SIZE-RELATED EFFECTS ON SEARCH TIMES IN NORTH AMERICAN GRASSLAND FEMALE UNGULATES[1]

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Abstract. Feeding and searching (=vigilance) rates arise as a result of many interrelated factors including trophic level, diet, reproductive condition, sex, habitat, body mass, and potential predation pressure. Because of unique ecological conditions in which the confounding influences of all but two of these variables could be minimized, we examined the hypothesis that body mass alone accounts for interspecific differences in search times, and tested it with females of four sympatric native North American ungulates (*Bison bison, Antilocapra americana, Ovis canadensis,* and *Odocoileus hemionus*).

When the effects of group size were controlled, smaller bodied species were more vigilant (per unit body mass) than larger ones. However, search times (ST) also scaled to body mass, and between 81 and 97% of the ST variance was explained by either exponential or power functions. To remove the potential bias that predators exert different influences on species of varying size, search times of bison in areas with and without their major predator, wolves (*Canis lupus*), were contrasted; search times did not differ between sites.

Our results highlight the importance of designing field research that controls for confounding variables prior to attempting to scale behavioral processes to ecological events.

Key words: antipredator behavior; body size; feeding activities; herbivores; prairies; predators; search times; size relationships; ungulates.

INTRODUCTION

A particularly conspicuous feature of group-forming vertebrates is that body-size variation is extreme; elephants and minnows each form conspecific groups yet their masses differ by more than 1 000 000 times (Schmidt-Nielsen 1984). The ecological implications of body-size variation have been explored in numerous contexts, including physical correlates (Peters 1983, Calder 1984) and some aspects of behavior (Clutton-Brock and Harvey 1983). For example, foraging is related in at least three ways to body size: (1) larger species require greater absolute amounts of food (McNab 1963, 1983, Eisenberg 1981, Belovsky and Slade 1986); (2) larger species tend to exploit open habitats (Jarman 1974, Geist 1978); and (3) species in open environments form large groups (Hamilton 1971, Pulliam 1973, Jarman 1974, Underwood 1983). These trends could result because larger species require more time to forage and because nutritious food is situated primarily in open areas. Alternatively, large species may form groups in open areas for reasons unrelated to food, such as enhanced protection from predators (Pulliam and Caraco 1984). However, small species also form groups, sometimes in the absence of conspicuous predator pressures or rich food patches. Moreover, large and small species may differ in diets, habitats, vulnerability to predators, reproductive demands, and other interrelated factors. Understanding how, when, and why size-related variability occurs in foraging and antipredator biology is difficult, especially because it is rarely possible to separate the influence of one variable from another.

In large mammalian herbivores, feeding rates are scaled not only to body size (Bunnell and Gillingham 1985) or rumenoreticulum volume (Demment 1982), but are also influenced by myriad proximate factors including predators (Schaller 1972, Risenhoover and Bailey 1985), group-size effects (Berger 1978, Lipetz and Bekoff 1982, Berger et al. 1983) and other variables (Table 1). Because foraging and antipredator activities are inextricably linked, it is necessary to reduce the effect(s) of antipredation activities as a confounding variable before it is possible to examine directly potential body-mass influences on foraging time. This manipulation has proved difficult in a practical sense because food habits impose differing requirements (McNab 1983), and different species often satisfy their demands through existence in habitats that are not comparable. While it has been convenient to ignore these confounding variables (including group size) (e.g.,

TABLE 1. Summary using selected examples of ecological variables that modify searching and feeding rates of large herbivores.

Variable	Species	Reference
Sex	red kangaroo	Short 1986
	bison	Hudson and Frank 1986
Habitat	several African antelope	Underwood 1982, 1983
	reindeer	Trudell and White 1981
Food dispersion	kudu	Owen-Smith 1979
		Bunnell and Gillingham 1985*
Season	African buffalo	Sinclair 1977
	horses	Duncan 1980
Food stage	elk	Hudson and Watkins 1986
	moose	Belovsky 1981
Group size	bighorn	Berger 1978
	ibex	Alados 1985
Predation	pronghorn	Berger et al. 1983
Reproductive condition	red deer	Clutton-Brock et al. 1982
	horses	Berger 1986
Position within a group	pronghorn	Lipetz and Bekoff 1982
Insects	horses	Hughes et al. 1981
	reindeer	Espmark and Langvtan 1979

* A general review emphasizing large herbivores.

Bunnell and Gillingham 1985, Belovsky and Slade 1986) in the construction of realistic time budgets, the influences of multiple factors must be considered (Robbins 1983).

On the central North American prairies, opportunities exist to minimize many of the above potential sources of confusion when assessing time allocated to searching for potential predators and to feeding. During a 3–4 wk period in late winter/early spring, ungulates (and especially pregnant females) are protein starved (Blaxter 1964, Robbins 1983), and in Badlands National Park, South Dakota, four species congregate on the same plateaus to feed upon newly emergent and highly proteinaceous grasses. The species are (in order of decreasing size) bison (*Bison bison*), mule deer (*Odocoileus hemionus*), bighorn sheep (*Ovis canadensis*), and pronghorn (*Antilocapra americana*). These congregations offer unique possibilities to examine how body size impacts feeding and searching times in the absence of contrasting ecological variables (but see Results: Effects of Predation on Search Times for the influence of potential predation).

Here we report results in three areas of body size-feeding-antipredator relationships. First, we examine the hypothesis that body mass exerts no influence on ungulate search times. While many ecological sources of variation can be controlled simply by carefully selecting when and where field data are collected, group

sizes cannot. Thus, we secondarily investigate how group size and individual position within groups affect searching rates. Third, we account for a potential bias in our data. Since the major predator of bison, wolves (*Canis lupus*), no longer occurs in Badlands National Park, the patterns we report could arise merely because bison are no longer vigilant. Hence, to examine the validity of using Badlands bison search rates in the absence of predation pressures, we contrast their search rates with those in Wood Buffalo National Park, (Alberta and Northwest Territories) Canada, where bison are regularly preyed upon by wolves (Fuller 1966, Oosenberg and Carbyn 1985).

METHODS

Study period and locations

Data were gathered during March of 1985 and 1986 in the Sage Creek Wilderness Area (≈ 250 km^2 in size) of Badlands National Park (BNP) in southwestern South Dakota. This is the largest intact natural mixed-grass prairie ecosystem with free-ranging bison in North America. Steigers (1983) offers a detailed description of the study site. During late August and early September, 1985, data were collected on bison in Wood Buffalo National Park (WBNP), a reserve of 44 800 km^2 with the largest free-roaming population of bison in the world. Unlike Badlands, Wood Buffalo National Park contains expansive boreal forests and several large salt plains along the Peace-Athabasca-Slave River lowlands (Soper 1941). Estimated population sizes of bison in the two parks are 450 (BNP) and 6000 (WBNP).

Study animals

In addition to bison, there were ≈ 75 bighorn, 300 pronghorn, and 500 mule deer at BNP. White-tailed deer (*O. virginianus*) also occur, but because they were observed infrequently they were excluded from analyses. Not all species could be sampled equally due to differences in population size, yet except for white-tailed deer all species congregated on the grassy plateaus and tablelands where data were collected. The following mass estimates were used: pronghorn, 37 kg; bighorn, 46 kg; mule deer, 51 kg (Jones et al. 1983); and bison, 400 kg (J. Berger, *personal observation*).

Data collection and statistical analyses

Randomly selected groups were observed with binoculars or spotting scopes for standard 180-s periods. (Of 684 timed observation sessions, 96% lasted 180 s while 4% ranged from 60 to 177 s in length.) Periods when an animal's foraging behavior was interrupted by social interactions, elimination behavior, grooming, or resting for >10 s were omitted (see Berger et al. 1983).

Data were collected on foraging adult females to minimize the greater variability that occurs among males (Berger 1978, Risenhoover and Bailey 1985).

TABLE 2. Statistical summary of differences between centrally and peripherally located Badlands animals, in (A) vigilance (search) time and (B) variability in vigilance time, per 180-s observation period. Comparisons were by Mann-Whitney U Test in (A) and by F test for homogeneity of two independent samples in (B).

	Group size†	Pronghorn	Bighorn	Mule deer	Bison
(A)	2–5	$U = 64*$	NS	$U = 38***$	NS
	c, p	34, 16	41, 27	29, 18	19, 17
	6–10	$U = 89*$	$U = 24**$	$U = 135***$	NS
	c, p	23, 14	38, 21	37, 30	40, 27
	11+	$U = 57.5*$	$U = 97***$	NS	NS
	c, p	13, 24	37, 19	44, 24	46, 15
(B)	2–5	$F = 7.46**$	NS	$F = 14.44**$	NS
	6–10	NS	NS	$F = 3.01**$	NS
	11+	$F = 18.10***$	$F = 6.85**$	$F = 13.13***$	NS

$* P < .05; ** P < .01; *** P < .001;$ NS = not significant.

† Sample sizes of both central (c) and peripheral (p) animals are given in (A).

Animals resting within view of the foragers were classified as part of that group. When groups were small (four or fewer), sampling could usually be done on all animals simultaneously. In larger groups, focal animals were selected. Individual positions within groups were noted as central or peripheral. If individual positions during a foraging bout shifted, data on these groups' members were excluded. Differences in sample sizes among species were minimized as much as possible by lumping the data into four group-size categories: 1, 2–5, 6–10, and 11+ individuals. An animal was considered "searching" when its head was raised above its shoulders or its attention was focused on an area or object. This "attention" posture (Geist 1971) is easily distinguishable from feeding postures, when animals' heads are oriented toward the ground.

The effect of group size on search time was examined both within and between species using standard parametric and nonparametric techniques. The time variable was transformed (log X + 1, where X = time), a preferable method when a skewed proportion of the values is small (Zar 1984). Data for central animals were analyzed using a two-factor completely randomized ANOVA (Norusis 1986), which revealed significant group-size and species effects (F = 90.21, P < .001; F = 34.13, P < .001; respectively) as well as interaction effects (F = 2.512, P < .001). Simple interaction effects were examined by treating group size and species each as single factors in a one-way ANOVA, comparing group sizes and the different species while holding the other variable constant. These analyses supported the two-way ANOVA with significant group-size and species effects. Because ANOVA may reveal intergroup differences but not where they occur (i.e., between which groups), Student-Newman-Keuls Multiple Range tests (SNK) were performed.

Search time (ST) was divided by body mass (BM) for each species, and the corresponding values of ST per unit body mass were compared, to determine whether a species' size in itself was responsible for possible ST differences. Because a proportional relationship did not exist, four regression equations (linear,

log transformation, exponential, and power) were generated to predict ST (Y) from female body mass (X).

RESULTS

Position effects

The position of a foraging animal within a group affected its searching rate. Individuals on the periphery scanned more than those in the center and exhibited a higher degree of variability in levels of scanning (Table 2). Differences between central and peripheral pronghorn were significant for all group sizes. Yet, search times of peripheral animals in the smallest (2–5) and largest (11+) groups were more variable than those of centrally located pronghorn (Table 2).

Position effects did not occur for bighorn sheep foraging in small groups (2–5), but differences between centrally and peripherally situated foragers became progressively more significant as group size increased (Table 2A). Variability in foraging location within the group did not occur in bighorn except when groups were of 11 or more animals (Table 2B). On the other hand, mule deer exhibited strong position effects in both small and mid-sized groups but showed none in larger aggregations. Peripheral deer were strikingly more variable.

Bison females did not conform to these trends. They rarely scanned their environments while foraging, and position within the group had no effect on search time (Table 2).

Group-size effects

Because the search times of peripheral animals tended to be more variable than those of centrally located ones, only data on central individuals were used in evaluating group-size effects. For all species, mean search time declined with group size, though differences were consistently the most striking between solitary foragers and those in groups of two to five (Table 3). On average solitary pronghorn does spent 4.4% of each observation period foraging, while single bison cows fed for ≈61% of the time; bighorn ewes and mule deer does were intermediate.

TABLE 3. Search time (mean percentage of 180-s observation periods) in centrally foraging adult females in Badlands National Park, by group size.

	Group size					F†	P
	1		2–5		6–10	11+		
Pronghorn	95.5	*	9.4		7.8	4.4	105.44	.001
Bighorn	62.2	*	38.3	*	21.1	17.2	23.20	.001
Mule deer	64.4	*	27.2	*	8.8	8.3	60.20	.001
Bison	38.8	*	4.4		1.1	1.1	23.50	.001

* $P < .05$.

† One-way ANOVA (F) values given for each species, and within species (SNK) values sharing common underline are not statistically distinguishable. Sample sizes as indicated in Table 2, and for solitary animals (in order) are 7, 6, 10, 7.

Among all species, searching was lowest in largest groups, but no statistical differences were evident between groups of 6–10 and 11+. Search time differences between groups of 2–5 and 6–10 occurred only in bighorn sheep and mule deer; individual pronghorn does differed from bighorn and deer in that no further benefits in foraging time were achieved with increasing group size (Table 3). Female bison spent very little time searching; once they were in groups of two or more cows, >95.5% of their time on the average was spent feeding although their group sizes varied from 2 to 178 animals.

Interspecific comparisons

Variation in scanning was noticeable when compared among species; solitary foragers allocated the greatest proportion of time to nonforaging activities (Table 3). Solitary females constituted a rare subset of the population; pronghorn 0.7% ($N = 996$), bighorn 0.9% ($N = 661$), mule deer 0.9% ($N = 1121$), and bison 0.4% ($N = 1949$).

Among species, search times were consistently and significantly different between bighorn and mule deer for all group-size comparisons except solitary individuals (Table 4). In contrast, pronghorn differed from mule deer for only the two smallest group sizes, whereas bighorn and pronghorn differed for all group sizes (Table 4). Regardless of group size, bison cows always spent a greater amount of time feeding. A one-way ANOVA for all group sizes revealed significant species ($P < .001$) effects (Table 4).

Body-size effects

If the above interspecific differences arise simply because smaller species are more vulnerable to predators than larger ones and, hence, allocate more time to searching for predators, then smaller species should be more vigilant (per unit body mass) than larger ones. This is the case when simply dividing the species search times (reported in Table 3) by the species masses listed in Methods: Study Animals. For instance, solitary pronghorn females were ≈27 times as vigilant per unit body mass as solitary bison cows.

However, rather than expecting a proportional relationship between species mass and search time, it may be that ST is scaled directly to body mass. This possibility was examined independently for each of the four group sizes indicated earlier by using power ($Y = A \cdot X^B$), exponential ($Y = A^{BX}$), linear ($Y = A + [BX]$), and log ($Y = A + B \log[X]$) functions, where Y = search time, A is the intercept, B is the regression coefficient, and X is body mass. For all group sizes the minimum ST variation explained by the exponential and power equations was 81%, whereas for group sizes 1, 2–5, and 6–10 these functions accounted for between 88 and at least 96% of the variance; linear and log transformations were less able to predict ST (Table 5). Despite the use of only four species a good deal of variance was explained once other factors were controlled for.

Effects of predation on search times

Small carnivores such as coyotes (Canis latrans) and bobcats (Lynx rufus) may prey on females or young of species the size of pronghorn, bighorn, and mule deer but not bison. Consequently, it seems reasonable to expect that BNP bison search times could be low simply because they have become habituated to an environment lacking in natural predators, especially since data for other species demonstrate greater search time with increasing predation pressure (Berger et al. 1983).

TABLE 4. Statistical summary of interspecific comparisons of search times (one-way ANOVA followed by Student-Newman-Keuls; $P < .05$).

Comparison	Group size			
	1	2–5	6–10	11+
Pronghorn vs. bighorn sheep	*	*	*	*
Pronghorn vs. mule deer	*	*	NS	NS
Pronghorn vs. bison	*	*	*	*
Bighorn sheep vs. mule deer	NS	*	*	*
Bighorn sheep vs. bison	*	*	*	*
Mule deer vs. bison	*	*	*	*
$F =$	6.42	3.58	5.27	7.14
$P <$	.02	.03	.01	.001

TABLE 5. Comparison of regression equations predicting mean search time from mean ungulate body mass for each of four group sizes.

Group size	A	B	r^2	A	B	r^2
	Linear			Exponential		
1	129.865	−0.241	0.79	136.514	−0.003	0.92
2–5	24.658	−0.006	0.77	32.504	−0.001	0.97
6–10	5.684	−0.014	0.42	6.338	−0.008	0.88
11+	4.236	−0.007	0.61	4.312	−0.003	0.81
	Log			Power		
1	271.069	−39.944	0.85	997.237	−0.565	0.96
2–5	56.863	−9.248	0.73	6013.092	−1.493	0.95
6–10	13.263	−2.166	0.41	680.969	−1.334	0.88
11+	8.259	−1.149	0.60	21.986	−0.465	0.81

If this were the case, the relation between body mass and search times reported above would result not from species differences in size per se but from the loss of large (natural) predators.

To investigate potential predator effects, bison search times in Wood Buffalo and Badlands national parks were compared. The data in WBNP were collected both in boreal forests and in grasslands, but to facilitate comparisons with Badlands animals only the WBNP grassland data were contrasted. As in BNP, group-size influences on WBNP cow search times were evident ($F = 25.36$; df = 3, 184; $P < .001$), but between-site comparisons show no differences in search times ($F = 0.053$; NS). Hence, despite the presence of wolves, bison in WBNP were no more likely to scan their environments than were BNP bison.

DISCUSSION

Factors affecting searching and grouping

Numerous variables influence group formation (Hamilton 1971, Pulliam 1973, Alexander 1974). Among African antelopes feeding style and body size are correlated (Jarman 1974), and together they exert major influences on grouping (Underwood 1982). Not unexpectedly, small territorial, monogamous antelopes such as klipspringers (Oreotragus oreotragus) use different tactics to avoid predators than do larger, polygynous, and more mobile ones (Jarman 1974, Tilson 1980, Eisenberg 1981). In addition to conspicuous interspecific differences, intraspecific variation occurs in antipredator behavior. In both North American and African ungulates, group size and position within different-sized groups affect scanning and foraging times (Berger 1978, Lipetz and Bekoff 1982, Underwood 1982). And, although group size and position effects may persist even when compared among populations, subtle factors are also influenced. Where predation pressure varies and affects antipredator behavior, differences should be reflected in at least grouping or search times, or both. This has been verified for pronghorn in the Great Basin Desert where individuals under heightened predation pressures by humans scanned more, formed larger groups, and foraged less efficiently than nonharassed individuals (Berger et al. 1983).

Body-size effects

How individuals of species of disparate body size allocate time to feeding and predator surveillance has been reported in taxa that vary from insects to large mammals (Hoogland 1979, Belovsky 1981, Elgar et al. 1984, Alados 1985, Stacey 1986). The most cogent theme emerging from such work is that searching rates are greater in smaller than in larger species. However, drawing inferences from studies of species that differ widely in their patterns of habitat use, group sizes, reproductive requirements, and predator pressures makes it difficult to compare results. The data reported here on North American prairie ungulate females demonstrate that search times are *not* merely related to body size in general; they scale directly to body mass (Table 5) and explain between 81 and 97% of the time spent searching (or foraging) once group size and other factors are taken into account. Once the influence of body mass is controlled, search time disparities among bison, pronghorn, bighorn, and mule deer disappear. These results support the hypothesis that differences in predator scanning among prairie ungulate females are related to body size.

Ecologically, body size is important because it influences metabolic rate, density and biomass, and trophic adaptations (Kleiber 1961, McNab 1980, 1983, Peters 1983, Calder 1984), while behavioral implications include the adoption of different tactics to avoid predation (Eisenberg 1981) and modification of mating behavior due to intraspecific competition (Ryan 1985). What is evident from the present results is that physical variables such as body size ($F = 34.13$) exerted a lesser influence on search times than did social parameters such as group size ($F = 90.21$), though interaction effects between these two factors were also significant ($F = 2.512$; $P < .01$). Hence, both body and group size are essential physical and socioecological variables that

must be considered (in addition to those listed in Table 1) when evaluating foraging or searching behavior; they cannot easily be dismissed if predators have an impact on foraging or grouping. Unfortunately some prior studies have failed to allude to the potential influences of these variables.

Predation and other sources of bias

While it is not surprising that a variety of size-related scaling effects occur in ecology (Peters 1983, Calder 1984), a unique feature about the data reported here is that highly variable and often cumbersome behavioral frequencies can be predicted by knowledge of body size once group size and other effects are controlled. Thus, it is somewhat surprising that one-dimensional comparisons of feeding styles and body mass have also detected strong relationships especially when differences such as habitat, sex, and food are not mentioned (see also Table 1).

However, our Badlands data are not without problems of their own. The search time similarities between BNP and WBNP bison could result because: (1) bison are large-bodied generalist herbivores that need to fulfill their energy and nutrient requirements by feeding often (Belovsky and Slade 1986, Hudson and Frank 1986); or (2) WBNP bison had not been attacked by wolves immediately prior to periods when our data collection occurred. Both explanations have merit: if predation had no influence on search times then results from the two study sites should not differ (as our results show). However, bison become very attuned to wolves once predation is likely. Most predation in WBNP occurs in winter, when bison leave forested areas and inhabit open plains. Since our data were collected in late summer, different search patterns might have resulted had our efforts commenced during winter. For example, bison have run as far as 16 km in 1 d and up to 81 km over a 3–4 d winter period when pursued by wolves (Oosenberg and Carbyn 1985); moreover, bison leave forested areas when disturbed by predators to stand on open roadway cuts where visibility is greater (J. Berger, *personal observation*). While not quantified, the loss in feeding time during such periods of potential predation would surely exceed the mean ($\approx 2\%$) debit incurred among cows in groups of two or larger when predators are not present.

Although some sources of bias can be controlled, either by statistical methods or through experimental designs even in unstructured field settings, others cannot. It would have been ideal to compare WBNP and BNP animals when females suffered identical gestational demands, inhabited the same environments, and fed upon the same food. Obviously, this is impossible. Further, it would have been ideal to compare additional ungulates feeding in the same habitats on the same plant species, but few North American ecosystems offer opportunities for contrasting even four species simultaneously. Still, the present results highlight some of the straightforward relationships that emerge when controlling for numerous sources of bias. As field studies proliferate, it will be intriguing to see how innovative designs uncover relationships between body size, foraging, and antipredator behavior.

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