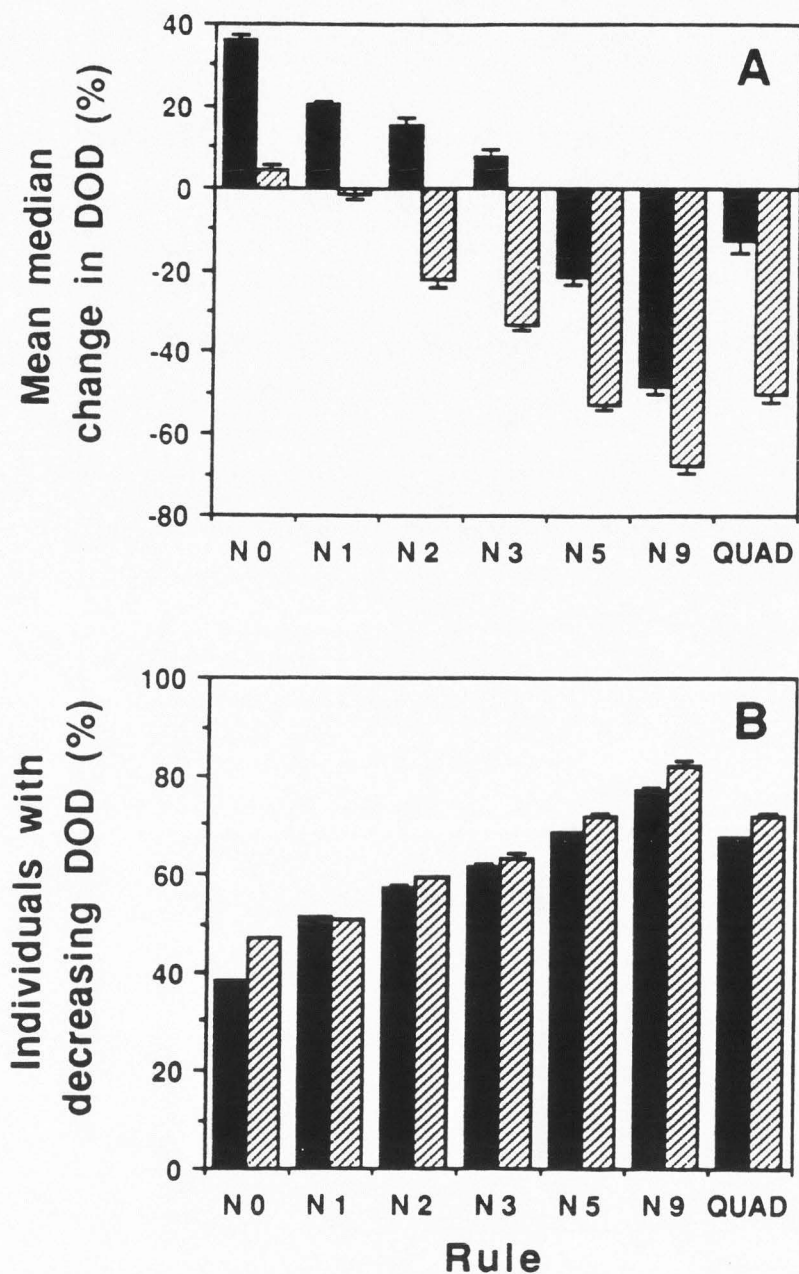
Figure II-3. Comparison of seven different rules using all individuals (closed bars) and central individuals (hatched bars). Results are given as mean ($\pm$SE) median change in DOD (A) and the percentage of individuals decreasing their DOD (B). The Quadrant Rule (Quad) is listed last.
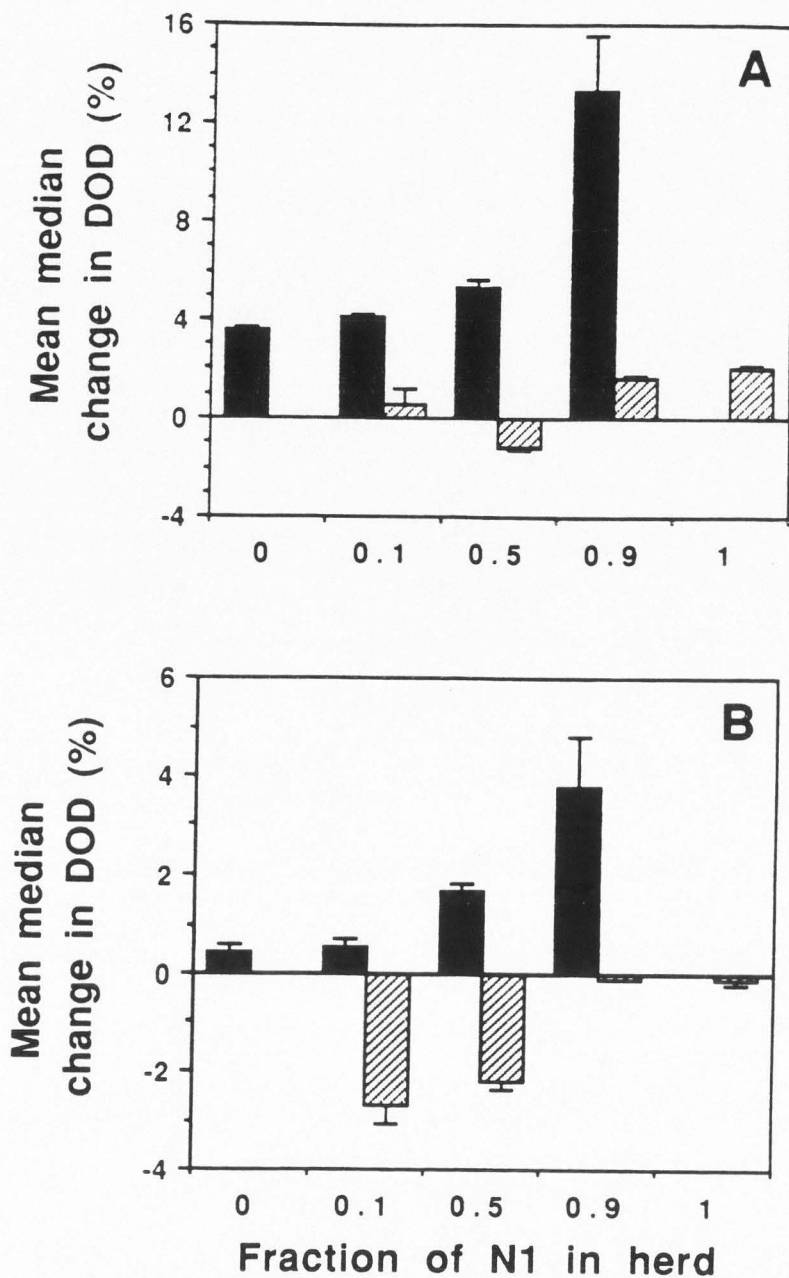
Figure II-4. Comparisons of the two strategies N0 (closed bars) and N1 (hatched bars) interacting at various relative proportions. Results given as mean median change in DOD using all (A) and only the central individuals (B). One hundred simulations were used per proportion. Error bars are $\pm$ 1 SE.

CHAPTER III

ACCURACY OF GROUND OBSERVERS IN DETERMINING UNGULATE LOCATIONS WITHIN HERDS

ABSTRACT

Ground observers diagrammed individual animal locations in small herds of resting Rocky Mountain elk (*Cervus elaphus*). Simultaneously, a remotely controlled airplane was used to photograph the herds from above. The distance discrepancy between expected animal locations (from aerial photographs) and observed animal locations (from observer diagrams) averaged 5.6 body lengths (BL). Projecting observations onto axes parallel and perpendicular to the observers' lines of sight revealed that the discrepancy along the parallel axis (5.0 BL) was significantly greater than along the perpendicular axis (1.7 Bl). Some observers performed better than others in judging perpendicular-axis locations, some herds were more accurately diagrammed than others, and observers were not necessarily consistent in diagramming different herds. Average observer accuracy along the perpendicular axis decreased with the number of elk per group. The orientation of the herd also affected average observer accuracy. Observer diagrams were also analyzed for categorical location of animals (i.e., the placement of individuals into general categories such as front or back, central or peripheral). Accuracy ranged from 31 to 89% depending on the distance measurement and the category.

INTRODUCTION

The study of gregarious organisms has focused mainly on the question of why individuals group. Recently, this has meant quantification of individual behaviors varying with location within groups. Such research has been spread across taxonomic boundaries, many times focusing more on behaviors than on the organisms. For example, recent research has addressed the three-dimensional locations of swarming insects and schooling fish, ground and air locations of birds in flocks, male locations in bird and large mammal leks, and vigilance and foraging success according to location within monkey troops and ungulate herds (e.g., Major & Dill 1978; Partridge *et al.* 1980; Caraco & Bayham 1982; Shinn & Long 1986; Berger & Cunningham 1988; Gosling & Petrie 1990; Janson 1990a, 1990b; Gibson 1992). Although these studies involved unrelated organisms and may have had quite different objectives, they were usually interested in variation in individual behavior according to location within groups. Such variation may be a result of ecological pressures such as predation, resource distribution, and competition and is often documented as differences in foraging success, vigilance towards conspecifics and predators, and social status and leadership roles (Alexander 1974; Wrangham & Rubenstein 1986).

The study of behavioral variation in gregarious species requires different levels of accuracy in sampling spatial locations. This resolution

is particular to each investigation and the question or questions asked. Measurements may range from simple inclusion in a group or not, such as individuals being closer to one set of organisms than another, to precisely mapped locations of individuals within a group (Alados 1985; Caraco & Bayham 1982). The level of accuracy required in each investigation is not always apparent at the outset. One example of this concerns the study of spatial relationships in schooling fish. Early work considered only the two-dimensional structure of fish schools, mainly because of limitations in photographic techniques. The belief was that fish swam in a lattice formation along two-dimensional planes stacked vertically and received a hydrodynamic benefit from schooling. Innovative techniques in measuring three-dimensional fish locations demonstrated that fish were not positioning themselves in horizontal planes (Partridge & Pitcher 1979). Fish seemed to be more concerned with retaining maneuverability and visual range than with the hydrodynamic effects of neighbors (but see Abrahams & Colgan 1987). For this example an improved sampling method allowing higher data resolution resulted in new findings contrary to popular belief.

Studies of gregarious ungulates vary widely in the number of animals considered and the types of spatial measurements used. Recent studies have considered mother/young distances as well as those of other paired individuals and nearest neighbors (Lagory *et al*. 1981; Byers & Byers 1983; Crowell-Davis 1986; Lagory 1986; Ralls *et al*. 1987; Fitzgibbon

1989; Green *et al.* 1989; Green 1992a). Generally speaking, spatial location has been coarsely measured, with individuals usually placed in categories. For example, evaluation of larger numbers of individuals ranged from measuring the progressive order of individuals in transit to estimating distances between nearest neighbors and between grouped individuals (Gilbert & Hailman 1966; Reinhart 1983; Stuwe 1986; Schulte & Klingel 1991). In addition, some studies have considered the locations of individuals relative to others, i.e., near the center or edge of the group (Underwood 1981; Lipetz & Bekoff 1982; Underwood 1982; Berger *et al.* 1983; Alados 1985; Berger & Cunningham 1988; Prins 1989; Prins & Iason 1989; Fitzgibbon 1990a, 1990b; Balmford & Turyaho 1992).

As these studies varied in measurement methods, they also considered a wide variety of ungulate species in natural and artificial settings. Crowell-Davis (1986) observed mother/young relationships of Welsh ponies on a farm while Schulte and Klingel (1991) observed domesticated camels. Semiwild cattle were studied by Reinhart (1983). Others have observed wild ungulates held in captivity (Gilbert & Hailman, 1966; Ralls *et al.* 1987). The majority of the studies considered wild ungulates from natural settings in Africa, North America, and Europe (see above).

The first purpose of this chapter was to measure the accuracy of ground observers in determining elk locations within herds. I compared observer estimates to known animal locations. The second purpose was to

evaluate ground observers' ability to assess the elk locations relative to other individuals, the progressive order of individuals, and the radial location of individuals (i.e., central versus peripheral locations).

METHODS

Small herds of Rocky Mountain elk (*Cervus elaphus*) were diagrammed by ground observers and simultaneously photographed with a remotely controlled airplane. The estimated animal locations (from observer diagrams) were compared to the true animal locations (from the photographs) and these data analyzed to see how accurately observers estimated animal locations. Data were also used to assess the accuracy of observer techniques employed in other gregarious ungulate studies.

The experiment was conducted on the afternoon of 30 March 1989 at Hardware Ranch, Utah, an elk winter feeding area. The refuge is maintained by the Utah Division of Wildlife Resources and consists of a large meadow bordered by low hills (Fig. III-1). Within this meadow three to four groups of wild elk were present: herd A was free-ranging, herd B was confined to pen 1, and herds C and D were subgroups of a larger herd in pen 2.

The equipment used to photograph each elk group consisted of a Senior Telemaster model airplane carrying a 35 mm Ricoh camera. The camera was equipped with an autowinder, a databack, and an electronic shutter release. The 2.4 m wingspan airplane and the camera were

controlled with a Futaba Conquest AM six-channel radio operating five servo units mounted in the plane.

The photographic accuracy of this equipment was tested using a calibration grid composed of nine 77 cm high barrels spaced 10 m apart in a three-by-three grid arrangement. The airplane was flown over the grid at various altitudes by three different controllers. Photographs were taken during each pass and later analyzed for comparison to ground measurements. I considered the average error of 1.6% ($\pm$0.3, 95% CI) between photographs and true locations to be trivial; therefore, all photographed point coordinates were considered true locations.

The field procedure consisted of observers diagramming elk locations within four herds. Each herd was simultaneously diagrammed and photographed. The airplane was flown four times, once over each elk group, within a 1-h period. The airplane controller was located in a parking lot approximately 1 km from the herds, while the three observers with binoculars or spotting scopes were stationed on a hill approximately 0.8 km from the herds (Fig. III-1). The slope of the hill was 10%, although the apparent viewing angle, accounting for the elevation of each herd and the distance from observers, varied from 1.0 to 3.0°. Only observer 1 had prior field experience with ungulates. On a diagram sheet each observer drew the animal head positions represented by circles, animal orientations represented by trailing lines, interanimal distances given in body lengths

(BL = the longest measurement of animal length), and a scale indicating average animal body length.

These diagrams were digitized and then transformed to be comparable with one another and the photographed elk locations. To facilitate comparisons, I transformed all coordinates in three ways. I determined the average animal location in each diagram or photograph and made it the origin of a Cartesian coordinate system. Animal locations were then scaled relative to the center of each group. Points were also scaled according to the average body length estimated by observers for each diagram and calculated from the digitized head and tail points from each photograph. Lastly, points were rotated so that the y-axis was parallel to the observer's line of sight (e.g., Fig. III-2).

The data analysis was partitioned so as to answer three questions: how accurate were observers, how could they be improved, and how do these results apply to other studies? To answer the first question, I calculated the distance, or exact "discrepancy," between observed and true animal head point locations relative to the center of the herd. This was performed for Euclidean and x-axis and y-axis distances. I only analyzed data for reclining (i.e., resting) animals common to all observer diagrams for each herd.

The experimental design was a repeated measure with three treatments in a mixed univariate analysis general linear model (SAS 1989). This allowed me to test for the effects of different observers

(treatments), of different herds (groups), and the interaction of observers and herds, on discrepancy. I also tested whether mean discrepancies were different from zero. (Differences were considered significant at $\alpha=0.05$.)

I next investigated whether or not observer inaccuracies could be corrected or at least improved. First, observed animal locations were regressed on true animal locations to predict individual observer error for each diagram. Standard ANOVA and linear regression were used with the Euclidean, x-axis, and y-axis distances. Regression analyses were compared for differences within observers. Results suggested that observer discrepancies might arise from a simple scaling problem.

Second, I scaled herd diagrams with herd photographs to see if observers had correctly diagrammed elk locations but incorrectly estimated body lengths, or the scale of the diagram. I calculated the herd width, the largest distance between any two animals along the x-axis, for each herd photograph and its corresponding observer diagrams. This procedure was repeated for herd length along the y-axis. Diagram points were then scaled by the photograph scaling factor along each axis. These factors were the herd photograph width divided by diagram width along the x-axis, and herd photograph length divided by diagram length along the y-axis. This resulted in diagrammed herds having the same overall dimensions as the corresponding photographed herd. Another discrepancy analysis was performed on these scaled data.

The next set of analyses compared my results to published studies on gregarious ungulates -- an analysis of the general locations of individuals, or categorical elk locations. Categorical elk-location analysis consisted of assessing the exact order of animals, identifying the front and back individuals, indicating the extreme individuals, and distinguishing between central and peripheral animals. In each case the percentage of animals correctly placed was scored for each diagram.

The order of animals was calculated from the inside to the outside of the herd (Euclidean distance), from left to right (x-axis distance), and from front to back (y-axis distance), for each photograph. Identical methods were used for each diagram and these results compared to the photograph results. A similar procedure was conducted for general animal location by splitting photographed and diagrammed herds into one-half sections and again scoring observer diagrams according to photographed herds. For the "front" analysis, I assessed the number of animals correctly placed in the front one-half of the herd for Euclidean distance, the left side for the x-axis, and the bottom for the y-axis. For the "center" analysis I calculated the number of animals correctly placed in the more central half of the herd. These animals had the smallest Euclidean distances or the closest coordinates to zero on the x-axis and y-axis. All sample sizes were truncated for herds with an odd number of animals. A similar analysis was performed for "extreme" individuals; I chose the two animals with the

largest Euclidean distance or, for the x-axis and y-axis, animals with the most negative and positive locations.

For the last categorical analysis, I distinguished between central and peripheral animals using previously published definitions. Fitzgibbon (1990a) defined peripheral individuals as those with no neighbors within a 180° arc and all others central individuals. Similarly, Green *et al.* (1989) defined peripheral individuals as those with no neighbors within a 90° arc on the side away from the group center. Central individuals were those surrounded by neighbors on all four sides. All other individuals must be considered intermediate since Green's two definitions are not mutually exclusive. Using these definitions, I placed animals in either central, peripheral, or intermediate categories and compared the results from observer diagrams to photographs.

The final analysis was exploratory in nature and addressed the effects of herd characteristics on the accuracy of observer diagrams. ANOVA and linear regression analysis were used to check for correlations of discrepancy and percentage correct with herd size (all visible animals) and herd orientation (the direction of the major axis of the herd). The herd orientation for each photograph was estimated as the slope of the line found by regressing the y-axis on the x-axis coordinates.

RESULTS

The average observer discrepancy (5.6±0.6 BL) was significantly different from zero (df=66, t=8.38, P<0.0001). This was similar to the discrepancy parallel to the line of sight (5.0±0.7 BL along the y-axis) but much larger than the discrepancy perpendicular to the line of sight (1.7±0.2 BL along the x-axis), although both were significantly different from zero (df=1, t=7.50, P<0.0001; df=1, t=7.64, P<0.0001, respectively). Observer discrepancies were not different in Euclidean or y-axis distances, but were significantly different in the x-axis distance (Table III-1). Differences were also seen between herds for Euclidean, x-axis, and y-axis distances. Lastly, there were herd/observer interaction effects for Euclidean, x-axis, and y-axis distances.

It appears that some observers performed better than others in judging x-axis locations. This is apparent when comparing the average discrepancies of the observers (Table III-2). Some herds were more accurately diagrammed than others; the mean discrepancy in Euclidean distance ranged from 1.7 to 7.3 BL (Table III-2a). And observers were not necessarily consistent between herds; there appeared to be an observer-herd interaction.

The scaling of the diagrams to the photographs decreased the average herd discrepancies substantially; Euclidean discrepancy declined by 48% while x-axis and y-axis discrepancies were reduced by 29 and 51%,

respectively. Reductions in the individual herd discrepancies were varied, ranging from 19-76% (n=10), with six of these over 50%. The y-axis and Euclidean distances for Herd A were exceptions and increased 29 and 6%, respectively.

I accessed observer accuracy without modifying point locations by scoring observers according to how well they ordered or grouped individuals. The accuracy varied greatly between different measures and distances, ranging from 31 to 89% (Table III-3).

Analysis of the literature definitions of central and peripheral indicated that both techniques were fairly accurate, but suggested that Fitzgibbon's 180° was more reliable than Green's 90°. The observer average across herds was 81% ($\pm$5) for 90° and 89% ($\pm$2) for 180°. The herd average, across observers, was 81% ($\pm$6) for 90° and 88% ($\pm$7) for 180° and for 180°.

The last results concern an exploratory analysis approach searching for factors correlated with observer discrepancy and percent accuracy. ANOVA and linear regression analysis indicated that the Euclidean and y-axis discrepancies were correlated to the herd axis direction (df=1, F=12.01, P=0.074, R^2=0.8573; df=1, F=17.59, P=0.052, R^2=0.8979). Similarly, the x-axis discrepancy was significantly correlated to group size, indicating an increase in discrepancy with increase in the number of animals (df=1, F=18.63, P=0.050, R^2=0.9031).

DISCUSSION

Ungulate field studies often require accurate assessment of animal location in relation to conspecifics, environmental structures, or the observer. The last can be accomplished by estimating distances, as in flight distances in white-tailed deer, and then measuring those distances (Lagory 1987). Most studies either estimate the absolute distance between individuals or visually place individuals into spatial categories. These observations are invariably made from the ground at a distance of 1-500 m (e.g., Crowell-Davis 1986; Prins 1989). Some of the observers are checked for accuracy at a later date, but most are not or are checked incorrectly. The absolute distance is often measured as the distance between two individuals, as in mother and young dyad distances or as nearest-neighbor distances.

My results indicate that ground observers judged elk locations poorly and, on average, misjudged locations by 5.6 BL. This was true for all three observers, regardless of prior experience observing large ungulates. If I estimate an adult elk BL at 1.5 m, I have an average error of 8.4 m, a rough estimate of the error associated with estimating distances between individuals.

Most of the studies concerning spatial location in dyads are concerned with very close associations and utilize distance categories in estimation. For example, Ralls *et al.* (1987) estimated various ungulate

mother/young distances at <1, 1-2, and >2 m, while Green (1992a, 1992b) used 1 and 10 m boundaries for estimation. My results have little application to studies such as these where observers are in close contact with the subjects, the subjects are within a few meters of each other, or fairly liberal distance categories are used. One notable exception is Byers and Byers (1983) in which pronghorn mother/young distances averaged 50-75 m and showed high variance. The exact distance estimates were made while mothers were grazing away from hidden fawns. My results suggest that the high variability about the mean may be less a result of the mother/young interaction and more a result of observer error.

Studies estimating nearest-neighbor distances are less easy to summarize, but address interanimal distances from 1 to 100 m, use various observer distances, and concern animals within groups. Sometimes categories were used, as with Alados (1985) where an animal within 50 m of a group was considered a member of that group. Mostly distances were estimated within 1 m or 1 BL for a focal animal and its nearest neighbor (Lagory *et al.* 1981; Lagory 1986; Fitzgibbon 1990a). In one study the average nearest-neighbor distance was estimated for groups of 200 buffalo (Prins 1989). Another study gave little information on the method, result, or error (Underwood 1982).

Most of the studies estimating nearest-neighbor distance do not give enough information to evaluate the possible observer error. For example, I have demonstrated that ground observers did better in judging distances

perpendicular to their line of sight rather than parallel, on average 2 versus 6 BL, respectively. These results were true for all three observers and were not surprising. One would expect distance estimation to be better from left to right than from front to back, as inaccuracies in depth of field estimation increase rapidly with distance. Yet few studies indicate the spatial relationship of the observer and the subjects. My results suggest that estimates made from animals aligned perpendicular to the observers' line of sight are more accurate than estimates from other alignments. In fact, the spatial relationship of a focal animal and its neighbors may affect the ability of the observer to choose the correct animal for the nearest neighbor.

Although observers did poorly on average, they diagrammed some herds more accurately than others (compare Herds A and C in Table III-2a). This was supported by the finding of significant herd effects and high variances associated with average herd discrepancies. One obvious difference in the herds was the group size. I found that the x-axis discrepancy was significantly and positively correlated with group size, suggesting that diagramming becomes harder as the picture becomes more complex. The y-axis discrepancy was not found to be correlated to group size. I suggest that the observers' poor diagramming along the y-axis masked any group size effect.

Another difference between the herds was the general orientation of the herd. Herd A's major axis was oriented along the x-axis while the

other three herds' major axes were oriented more along the y-axis. I found a significant correlation between herd axis direction and the average Euclidean and y-axis discrepancies. I suggest that herds oriented along the x-axis are more accurately diagrammed by observers.

Observers were consistent in their errors. The fact that average herd discrepancy was reduced by one half when diagrams were scaled to photographs suggests that observers underestimated body length size on diagrams. This assertion is also supported by ANOVA and linear regression results which indicate inaccurate but precise observer diagramming; high correlations were found in significant regressions of diagram and photograph locations. Overall, observers appear to be consistent in their discrepancies, depending upon the measurement, although still inaccurate. Average herd discrepancy remained high at 3 BL even after scaling.

Few studies have measured exact distances between individuals when observing grouped ungulates (see exceptions above). Most have relied on the order or categorical classification. Observation of the order of moving individuals has been used mainly on captive ungulates such as wild fallow deer and semiwild domesticated cattle and camels (Gilbert & Hailman 1966; Reinhart 1983; Schulte & Klingel 1991). The flight order, the first to move, was observed as five age-sex classes in wild white-tailed deer (Stuwe 1986).

My observers were poor at ordering individuals. They were correct only one-third of the time for Euclidean distance and about one-half of the time for the x-axis and y-axis. These observations, however, were made of stationary groups and not of mobile animals walking along a relatively straight path. Most studies relying on the accurate ordering of animals placed observers close to the subjects and relied on straight-line paths.

Most studies used spatial categories to describe ungulate locations within animal groups. The methods can be placed into two groups, arbitrary and radial. Two studies placed animals in arbitrary categories according to the general direction of movement of the group. Underwood (1982) scored animal locations as frontal, flanking, rear, central or unclassified. Prins (1989) used similar methodology and scored animal locations according to the front 10%, subfront 10%, center-front 10%, center 40%, center-rear 10%, subrear 10%, and the rear 10%. The location of the observer is not given in either study, although from the categories chosen by Prins (1989) it appears that animal groups moved perpendicular to the observer's line of sight (along the x-axis of my study). I found that along the x-axis observers placed elk correctly in the front one-half of the group 89% of the time and in the center one-half 80% of the time. Similar percentages were found for the y-axis.

Most ungulate studies describe individuals according to radial locations, as central and peripheral members of the group. Most of these give no clear definition separating the two categories (e.g., Underwood

1981; Lipetz & Bekoff 1982; Berger *et al.* 1983; Alados 1985; Berger & Cunningham 1988; Prins & Iason 1989; Balmford & Turyaho 1992). For example, Alados (1985) defined a central animal as one surrounded by other animals, although it is unclear what the operational definition of "surrounded" is. Given this uncertainty, I first tested the accuracy of observers in choosing the two most peripheral, or extreme, animals. Observers chose correctly the two elk furthest from the group center 54% of the time, the two elk flanking the group along the x-axis 67% of the time, and the elk closest and furthest from the observer along the y-axis 59% of the time.

I next took two operational definitions and tested them with the observer diagrams (Green *et al.* 1989; Fitzgibbon 1990a, 1990b). In general, observers averaged 80-90% accuracy. Fitzgibbon's 180° was better than Green's 90° and appears easier for observers to use in the field as less observer discrimination and calculation is required.

I have shown that a substantial amount of error is associated with diagramming the spatial location of ungulates. This error is more pronounced when estimating distance locations than when categorizing animals in groups. Whether or not the error in diagramming ungulate groups affects a study's conclusions depends on the accuracy needed for that data. Studies which are mostly concerned with relative animal spatial location (e.g., Byers & Byers 1983; Prins 1989; Fitzgibbon 1990a)

are probably more affected than ones concerning group size and vigilance behavior (e.g., Lipetz & Bekoff 1982; Lagory 1986).

The accuracy in diagramming spatial location varies with the methods used, or the resolution needed in the study. Observers were correct 89% of the time when diagramming the front of the group and only 58% of the time when describing the individual order along the x-axis.

I conclude that ground observers are poor but consistent in describing actual animal locations and fair in estimating categorized animal locations. This consistency suggests that observer diagrams may be corrected, within limits. I have two suggestions for improving these types of spatial studies; determine the amount of error allowable for the study and test observers *a priori* to determine their accuracy level. To improve the accuracy of observer estimates I suggest performing calibration procedures before observers begin field observations. The testing of observers may allow the use of linear regression to reduce individual observer error in the field.

One way to calibrate observers is to have them view stationary subjects under simulated field conditions. For example, objects similar in size and shape to actual subjects are placed randomly in groups and diagrammed by observers from the expected viewing angle and distance. (In most cases viewing distances are large and angles small so that group movement will not have a significant effect on viewing angle.) Numbers and arrangements per group should be varied to simulate field encounters.

Analyses similar to ours should be performed with ANOVA and regression

to calibrate each observer's mean discrepancy and error interval.

Observations of animal locations in the field can then be partially

corrected.

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Table III-1. ANOVA results for (a) Euclidean, (b) x-axis, and (c) y-axis distances.

(a)

Source	df	F	P
Herd	3	7.74	0.0005
Observer	2	1.02	0.3673
Herd * Observer	6	5.67	0.0001
Residual (Observer (Animal Herd))	66	8.38	0.0000

(b)

Source	df	F	P
Herd	3	7.09	0.0008
Observer	2	6.60	0.0024
Herd * Observer	6	9.96	0.0000
Residual (Observer (Animal Herd))	66	7.64	0.0000

(c)

Source	df	F	P
Herd	3	6.63	0.0016
Observer	2	0.01	0.9853
Herd * Observer	6	2.59	0.0259
Residual (Observer (Animal Herd))	66	7.50	0.0000

Table III-2: Mean discrepancy (±SE) for (a) Euclidean, (b) x-axis, and (c) y-axis distances for observer diagrams.

(a)

Observer	Herd			
	A	B	C	D
1	1.6 (1.5)	8.5 (4.7)	4.4 (3.4)	6.7 (2.6)
2	2.3 (1.1)	6.9 (3.8)	5.3 (3.9)	8.1 (2.6)
3	1.3 (1.1)	9.2 (5.4)	5.4 (4.0)	7.1 (2.4)
Mean	1.7 (1.2)	8.2 (0.9)	5.0 (1.4)	7.3 (1.1)

(b)

Observer	Herd			
	A	B	C	D
1	0.4 (0.2)	2.7 (4.7)	0.7 (0.6)	1.1 (0.7)
2	1.5 (0.6)	1.6 (1.1)	1.0 (0.7)	3.4 (1.7)
3	0.2 (0.1)	2.3 (1.9)	1.5 (0.9)	3.7 (1.7)
Mean	0.7 (0.4)	2.2 (0.3)	1.1 (0.4)	2.6 (0.3)

(c)

Observer	Herd			
	A	B	C	D
1	1.5 (1.5)	7.9 (4.7)	4.4 (3.3)	6.7 (2.8)
2	1.5 (1.4)	6.6 (4.0)	5.2 (3.8)	6.9 (3.2)
3	1.3 (1.1)	8.6 (5.7)	5.1 (4.1)	5.5 (3.1)
Mean	1.4 (1.2)	7.7 (1.0)	4.7 (1.4)	6.2 (1.1)

Table III-3: Percentage correct (±SD) in determining animal placement for various distance measurements and methods.

Distance Measure	Method							
	Order		Front		Center		Extreme	
Euclidean	31	(20)	-	-	77	(16)	54	(9)
X-axis	58	(28)	89	(13)	80	(15)	67	(41)
Y-axis	52	(39)	85	(19)	72	(18)	59	(42)
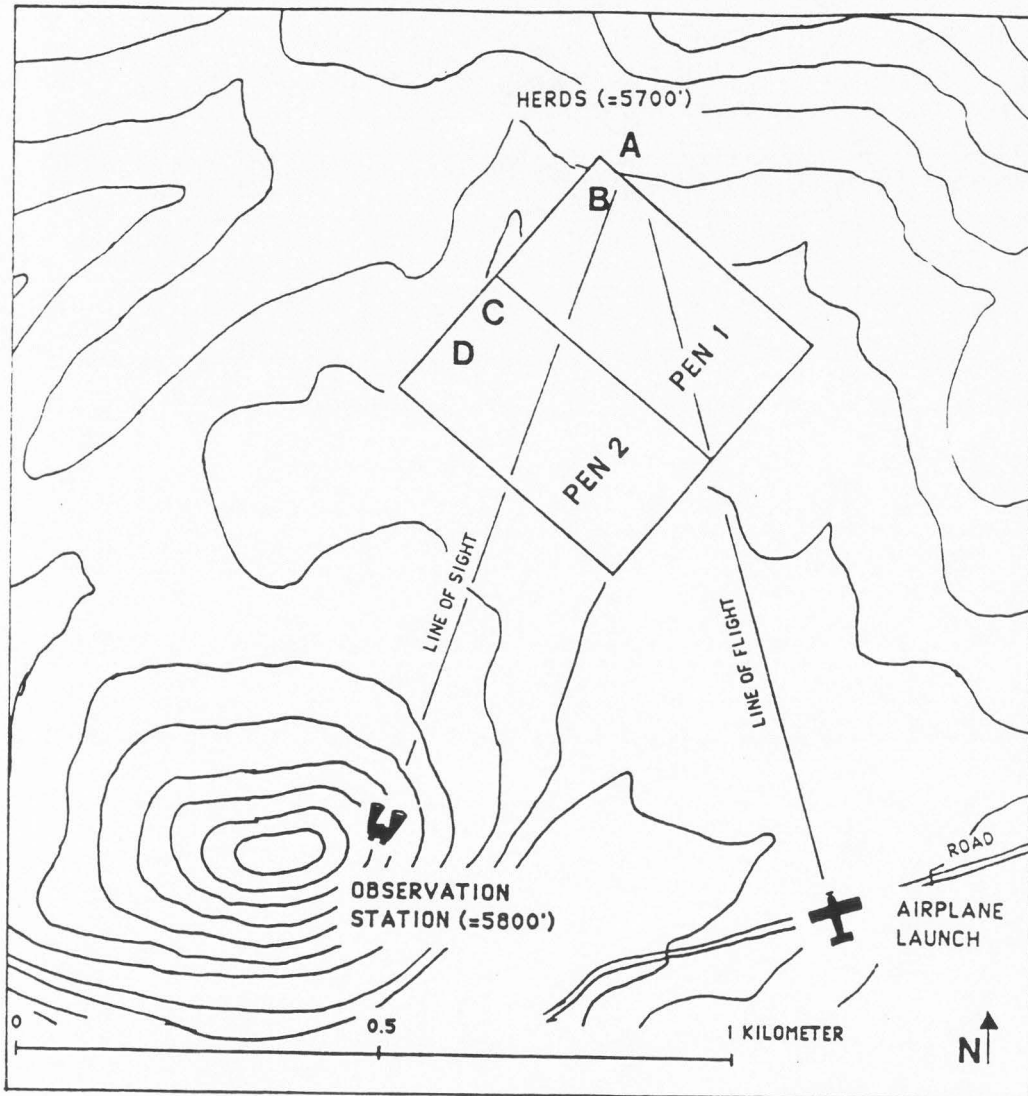
Figure III-1. Hardware Ranch study area with 12.2 m contours and approximate herd positions labeled as A-D.
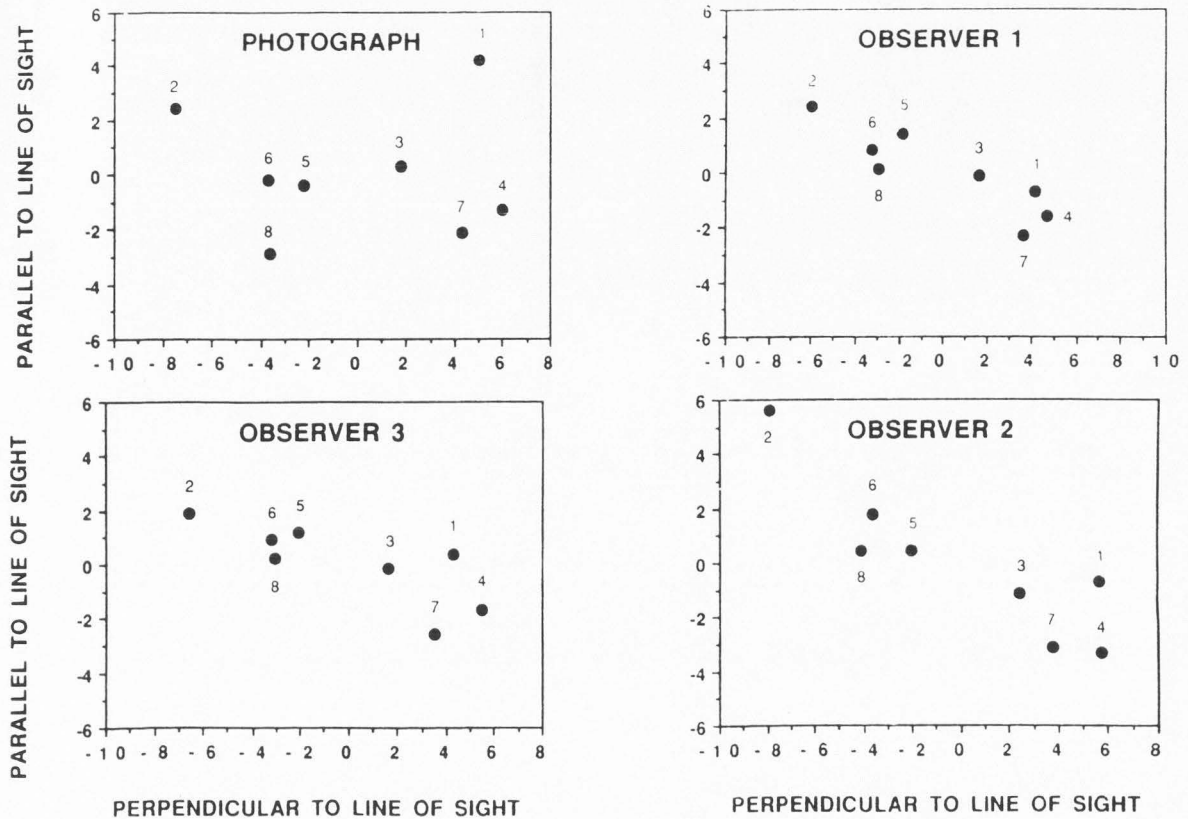
Figure III-2. Diagrams of Herd A taken from a photograph and three observer sketches. Points are numbered for comparison and represent the head location of each animal. Units are average animal body length.

CHAPTER IV

SPACING OF BISON WITHIN HERDS ON ANTELOPE ISLAND

ABSTRACT

Bison herds on Antelope Island, Utah were photographed from an airplane during a three-month period. Interbison spacing was measured, and cover habitat was estimated for each herd. Regression models suggested that the group size and the visibility in an area were important indicators of average nearest-neighbor distance. Other significant indicator variables were the geographical location of the herd, time photographed, and activity variables.

INTRODUCTION

Ungulates are typically thought to aggregate in response to proximate causal factors such as resource distribution and predation (Alexander 1971; Jarman 1974; Wrangham & Rubenstein 1986). For example, large migrations of wildebeest and other African ungulates in the Serengeti Plains are highly correlated with the seasonal distribution of food (see Maddock 1979). The evolution of highly gregarious species, such as bison in North America, may have been a result of ultimate causal factors such as past predation pressure in the Pleistocene that may or may not be reenforced by current predation pressure. (For a general discussion of the evolution of bovid sociality see Eisenberg 1981.) Ungulates

susceptible to predation are usually quite vigilant and actively monitor

conspecifics for reactions to predators (see Elgar 1989). Vigilance is

related to group size and properties of the habitat, such as topography and

vegetative cover (Lima 1987a, 1987b; Lima & Dill 1990). Some

researchers have observed that gregarious species close ranks when they

feel threatened (e.g., Kitchen 1974; pers. obs.). This may occur when

predators are nearby or hard to detect or when visual contact with

conspecifics is limited. The purpose of this study was to investigate the

relationship of bison spacing to other herd and environmental

characteristics.

A number of studies have investigated different aspects of grouping

behavior in ungulates. Few have measured interanimal distances in

groups and the factors affecting such distances. Prins (1989) visually

estimated average nearest-neighbor distance (NND) for groups of African

buffalo during different seasons in Tanzania. Others estimated NND for

selected individuals in African antelope, white-tailed deer, and bison

mother/daughter dyads and adult groups (Lagory *et al.* 1981; Underwood

1982; Lagory 1986; Rutberg 1986; Green 1992a, 1992b).

In contrast, many researchers have characterized various ungulate

herds in terms of size and group composition. For example, water buffalo

and African buffalo herds demonstrate a fusion-fission pattern of grouping

that is influenced by herd size (Tulloch 1978; Prins 1989). A similar

pattern with diffuse social units has been found in nonterritorial eland and

territorial Thompson's gazelles (Hvidberg-Hansen & De Vos 1971; Underwood 1981). Other studies have concentrated on herd composition and size in European and American bison (Krasinski 1978; Oosenbrug & Carbyn 1985; Calef & Van Camp 1987). Berger and Cunningham (1988) compared feeding patterns and group size among four ungulate species: bison, bighorn sheep, pronghorn, and mule deer. Lagory (1986) considered habitat effects on group size and interanimal spacing in white-tailed deer.

The most commonly cited factor extrinsic to the herd is predation pressure. Carbyn and Trottier (1987) showed that bison calves exhibit more intense grouping behaviors than adults and form small subgroups within herds called calf pods. A study comparing bison from areas with and without wolf predation suggested that adult behaviors do not differ between sites (Berger & Cunningham 1988).

Other environmental variables such as visibility and available cover influence antipredatory behaviors and intraspecific interactions (Green et al. 1989). Studies with white-tailed deer suggested that group size decreases as visibility decreases (Hirth 1977) and that NND decreases as visibility decreases (LaGory 1986). Prins (1989) showed that group size, NND, and vegetation type were related in African buffalo groups. Lastly, other African ungulates showed increased vigilance in closed habitats and decreased NND (Underwood 1982). These and other studies suggest that many factors affect spacing in gregarious ungulates. I hypothesize that interanimal spacing is dependent on the number of animals in the herd

and the ability of individuals to view their surroundings. These proposals were investigated with bison on Antelope Island. The study was carried out in three parts. The first concerned adaptation of habitat-sampling methods for use on Antelope Island. The second compared two different methods of assessing the ability of bison to visualize conspecifics and predators. The third related visibility and other factors to interbison spacing.

METHODS

Two types of data were collected for this study. Bison herds were photographed to measure interanimal spacings, and habitat measurements were taken at selected herd locations to estimate animal visibility. I consider visibility to be the ability of bison to view other individuals, particularly conspecifics and predators. Data were collected from Antelope Island in the Great Salt Lake in Utah, USA. The island is characterized by a ridge extending north-south and a gently sloping eastern aspect. The northern end has gently sloping hills and ridges. The vegetation is dominated by grasses, with less than 1% of the surface area covered by trees (for a detailed description see Wolfe & Kimball 1989). Approximately 500 bison reside on the island. The animals have been rounded-up annually since the fall of 1987, but otherwise they are free-ranging.

Bison were photographed from fixed-wing aircraft during the spring of 1990. The pilot flew directly over various bison groups at an altitude of

150-500 m. I positioned a Ricoh 35 mm camera, equipped with autowinder, databack, and a leveling bubble, on the side of the plane and photographed each bison herd during each 20-30 minute pass. Diagrams were drawn from projected images of each herd and interanimal spacing was measured from the 376 resultant diagrams. The procedure was similar to that used for measuring elk herds (see Chapter III), except locations were digitized according to three bison points: the center of the head, shoulder, and base of the tail. The points of each diagram were scaled according to the mean bison body length (BL).

Seven NND descriptors were calculated for each herd: mean, median, standard deviation, range, interquartile range, and minimum and maximum values. Preliminary regression analysis suggested that the mean NND of each photograph was as good a response variable as any of the others; therefore, it was used in the analysis. This value was the arithmetic mean of all NNDs without duplication of reflexive pairs, those NNDs shared between two animals.

Visibility measurements were made for 30 of the 101 photographed herd locations. Sampling was limited to the northern region of Antelope Island (Fig. IV-1), since the remainder of the island burned after the herds were photographed but before visibility sampling began. Data collection was limited further to site locations that could be identified from photographs. Only one time and location were used for each herd.

I adapted techniques from previous studies to estimate a bison's ability to scan its surroundings. In all cases map coordinates of previously photographed bison-herd sites were determined and a temporary transect, oriented parallel to the main axis of the herd, was established at each site. Three observer points were located at 20 m intervals along each transect with the middle point at the approximate herd center. At each observer point I measured the visibility of objects from various distances along four radii, one located in each quadrant (Fig. IV-2).

The "index" method utilized a "cover" pole to measure the density of cover in an area (adapted from Nudds 1977 and Griffith & Youtie 1988). This 2 m pole of white PVC pipe was marked every 20 cm with orange tape (Fig. IV-2) and placed at each distance location. At each observer point I scanned the cover pole and recorded the number of consecutive increment marks visible from the top of the cover pole. All observations were made from a height of 120 cm, the approximate eye level of a bison, and with binoculars to insure that only obstacles, and not poor eye-sight, affected readings.

The "scanning" method was used by Risenhoover and Bailey (1985) to quantify habitat cover in bighorn sheep. From the center of various habitats they estimated the percent of each quarter of the compass over which an object the approximate shoulder height of an adult sheep could be seen at 40 m. Percentages of the four quarters were then averaged. I modified the procedure and used two objects. The first, the "predator"

method, approximated the shoulder height of canid and felid predators (60 cm), and the second, the "conspecific" method, the shoulder height of a bison (120 cm).

Preliminary visibility data were gathered for seven sites on Antelope Island. The purpose was to discover the distance measurement representing the most variation between sites (see Nudds 1977). For example, island sites ranged from open grasslands to slightly wooded areas. Visibility might be 100% for all sites at a distance of 20 m but range from 0-100% for sites at a distance of 100 m. At 500 m the visibility might be 0% for all sites. Therefore the distance of 100 m would be the best of the three to distinguish visibility between sites. Analysis of variance was performed for all methods to determine the distance demonstrating the most variation between habitat types. This maximum was ascertained from the ratio of differences between locations to within locations, the F-statistics. Preliminary results indicated that 80 and 100 m reflected the most variation in cover, or visibility, between habitat types.

The final sampling procedure was developed from these preliminary results and other field considerations. Eighty meters was chosen as the primary measuring distance and bracketed with samples at 40 and 120 m. A random direction between 0 an 89° was chosen for the first quadrant of each point. To eliminate overlap in the scanning method the other three radii were placed at 90, 180, and 270° from the first.

Twenty-five different sites were sampled and analyzed for among-site differences. Sites located in grassy, flat areas were considered completely open and given the highest values for each method. The data collected at one site were duplicated for two different herds photographed in the same location. The General Linear Model procedure (SAS 1989) was used with sites and quadrants as groups or treatments, points as experimental units or subjects, and distances as repeated measures.

The average bison-spacing values (i.e., NNDs) were compared for the original dataset of 101 herds. A three-level nested analysis of variance with unequal sample sizes was performed. The purpose of this analysis was to determine if there were significant differences in average NND for herds between different sampling dates, between different locations on the same date, and between different photographic times. Differences were found between herds at different times and suggested that a regression analysis be performed.

Two classes of indicator variables were used in the regression analysis. The first, herd characteristics, included the number of animals, the number of active animals, and the polarization of the herd. The relationship between the number of animals in a group and the mean NND appeared to be curvilinear. This suggested a logarithmic transformation and resulted in the variable LOGN. Individuals within herds were scored according to activity, i.e., standing or reclining. The resultant variable, ACTIVE, was the fraction of the individuals standing

for each herd. The polarization of the herd was a measure of the general body orientation of individuals within each herd. Body orientation was a vector originating at the tail point and travelling through the head point. The vector direction was measured on a 360° scale and averaged for all herd members. The variable POLAR was then calculated as the standard deviation of body orientation.

The second class of indicator variables concerned environmental characteristics such as the time of day, the location of each herd, and the visibility within each area. The variable TIME was the number of minutes since 12:00 a.m. The geographical location of each group was given in kilometers north and east of Elephant Head, a rock point located in section 13 of the Antelope Island quadrangle topographic map (Fig. IV-1).

Nine variables, distinguished by distance and method, resulted from the visibility measurements. These variables were analyzed for correlation to one another and for influence in the regression models. Preliminary results indicated that only one visibility variable should be included in a regression model. The conspecific method at 80 m, variable VISIBILITY, was chosen. Other variables were excluded from the analysis either because they had little or no correlation with mean NND or were highly correlated with one or more of the selected variables.

The regression analysis consisted of switching between manual and automatic model-building procedures. Eight variables were initially entered in the NCSS Automatic Step-wise Regression Procedure (Hintze

1987). The procedure halted with a model in which no further addition or deletion of variables reduced the root mean error by more than 1%. Each model was evaluated and then variables were added and deleted manually. Evaluation consisted of looking at total R^2, number of variables, colinearity between indicator variables, and status of the residuals. When problems were encountered with the data, they were minimized through transformation, as with LOGN, or through partitioning of the data, as was done with VISIBILITY and ACTIVE (see Results).

The final models were selected according to four criteria: maximum R^2, and minimum s^2, the PRESS statistic, and Mallows' C_p. The PRESS statistic evaluates the influence of each data point on the model in the form of n validations in which the fitting sample for each is of size n - 1. Minimization reveals the model least influenced by any single data point. Choosing the smallest Mallows' C_p minimizes underfitting, where results in important estimated quantities are biased, and overfitting, which includes terms which contribute little or nothing to the model (see Myers 1990 for detailed explanations).

A second data set for bison group size and composition was provided by M. Wolfe and D. Hiller (pers. comm.). These bison groups were observed during May and June of 1987. I classified the groups according to the number of animals, the age class and sex (i.e., calf or adult female or male), and the location. I analyzed these data for patterns in group size and composition.

RESULTS

This section has two parts. The first part describes differences in visibility and interbison spacing within and between various sites. The second part concerns correlations between interbison spacing and various indicator variables. The visibility data revealed significant differences among sites for index, predator, and conspecific methods (Table IV-1). This variation between sites allowed the investigation of differences in visibility and interbison spacing (see Methods). There were significant differences between distances at the same sites, although distances were strongly correlated within sites. The conspecific method at 80 m contributed the most to the regression analysis, hereafter used for the variable VISIBILITY.

I found NNDs to be significantly different between days, between herds on the same day, and between different photographs of the same herd (Table IV-2). This last result suggests that the average interanimal spacing changes through time. Therefore, only one time per herd was included in the regression analyses. These analyses were carried out in two parts: models using all available sites and models distinguished by visibility. The results are summarized in Table IV-3.

In the first analysis two models were constructed for the original set of 30 herds. Model I contained six variables (five indicator variables) and demonstrated a significant relationship with mean NND (n=30, F=20.25,

$P<0.001$). This model allowed the lowest C_p value, a minimal PRESS statistic and s^2, and a large R^2 as compared to alternative models (Table IV-3). LOGN was the most influential variable in Model I, accounting for over half the variance. The addition of the VISIBILITY, EAST, NORTH, and POLAR variables helped explain almost three-quarters of the variance, although this estimate is probably inflated (S. Durham, pers. comm.). Additional indicator variables had little effect on the model.

An individual evaluation was conducted of each indicator variable. A graph of mean NND versus LOGN appeared to be linear, although variance decreased with LOGN (Fig. IV-3). Individual plots of EAST, NORTH, and POLAR variables with mean NND were acceptable, although they demonstrated high variability, especially near mid-values. The distribution of mean NND with VISIBILITY was peculiar with points amassed at 100%, the upper bound (Fig. IV-4). Transformation could not alleviate this problem. The distribution suggested splitting the variable into two different groups, equal to 100% and less than 100%. This was done in Models III and IV.

A closer examination of Model I revealed that colinearity between indicator variables was low. The parameters were all significantly different from zero ($P<0.04$). The residuals appeared normally distributed and independent (Durbin-Watson $D=2.18$, $P>0.10$), although two outliers distorted the normal probability plot.

A second analysis to minimize the influence of one of the outliers resulted in Model II. Unlike Model I, an adjacent photograph time was used for one herd. This reduced the influence of this outlier without reducing the sample size. Model II was very similar to Model I, including the same indicator variables except POLAR. With one less variable the R^2 increased while the s^2, PRESS statistic, and C_p values, decreased (Table IV-3).

The distribution of mean NND and VISIBILITY suggested that bison spacing differed according to bison visibility and spawned models III and IV. Two categories of habitat visibility were obvious: less than 100 and equal to 100% (Fig. IV-4). To address the possibility that a measuring distance larger than 80 m would have eliminated the latter group, I compared mean NND for the conspecific method at 80 m and 120 m. The comparison revealed no major differences, reducing the number of values equal to 100% by two. The data for Model III contained 16 herds with VISIBILITY values less than 100%. The regression analysis resulted in a five-variable model with LOGN, VISIBILITY, EAST, and POLAR. NORTH was not included, unlike Model I.

Model IV's data were the complement of Model III's, the remaining 14 data points where VISIBILITY values equaled 100%. The removal of VISIBILITY as a variable produced a six-variable model with previous indicators LOGN, EAST, and POLAR, and the addition of ACTIVE and TIME. The evaluation criteria for Models III and IV (Table IV-3) suggest

that division of the data into two subsets by VISIBILITY produced an improvement in three of the four categories.

The regression models indicate that two variables are strongly correlated with interbison spacing, LOGN and VISIBILITY. They were included in all models and accounted for most of the variance (Table IV-3). EAST was less important but included in all of the regression models. Lastly, the variables ACTIVE, NORTH, POLAR, and TIME contributed the least to the models.

Size and composition of groups were recorded for the 1987 data set (M. Wolfe & D. Hiller, pers. comm.). The female-to-male sex ratio for adult bison on Antelope Island in 1987 was approximately 1.2:1.0. Of the 403 known animals 18% were calves (Wolfe & Kimball 1989). One hundred fifty-four groups were classified according to age and sex. The group composition changed dramatically with size. Approximately 50% of the smaller groups (1-5 members per group) were composed entirely of males (Table IV-4). Larger groups were always mixed. The average group size was 21.8±28.9 (±SD; n=153). Groups composed entirely of bulls averaged 4.4±4.6 (n=36) and of cows 2.8±3.5 (n=4). Cow and calf groups were uncommon and averaged 7.0±8.1 (n=8). Mixed groups of all sexes and age classes were the most common and averaged 27.2±31.1 (n=117). By 1989 the herd was reduced to 350 adults with a sex ratio of approximately 2:1. Calves comprised approximately 19% of the population (n=81). Group composition data were not available for 1989-1990.

DISCUSSION

Many studies have investigated aspects of grouping behavior in

ungulates (e.g. Walther 1972; Jarman 1974; Leuthold & Leuthold 1975;

Lipetz & Bekoff 1982). The majority have focused on the effects of group

size on foraging, vigilance, and, in a coarse sense, spacing. Few have

measured interanimal distances and the factors that affect such distances,

yet this measurement may be the most informative. For example, Jarman

(1974) proposed that group size is limited by intraherd resource

competition at the upper bound and by predation at the lower bound. The

former is dependent on such resource characteristics as quality, quantity,

distribution, and density. Predation, on the other hand, may place a

maximum limit on interanimal spacing. These characteristics influence

and possibly determine the animal distribution within groups.

A few ungulate studies have estimated NND for selected individuals

or for entire groups. Underwood (1982) observed different species and

groups of African antelope for the effects of selected variables on vigilance.

While his results did not address directly the effects of cover and group

size on NND, he did conclude that the interaction between foraging and

surveillance (and cover, group size, and NND) is probably complex. Other

investigations observed white-tailed deer for NND and activity patterns

(Lagory *et al.* 1981) and for NND and group size in three different habitats

(Lagory 1986). Their results demonstrated that NND decreased as group size increased.

Studies with bison have not been as informative. Green (1992a, 1992b) sampled activities of bison mother/daughter dyads, but estimated NNDs at <1 and at <10 m. Rutberg (1986) described the dominance relationships in adult groups of bison. He observed focal animals within groups for foraging time and aggressive encounters. Additional data were taken for NND at the beginning and end of each bout. He found that the average NND measured for bison at four locations ranged from 4.5-6.5 m. The observation sites varied in percentage of green biomass and presence or absence of snow cover. Group size ranged from 25-34 animals.

Group size has been shown to affect ungulate behavior, especially vigilance behavior. Underwood (1982) found that the number of companions was inversely correlated with time spent looking in three of five African antelope species. He also found that vigilance was affected by habitat openness. Similar results were found in California bighorn sheep and fallow deer (Berger 1978; Schaal & Ropartz 1985). Berger (1978) also demonstrated that foraging efficiency increased as group size increased. A comparison of feeding patterns and group size between bison, bighorn sheep, pronghorn, and mule deer found that searching behavior (head raised) changed significantly with group size (Berger & Cunningham 1988). Female bison spent comparatively little time searching; in groups of two or more cows, greater than 95% of their time was spent feeding.

Prins (1989) demonstrated that the formation and breakup of herds, the fusion-fission pattern, is strongly influenced by group size. In addition, individuals in large groups grazed closer together and exhibited stronger place fidelity than did individuals in small groups.

These results differ from mine in various ways. The average bison NND was 5.9 ± 3.4 BL for the 30 groups analyzed, ranging from 1.4-13.8 BL, approximately 3-28 m. My data showed both a larger variation in group size (6-80 animals) and NND values than did those of Rutberg (1986). Bison spacing on Antelope Island was inversely related to group size. Animals in larger groups tended to have closer nearest neighbors than those in smaller groups. There was more variation in average NND among smaller groups than among larger ones (see Fig. IV-3). This variation may be related to herd composition.

Many studies have investigated the relationship between bison herd size and composition. In general, bulls are most often found in groups of fewer than 10 individuals, and mixed groups rarely contain more than a few hundred individuals. In European bison 56-89% of the bulls lived outside mixed aggregations during the winter (Krasinski 1978). Group size of males ranged from 1-15 for a herd of about 200 animals. In Wood Buffalo National Park, American bison had a mean group size of 13-25 animals in one area and 23-29 in another, depending on the season (Oosenbrug & Carbyn 1985). Similar bison in the Slave River lowlands of Canada formed mixed groups of 20-60 animals or mature bull groups of 2-

5 animals (Calef & Van Camp 1987). Group size and composition also varied with season. In late winter mixed groups averaged 37.3±2.6 individuals while bull groups averaged 2.7±0.2 individuals. The total population was greater than 500 individuals.

Antelope Island bison bulls appear to maintain segregated groups more often than previously reported. Bull-only groups comprised 24% of those observed in 1987 while cow-only and cow/calf groups comprised 3 and 5%, respectively. The majority of groups were mixed (76%). About one-half of the smaller groups (<6 individuals) were comprised entirely of bulls, and all bull groups contained fewer than 40 individuals. The prominence of small all-bull groups provides one explanation for the variance displayed in small-group average NND. Animal sex and age may play a significant role in selection of neighbors and NND. Group composition data were not available for the photographed herds.

I anticipated variation in animal spacing according to activity, the time of day, and different behaviors associated with those times, e.g., between active and resting stages. Bison on Antelope Island appeared to feed and move early in the morning and late in the afternoon and rest during midday. Others have made similar observations (see Green 1992b). My results show little correlation between mean NND and the time of day or the number of animals active in a group.

Environmental factors beyond the animal composition of the herd are thought to greatly influence ungulate behavior. The most commonly

cited is the influence of predation pressure, which was not a variable in this study. Other variables such as visibility and available cover can influence antipredatory behaviors and intraspecific interactions (Elliott *et al.* 1977; Van Orsdol 1984). For example, habitat characteristics appear to effect group size, interanimal spacing, and vigilance. Green *et al.* (1989) states that group size decreases from open to closed habitats. Studies with white-tailed deer suggest that group size decreases as cover increases, i. e., as visibility decreases (Hirth 1977). LaGory observed white-tailed deer for NND, activity patterns, and group size in three different habitats. His data demonstrate that NND decreased from open to closed habitats (Lagory *et al.* 1981; Lagory 1986). A study of group size, NND, and vegetation type in African buffalo groups demonstrated a strong effect of vegetation type on NND (Prins 1989). His data suggest that NND decreases from open to closed habitats, although visibility measurements were not made. Lastly, other African ungulates show increased vigilance from open to closed habitats and a decrease in NND (Underwood 1982). Similar results on fallow deer suggest that vigilance is higher in open versus closed areas (Schaal & Ropartz 1985).

Bison spacing on Antelope Island is correlated with vegetative structure. Mean NNDs are greater in areas of higher visibility. In fact, animals in completely open habitats (VISIBILITY = 100%) may be more influenced by the time of day and activity levels than those in more closed habitats (compare Models III and IV in Table IV-3).

The regression analysis suggested that seven factors are useful indicators of bison spacing on Antelope Island. The first and foremost is group size. In all but one regression model it was the best predictor of average NND. This suggests that group size plays an important role in determining animal distribution. Larger groups may decrease vigilance activity and allow for increased foraging time. The environmental variables were less correlated with mean NND than LOGN but were still significant model contributors. The visibility in an area or, inversely, the amount of cover, was a better indicator of bison spacing than either of the location variables (i.e., EAST and NORTH). Animals tended to be more spread out (larger NNDs) as visibility increased. The ACTIVE, POLAR, and TIME variables were coarse measurements of activity and only marginally useful in predicting NND.

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TABLE IV-1: Separate analysis of variance results for visibility data by method and distance.

ANOVA for Index method

Source of Variation	F	P	df
Site	12.62	<0.0001	19
Distance (Site)	120.25	<0.0001	2, 148

ANOVA for Predator method

Source of Variation	F	P	df
Site	13.59	<0.0001	19
Distance (Site)	77.77	<0.0001	2, 148

ANOVA for Conspecific method

Source of Variation	F	P	df
Site	12.85	<0.0001	19
Distance (Site)	62.59	<0.0001	2, 148

TABLE IV-2: Analysis of variance results for mean nearest-neighbor distance.

Source of Variation	F	P	df
Total	-	-	8410
Date	5.50	<0.01	8
Herd	6.22	<0.01	93
Time	1.95	<0.01	245
Error	-	-	8064

TABLE IV-3: Comparison of regression models using average nearest-neighbor distance as response variable according to indicator variables (VAR), total number of variables (p), number of herds (n), and four model evaluation criteria (see text). Variable abbreviations are A=ACTIVE, E=EAST, L=LOGN, N=NORTH, P=POLAR, T=TIME, and V=VISIBILITY.

Model	Filter	n	Var's	p	R^2	s^2	PRESS	C_p
I	-	30	LVENP	6	0.7831	2.97	49.3	6.8
II	-	30	LVEN	5	0.8193	2.15	40.3	2.2
III	V<100%	16	LVEP	5	0.8809	0.64	4.2	3.0
IV	V=100%	14	LATEP	6	0.9588	1.30	4.4	4.9

TABLE IV-4: Summary of group composition with group-size categories for original points, i.e. 30 herds. Numbers are frequencies (%).

Group Size	Number of Herds	Bull Only		Cow Only		Cow/Calf	
1	18	8	(44)	3	(16)	3	(16)
2-3	22	10	(45)	0	-	1	(05)
4-5	17	9	(53)	0	-	1	(06)
6-9	23	7	(30)	1	(04)	1	(04)
10-19	20	1	(05)	0	-	1	(05)
20-39	24	1	(04)	0	-	1	(04)
40-99	21	0	-	0	-	0	-
100-299	9	0	-	0	-	0	-
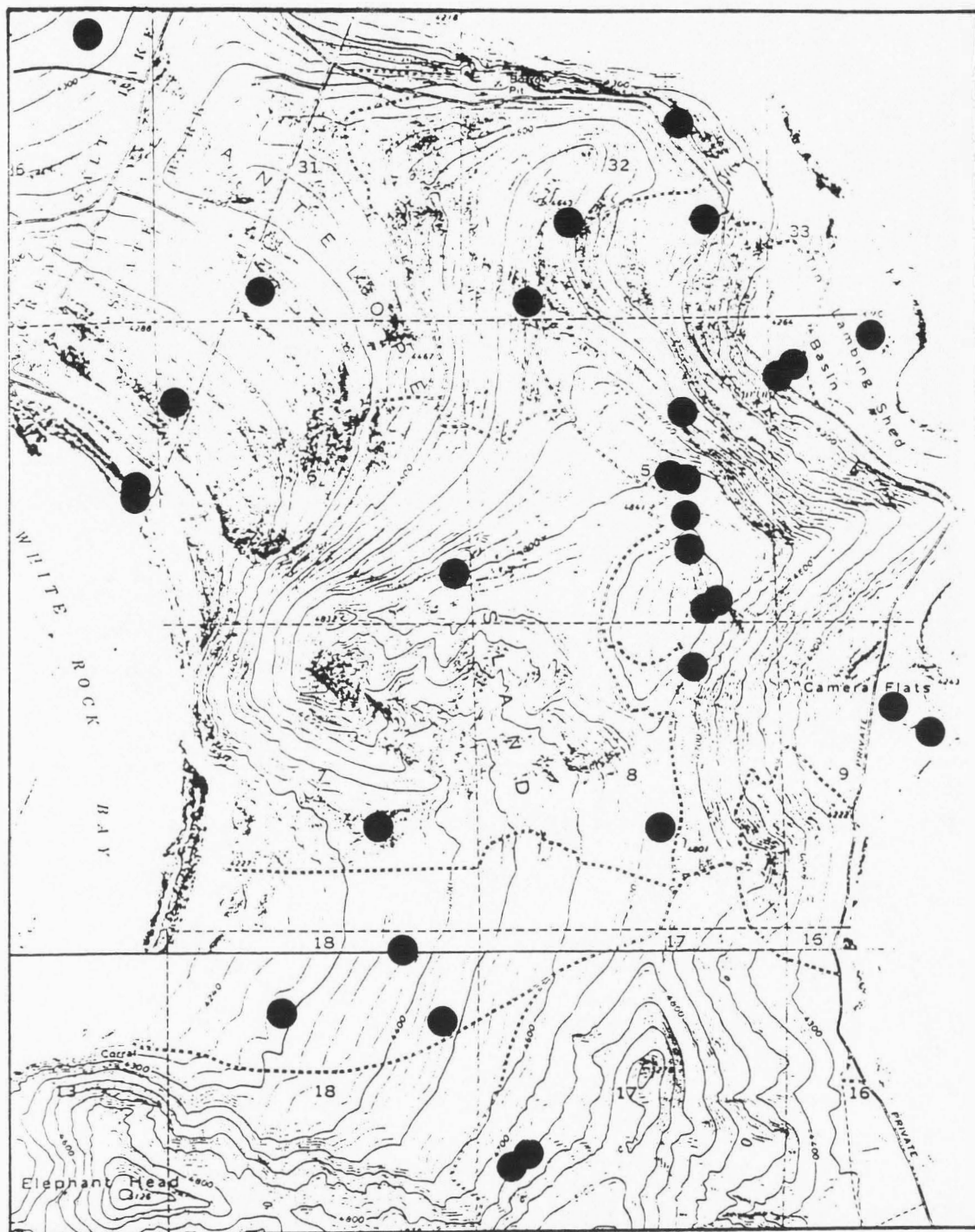
FIGURE IV-1. Map of Antelope Island with visibility sampling locations marked.

a)

Pole	Value	Height(m)
	1	2.0
	2	1.8
	3	1.6
	4	1.4
	5	1.2
	6	1.0
	7	0.8
	8	0.6
	9	0.4
	10	0.2
	11	0.0

b)

c)
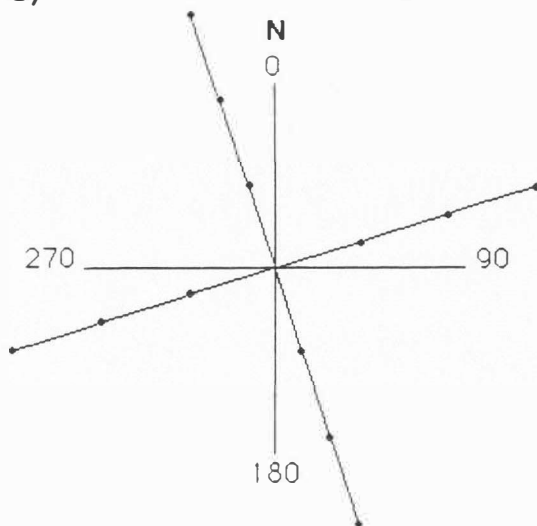
FIGURE IV-2. Equipment and procedure for measuring cover, or bison visibility. a) Cover pole with 20 cm increment markings and index numbers. b) Transect layout with 20 m between three points. c) Enlarged version of one observer point from transect showing four radii and distance measures used for cover pole locations.
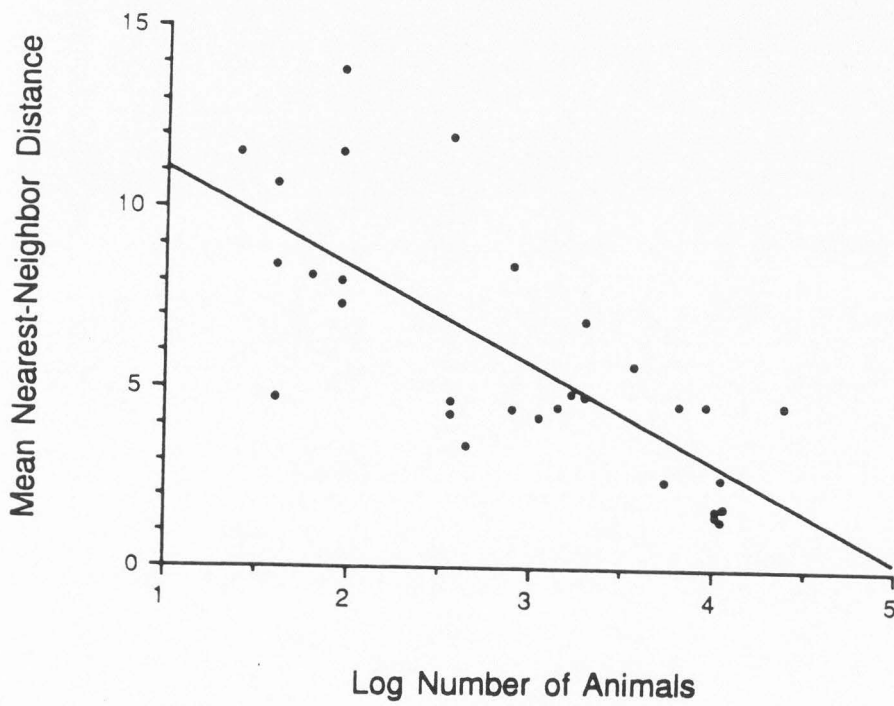
FIGURE IV-3. Graph of log transformation of number of animals (LOGN) with mean nearest-neighbor distance for original points (n=30).
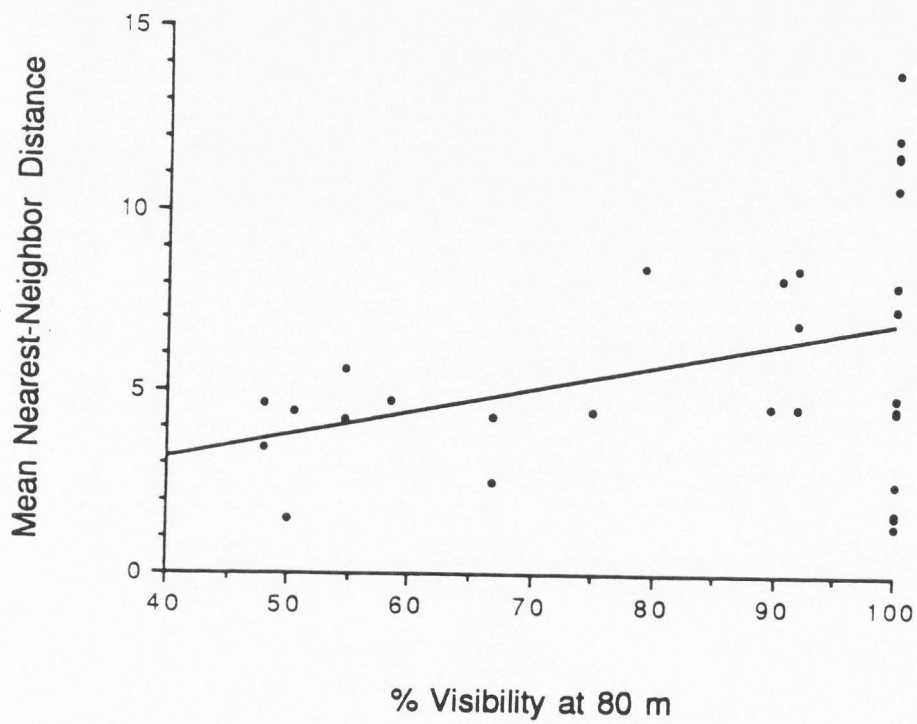
FIGURE IV-4. Graph of visibility at 80 m with mean nearest-neighbor distance for original points (n=30).

CHAPTER V

MODELING BISON BEHAVIOR WITH SIMPLE MOVEMENT RULES

ABSTRACT

The purpose of this exercise was to see if the simulation of simple movement rules could mimic bison behavior. Each simulation began with n individuals randomly located on a grid. After each time step, individuals moved according to a variety of near-neighbor rules. This process was repeated until the mean nearest-neighbor distance stabilized. Results showed that the overall means and variances of nearest-neighbor distances decreased as the number of individuals simulated increased. The number of near neighbors had little effect on these results. The results from the alternative rules were indistinguishable from one another, and all were different from real data. Results from randomly placed individuals were similar to real data.

INTRODUCTION

A variety of theoretical studies have been conducted on particle movement as applied to animal behavior, ranging from simple diffusion models to complicated automatons. My interest is with aggregation models, particularly those simulating individual animal movement. I will briefly review some of the early modeling efforts, recent object-oriented models, and particular models for ungulate behavior.

Early mathematical models of animal aggregation focused on the immediate space around an animal. In general, animals were hypothesized to reduce personal space and thus decrease the chances of being preyed upon (see Chapter I for a reviews of Brock & Riffenburgh 1960; Hamilton 1971; Vine 1971). Recent models have concentrated on predator foraging behavior, rather than on prey escape behavior, relying on traditional modeling methods like partial differential equations and passive diffusion simulations (Kareiva 1982; Cain 1985; DeJong & Saarenmaa 1985; Kareiva & Odell 1987; Benhamou & Bovet 1989). The most recent approach uses rule-based individual movement models which focus on the behavior of individual organisms (Packard *et al*. 1990; Folse *et al*. 1990).

Rule-based object-oriented models are used to simulate the behavior of individuals in particular environments. This approach to modeling aggregations and ungulate behavior is still in an early state. A few prototypic models are available, however. One model concerns lek formation in grouse and suggests that studies of the processes of lek formation, rather than the outcomes, may produce more insight into grouse behavior (Gibson *et al*. 1990). Folse *et al*. (1989) constructed an object-oriented model to simulate the effect of patch size on deer movement. The model is dynamic in the sense that the animal learns about habitat structure, plans movements, and accommodates changes in patchy habitat. Another ungulate model simulates moose foraging

behavior (Saarenmaa 1988; Saarenmaa & Nikula 1989). This model is similar to the deer model; it is an object-oriented representation of animals, their reasoning, and environment. It focuses on the problem of moose as a pest species on silviculture management in Finland. Others have developed similar moose-foraging models (e.g., Roese *et al.* 1991). (For a brief review of other ungulate models see Saarenmaa *et al.* 1988.)

The purpose of this chapter is to construct and analyze a different animal-movement model, the basis for which is an influential paper published on gregarious behavior and predation by Hamilton (1971). His main conclusion is that prey may group for selfish reasons, according to simple movement rules, and thereby reduce individual predation risk. I recently addressed the empirical aspect of this work (Chapter II) and now address the major theoretical point to see if simple rules can simulate bison grouping. My model simulates a modified version of Hamilton's (1971) nearest-neighbor rule (NN1), where individuals move toward their closest neighbors. If simple movement rules encourage and maintain aggregation in bison, then my simulations could account for much of the variation in bison data (Chapter IV).

METHODS

The model is a modified form of the automaton used previously (Chapter II). It simulated the movement of *n* identical objects, each of which was in one of three states at any time: "too far," "too close," or

"neutral." The current state of each individual was determined by the proximity of a neighbor or neighbors. The rules used were simple. Individuals moved randomly within the limits of a minimum and maximum distance from their nearest-neighbor distance (NND), or some group of near neighbors. Each simulation began with n individuals randomly located on a 500 by 700 grid; individuals could move anywhere thereafter. Each individual first determined its current state and then chose the next location based on this state, the predetermined distance of a move, and the angle to its nearest neighbor.

If an individual was farther than a maximum NND, its next movement was directly toward its nearest neighbor. Individuals closer than a minimum NND moved directly away. Individuals between the maximum and minimum moved a random direction to their next location. All new locations were determined before any animal was moved. The procedure was repeated for a fixed number of time steps. A number of other proximity rules were used to determine individual movements. The procedures were exactly as above except that the direction of movement was determined by averaging the angles to the n near neighbors.

Preliminary analyses were performed to determine appropriate model parameters. Simulations were conducted with 25 randomly located individuals, moving a distance of one-half or 1 bodylength (BL) every time step, and at various combinations of minimum (0-15 BL) and maximum (2-32 BL) distances. A move distance of 1 BL resulted in configurations

more like actual bison data than one-half BL. Most simulations stabilized by 200 time steps. The personal-space limits were selected from analysis of previous bison data. A maximum of 16 BL seemed to fit previous upper limits seen in bison data (Chapter IV), and a minimum of 1 BL was chosen to make it unlikely that individuals occupied the same location. A simulation run was deemed complete at 200 time steps. Multiple runs were completed from simulations beginning with the same parameters and a variety of random-number seeds.

Five near-neighbor rules were simulated. Individuals using the previously described nearest-neighbor rule (i.e., NN1) calculated new positions based solely on the first nearest neighbor. NN2-NN5 used 2-5 near neighbors in determining new positions. The number of individuals simulated were 3, 5, 10, 15, 20, 25, 35, and 50 for most models. Up to 50 different random-number seeds were selected to determine individual starting locations.

Two indicator variables were measured at the end of each run. The mean NND included one value for each reflexive pair of individuals, individuals which were each other's nearest neighbor. Mean subgroup size was the total number of individuals divided by the number of subgroups, where subgroup size was the number of individuals connected by nearest neighbors to one reflexive pair. The mean NND and mean subgroup size were determined at the end of each run for a particular rule. Additional runs were completed until these means were deemed stable, when the

same overall mean and standard error were attained after three consecutive simulation runs. Results were compared graphically.

RESULTS

A comparison of simulations of the five rules revealed few differences; therefore only results of NN1 and NN5 were reported. The major effect was produced by varying the numbers of individuals; NND decreased as the number of individuals increased (Fig. V-1). This decrease was associated with a substantial reduction in variance (e.g., ANOVA results for NN1 were df=5, F=9.55, P=0.027). The geometrical result was that as the density of individuals increased, individuals moved consistently closer, regardless of starting locations. Mean subgroup size showed a similar result; the variance decreased as the number of individuals increased. Unlike overall mean NND, there was little effect on overall mean subgroup size (Table V-1).

Small groups showed more variation in their mean NND than larger groups. For example, in NN1 the standard error of mean NND ranged from 0.1 to 6.3 BL, or from 1 to 73%, for various simulation runs of three individuals. In contrast, the same measurement for 50 individuals ranged from 3.0 to 4.2 BL, or from 45 to 58%. Surprisingly, this variability was not related to mean group size. The variability in mean NND for small groups resulted from random patterns within individual simulations. Preliminary monitoring of single simulation runs indicated that mean

NND varied with time. The system of individuals moved from low to high mean NND and back again irregularly. This erratic behavior resulted from individuals changing groups between time steps, although visual observation of the simulation runs revealed little change in group structure.

The simulation results were compared to expected results from randomly placed points. The mean NND and variance are dependent on the density of points and easily calculated using the formulas from Clark and Evans (1954). Density was determined from the number of individuals divided by the constant grid area. Unlike the previous simulations, the results from random points demonstrated an abrupt decrease in NND with an increase in the number of individuals (Fig. V-1). Variance decreased in a similar manner.

The model output and bison data were similar. Bison data from Chapter IV were grouped into categories and demonstrated the same trends as the simulated results: decreasing mean NND and standard error with increasing group size. The overall results were strikingly different; mean NND decreased rapidly as group size increased. The expected mean-NND and variance from the random distribution (Random) produced results different from the simulation data (Fig. V-1) but almost identical to the bison data (Fig. V-2).

DISCUSSION

My model is a less complicated facsimile of a simple model of animal spacing in two-dimensional space (Murai *et al.* 1979). It is mathematically and behaviorally simple, as opposed to earlier models (Brock & Riffenburgh 1960; Vine 1971; Saarenmaa 1988; Folse *et al.* 1989; Saarenmaa & Nikula 1989; Gibson *et al.* 1990). The model simulates animal aggregation according to individual movement rules developed from Hamilton (1971). It is dynamic in the sense that previous interactions affect subsequent actions.

The goal was to produce simulation results indistinguishable from real data. The results from different rules of my model were indistinguishable from one another. Mean NND decreased as the number of individuals increased and was associated with a decrease in variability. This pattern held for all rules. In contrast, the variance in mean NND was higher for smaller than for larger groups. This was true for individual simulation runs and for overall means.

Surprisingly, this variability was not related to mean group size. The variability in mean NND for small groups resulted from random patterns within individual simulations. Preliminary monitoring of single simulation runs indicated that mean NND varied, as did the standard error, with time. The system of individuals moved from low to high mean NND and back again irregularly. This erratic behavior appeared to result

from individuals changing groups between time steps, although visual observation of the simulation runs revealed little change in group structure.

The simulation results were distinguishable from real data, although comparisons of the model output and bison data suggested similar patterns. The difference was in degree. Large groups of bison were more tightly packed than smaller ones. Similarly, overall mean NND decreased as group size increased in the simulations. However, the bison data showed a rapid decrease in overall mean NND while the simulations did not. In fact, the Random results were a better match to the bison data than any of the simple rules.

In conclusion, there appear to be few differences between these simple-ruled models. The number of conspecifics an individual monitors has little effect on spacing as measured by mean NND. The simple rules do a poor job of simulating bison spacing. The bison data are better simulated by a random distribution of points in a fixed area than by the output of near-neighbor rules.

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Saarenmaa, H. 1988. Model-based reasoning in ecology and natural resources. In: *Proceedings: Resource Technology 88*, pp. 141-157. Int. Sym. Adv. Tech. Nat. Res. Mngt., Fort Collins, Colorado.

Saarenmaa, H. & Nikula, A. 1989. Managing moose damage in forest plantations: a deep model of animal behavior on a geographic information system platform. 9th Int. Work. Expert Sys. Applic., Avianon, France.

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Table V-1: The effect of the near-neighbor rule on the overall mean ($\pm$SE) subgroup size for various numbers of individuals per simulation. The overall means are 3.1($\pm$0.2) for near-neighbor one (NN1) and 2.8($\pm$0.1) for near-neighbor five (NN5).

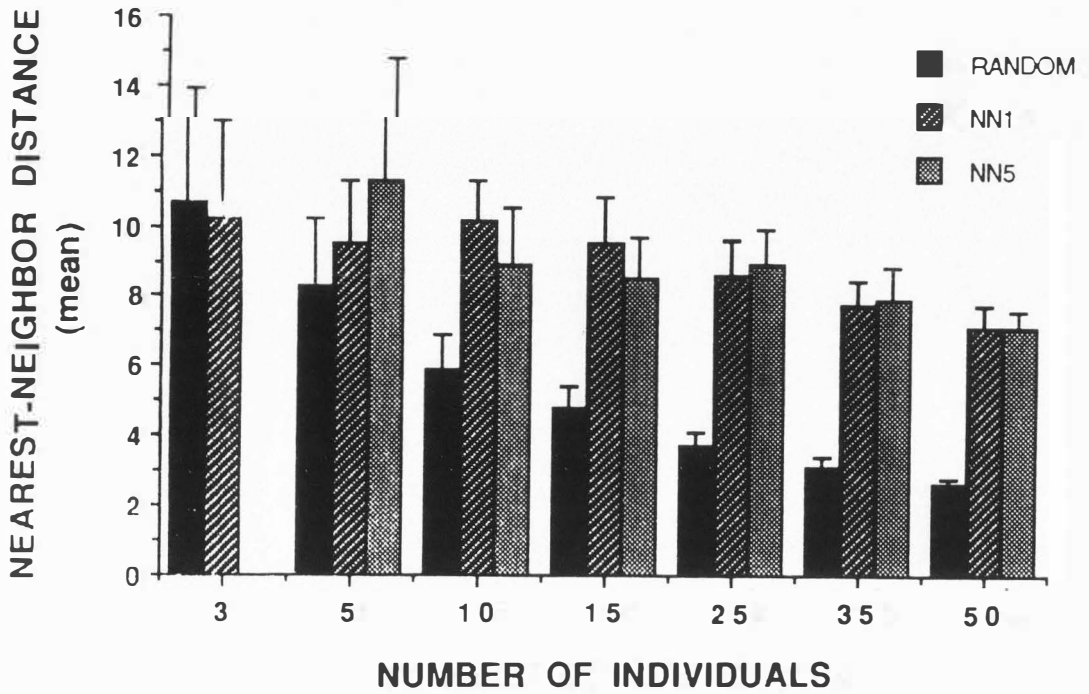| #	Rule Number			
	NN1		NN5	
3	3.0	(0.0)	-	-
5	2.7	(0.6)	2.9	(0.9)
10	3.0	(0.7)	2.9	(0.4)
15	3.0	(0.5)	2.7	(0.4)
25	3.3	(0.5)	2.9	(0.4)
35	3.2	(0.3)	2.8	(0.2)
50	3.2	(0.3)	2.7	(0.2)

Figure V-1. Effect of number of indi iduals on mean nearest-neighbor distance (±SE) for rules Random, near-neighbor one (NN1), and near-neighbor five (NN5).
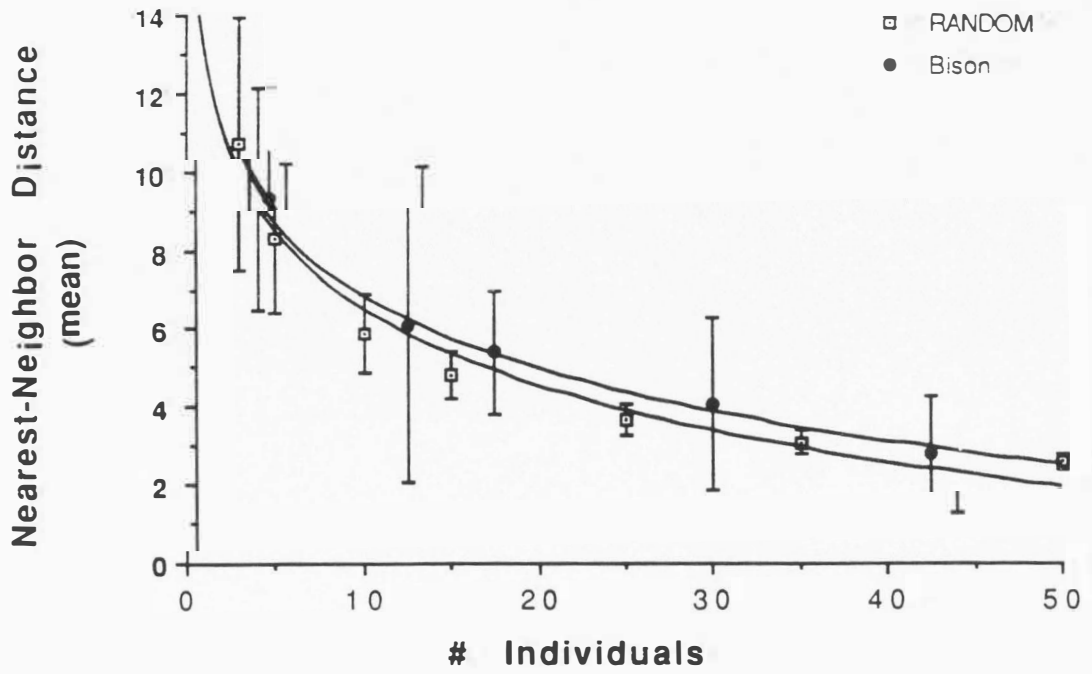
Figure V-2. Effect of number of individuals on mean nearest-neighbor

distance (±SE) for bison data and Random rule.

CHAPTER VI

DISCUSSION AND CONCLUSIONS

The topic of this dissertation is aggregation models of spatial relationships and gregarious behavior in ungulates. It addresses previous, current, and new models, evaluates data collection methods, and presents new data on interbison spacing. I shall briefly summarize my results and review other recent studies on ungulate spacing and social behavior.

The spatial position of large ungulates within herds has been a topic of discussion for some time. Gilbert & Hailman (1966) were of the first to measure group geometry in ungulates by focusing on the ordering of individuals in progressions. They found that captive fallow deer showed a predictable ordering of other individuals during flight. A recent example considered walking camels and demonstrated that there were no consistent leaders (Schulte & Klingel 1991). This large artificial breeding herd of domestic camels formed a loose association with few strong social bonds. When individual bonds did form, they were more likely to form in small rather than large groups.

Underwood (1981) considered a population of 80 eland functioning as a diffuse social unit. He observed animal social interactions and constructed a network of relationships among six classes of animals, each having a unique pattern of association. For example, cow groups were not stable centers of groups but were more like an interlocking series of

subgroups. Bulls were peripheral to most groups and not territorial. Underwood (1981) also found that aggregation was higher in the summer. He hypothesized that increased grouping was permitted by increased food quality and allowed protection from predation.

A strong association of individuals is referred to by Walther (1991) as social herding. In social herding, individuals are less likely to control the movements of conspecifics and more likely to maintain a relative position in the herd. This is in contrast to the active herding of individuals by males. Social herding is prominent in bison and African buffalo. Some of the latest work with spatial positioning in bison concerned mother/daughter interactions (Green *et al.* 1989; Green 1992a, 1992b). She made ground observations with binoculars of spatial relationships of mothers and daughters and central versus peripheral locations of calves within herds. Mothers and their young maintained closer contact in smaller than larger groups, suggesting that group size and protection of young are directly related. She also suggested that resting animals remained relatively close to each other, while grazing animals generally moved away.

The most thorough study of spatial position in ungulates was conducted on African buffalo. Prins (1989) used ground observations to estimate spatial positions of individuals within herds. He estimated the average nearest-neighbor distance (NND) for groups of 13-926 animals and categorized individual positions within the herd into one of seven areas.

These divisions ranged from the front 10% to the back 10%. He determined that spatial position is important for access to food and is strongly related to physical condition. His results indicated that cows maintained spatial positions as long as their reproductive status did not change. He also demonstrated that African buffalo in large herds grazed closer together than in small ones.

My results indicate that mean interbison spacing is strongly related both to the number of animals in the herd and to the cover in the immediate area. As numbers of animals increase, the mean NND decreases. Other important variables are the location of the herd on the island and activity level. The east-west location of each herd is mildly correlated with mean NND. I have no explanation for this correlation. Spacing might be related to the slope of each area, to the different types of forage available, or to some other property which was not measured.

The correlation of bison activity and spacing is more easily explained. Three variables relating to bison activity were mildly correlated with mean NND. These were time of day, whether animals were standing or reclining, and the variance in body orientation of herd animals. During data collection flights over the island I noticed that animals tended to recline by mid to late morning. If animals exhibit different spacing patterns according to gross activity (Green 1992b), then the mean NND would be expected to decline as the number of resting animals increased. My results indicate that mean NND increases with the number of animals

active. Lastly, the mild correlation between mean NND and variance in body orientation suggests that the degree of polarity of animal orientation may indicate different activities which, in turn, affect spacing.

The study of the influence of cover on ungulates has focused on vigilance behavior and group size. Cover has been considered mainly as an obstruction to vigilance, but for a discussion of its protective properties see Lazarus and Symonds (1992). Fitzgibbon has shown that cover can potentially increase the predation rate of cheetahs on Thomson's gazelles (Fitzgibbon 1990b). Individual Thomson's gazelles were preferentially selected if they were in small groups or alone, peripherally located in a herd with large NNDs, less vigilant than conspecifics, or in areas of high vegetation. Cheetahs hunted a greater proportion of grazing groups available to them in high versus low vegetation, as distinguished by a height of 30 cm (Fitzgibbon 1990a). Similar results for reduction of predation rates in larger groups were discussed by Green (1992b).

Recent studies on grouping behavior in brown capuchin monkeys focused on spatial relationships. Janson (1990a, 1990b) collected data on an individual's spatial positions relative to the center of the group and estimated distances according to equal-width concentric zones (i.e., inner, middle, and outer). Results show that as the amount of aggression an animal receives increases, time spent in the front and center of the group decreases. Predation pressure did not seem to be a major determinant of

adult spatial behavior. Spatial use was correlated with the percentage of time spent scanning for adult conspecifics.

My results suggest that obstructive cover reduces interbison spacing. Obstructive cover, as measured from a bison's viewpoint, explained about one-third of the variance of mean NND in bison herds. Furthermore, cover against the viewing of conspecifics is more important than against the viewing of predators. Bison spacing was more highly correlated to the cover reading at the height of a conspecific than either a relative cover index or the cover reading at the height of a predator.

All of the previously discussed studies used estimated distance measurements made by observers at ground level. I have demonstrated that observer bias occurred in a sample of elk spatial positions and is likely in most ungulate studies (Chapter III). The categorization of relative spatial location of individuals in groups may be a more realistic means of measuring distances and spatial positions. However, even estimation of relative positions may be in error. Studies which rely on accurate estimation of spatial positions should test the accuracy of the measurement.

There are numerous theoretical studies of movement ranging from simple diffusion models to complicated automatons. My concern is with aggregation models, particularly those simulating individual animal movement. Early models of animal aggregation concerned reducing the immediate space around an animal; the most prominent is Hamilton

(1971). His paper is frequently cited in support of the idea that individuals group to decrease predation risk (see Chapter II). The model is simple; move towards your nearest neighbor and reduce your risk of predation. I simulated this model and other similar but slightly more complicated rules. The results suggest that Hamilton's model has little effect on reducing predation risk although the model did fare better than a random movement model. However, the more complicated rules reduced predation risk by as much as two-thirds. These results suggest that individuals consider multiple neighbors when choosing new locations.

Recent models have concentrated on predator foraging behavior while the most current models take a rule-based approach to simulate behavior of individual organisms. (For a brief review of the old and the new see Folse *et al.* 1990; Packard *et al.* 1990.) Rule-based models are used to simulate the behavior of individuals in particular environments. This approach to modeling aggregations and ungulate behavior is still in an early state; however, a few prototypic models are available for lek formation in grouse and ungulate behavior (Saarenmaa 1988; Saarenmaa *et al.* 1988; Folse *et al.* 1989; Saarenmaa & Nikula 1989; Gibson *et al.* 1990; Roese *et al.* 1991).

The model developed in Chapter V simulates animal aggregation according to simple individual movement rules (Hamilton 1971). It is similar to the simple model of animal spacing in two-dimensional space of Murai *et al.* (1979), although less complicated, and dynamic in the sense

that previous interactions affect subsequent actions. Five simple rules were simulated and produced similar animal spacing results. These results were distinguishable from bison spacing data. In fact, the latter were more similar to expected results from a random distribution of points (see Chapter V). These simple models are inadequate for simulating gregarious behavior in bison. Improvements might include addition of separate age and sex classes as suggested by Prins (1989) or of separation of particular activities, such as fighting, foraging, loafing, and resting. Alternatively, the rules may be adequate but not the measurements. Maybe comparisons should be made of all interanimal spacing, not just the near neighbors. The latter may be a better descriptor of interanimal spacing and subgroup distribution.

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APPENDICES

Permission Letter

15 June 1993
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risk? J. theor. Biol.

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Permission Letter

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Mr. Vasu Nugala

★   Permission Letter

29 May 1993
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Permission Letter

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Permission Letter

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