

THE EFFECT OF COLONY SIZE ON INDIVIDUAL ALERTNESS OF PRAIRIE DOGS (SCIURIDAE: *CYNOMYS* SPP.)

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Abstract. From 1974 to 1976, I examined individual alertness of two species of squirrels (Sciuridae): loosely colonial white-tailed prairie dogs (*Cynomys leucurus*) and densely colonial black-tailed prairie dogs (*C. ludovicianus*). By observing single adults for 30-min periods and recording various measures of alertness, I investigated the effects on individual alertness of four variables, all of which are directly related to ward (subcolony) size and ward density. Conclusions were based on data from 188 white-tail observations and 280 black-tail observations. Individual alertness consistently correlated negatively with effective increases in ward size and ward density. I discuss various hypotheses that might explain these negative correlations, and conclude that decreased individual alertness is an important benefit of prairie dog coloniality.

It must usually be easier for a predator to remain undetected while approaching a solitary individual, for which only one individual's detection system must be avoided, than while approaching a group, for which numerous individuals' detection systems must be avoided. When individuals within a group give some sort of intentional or unintentional alarm signal after detecting a predator, it follows that one possible benefit of group living for individuals of prey species is an increased awareness of predators. That is, individuals within a group can sometimes benefit from the predator-detecting abilities of other group members, and are thereby less likely than solitary individuals to fall victim to a surprise predatory attack. This simple point was made by Galton (1883) almost 100 years ago, and has since been elaborated by numerous investigators (e.g. Lack 1968; Goss-Custard 1970; Pulliam 1973; Dimond & Lazarus 1974; Treisman 1975a, b; and references therein). Further, the probability that a member of a large group will himself be captured when a predator strikes is smaller than that for a member of a smaller group, due to 'selfish herd' effects (Hamilton 1971; Vine 1971). Relevant data from natural populations are available from studies of wintering shorebirds (Page & Whitacre 1975); laughing doves, *Streptopelia senegalensis* (Siegfried & Underhill 1975); bank swallows, *Riparia riparia* (Hoogland & Sherman 1976); and prairie dogs, *Cynomys* spp. (Hoogland 1978b).

When an individual's awareness of predators is higher in groups because of the vigilance and alarm signals of other group members and when the risks of predation within groups are lowered because of selfish herd effects, it follows that individuals of large groups might be able to reduce their own alertness and still be safer from predators than individuals of smaller groups. In large groups, the total collective amount of time devoted to alertness to predators can be high even though each individual's contribution might be small. That is, while maintaining an increased or at least an equivalent safety from predators, individuals of large groups might be able to devote proportionately less time to being cautious and alert for predators, and proportionately more time to feeding and other activities, than individuals of smaller groups (see references above and below). These same arguments apply to individuals of densely populated (versus sparsely populated) groups. For similar reasons, individuals at group centres might be able to be less watchful than individuals at group edges.

There have been several studies of individual alertness within natural populations. For birds, Murton (1968) reported that solitary wood pigeons, *Columba palumbus*, are more wary than are flocking individuals, and that peripheral flock members feed more slowly than do central flock members. For dark-eyed juncos, *Junco hyemalis*, Sabine (1949) observed that individuals within flocks feed faster than isolated individuals; the same is true for rooks, *Corvus frugilegus* (Feare et al. 1974), and bar-tailed godwits, *Limosa lapponica* (Smith & Evans

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1973). For yellow-eyed juncos, *Junco phaeonotus*, Caraco (1978) found that individual alertness varies inversely, and that feeding rate varies directly, with group size. In four different species of geese (*Anser* and *Branta*), individual vigilance correlates negatively with group size (see summary by Lazarus & Inglis 1978). Similar avian trends are suggested by laboratory studies (e.g. Powell 1974 and references therein). For mammals, Svendsen (1974) reported for yellow-bellied marmots, *Marmota flaviventris*, that solitary females are more watchful than colonial females, but sample sizes were small. Also for the yellow-belly, Armitage (1962) reported that peripheral colony residents seem to be more cautious than central residents. For the olympic marmot, *M. olympus*, Barash (1973) found that adults and yearlings in 'feeding groups' are less wary than the same adults and yearlings when solitary, but sample sizes were again small. Apparently, there have been few other serious investigations of individual vigilance in mammals.

In this report, I examine various effects of colony size and colony density on the individual alertness of adult prairie dogs. Specifically, I investigate the hypothesis that decreased individual alertness is a benefit of prairie dog coloniality. The effects of group size and group density on individual alertness have rarely been so rigorously examined. Elsewhere, I have investigated other possible benefits of prairie dog coloniality (Hoogland 1978b), as well as possible costs (Hoogland 1978a).

Prairie dogs are large, diurnal, colonial rodents of the squirrel family (Sciuridae). Of the five species, all in North America, that are currently recognized (Pizzimenti 1975), I studied two: white-tailed prairie dogs, *Cynomys leucurus*, and black-tailed prairie dogs, *C. ludovicianus*. Behaviour, ecology, and natural history of white-tails and black-tails have been summarized by King (1955, 1959), Tileston & Lechleitner (1966), Clark (1977) and Hoogland (1978a, b; see other references therein). In both species, individuals that detect predators usually both visually and vocally alarm other ward residents (Hoogland 1978b). For the purposes of this report, the most important difference between white-tails and black-tails concerns the degree of coloniality. Studies with marked animals have demonstrated that, although white-tails are definitely colonial, their colony and ward (subcolony; see below) densities are markedly lower than black-tail colony and ward densities. White-tail ward densities range from

1.47 to 5.65 adults per ha, with a mean \pm SD of 3.20 ± 1.40 ; black-tail ward densities range from 7.52 to 32.7 adults and yearlings per ha, with a mean \pm SD of 14.8 ± 9.67 (Hoogland 1978b). Further, absolute colony and ward sizes, with respect to both number of residents and physical area occupied, are smaller for white-tails than for black-tails (Hoogland 1978b). Within both species, gross social structure apparently does not vary with colony/ward density or absolute size. For example, black-tails are organized into harems known as coteries (King 1955) in colonies/wards of all densities and absolute sizes.

Methods

White-tail study sites were in the vicinities of Laramie, Wyoming, (elevation: 2200 m) and Walden, Colorado (elevation: 2500 m). The main study ward was located on the Arapaho National Wildlife Refuge, approximately 8 km southwest of Walden. Floral, faunal, and climatic conditions of the Laramie and Walden areas have been described by Clark (1977) and Tileston & Lechleitner (1966), respectively.

Black-tail study sites, including the main study ward, were within Wind Cave National Park (elevation: 1300 m), approximately 10 km north of Hot Springs, South Dakota. This area has been described by King (1955), who also studied black-tails at Wind Cave.

The white-tail and black-tail main study wards, as well as most of the other wards used for investigations, were protected from shooting, poisoning, and other forms of unnatural disturbance. All data were collected between April 1974 and July 1976.

The typical white-tail and black-tail colony is usually divided into two or more wards (King 1955), or subcolonies, by a small stream, a hill, a row of trees, etc. Residents of one ward can sometimes see or hear residents of an adjacent ward, but movements and interactions between wards are uncommon. When a predator attacks at one ward, residents of adjacent wards usually seem unconcerned. All investigations in this report involved wards rather than entire colonies.

Elsewhere I have detailed my methods for live-trapping, handling, and marking prairie dog adults and young (Hoogland 1977). Each year, all the residents of the white-tail and black-tail main study wards were both ear-tagged and colour-marked.

Quantification of Individual Alertness

To quantify individual alertness, I used stopwatches and handcounters and observed single prairie dogs for periods of 20 to 30 min; 520 such samples were taken, amounting to a total of 228 h of observation. All data were from adults and yearlings; that is, I did not examine individual alertness of juvenile prairie dogs. I only started to observe a prairie dog that was foraging under undisturbed conditions and showed none of the signs (see below) of individual alertness. Observations were discontinued during extended aggressive interactions such as black-tail territorial disputes. Mainly because of visual fatigue, trying to observe single animals for more than 30 min proved to be difficult. During each observation period, I recorded the following apparent measures of individual alertness, as described below: (A) number of headbobs, (B) amount of time devoted to headbobbing, (C) number of upright alerts, and (D) amount of time devoted to alert postures.

(A) Number of headbobs. While foraging on all fours, adult prairie dogs frequently lift their heads for short periods (0.2 to 5.0 s) and appear to quickly examine the surroundings. Each such lifting of the head was scored as a 'headbob', and was recorded with a handcounter (counter 1).

(B) Amount of time devoted to headbobbing. By means of a cumulative-time stopwatch (watch 1), I recorded the total elapsed time devoted to headbobbing during each observation period.

(C) Number of upright alerts. Often a prairie dog suddenly stops all previous activity, stands on its two hind legs, and appears to search for danger. This 'upright alert posture' (Clark 1977) is probably universal among burrowing, group-living squirrels (see Hoogland 1977 for references). By means of a handcounter (counter 2), I recorded each upright alert.

(D) Amount of time devoted to alert postures. Whenever there is real or suspected danger at a prairie dog ward, individuals therein assume any of a number of possible 'alert postures', of which an upright alert is one example. For white-tails, the numerous alert postures (upright extended, upright slouched, down sitting, down coiled, etc.) have been described by Clark (1977), and are similar to those described for other squirrels; I found black-tail alert postures to be essentially identical to those of white-tails. By means of a cumulative-time stopwatch (watch 2), I recorded the total elapsed time

devoted to alert postures during each observation period. It was sometimes difficult to distinguish between extended headbobs and alert postures. Individuals usually continued to chew vegetation during a headbob, but always stopped chewing when in an alert posture, and this difference was often helpful. Chewing during a headbob usually did not last for more than approximately 3 s; during those rare periods when it was possible to record headbobs but impossible to detect chewing (e.g. when a prairie dog's back was directly facing the observer), watch 1 was stopped and watch 2 was started after a single headbob had lasted for an estimated 3 s, unless the relevant individual clearly was not in alert. With this convention, it is probable that time devoted to an extended headbob was sometimes inaccurately assigned to time devoted to alert postures. Errors in this context were probably slight.

With data measuring A, B, C, and D, I was able, except for those cases involving missing data (see Tables Vb and VI), to compute four independent measures of individual alertness per observation period for my analyses: (1) headbobs per individual per minute, (2) proportion of time devoted to headbobbing, (3) upright alerts per individual per hour, and (4) proportion of time devoted to alert postures. I also computed two derived measures of individual alertness: (5) mean length of each headbob and (6) proportion of time devoted to both headbobbing and alert postures. The mean length of each headbob was derived by dividing the amount of time devoted to headbobbing (B) by the number of headbobs (A); the proportion of time devoted to both headbobbing and alert postures corresponded to the simple sum of (2) and (4), except in those cases involving missing data (see Hoogland 1977). I assumed that each of these six measures is associated with the detection of both predators and visual alarms of conspecifics (which warn of predators; see Hoogland 1978b), and that increases therein indicate increased individual alertness. Alternative interpretations are discussed in the sections that follow.

With respect to the presence of aboveground juveniles (Tables III and IV), data were classified as post-emergence after approximately 50% of the young at the relevant main study ward had already emerged from their natal burrows for the first time, and as pre-emergence otherwise. For white-tails, the date beyond which all data were classified as post-emergence in

1974, 1975, and 1976 was 22 June; for black-tails, the date for all three years was 20 May.

From day to day, I tried to avoid the repeated observation of the same individuals at the various wards. Such avoidance was easy at the main study wards, whose residents were all colour-marked. At other wards, I varied those areas within which I observed individuals. My 520 observation periods involved at least 250 different animals, one-half of which were colour-marked. There was no indication that individual alertness of colour-marked individuals differed from that of unmarked individuals.

Only data from prairie dogs that were observed for more than 5 min were used for my analyses. Data from the same individual that were not separated by more than 30 min were combined. Individual alertness of a single prairie dog varies tremendously over time (Hoogland, unpublished). Therefore, I assumed for this report that data from the same individual that were obtained from observation periods separated by at least 30 min were independent; in general, however, observations from the same individual were usually separated by at least several days (over 50% of all cases).

Individual alertness of prairie dogs might also be a function of sex, age, populational sex ratio, and populational age structure. Since I could only determine values for these variables at my single white-tail and black-tail main study wards, I assumed that the results of Tables I to VI were not biased by effects of such variables. As noted above, I recorded individual alertness of both adults and yearlings. Whereas white-tails usually breed as yearlings, black-tails do not breed until at least two years old (King 1955; Tileston & Lechleitner 1966; Clark 1977). Black-tail yearlings can only be distinguished from adults upon close examination. In this report, the term 'adult' refers to both adults and yearlings.

Some of the results in this report could be explained or could have been intensified by differential responses to human observers rather than by differential wariness to natural predators. To reduce the likelihood of such a bias, I (a) only recorded data when I was positioned within a hide (tent or vehicle), and (b) only recorded data after waiting at least 15 min after entrance into the hide (I waited longer if there were any signs of disturbance). Further, most of my data were from wards that were commonly exposed to humans. Also, as noted above, I only began to observe an individual that was foraging

under undisturbed conditions. Regarding the effect of first morning emergence (Table V), I only monitored first emergers if I had positioned myself in a hide before the first emergence of any prairie dog from its burrow.

For both white-tails (e.g. Clark 1977) and black-tails (e.g. King 1955; Lund 1974), there have been estimates from natural populations of individual alertness of adults. But methods and techniques of these previous studies have differed substantially, so that data from them cannot be legitimately combined or compared. All data in this report are my own.

Within a ward, aboveground ward size varies directly with aboveground ward density. I was unable for any of my analyses to determine whether one or both of these factors was mainly responsible for the observed results.

Statistical Analyses

I analysed most data in this report by non-parametric statistical methods. However, it was impossible to separate effects on individual alertness due to (a) ward size and (b) the presence of aboveground juveniles; other effects were easily separable. To examine (a) and (b), a two-way analysis of variance was called for. Because non-parametric methods for complex two-way analyses of variance are not available (Conover 1971), I used parametric two-way analyses of variance to examine the simultaneous effects of both (a) and (b) on the various measures of individual alertness. Transformations of data, which are indicated in Tables I and III, were often required to achieve significant equality of variances. The critical significance level for equality of transformed variances (and only for these analyses) was set at $P = 0.010$ rather than the conventional $P = 0.050$, since a parametric two-way analysis of variance is relatively insensitive to violations of the assumption of equality of variances (Dixon & Massey 1969).

Ward sizes were determined by repeated counts of visible residents or by estimates of physical areas occupied (on the assumption that there is a fixed relationship between physical area occupied and number of residents; see Hoogland 1977). For my analysis of the effect of ward size on individual alertness, I categorized each white-tail and black-tail ward as either 'small' or 'large', for two reasons. First, sample sizes from wards of different sizes were highly variable; that is, there were numerous data from certain ward sizes, and few data from other

ward sizes. Second and more important, small and large wards seemed to have real biological meaning; that is, my sample of wards for both species seemed to dichotomize well into the categories small and large. For white-tails, small wards contained fewer than eight resident adults, and large wards contained more than 15 resident adults. For black-tails, small wards contained fewer than 30 resident adults, and large wards contained more than 80 resident adults. I did not observe intermediate-sized wards for either species, although they probably exist. For interspecific comparisons, I assumed that my sample of white-tail and black-tail wards included a proportion of small and large wards that was representative and realistic for each species.

Data shown in tables and text are means \pm SD (one standard deviation). Sample sizes (N 's) in tables and text indicate numbers of observation periods, not numbers of different animals observed (see above). All significance levels resulted from two-tailed statistical tests. For more statistical details, see Hoogland (1977).

Results

I investigated the effects of the following variables on the individual alertness of white-tail and black-tail adults: (a) ward size (including interspecific differences), (b) the presence of aboveground juveniles, (c) first morning emergence, and (d) intraward position. Each of these variables is directly related to effective ward size and ward density. The results of my investigations are discussed below.

The Effect of Ward Size and Interspecific Differences

If decreased individual alertness is a benefit of prairie dog coloniality, then individuals of large wards should be less watchful than individuals of smaller wards, and should thereby have more time for feeding and other activities. To test this prediction, I observed white-tail and black-tail adults of small and large wards. For white-tails, I observed 182 adults (from five small wards and five large wards) for a mean of 23.7 ± 7.04 min per observation period (Table Ia). For black-tails, I observed 269 adults (from four small wards and four large wards) for a mean of 27.9 ± 5.15 min per observation period (Table Ib). By all measures, individuals of large wards were less wary than individuals of small wards for both white-tails and black-tails. Many of these differences were

significant ($P < 0.050$, (parametric) two-way analysis of variance).

As noted above, absolute ward sizes are greater for black-tails than for white-tails. In my sample of wards, even 'small' black-tail wards usually contained more residents than 'large' white-tail wards. Because of the effect of ward size on individual alertness (Table I), it follows that black-tails should be less vigilant than white-tails. The same prediction follows from the fact that ward densities are higher for black-tails than for white-tails. To test this prediction, I observed 188 white-tails and 280 black-tails (Table II); with a few additions, data for this comparison were from the same observations as those for Table I. With only one exception, for which there was no significant difference, black-tails proved to be significantly less wary than white-tails for the various measures of individual alertness ($P < 0.050$, Mann-Whitney U -test). I was unable to determine whether these differences resulted from effects due to absolute ward size or from effects due to ward density. As discussed below, there were at least four possible sources of error in this comparison.

First, the sensory capacities of black-tails might somehow be superior to those of white-tails, so that the former can safely devote proportionately less time to individual alertness than the latter. While simulating predatory attacks by badgers, *Taxidea taxus* (Hoogland 1978b), or while studying individual alertness, I detected no evidence that individual black-tails are somehow intrinsically better than individual white-tails at detecting danger.

Second, interspecific differences in Table II might have been biased by the presence of aboveground juveniles, which leads to decreased individual alertness (see below). Because proportionately more white-tail observations (75.5%) than black-tail observations (43.6%) occurred after most of the juveniles had first emerged and were aboveground, any biases in this context were presumably conservative.

Third, if white-tail predators are, or historically have been, more efficient or more numerous than black-tail predators, then this factor might explain the higher individual alertness of white-tails. Available information suggests that white-tail and black-tail predators are probably qualitatively the same (Hoogland 1978b). At the present time, however, it would be difficult to quantitatively compare white-tail and black-tail predators.

Table I. The Effect of Ward Size on Individual Alertness of (a) White-tails and (b) Black-tails

	Size of wards		Significance* of these differences
	Small (<i>N</i> = 63 from 5 wards)	Large (<i>N</i> = 119 from 5 wards)	
(a) White-tails			
Headbobs per individual per min	6.03 ± 2.43	5.48 ± 2.82	<i>P</i> = 0.710
Mean length of each headbob (s)	3.39 ± 2.09	2.79 ± 1.35	<i>P</i> = 0.151†
Proportion of time devoted to headbobbing	0.303 ± 0.130	0.244 ± 0.113	<i>P</i> < 0.001
Upright alerts per individual per hour	16.5 ± 13.6	14.6 ± 11.6	<i>P</i> = 0.938‡
Proportion of time devoted to alert postures	0.205 ± 0.148	0.142 ± 0.126	<i>P</i> = 0.003
Proportion of time devoted to both headbobbing and alert postures	0.508 ± 0.158	0.386 ± 0.136	<i>P</i> < 0.001
(b) Black-tails			
	Small (<i>N</i> = 74 from 4 wards)	Large (<i>N</i> = 195 from 4 wards)	Significance* of these differences
Headbobs per individual per min	5.11 ± 2.27	5.06 ± 2.54	<i>P</i> = 0.768‡
Mean length of each headbob (s)	5.08 ± 3.39	2.84 ± 1.54	<i>P</i> < 0.001**
Proportion of time devoted to headbobbing	0.284 ± 0.120	0.201 ± 0.072	<i>P</i> = 0.002**
Upright alerts per individual per hour	11.5 ± 12.3	10.9 ± 10.2	<i>P</i> = 0.247‡
Proportion of time devoted to alert postures	0.112 ± 0.131	0.094 ± 0.103	<i>P</i> = 0.222‡
Proportion of time devoted to both headbobbing and alert postures	0.411 ± 0.128	0.326 ± 0.164	<i>P</i> < 0.001‡

*Unless otherwise noted, all data were analysed by a parametric two-way analysis of variance.

†These data could not be legitimately compared due to inequality of variances. No transformation could remove this inequality. When the assumption of equal variances was ignored, the significance level was as shown.

‡To stabilize variances, square root or log transformations of the raw data were analysed in these cases. The untransformed data are shown.

**Mean length of each headbob was not recorded at small black-tail wards before the first emergences of juveniles from their natal burrows. The data shown came from small (*N* = 28) and large (*N* = 59) wards only after juveniles were already aboveground. These data were analysed by the Mann-Whitney *U*-test.

Fourth, differences shown in Table II might have been biased by interspecific differences in visibility within the habitat. Increased visibility within a ward almost surely facilitates the detection of both predators and the visual alarms of conspecifics: if visibility within wards is greater for black-tails than for white-tails, then this difference might explain why black-tails are less wary. In fact, numerous lines of evidence indicate that black-tails can better survey their surroundings (i.e. have higher intraward visibilities) than white-tails (Hoogland 1978b). But most of the interspecific differences in visibility probably result from active modifica-

tion and removal of potential protective cover by individual black-tails, rather than from mere passive differences in habitat (Hoogland 1978b). Such modification and removal by black-tails presumably function to enhance an already improved ability to detect predators and visual alarms of conspecifics. That is, increased visibility can enhance an improved ability to detect predators or conspecifics' visual alarms, but is probably never the cause of initial improvements in this ability. Increased visibility probably only works to the prey's, rather than the predator's, advantage when the prey animals are group-living, so that the increased visibility for the

Table II. Interspecific Comparison of Individual Alertness: White-tails versus Black-tails

	White-tails (<i>N</i> = 188 from 13 wards)	Black-tails (<i>N</i> = 280 from 8 wards)	Significance* of these differences
Headbobs per individual per min	5.67 ± 2.73	5.07 ± 2.47	<i>P</i> = 0.014
Mean length of each headbob (s)	3.06 ± 1.74	3.20 ± 2.37	<i>P</i> = 0.393
Proportion of time devoted to headbobbing	0.275 ± 0.121	0.208 ± 0.097	<i>P</i> < 0.001
Upright alerts per individual per hour	15.6 ± 12.5	11.1 ± 10.8	<i>P</i> < 0.001
Proportion of time devoted to alert postures	0.166 ± 0.138	0.099 ± 0.112	<i>P</i> < 0.001
Proportion of time devoted to both headbobbing and alert postures	0.432 ± 0.155	0.349 ± 0.159	<i>P</i> < 0.001

*All data were analysed by the Mann-Whitney *U*-test.

collective group outweighs the cost of increased conspicuousness (see Hoogland 1978a and 1978b for a more complete discussion of the role of visibility within prairie dog wards).

The Effect of Aboveground Juveniles

For both white-tails and black-tails, dramatic annual increases in aboveground ward size and ward density occur following the first emergences of 3- to 5-week-old juveniles from their natal burrows. If individual vigilance correlates negatively with the aboveground presence of nearby conspecifics (underground individuals are presumably incapable of detecting predators), then adult prairie dogs should be less watchful after the first emergences of juveniles than they are beforehand. That is, post-emergence adults should be less wary than pre-emergence adults if decreased individual alertness is a benefit of prairie dog coloniality and if juveniles are capable of detecting predators. To test this prediction, I monitored white-tail and black-tail adults both before and after the first emergences of juveniles from their natal burrows; with few additions or deletions, data for these comparisons were from the same observations as those for Table I. Relevant white-tail and black-tail data are shown in Tables IIIa and IIIb, respectively. For the most part, adults of both species were less vigilant in the presence of aboveground juveniles, and some of the differences were significant (*P* < 0.050, (parametric) two-way analysis of variance).

It might seem surprising that white-tail and black-tail adults were less wary after the first emergences of juveniles. Perhaps parents, at least, should have been more watchful in the

presence of aboveground juveniles in order to protect their offspring better from certain dangers, such as attacks by aerial predators, that were non-existent to underground juveniles. For both white-tails and black-tails, juvenile interactions with adults usually involve only the juveniles' mothers on the day or day after first emergence; on these days it did seem that white-tail and black-tail mothers were especially watchful, but I did not rigorously investigate this possibility. However, in both species the exclusiveness of interactions between juveniles and their mothers terminates shortly after the juveniles' first emergences, and the juveniles begin to interact with numerous other adults (King 1955; Tileston & Lechleitner 1966; Clark 1977). Thus, there probably is no significant advantage for those parents that are especially wary shortly after their juveniles' first emergences. In this context, it is also relevant to point out that many of the post-emergence adults that were observed during any one year had not reared any offspring; this was true each year for approximately 10% of the observed white-tails and approximately 40% of the observed black-tails.

Following the first emergences of juveniles from their natal burrows, black-tail aboveground ward density usually increases by 50% to 100% (King 1955; Tileston & Lechleitner 1966; Hoogland 1978b). By contrast, white-tail aboveground ward density usually increases by 150% to 400% following the first juvenile emergences (Tileston & Lechleitner 1966; Clark 1977; Hoogland 1978b). It follows that the effect of aboveground juveniles on individual alertness of adults should be more pronounced for white-

Table III. The Effect of the Presence of Aboveground Juveniles on Individual Alertness of (a) White-tails and (b) Black-tails

	Stage of annual cycle		Significance* of these differences
	Before the emergence of young (<i>N</i> = 46 from 5 wards)	After the emergence of young (<i>N</i> = 142 from 5 wards)	
(a) White-tails			
Headbobs per individual per min	7.05 ± 2.68	5.25 ± 2.61	<i>P</i> = 0.001
Mean length of each headbob (s)	2.23 ± 1.66	3.40 ± 1.67	<i>P</i> < 0.001†
Proportion of time devoted to headbobbing	0.271 ± 0.148	0.264 ± 0.116	<i>P</i> = 0.028
Upright alerts per individual per hour	20.1 ± 15.6	14.1 ± 11.0	<i>P</i> = 0.007‡
Proportion of time devoted to alert postures	0.195 ± 0.132	0.156 ± 0.139	<i>P</i> = 0.875
Proportion of time devoted to both headbobbing and alert postures	0.466 ± 0.191	0.421 ± 0.140	<i>P</i> = 0.048
(b) Black-tails			
	Before the emergence of young (<i>N</i> = 149 from 4 wards)	After the emergence of young (<i>N</i> = 121 from 6 wards)	Significance* of these differences
Headbobs per individual per min	5.32 ± 2.68	4.77 ± 2.14	<i>P</i> = 0.009‡
Mean length of each headbob (s)	1.90 ± 0.935	2.84 ± 1.54	<i>P</i> < 0.001**
Proportion of time devoted to headbobbing	0.139 ± 0.057	0.201 ± 0.072	<i>P</i> = 0.001**
Upright alerts per individual per hour	11.4 ± 11.6	10.7 ± 9.75	<i>P</i> = 0.067‡
Proportion of time devoted to alert postures	0.106 ± 0.120	0.091 ± 0.100	<i>P</i> = 0.793‡
Proportion of time devoted to both headbobbing and alert postures	0.363 ± 0.172	0.333 ± 0.141	<i>P</i> = 0.762‡

*, †, ‡ See Table I.

**Mean length of each headbob was not recorded at small black-tail wards before the first emergences of juveniles from their natal burrows. The data shown came from large wards only. Sample sizes for pre- and post-emergence were 23 and 59, respectively. These data were analysed by the Mann-Whitney *U*-test.

tails than for black-tails. To test this prediction, I computed the ratios for pre-emergence individual alertness to post-emergence individual alertness (Table IV); large ratios presumably indicate a more pronounced effect from aboveground juveniles than smaller ratios. White-tail and black-tail pre-emergence to post-emergence ratios (for number of headbobs, mean length of each headbob, etc.) were computed directly from Tables IIIa and IIIb, respectively. With only one exception, the effect of aboveground juveniles was more pronounced (i.e. ratios were higher) for white-tails than for black-tails for the various measures of individual alertness. These interspecific differences might have been intensified because white-tail young mature

physically and behaviourally more quickly than do black-tail young (Tileston & Lechleitner 1966; Clark 1977; Hoogland 1978b): white-tail young probably became competent watchers and competent visual and vocal alarmers more quickly than did black-tail young, and thereby might have more quickly absorbed some of the sentry burden. I did not rigorously investigate the latter possibility (by a time-series analysis, for example).

The Effect of First Morning Emergence

Within a ward, the first prairie dogs that emerge from their burrows in the morning are effectively at a reduced ward density (and are effectively in a 'smaller' ward) until most of the

Table IV. Interspecific Comparison of the Relative Effect of the Presence of Aboveground Juveniles on Individual Alertness

	Ratio of pre-emergence (of young) data to post-emergence data		White-tail ratio/ Black-tail ratio
	White-tails	Black-tails	
Headbobs per individual per min	1.34	1.12	1.20
Mean length of each headbob (s)	0.66	0.67	0.99
Proportion of time devoted to headbobbing	1.03	0.69	1.49
Upright alerts per individual per hour	1.43	1.07	1.34
Proportion of time devoted to alert postures	1.25	1.16	1.08
Proportion of time devoted to both headbobbing and alert postures	1.11	1.09	1.02

other ward residents have also emerged. If decreased individual alertness is a benefit of prairie dog coloniality, it follows that, immediately after emergence, first emergers should be more wary than later emergers. To test this prediction, I started to observe first emergers immediately after their initial emergences, when no or few (≤ 3 or 4) other ward residents had also emerged, and compared these data with data from the same colour-marked individuals observed at later times on the same mornings, when most of the other ward residents had also emerged. I collected 'control' data from late emergers immediately after their initial emergences, when most of the other ward residents were aboveground and foraging, and again from the same individuals at later times on the same mornings, when most of the other ward residents were still aboveground and foraging. The prediction was that the two sets of data from each first emerger would be markedly different (with greater alertness immediately after emergence), due to marked differences in effective ward density; and that the two sets of control data from each late emerger would be similar, due to lacking differences in effective ward density.

For white-tails (Table Va), I observed individuals for 20-min periods and collected 18 paired sets of data from first emergers (from five wards) and nine paired sets of control data from late emergers (from two wards). For black-tails (Table Vb), I observed individuals for 30-min periods and collected 25 paired sets of data from first emergers (from three wards) and 24 paired sets of control data from late

emergers (from one ward). For both species, data from first and late emergers were collected from equal proportions of small and large wards whenever possible. For three of the four measures of black-tail individual alertness, first emergers were significantly more cautious immediately after their emergences than at the later times ($P \leq 0.009$, Wilcoxon matched-pairs signed-ranks test). By contrast, late emerging black-tail controls were not more wary immediately after their emergences than at the later times for any of the various measures of individual alertness ($P > 0.100$, Wilcoxon matched pairs signed-ranks test). The white-tail data suggested a similar conclusion, but were less convincing. However, note that for four of the six measures of white-tail individual alertness, controls were more often less watchful immediately after their emergences than at the later times; for only one of the six measures of white-tail individual alertness was this true for first emergers.

Because individual prairie dogs within small groups are probably more vulnerable to predation than individuals within larger groups, it might be especially profitable for predators to concentrate their efforts on the first morning emergers within a ward. If so, then this factor, rather than effective differences in ward density and ward size, might have been the cause or might have intensified those differences shown in Table V. During my three-year study, I did not detect any obvious attempt by predators to hunt either most often or most diligently just when first emergers were beginning to appear in the morning. In fact, I never observed an

attack on one of the three to four first emergers within a ward, even though I was often ($N = 250$ mornings) positioned in a hide at one of the various wards before such first emergences. I realize, however, that my arrival at or my presence in the hide might have deterred attacks by such skittish predators as coyotes (*Canis latrans*) and bobcats (*Lynx rufus*).

The Effect of Intraward Position

Individuals at an edge of a prairie dog ward are almost invariably surrounded by fewer con-

specifics than are individuals at the centre of the same ward, and the former are thereby effectively at a lower ward density (in a 'smaller' ward) than the latter. If reduced individual alertness is a benefit of prairie dog coloniality, then peripheral ward residents should be more wary than central residents. To test this prediction, an assistant and I observed central and peripheral residents of the same wards during exactly the same time periods; we alternated roles, with me observing the central animal

Table V. The Effect of First Morning Emergence on Individual Alertness of (a) White-tails and (b) Black-tails

	No. of individuals that are more watchful/ less watchful at emergence than at a later time (Significance*)	
	Controls ($N = 9$ from 2 wards)	First emergers ($N = 18$ from 5 wards)
(a) White-tails		
Headbobs per individual per min	6/3 (0.20 < P < 0.30)	11/7 ($P = 0.372$)
Mean length of each headbob (s)	4/5 (0.80 < P < 0.90)	7/9 ($P = 0.796$)
Proportion of time devoted to headbobbing	6/3 (0.50 < P < 0.60)	12/4 ($P = 0.079$)
Upright alerts per individual per hour	3/6 (0.50 < P < 0.60)	9/9 ($P = 0.617$)
Proportion of time devoted to alert postures	2/7 (0.05 < P < 0.10)	11/6 ($P = 0.177$)
Proportion of time devoted to both headbobbing and alert postures	3/6 (0.50 < P < 0.60)	11/5 ($P = 0.044$)
	No. of individuals that are more watchful/ less watchful at emergence than at a later time (Significance*)	
	Controls ($N = 24$ from 1 ward)	First emergers ($N = 25$ from 3 wards)
(b) Black-tails		
Headbobs per individual per min	12/11 ($P = 0.693$)	19/6 ($P = 0.009$)
Upright alerts per individual per hour	8/9 ($P = 0.868$)	13/7 ($P = 0.332$)
Proportion of time devoted to alert postures	12/12 ($P = 0.587$)	21/4 ($P = 0.003$)
Proportion of time devoted to both headbobbing and alert postures	15/9 ($P = 0.123$)	22/3 ($P < 0.001$)

*Data from adults immediately after their emergences in the morning and data from these same adults at later points of the same mornings were all compared by the Wilcoxon matched-pairs signed-ranks test. Differences in sample sizes resulted from ties (which are ignored by the Wilcoxon matched-pairs signed-ranks test) and missing data.

sometimes and the assistant doing so the other times. We collected data only from black-tails, by simultaneously observing central and peripheral individuals from each of 26 pairs (from 10 wards) for a mean of 27.5 ± 12.3 min per observation period (Table VI; these data do not appear in any other table). Edges of black-tail wards can be easily identified by the tall vegetation there (Hoogland 1978b), and peripheral individuals chosen for observation were near such edges; central individuals were removed from such edges and were located approximately at ward centres. By all four measures of individual alertness, peripheral black-tail adults were more cautious than central adults, and three of these differences were significant ($P \leq 0.010$, Wilcoxon matched-pairs signed-ranks test). Peripheral individuals sometimes became more central during the course of observation, and vice versa; individual alertness seemed to correlate as predicted (i.e. alertness seemed to decrease with movement towards the ward centre), but sample sizes were too small for statistical analysis.

If peripheral black-tails were consistently closer to the hide containing me and my assistant during centre-edge observations, then differences in Table VI might have resulted from or been intensified by a differential wary response of peripheral individuals to humans rather than from effective differences in ward density. However, there was no significant association between the greater individual alertness and that individual closer to the hide. Further, for 24 of the 26 paired observations for which I recorded the relevant information, central individuals were closer to the hide 16 times, and peripheral individuals were closer the other eight times.

Discussion

Daily activity patterns, which indicate proportions of time devoted to various activities such as feeding and wariness of predators, have been described for numerous species. But only rarely have there been attempts to determine what factors lead to a particular activity pattern. In this report, I investigated the effects of ward size and ward density on the daily activity patterns of white-tailed and black-tailed prairie dogs, and I tried to determine whether decreased individual alertness is a benefit of prairie dog coloniality. There are other factors besides group size and group density, of course, that influence daily activity patterns (e.g. see Caraco 1978 and Lazarus & Inglis 1978); such factors are unrelated to coloniality, and were not investigated.

At least four variables determine the effective aboveground size and density at a prairie dog ward: (a) ward size itself (i.e. the number of residents living there); (b) the presence of aboveground juveniles that have emerged from their natal burrows; (c) first morning emergence, with first emergers being at effectively low densities until most of the other ward residents have also emerged; and (d) intraward position, with peripheral ward residents being at lower effective ward densities than central residents. By observing single prairie dogs for 30-min periods, I examined the effect of each of these variables on individual alertness (Tables I to VI). Individual alertness consistently correlated negatively with effective increases in ward size and ward density, and densely colonial black-tails were less alert than loosely colonial white-tails.

Throughout this report, I have assumed, as have numerous investigators before me (see references in Hoogland 1977), that sciurid

Table VI. The Effect of Intraward Position on Individual Alertness of Black-tails

	No. times that edge individual is more watchful than centre individual	No. times that edge individual is less watchful than centre individual	Significance* of these differences
Headbobs per individual per min	15	6	$P = 0.009$
Upright alerts per individual per hour	15	8	$P = 0.086$
Proportion of time devoted to alert postures	21	5	$P = 0.001$
Proportion of time devoted to both headbobbing and alert postures	16	5	$P = 0.005$

*All centre-edge paired data were analysed by the Wilcoxon matched-pairs signed-ranks test. Differences in sample sizes resulted from ties (which are ignored by the Wilcoxon matched-pairs signed-ranks test) and missing data.

alert behaviours function to detect predators and visual alarms of conspecifics. Regarding individual alertness of black-tails, King (1955, page 101) hypothesized that 'this constant alertness of the prairie dog has often incorrectly been interpreted as a guard against predatory attacks; instead, its social function is to watch the threatening activities of other prairie dogs.' I agree that individual alertness of prairie dogs might sometimes facilitate observations of the threatening activities of competing conspecifics (territorial invasions, harassment of offspring, etc.). But I do not agree that close watching of such threatening activities is the primary function of individual alertness. If close watching of conspecifics' threatening activities were the primary function, then individual alertness should correlate with effective increases in ward size and ward density, since such increases mean increases in the numbers of nearby competitors whose threats will presumably command attention. In particular, it follows from King's (1955) hypothesis that individual alertness of prairie dogs should be more pronounced (a) in large rather than small wards, and for black-tails rather than white-tails, (b) after the first emergences of juveniles from their natal burrows rather than before, (c) after most of the other ward residents have emerged in the morning rather than before, and (d) for central rather than for peripheral ward residents. These four predictions from King's (1955) hypothesis are exact opposites of those predictions that follow from the hypothesis that individual alertness of prairie dogs functions to detect predators and visual alarms of conspecifics. Results from this study, at least, indicate that individual alertness of prairie dog adults has probably evolved mainly in the context of detecting predators and conspecifics' visual alarms. Data from simulated attacks of badgers also support this conclusion (Hoogland 1978b).

Increased competition for various resources such as food, burrows, and mates is an automatic cost of prairie dog coloniality (Hoogland 1978a). It follows that such competition is probably more intense in large wards than in smaller wards, for black-tails than for white-tails, for central ward residents than for peripheral ward residents, etc. On the basis of my results (Tables I to VI), I conclude that decreased individual alertness is probably an important benefit of prairie dog coloniality. But such decreased individual alertness might merely reflect the effects of increased competition.

Individuals in large wards, for example, might devote less time to alertness than individuals of smaller wards because of the former's pressure, resulting from increased competition, to devote more time to searching for food, defending burrows and mates, etc. That is, even though individuals in large wards might seem to have more time to feed, their actual intake of food might be lower because of lower food availability and greater pressure to devote time to defence of burrows and mates. Caraco (1978) makes a similar point for yellow-eyed juncos. For prairie dogs, I was unable to determine to what extent the benefit of decreased individual alertness is offset by the cost of increased competition.

Although I conclude that decreased individual alertness is probably an important benefit of prairie dog coloniality, I was unable to examine directly the effect of such decreased individual alertness on reproductive success. That is, I was unable to determine, for example, whether those individual prairie dogs of large wards that devote less time to individual alertness than individuals of smaller wards are thereby able to rear more offspring. Such a determination for prairie dogs would be difficult for two reasons. First, individual prairie dogs are exceedingly difficult to live-trap (Hoogland 1977). Thus, it would be difficult to compare reproductive success with ward size, for example. Second and more important, it would be difficult to determine whether increases in reproductive success, if they occur, result from decreased individual alertness or from some other possible benefit of prairie dog coloniality (Hoogland 1978b). Observed increases in reproductive success in larger wards, for example, might result directly from reduced predation therein rather than from effects of decreased individual alertness. It seems likely that consistent reductions in individual alertness would eventually lead to gains in reproductive success, but for now the conclusion that decreased individual alertness is a selective benefit of prairie dog coloniality must remain tentative.

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