Vigilance and group size in springbok

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ABSTRACT

Wild springbok *Antidorcas marsupalis*, in the Ethosha National Park, were observed while feeding in groups of varying size, and the numbers of vigilant (neck erect, head up) animals recorded. The proportion of vigilant springbok declined as group size increased. However, an individual's feeding time apparently does not increase and may even decline in groups larger than about 25 animals. These findings are discussed in relation to anti-predator and other benefits resulting from grouping.

1 INTRODUCTION

Modern reviews of the variety of ways by which animals may gain protection from predators, and simultaneously enhance their feeding efficiency by gathering in groups, have been undertaken by Bertram (1978) and Rubinstein (1978). However, the relationships between anti-predator behaviour and feeding behaviour are complex and are not yet clearly understood (Bertram 1979). Somewhat surprisingly, the many different species of gregarious African antelopes have largely been ignored by students interested in investigating the costs and benefits attending the relationships between feeding efficiency and predator detection in animal groups.

This report deals with aspects of the vigilance and feeding behaviour of springbok *Antidorcas marsupialis* in relation to group size in the Etosha National Park. Springbok are well suited for studies of this topic, since they generally form conspicuous, discrete groups and typically inhabit open, gently undulating country covered in short grass and scattered small bushes.

2 METHODS

Groups of springbok were observed while feeding undisturbed during 1–4 July 1978, using binoculars from inside a motor vehicle at distances normally of 500 m. Animals were counted as members of a group if they were within 50 m of each other (normally they were much closer together) and the smallest group was taken as three individuals. Singletons and duos were excluded, since they were almost invariably territorial males. I recorded the numbers of individuals with their heads down (feeding) among the vegetation and the numbers of individuals with their heads up and necks erect (looking around, vigilant), during single uninterrupted scans of each group. The data were spoken into a tape recorder and later transcribed. Repeat observations of the same group were unlikely, since usually not less than 0,5 km separated the groups observed on any one day, and widely separated different areas were surveyed on each day. I did not record information separately for different age, sex or social-status classes of springbok. In July most of the juveniles feed independently of their mothers, and approach adults in size. Associations of springbok on their way to and from watering sites were not sampled. Thus, only largely static groups of feeding animals were recorded. Groups containing one or more individuals resting and/or ruminating while lying on the ground were not included in the sample.

3 RESULTS

Figure 1 summarises the data, and shows that the proportion of feeding (head down) springbok initially increased as group size increased. A log-log regression model in linear regression best fits the head-down/group-size curve ($y=81{,}23 + 3{,}77x$, $t=3{,}77$, $P<0{,}01$, $N=85$), where y is the number of animals with head down and x is group size. In other words, springbok in small groups raise their heads more frequently, and/or for longer, than individuals in medium-sized groups, but above this an individual's feeding time, as measured here, apparently does not increase and may even decline in groups larger than about 25 animals. This cannot be related to a frequency distribution of the 85 groups in the sample, since I deliberately biased my observations in favour of large groups. However, based on aerial counts, made by H. H. Berry, of springbok (drinking groups excluded) at Etosha in July 1976, mean group size (discounting single animals and groups smaller than three) was 28,2 (S.D. = ± 40,1, range 3–350, N = 250).

4 DISCUSSION

Springbok are an important prey item for lions *Panthera leo* and some other large carnivores in semi-arid areas of southern Africa (Eloff 1973; Berry pers. comm.). According to Schaller (1972), the success rate of lions increased when hunting solitary members of social ungulates, rather than animals in groups, probably because of the groups' better vigilance; also perhaps the solitary individuals are at a disadvantage in some other way.

A springbok standing erect, with head held high, is presumably better able to detect visually an approaching predator than one feeding with its head low down in the vegetation. Thus, increased vigilance, and presumably reduced risk of predation, is achieved at the cost of time spent feeding. Bertram (1979) investigated how ostriches *Struthio camelus* resolve this time–allocation problem, and showed that individual vigilance declined as group size increased, through a decrease in the frequency with which the birds raised their heads. Bertram concluded that, while grouping when feeding results in only a slight reduction in the group's vulnerability to successful predator attack, grouping considerably reduces an individual's vulnerability. However, the ostrich data were obtained only from very small groups (up to four birds). Larger groups, had they occurred, might have been found to show increased predator-detecting ability, as has been occasionally demonstrated experimentally in some other species of birds (Powell 1974, Siegfried and Underhill 1975; Kenward 1978). In any event, feeding springbok apparently behave similarly to ostriches in that they are able to reduce their rate of vigilance, and presumably also the risk of predation, through joining companions. Reduced vigilance enables a springbok to feed at a faster rate but this does not necessarily equate with an increased total intake of food, since feeding efficiency is influenced by a variety of factors in addition to predation (Bertram 1978, 1979).

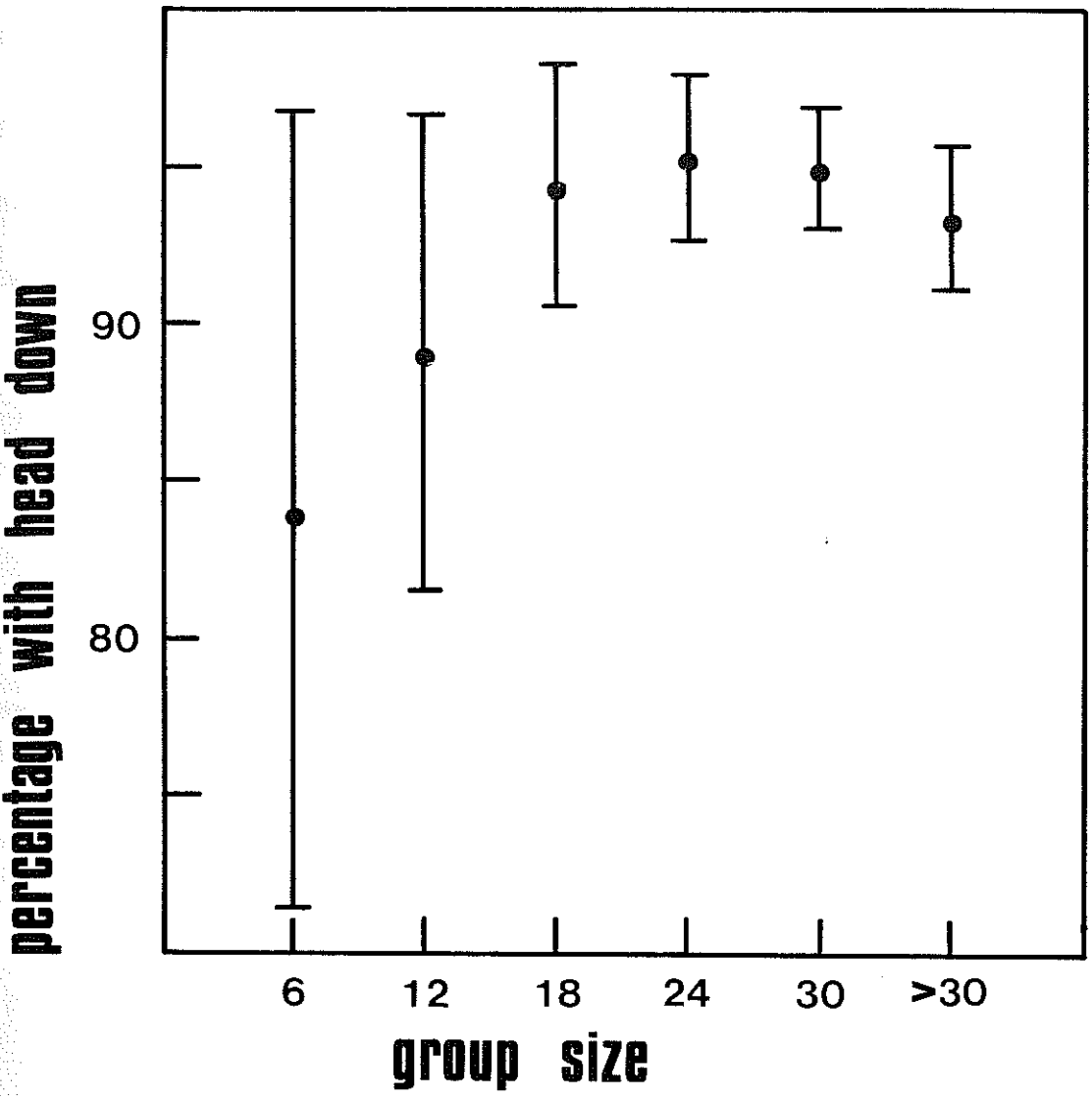

FIGURE 1: Relationship between mean percentage of animals feeding (head down) and mean group size in springbok. The vertical bars show one standard deviation on either side of the mean. Based on 85 groups containing from three to 105 animals.

The mean group size (28,2) of mixed springbok herds observed in July 1976 can be compared with that (18,7 ± 16,4, range 3–90, N = 32) recorded in the same month some 20 years ago by Bigalke (1970) in the Etosha Park. Although springbok herd size and composition can be very variable in relation to season, year and region (David 1978), it seems that the species generally fits the gazelle pattern in having herds averaging 10–30 animals (Estes 1967). The results of the present study hint at the existence of an optimal group size for fastest feeding of about 20 animals, during the period that the observations were made. Investigations of the mechanisms and the selective bases for upper size limits in flocks of bird species have revealed complicated and not yet fully understood interrelationships between anti-predator and other benefits resulting from grouping, but clearly improved predator detection does not go on increasing with group size above a certain limit, beyond which it may even decline (Siegfried and Underhill 1975; Bertram 1978).

Apart from protection against predators, or parasites (Duncan and Vigne 1979), and an enhanced feeding rate, there are certainly other benefits attending grouping, such as courtship and mate selection. In practice, there are many different and changing pressures, involving ecological factors and within-group interactions, operating to modify a social species' optimal group size (Bertram 1978). Ultimately, however, food availability is likely to be most important in determining the size of springbok feeding groups, as found for barnacle geese *Branta leucopsis* by Drent and Swierstra (1977).

The nature of the springbok's food supply is such that animals in small groups probably do not compete directly to any significant extent over food. However,

the animals must spend more time on feeding when food becomes scarce and this initially will favour an increase in group size, because of a reduction in time spent on vigilance. Further depletion of food stocks will contribute to an increase in the distance travelled by animals in searching for food. This should lead to further increases in group size if, as proposed by Cody (1971, 1974) for finch flocks in the Mohave desert, springbok can exploit scarce food more efficiently in an area if they forage over it as a single large herd, since such behaviour will enable the animals to avoid interference between themselves and so optimise their return times. In other words, springbok in large herds can avoid revisiting places where they have recently fed, whereas smaller groups foraging independently would often expend energy and time covering ground denuded by previous foragers. There is some evidence in support of the general applicability of Cody's thesis, from theoretical considerations (Charnov, *et al.* 1976) and occasional studies of different species (see Heinrich 1978), but definitive conclusions cannot yet be drawn. Nevertheless, one might now view in some new light the erstwhile sporadic appearance of enormous congregations of springbok, known as *trekbokken* (see Bigalke 1972), as being perhaps an extreme point on a continuum of optimal behaviour for economical foraging under changing ecological circumstances. This view is incompatible with earlier interpretations by Wynne-Edwards (1962), and others, of springbok treks being mass irruptions evolved by the species to ensure its survival when conditions for life become extremely adverse in arid areas. Similarly, Child and le Riche (1969) do not provide convincing factual or inductive evidence for their opinion that springbok treks are spectacular dispersal movements from areas of high population density.

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