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Group Size, Foraging, and Antipredator Ploys: An Analysis of Bighorn Sheep Decisions

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Summary. I. Several aspects of the foraging behavior of California bighorn sheep (*Ovis canadensis californiana*) were studied in homogeneous habitats in the interior of British Columbia, Canada. The manner in which an individual sheep foraged was based upon the size of group within which it was found.

2. In small groups (five or less individuals) sheep foraging efficiency was poor and interruptions of foraging to scan the environment were frequent.

3. Alarm vocalizations and other conspicuous behaviors tend to alert their neighbors to the presence of disturbances. It appears that these signals cannot be based solely as the result of kin selection.

Introduction

Much attention has focused on the relationships between group size, individual fitness, and predator avoidance in vertebrates (Alexander, 1974; Hamilton, 1971; Maynard Smith, 1965; Moriarity, 1976; Murton et al., 1966; Smith, 1977; Taylor, 1976, 1977; Wilson, 1975). It is commonly reported that one of the benefits derived by individuals in large groups is added protection from predators. In mammals, this protection through grouping may be achieved principally in two ways. First, an increased number of visual, auditory, or olfactory sensory organs are available for predator protection. Second, by grouping together the probability of any single individual succumbing to the attack of a predator usually is minimized. Other social adaptations for detecting and avoiding predators include learning signals that indicate their presence (Kruuk, 1964; Seghers, 1973; Walther, 1969) and attraction to rapid movements of group members (kinopsitic behavior) (Wilson, 1975).

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Social adaptations utilized in predator detection have been studied in ungulates (Altmann, 1956; Klingel, 1967; Walther, 1969) and in other mammals (see Kruuk, 1972; Schaller, 1972). Additionally, the role of warning vocalizations in relation to individual fitness as an adaptive strategy to reduce predation has been considered in ungulates by Hirth and McCullough (1977) and Smythe (1977). However, to my knowledge no studies of ungulates have concentrated on, or quantified the relationships between the time budgeting of foraging activities and predator surveillance activities in different sized groups.

The present study considered the following questions: 1) Do individuals in large groups forage more efficiently than those in small groups?, 2) Are individuals in large groups more likely to detect predators than those in small groups?, 3) Can explosive snorting sounds and other conspicuous behaviors in solitary or non-related individuals be explained on the basis of individual selection?

Methods

1. Study Period and Location. Data on California bighorn sheep (*Ovis canadensis californiana*) were collected from May to November 1976 in the Chilcotin-Cariboo region of the central interior of British Columbia, Canada. The study site was situated near the confluence of the Chilcotin and Fraser Rivers and it was composed mainly of northern grasslands (see Demarchi and Mitchell, 1973 for a more detailed description of the study site).

2. Definitions. For bighorn sheep (hereafter referred to as sheep) several patterns of activity were noted and these are described below.

1. Foraging Behavior. The time period during which sheep were involved in obtaining food (grazing, browsing, or searching). I have subdivided foraging into five components.

a) Down (*D*). The mouth is either in contact with food or in a downward position with the head oriented to the ground.

b) Search (*S*). The head is lowered near the ground and the sheep are walking, presumably while looking for food.

c) Up (*U*). The head is raised in a normal standing position and rumination may occur. Several variations may occur. For example, when sheep become aware of potential danger during foraging they may: 1) stare at it in an 'attention' posture (Geist, 1971); 2) use an 'alarm' posture (Geist, 1971); 3) run; or 4) use any combination of these patterns. If sheep do not run and foraging is resumed, they often will lift their heads without looking directly at the disturbance and without making noticeable reference to it.

d) Look Around (*LA*). The head is moved (although not necessarily continuously) in several directions, presumably to look around. *U* always precedes this stage if sheep were *D*.

e) Walk (*W*). The head assumes a normal upright position and the sheep walk. This stage is in contrast to *S* during which sheep also walk but with their heads down.

2. Resting Period (*RP*). The sheep lie on the ground. Usually when more than one sheep rests they do so adjacent to one another.

3. Foraging Ratio (*FR*):

$$FR=\frac{D+S}{U+LA+W+D+S}\times 100.$$

No caloric nor plant ingestive values are implied by *FR*. It simply is a percentage measure of how much time is spent in the acquisition of food.

4. False Alarm. When one or more sheep jump and/or run momentarily in an apparent alarm and they are successful in causing at least one member of the same group to become startled and run. Feeding is resumed immediately following the false alarm.

3. Data Collection. Rams, ewes, solitary sheep, and mixed bands were selected at random and each component of foraging behavior was timed. When groups were small, usually four or less, all members could be observed simultaneously. When groups were larger, a focal animal was monitored. Most frequently though, a few adjacent sheep could be viewed and their 'times' recorded. Data were collected with the aid of a stopwatch and a spotting scope and then recorded directly into a tape deck or onto note cards.

Components of foraging were timed only after at least one of the following conditions were met: 1) sheep had previously been in *RP's*; 2) they had been grazing rather than browsing (because the former is a more continuous activity); or 3) they were feeding passively without perceptable prior disturbances. Finally, I recorded foraging behavior when sheep were in homogeneous grassland habitats (Agropyron-Poa associations) rather than in broken areas with much debris, talus, etc. In these areas it would have been difficult for me to judge whether sheep watched where they walked, searched for food, or looked for other animals. Periods during which I did not record foraging were those that were interrupted frequently by social interactions. Lambs were excluded from computations of group size, foraging ratios, resting positions, and false alarms. At this early age, the attention and alarm postures of lambs are ignored by ewes.

Results

1. Group Size

A total of 258 sheep were timed for 66,779 seconds while foraging in various sized groups. Average foraging ratio per sheep increased significantly with group size (Fig. 1). Also, in small groups or when solitary, sheep tended to be more variable in their *FR* than were those from larger groups (see legend in Fig. 1). As might be expected, solitary individuals or those in small groups (one to five individuals) were more likely to interrupt foraging activities to remain up, to look around, or to walk, than were sheep in larger groups (Fig. 2). This was measured by the average number of interruptions (*NI*) per 100 seconds of foraging.

The data in Figures 1 and 2 suggest a threshold at which additional group members confer very little benefit to those already in the group. I determined that, benefit to the 'average' individual ceased at the region where either *FR's* or *NI's* no longer changed significantly with increasing group size. In other words, since correlation coefficients were not significant ($P > 0.05$) when group sizes were larger than five, individuals in bands larger than this gained little through associating with additional conspecifics.

These results were also very obvious from field observations. For example, solitary sheep were noticeably more 'nervous' than conspecifics in larger groups. Solitary sheep, especially ewes, commonly ran from ridge to ridge and looked around. Also, during foraging they appeared to lift their heads quite often. In contrast, those individuals that foraged in larger groups seemed to 'mow' down grasses and they infrequently lifted their heads.

During the non-rut, foraging by solitary Class III and IV rams (the largest horned and most independent sheep; Geist, 1971) was quantified on only four occasions. As previously shown, variability is great in solitary foragers so these data on rams must be viewed with caution. These rams spent more than 50% of foraging bouts in *LA* or *W* components (55, 68, 70 and 75%). During the rut, again only a few instances of foraging were timed ($n = 6$). However,

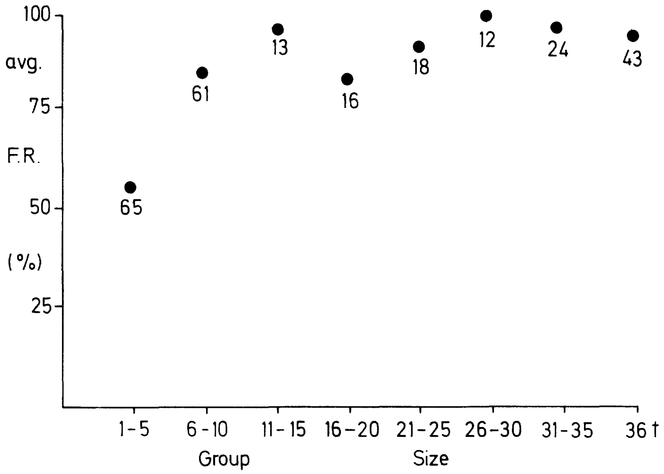

Fig. 1. Mean foraging ratio (*F.R.*) per individual in a given group. The Spearman rank correlation coefficient of +0.60 ($P<0.01$) is given for all 252 observations. Points on the graph represent group means and respective sample sizes are shown by small numbers. Coefficients of variation (in parentheses) and sample sizes for specific groups are: *1*; 21 (88.8): *2*; 8 (45.4): *3*; 10 (24.2): *4*; 21 (28.3): *5*; 5 (45.1): *6*; 20 (42.5): *7*; 11 (58.0): *8*; 10 (35.1): *9*; 10 (34.6): *10*; 19 (27.0): *11–15*; 13 (24.6): *16–20*; 16 (18.0): *21–25*; 18 (13.8): *26–30*; 12 (6.2): *31–35*; 24 (17.4): *36+*; 43 (22.3)

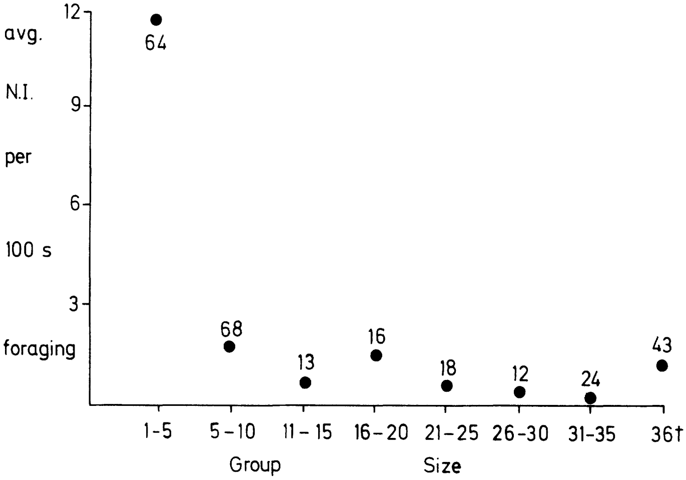

Fig. 2. Average number of interruptions (N.I.) per 100 s of foraging in a given group. The Spearman rank correlation coefficient of −0.87 ($P<0.001$) is given for all 258 observations. Points on the graph represent group means and respective sample sizes are shown for all numbers. Sample sizes for specific groups up to 10 are shown below. *1*, 18; *2*, 8; *3*, 10; *4*, 21; *5*, 7; *6*, 17; *7*, 11; *8*, 11; *9*, 10; *10*, 19

the results were similar and Class III and IV rams averaged 69, 70, 74, 83, 89, and 90% of their time in *LA* or *W* components.

2. *Conspicuous Behaviors and False Alarms*

Bighorn sheep and many other ungulates as well frequently use alarm vocalizations or snorts and characteristic postures during confrontations with predators. For instance, when male or female bighorn sheep are startled at close range by a predator (i.e. a bear) they immediately run. However, when danger is not as close, (whether it be a coyote or a human at a distance) sheep may: 1) snort; 2) perform a 'functional' circle; 3) step forward and kick at the ground; or 4) head bow. All of these behaviors are rare (Geist, 1971), but they do occur whether individuals are solitary or in groups. These behaviors alert conspecifics (when individuals are not solitary) which then orient to the disturbance, or they may run in response to a lead individual. These behaviors also alert predators (on many occasions I was cued in to the location of the vocalizing individual).

I observed groups as large as 136, yet with that many individuals (and hence more chances for alarm) false alarms were surprisingly rare. Typically, a small fraction of a group would be startled. The largest proportion of any group participating in flight (80%) occurred when group size was small (five). The largest number of startled sheep was nine but these sheep represented only 20% of the group of 45. In the Chilcotin false alarms occurred very infrequently; seven times in seven months of investigation (896 hours of observation).

Discussion

1. *Group Size*

The number of members that a group contains depends on many variables, of which the most important include openness of terrain, the availability and distribution of resources, and predator pressures (Alexander, 1974). It is not surprising that under the cover of darkness fish schools disperse (Williams, 1966) nor that food ultimately limits the formation of group size in many species of ungulates (Jarman, 1974; Schaller, 1967). As has been demonstrated on numerous occasions, when resources are clumped (even when the environment is characterized by 'good' visibility) groups may also be clumped into a small area. Evidence for this clumping is obtained from artificial feeding stations where a large number of animals may congregate, such as at a limited food resource (see Wilson, 1975). In feral horses (*Equus caballus*) and feral asses (*E. asinus*) the most 'nervous' individuals are usually the last to approach such a resource (e.g. a waterhole), and if others are not present they may not approach it at all (Berger, 1977; Moehlman, 1974). Even in large foraging aggregations one must wonder what the probable reason is for an individual who exhibits nervousness and why it frequently scans its environment. Do members of a herd (or solitary individuals) look for conspecifics *or* do they look for predators?

With respect to foraging ratios and the number of interruptions, there is no difference in scanning for predators or conspecifics in bighorn sheep. The fact remains that for sheep, when group sizes are small or individuals are solitary, they: 1) forage less efficiently (as measured through *FR's*); and 2) they interrupt foraging more frequently than sheep in larger groups. In short, sheep in small groups are poor foragers.

Whether sheep seek larger groups so they may reduce time spent scanning or because conspecifics may then buffer them from predators (Hamilton, 1971; Pulliam, 1973) is uncertain. But these categories are not mutually exclusive alternatives and both factors may interplay in decision making (Altmann, 1974). However, enhanced predator detection is certainly implicated since larger bands (whose individuals spent less time in surveillance) were more difficult for me to approach. Hoogland (1977) reported similar findings for black and white-tailed prairie dogs (*Cynomys ludovicianus* and *C. leucurus*). Residents in larger wards spent less time in 'watching' activities, yet still detected predators earlier than conspecifics in smaller groups. The most plausible explanation for increased alertness in larger groups is that more sensory apparatus (visual, olfactory, auditory systems) is available for predator detection.

2. *Social Facilitation*

Another form of antipredatory behavior in herd dwelling ungulates is following other individuals, a behavior pattern that first appears in filial imprinting (Hess, 1962; Lent, 1974). At this early age it obviously is adaptive for infants to follow their mothers. As bighorn lambs age they group together and play with peers. In fact, lambs of one age interact very differently with those of various ages. For instance, Berger (1978) found that during 'contact' play, lambs interacted with only similarly aged individuals, whereas they chased and followed lambs of any age during 'locomotor' play. The lack of choice for similar age partner preferences during 'locomotor' play was interpreted as selection for the ability to follow any conspecific regardless of age (see Berger, 1978). Simply stated, when one animal runs others follow (Autenrieth and Fichter, 1975; Walther, 1969; and others). By following conspecifics, individuals that have not yet observed danger are quite apt to avoid it by running. Of course, at some point excessive energy expenditure (for example nervousness or unnecessary flight) is obviously detrimental and will be selected against. And, as previously shown, sheep typically exhibited few false alarms.

3. *Behaviors Conspicuous to Predators*

Several different functional explanations have been offered for vocal signals and conspicuous postures in ungulates. Hirth and McCullough (1977) presented evidence that snorting sounds occurred more often in groups of female white-tailed deer (*Odocoileus virginianus*) than in males, and they suggested that this behavior evolved through kin selection. Their interesting hypothesis remains untested, however, because the genetic relationships of their study population were unknown. Since alarm vocalizations appear to be ubiquitous among many male and female, solitary, and non-related ungulates (see examples in Schaller, 1972, 1977; Du Plessis, 1972), there may be other explanations that coincide with the kin selection hypothesis for these vocal signals.

Several factors may interplay and account for explosive snorting sounds in bighorn sheep (and other ungulates too). Snorting may be envisioned to lie along a continuum represented by warning at one extreme and threat (directed toward conspecific intruders) on the other. Depending upon genetic relationships, warnings may then be given to kin (as suggested by Hirth and McCullough). Marler (1975), p.16) stated that in colobus monkeys (*Cercopithecus* spp.) variations of the same call are given, "one serving as threat, another as alarm." Alternatively, Smythe (1970, 1977) suggested that vocal snorts in ungulates could serve as 'pursuit-invitation' signals.

Another possible explanation for vocal alarms is that they are a respiratory displacement activity (Spurway and Haldane, 1954) which may have developed as an evolutionary by-product. For instance, many species of ungulates, primates, rodents, and even humans elicit audible responses when startled or suddenly excited; particularly in novel situations (see Andrews, 1963). It is possible that such vocal behavior in ungulates could have developed as a displacement activity. And, since predation appears to be rare in vocalizing individuals (Brown, 1975, p. 200), it seems selection would not disfavor individuals that call. Conspecifics could than learn that snorts signal a new stimulus just as 'attention' postures do.

Finally, conspicuous postures (kicking the ground, etc.—see Results) and explosive snorting sounds, which occur among solitary individuals and/or those in groups, may function as interspecific aggressive signals rather than intraspecific warning devices (or perhaps, both). Linsdale and Tomich (1953) suggested that these behaviors serve to cause a potential intruder to move so that its identity may be assessed.

It is apparent that the study of conspicuous behaviors, at least in bighorn sheep, is exceedingly difficult. Not only is the interaction between intrinsic (e.g. motivational) and extrinsic factors complex, but the lack of these behaviors in populations that no longer persist under natural conditions is widespread (i.e. in those populations frequently bombarded with peripheral stimuli such as direct human disturbances, airplanes, dogs, etc.). Further and careful quantitative study of conspicuous behaviors in ungulates is necessary to better understand their evolutionary development. With respect to vocal alarms, it appears that for bighorn sheep they may not be explained as the outcome of one selective pressure, but rather they may comprise components of threat, displacement, and warning.

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