THE EVOLUTION OF COLONIALITY IN WHITE-TAILED AND BLACK-TAILED PRAIRIE DOGS (SCIURIDAE: Cynomys leucurus and C. ludovicianus)

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Abstract. In a 6-yr study, I investigated possible selective bases for coloniality in two species of squirrels (Sciuridae): loosely colonial White-tailed Prairie Dogs (Cynomys leucurus) and densely colonial Black-tailed Prairie Dogs (C. ludovicianus). White-tail study sites were in Wyoming and Colorado, USA; Black-tail study sites were in Colorado and South Dakota. I examined three hypotheses that might explain the evolution of coloniality: (a) shortage of suitable habitat, (b) social facilitation of foraging, and (c) reduced predation. The apparent surplus of unused suitable habitat and the absence of isolated individuals both indicated that prairie dogs are not forced to live together because of habitat shortages. An analysis of prairie dog foraging patterns indicated that there is no social facilitation of foraging in terms of either (a) group hunting of either large or elusive prey, (b) the location of large, scattered food supplies, (c) modification of the soil in order to effect the growth of vegetation that is more favorable or more abundant than that which would otherwise result, or (d) group defense of foraging grounds. Three lines of evidence indicate that reduced predation may be the most important benefit of prairie dog coloniality. First, simulated predatory attacks by badgers (Taxidea taxus) indicated that individuals in large wards (subcolonies) detect predators more quickly than do individuals in smaller wards; further, Black-tails detect predators more quickly than do White-tails. Second, individuals in large wards devote proportionately less time to alertness (i.e., scanning for predators) than do individuals in smaller wards, and Black-tails are less vigilant than are White-tails. Third, breeding synchronization and center-edge differences in individual alertness both indicate the possible importance of selfish herd effects. Interspecific differences in ward size and ward density may ultimately result because White-tail habitats contain significantly more protective cover than do Black-tail habitats.

Key words: breeding synchronization; coloniality; Cynomys leucurus; Cynomys ludovicianus; individual alertness; prairie dog; predation; selfish herd effects; social facilitation of foraging.

INTRODUCTION

Like other animals that live in groups (Alexander 1974, Hoogland and Sherman 1976), prairie dogs (Sciuridae: Cynomys spp.) experience several disadvantages of group-living. For example, by being in colonies, individual prairie dogs experience increased aggression and increased transmission of ectoparasites (Hoogland 1979a). In view of such costs, it is not obvious why coloniality has evolved in prairie dogs (or, more generally, in any animal). Possible selective contexts for the evolution of coloniality have been examined for several bird species (e.g., Horn 1968, Krebs 1974, Emlen and Demong 1975, Snapp 1976), but there have been few comparable studies with mammals. In this report, I examine coloniality in two species of squirrels: loosely colonial White-tailed Prairie Dogs (C. leucurus), and densely colonial Black-tailed Prairie Dogs (C. ludovicianus). Specifically, I investigate whether prairie dog coloniality has evolved in the context of either (a) a shortage of suitable habitat, (b) social facilitation of foraging, or (c) reduced predation.

MATERIALS AND METHODS

The study animals

Prairie dogs are large (700–1500 g), diurnal, colonial rodents. The typical prairie dog colony is subdivided into two or more wards (King 1955), or subcolonies, by a strip of tall vegetation, a small stream, a hill, etc. Residents of one ward can sometimes see or hear residents of an adjacent ward, but communications and interactions between wards are rare. All investigations in this report involved wards rather than entire colonies.

Most importantly, at least for this study, White-tails and Black-tails differ in the degree of coloniality in two obvious ways. First, White-tail colony and ward densities, measured in terms of the number of adults and yearlings per hectare, are significantly lower than Black-tail colony and ward densities (P = .014, MW) (Fig. 1b). Second, absolute colony and ward sizes, measured in terms of the number of adult and yearling residents, are predictably smaller for White-tails than for Black-tails (P = .005, MW) (Fig. 1a). Whereas I have seen numerous Black-tail wards that contained...
hundreds, and even thousands, of adults and yearlings. I have never seen a White-tail ward that contained more than \( \approx 100 \) adults and yearlings (see also Lechleitner 1969, Torres 1973, Clark 1977).

Black-tails within a ward are organized into social units known as coteries (King 1955). The typical coterie contains a single adult male and his harem of 1–6 females, along with yearlings and juveniles. Coteries members restrict foraging and other activities to a well-defined coterie territory that contains scores of burrow entrances; the mean size of a coterie territory is 0.26 ± 0.12 ha (Hoogland 1980, see also King 1955). White-tail social organization within a ward is poorly understood: individuals seem to have well-defined, overlapping home ranges (i.e., individuals do not forage over the entire ward), but harems and other obvious subgroupings do not occur. Foraging patterns of both White-tails and Black-tails usually keep individuals in those areas that contain nearby burrow entrances (i.e., individuals do not forage outside the boundaries of the home ward).

Whereas White-tails of both sexes usually breed in the spring of their 1st yr, Black-tails of both sexes usually do not breed until at least 2 yr of age. That is, White-tail yearlings do breed, but Black-tail yearlings (in South Dakota, at least) usually do not breed. I use the term “adult” in this report to indicate prairie dogs \( \geq 2 \) yr old.

At the outset of my study, I hypothesized that possible benefits of prairie dog coloniality should be greater (a) for individuals of large wards than for individuals of smaller wards and (b) for Black-tails (large, densely populated wards) than for White-tails (small, sparsely populated wards). Whenever possible, I therefore attempted to investigate benefits both intra- and interspecifically. Of course, factors other than the density and absolute size of wards and colonies affect the benefits of prairie dog coloniality. Because such latter factors probably vary more between species than within species, I consider my intraspecific comparisons with ward size to be more valuable than my interspecific comparisons. As discussed below, I never detected either a White-tail or a Black-tail living solitarily. Thus, I was unable to compare noncolonial and colonial prairie dogs with respect to the benefits of coloniality.

**Study sites, study periods, and marking procedures**

White-tail study sites were in the vicinities of Laramie, Wyoming (elevation = 2400 m), and Walden, Colorado (elevation = 2600 m). Black-tail study sites were in the vicinities of Fort Collins, Colorado, and Hot Springs, South Dakota (elevation for both = 1300 m). Many of the White-tail sites were on or near Walden’s Arapaho National Wildlife Refuge, and many of the Black-tail sites were within Hot Springs’ Wind Cave National Park; at both of these places, prairie dogs were protected from shooting, poisoning, and other forms of human disturbance. My single White-tail and Black-tail main study wards, where all the residents were ear-tagged and color-marked each year, are described elsewhere (Hoogland 1977).

Data for this report were collected over a 6-yr period, from 1974 through 1979. However, most data were collected between April of 1974 and August of 1976.

To capture prairie dogs, I used 15 × 15 × 60 cm National Double-door Live Traps (for adults) and 10 × 10 × 40 cm National Single-door Live Traps (for juveniles); for bait, I used whole oats. For permanent identification of individuals, I used National “fingerling” ear-tags; for visual identification from distances as great as 300 m, I used Nyanzol D fur dye. Trapping
and marking details can be found elsewhere (Hoogland 1977, 1979a).

**Experiments with the weasel and badger**

To study the responses of prairie dogs to predators, I used a single stuffed mink (*Mustela vison*) and three stuffed badgers (*Taxidea taxus*). The mink, termed "weasel" in this report, was stuffed in a lifelike pose and, for pulling, was mounted on a cardboard sled: this was the best simulation that I could find of a long-tailed weasel (*M. frenata*), a probable predator on prairie dogs (J. L. Hoogland 1977 and personal observation; C. N. Hillman, personal communication). The stuffed badgers used were museum skins and were therefore abnormally flattened; each badger was mounted on a cardboard sled and was assumed to simulate a live badger, which is a known predator on prairie dogs (Smith 1958, Tileston and Lechleitner 1966, Clark 1977, J. L. Hoogland 1977 and personal observation). Before each experiment, the weasel or badger was concealed in a large, black plastic bag to which the prairie dogs had become habituated for several days. The predator was pulled from its concealed position by means of fishing wire that led from the predator to the blind containing me and an assistant; pulls were made when there were no signs of disturbance among any of the aboveground foraging ward residents. With stopwatches and handcounters, I recorded information while the assistant pulled the predator. White-tail experiments were conducted in July of 1975 and June–July of 1976, when juveniles had been aboveground for 4–6 wk and were approximately 50% of adult mass. Black-tail experiments were conducted in August of 1975 and July–August of 1976, when juveniles had been aboveground for 8–12 wk and were approximately 50% of the adult mass. During the summer months, prairie dogs are most likely to be active and aboveground in early morning (approximately 0600 to 1100) and late afternoon (approximately 1500 to 1800) (e.g., King 1955, Clark 1977), and experimental runs were performed at these times.

The weasel was always positioned at the approximate center of a ward, 2 m from a randomly chosen burrow entrance. The badger was always positioned at a peripheral ward position. For most experimental runs, the badger was placed 30 m from an outermost peripheral burrow entrance that had an associated burrow mound with a diameter of at least 1 m. For these experiments, which were used for all intraspecific comparisons with ward size, the badger was pulled at a constant rate of 11 cm/s until 1 min after the first "whole ward" response (see below), at a rate of 22 cm/s for the next 5 min after the first "whole ward" response, and then at a rate of 33 cm/s until the badger reached the blind. For a small number of experimental runs used for some of the interspecific comparisons, the badger was positioned 16 m from an outermost peripheral burrow entrance of any kind (i.e., with or without an associated burrow mound). For these latter experiments, and for all experiments with the weasel, the predator was first pulled at a rate of 6 cm/s and then at a rate of 12 cm/s by a complicated method that involved starts and stops (Hoogland 1977). My pulling rates for intra- and interspecific comparisons were not necessarily realistic. However, predators such as badgers and coyotes (*Canis latrans*) may either run or walk slowly through a ward while hunting for prairie dogs, and both of these methods commonly involve several stops and starts.

A stopwatch was started as soon as the badger or weasel was first exposed from its concealed position. The first visual alarm was scored when the first prairie dog responded to the predator with either an alert posture or sudden run. The first vocal alarm, or alarm call, was detected by listening closely after the exposure of the predator. Because of difficulties with audibility, no attempt was made to record the first alarm call on windy days. The first "whole ward" response was recorded when most or all of the ward residents were alert together for the first time.

For experiments with the weasel or badger, I assumed that the prairie dogs responded to my stuffed specimens as they would have responded to live predators. Limited observations of live long-tailed weasels and badgers indicate that this assumption was probably justified (J. L. Hoogland 1977 and personal observation). The nature of the two types of outermost burrow entrances used for positioning the badger was arbitrarily determined, and I assumed that the appropriateness of the type of burrow entrance chosen for positioning did not vary within or between species. To take a specific example: I assumed that the outermost peripheral burrow entrances with associated 1-m burrow mounds were not significantly farther removed from areas of prairie dog activity in small wards than in larger wards. To reduce the possibility of biases related to badger positions that may have been unusual for any unknown reason, I pulled the badger three times from at least five different positions at each ward when possible, for a total of 3 × 5 = 15 pulls per ward.

All Black-tail experimental runs with the weasel and badger were conducted at Wind Cave National Park, where there is no grazing by cattle (*Bos sp.*) or horses (*Equus caballus*); I assumed that the limited grazing at Wind Cave by buffalo (*Bison bison*) is natural. On the other hand, several of the White-tail wards used for experiments with the weasel and badger were moderately to heavily grazed by cattle or horses. There was no relationship between the amount of grazing and White-tail ward size in my sample of wards, and I therefore assumed that my intraspecific comparisons with ward size were not biased by the effects of grazing. Any biases in the interspecific comparisons caused by unnatural grazing at the White-tail wards should have been conservative (Hoogland 1977).
During experimental runs within a prairie dog ward, only residents at that ward usually responded to the weasel or badger. That is, residents of adjacent wards usually did not respond to the stuffed predator. During attacks by live terrestrial predators, I observed the same pattern.

A more detailed description of my experiments with the weasel and badger can be found in Hoogland 1977: Chapter 2.

Statistical procedures

For reasons outlined elsewhere (Hoogland 1977, 1979), most data in this report were analyzed by nonparametric statistical methods (Conover 1971). However, to examine the effect of ward size on individual alertness (Fig. 6), I used a parametric two-way analysis of variance in order to remove the confounding effects of another variable (the presence of above-ground juveniles; see Hoogland 1979b), simply because nonparametric methods for complex two-way analyses of variance are not available (Conover 1971). I have used the term “ward rank” to refer to ward size, with respect to the number of adult and yearling residents, relative to the sizes of other wards. A ward with a rank of 2 contained more adults and yearlings than did a ward with a rank of 1, for example, but the magnitude of the differences could not be accurately determined. Ward rankings were determined either (a) by color-marking of all residents (N = 1 or 2 wards for each species), or (b) by using the maximum of several counts of active prairie dogs taken at different times on different days. I did not investigate the possibility of a relationship between ward size and ward density for either species. 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 for each species. For these same comparisons, I made no attempt to distinguish between those differences resulting from differences in ward size and those resulting from differences in ward density.

All significance levels in this report resulted from two-tailed statistical tests. Numbers in tables are means ± SE (one standard deviation), numbers in figures are means ± SE (one standard error), and numbers in figures above SE lines indicate sample sizes. I have used the abbreviations KRC and MW in the text to indicate the Kendall rank correlation test and Mann-Whitney U test, respectively.

Possible explanations for the evolution of prairie dog coloniality

Explanation number 1: shortage of suitable habitat?

A shortage of suitable habitat could force individuals to live closer together than would otherwise be advantageous. In coloniality caused by a shortage of suitable habitat, colony members do not gain from the proximity of nearby conspecifics as they do in coloniality caused by either social facilitation of foraging or reduced predation (Alexander 1974): that is, coloniality resulting from a shortage of suitable habitat involves all the costs of coloniality with no real benefits, and might be considered equivalent to “forced coloniality.” A possible importance of limiting habitat has been suggested for Cliff Swallows (Petrochelidon pyrrhonota) (J. Emlen 1952), Bank Swallows (Riparia riparia) (S. Emlen 1971), Barn Swallows (Hirundo rustica) (Snapp 1976), and several species of both sea-birds (Lack 1968) and weaver birds (Ploceinae) (Crook 1964). For mammals, similar shortages of habitat might be important for northern elephant seals (Mirounga angustirostris) (Bartholomew 1952) and Belding’s ground squirrels (Spermophilus beldingi) (Sherman 1976). For prairie dogs, I examined whether coloniality has evolved or is maintained by a shortage of suitable habitat by investigating (a) the annual usage pattern at ward sites, (b) the possibility of unused habitat within or near colonies, and (c) the possibility of isolated prairie dogs.

Continued use of the same ward site.—Several investigators have reported the long-term use of a particular ward site by both White-tails (Tileston and Lechleitner 1966, Clark 1977) and Black-tails (King 1955, Koford 1958, Tileston and Lechleitner 1966, Lo-vaas 1973, M. Garrett, personal communication; Z. Halpin, personal communication; J. L. Hoogland, personal observation). This evidence might indicate a shortage of suitable habitat, whereas frequent changes in the location of ward sites might indicate an abundance of suitable habitat. However, long-term use of ward sites might also result even when there is an abundance of suitable habitat if emigration is dangerous or if colonization of new habitat requires a large commitment of time and energy. As with small mammals in general (e.g., Lidicker 1975), emigration is probably dangerous for prairie dogs (e.g., King 1955: 37). Further, the invasion of new suitable areas, involving clipping of tall vegetation (Black-tails only; see below) and excavation of new burrows, is probably a long and difficult process. It follows that the long-term use of the same prairie dog ward sites is only weak evidence for a shortage of suitable habitat.

The presence of unused habitat.—If habitat is limiting for prairie dogs, then there should be few areas of unused suitable habitat. Unfortunately, suitability of a particular patch of habitat can only be unequivocally determined by actual use of that patch; that is, if prairie dogs do not live in a particular patch of habitat, then it is impossible to verify that that patch is suitable. With this reservation in mind, I qualitatively examined the levelness, soil type, and vegetation of the habitat that bordered prairie dog colonies. Every White-tail colony (N = 10) and Black-tail colony (N = 12) that I examined was bordered on at least one edge by unused habitat that appeared to me to be suit-
able for colonization. That is, prairie dogs of every colony seemed to be more clumped (i.e., more colonial) than required by habitat availability, and this suggests that a shortage of suitable habitat has not been important in the evolution or maintenance of prairie dog coloniality.

For both White-tails (Clark 1977) and Black-tails (King 1955, Lovaas 1973, J. E. Cole, M. Garrett, and Z. Halpin, personal communications, J. L. Hoogland, personal observation), the physical area occupied by a ward has repeatedly been observed to increase for those wards studied for several years; on the other hand, decreases in the physical areas occupied by wards have not been reported. For example, Clark’s (1977) study ward increased from 10.9 ha in 1966 to 13.2 ha in 1967–1968; King’s (1955) “ward A” increased from 2.10 ha in 1948–1949 to 2.95 ha in 1950. Ward expansions of this sort again suggest the availability of surplus suitable habitat, but the possibility remains that the observed areas of expansion were unsuitable prior to their initial use. For Black-tails, the occasional appearance of new wards at previously uncolonized sites (e.g., J. E. Cole, R. Klukas, and M. Garrett, personal communications) also suggests the availability of surplus suitable habitat.

The absence of isolated prairie dogs.—If prairie dog coloniality results mainly from a shortage of suitable habitat, then, despite the dangers of emigration and colonization cited above, individuals should at least occasionally isolate themselves whenever there are patches of habitat that are large enough for only one animal and whenever patches are too large to be saturated by the local population. Such isolation would circumvent the costs of coloniality, and would not involve the loss of (nonexistent) benefits. Isolated prairie dogs have not been reported in the literature. During each year of my study, I carefully examined the Walden and Wind Cave National Park vicinities in search of isolated prairie dogs. I never detected either an isolated White-tail or an isolated Black-tail (possibly because isolates are so vulnerable to predation; see arguments below), and this suggests that prairie dog coloniality does not result from a mere shortage of suitable habitat.

Explanation number 2: social facilitation of foraging?

Coloniality might evolve if groups of individuals are somehow able to secure more or better food per individual than are solitary individuals. Such social facilitation of foraging can occur in numerous ways (e.g., see Bertram 1978). For prairie dogs, there are at least four types of social facilitation of foraging by which coloniality may have evolved or may be maintained: (a) group-hunting of large or elusive prey, (b) location of large, scattered food supplies, (c) "farming," and (d) group-defense of foraging grounds. For Black-tails, these four possibilities are considered below; White-tail foraging patterns are poorly understood, and White-tails are therefore only briefly considered.

Group-hunting of large or elusive prey.—Some predators depend on large or elusive prey that can be easily captured only by groups of cooperating individuals. Single individuals of these predatory species are only rarely successful at hunting large or elusive prey items and usually obtain less food per individual than do individuals of cooperating groups. Examples of group-hunters of this sort probably include lions (Panthera leo) (Schaller 1972), Cape hunting dogs (Lycaon pictus) (Lawick and Lawick-Goodall 1971), spotted hyenas (Crocuta crocuta) (Kruuk 1972), wolves (Canis lupus) (Mech 1970), and killer whales (Orcinus Orca) (Martinez and Klinghammer 1970).

I never detected any evidence for group-hunting by prairie dogs. Further, observations of foraging individuals and analyses of feces and stomach contents both show that White-tails and Black-tails are almost strictly herbivorous (Whitehead 1927, Stockard 1930, Kelso 1939, King 1955, Koford 1958, Tileston and Lechleitner 1966, Summers and Linder 1978, Rogers-Wydeven 1979). Those few arthropods that are eaten (mostly grasshoppers, Acrididae) are small and can be easily captured by solitary individuals. Thus, there is no obvious context in which group-hunting of prey could be important for prairie dogs.

Certain plants within a Black-tail ward occasionally grow as tall as 50–150 cm (King 1955), presumably leading to interference with the prairie dogs’ range of vision. Most of these tall plants are eventually removed by the prairie dogs by either clipping or uprooting (see below). Perhaps certain tall plants can only be removed easily by groups of cooperating individuals; that is, one benefit of Black-tail coloniality might be the increased ability of cooperating individuals to remove tall plants. On numerous occasions (N > 20), I observed single Black-tails removing plants that were tall and/or tough and probably difficult for the prairie dogs to handle (e.g., mullein, Verbascum sp.; thistle, Cirsium sp.). On the other hand, I observed cooperative removal only two times. Thus, groups are not required, at least, for the removal of tall plants, and it seems unlikely that cooperative removal has been important in the evolution of Black-tail coloniality.

Location of large, scattered food supplies.—When food supplies are predictably (a) so large that they cannot be easily consumed by single individuals and (b) so scattered that solitary foragers only rarely find them, then groups of cooperating foragers may be able to secure more food per individual than can solitary foragers (Ward 1965, Horn 1968, Ward and Zahavi 1973, Alexander 1974, Krebs 1974, Erwin 1978, 1979). Three lines of evidence indicate that the location of large, scattered food supplies (herein called bonanzas)
has not been important in the evolution of Black-tail coloniality.

First, when the location of bonanzas is important, then individuals within colonies should be selected to be legitimately concerned for the food requirements of other colony members, one or more of which might be the finder of a bonanza at some later time; a system of reciprocity (Trivers 1971) involving food-finding signals is expected to evolve in this case. Such signalling may occur in Great Blue Herons (Ardea herodias) (Krebs 1974), Oilbirds (Steatornis caripensis) (Snow 1961), and a few other species (see Ward and Zahavi [1973] for other possible examples). By contrast, if coloniality is not dependent on locating food bonanzas, then individuals will probably be selected to maximize the capacity to “parasitize” the food-finding of other colony members and to minimize those behaviors that might alert others to personal food-finding success (Hoogland and Sherman 1976); no bonanza-finding signals are expected in this latter case, but parasitism should be common (see Horn 1968, for a possible case of this form of parasitism in Brewer’s Blackbirds (Euphagus cyanocephalus)). Though I was alert to this possibility, I never detected any mechanism (vocal, visual, or otherwise) by which individual Black-tails inform other colony residents about food sources; the same is true for White-tails. This information suggests that the location of bonanzas is not important for prairie dogs, but I realize that food-finding signals might be extremely subtle and practically immune to human detection.

Second, as noted above, individual Black-tails restrict essentially all of their foraging to the home coterie territory; e.g., in 1979, behavioral observations showed that individuals did over 99% of their foraging in the home coterie territory. Further, each coterie member usually has access to the entire coterie territory, and regularly traverses a large proportion of that territory during any single day; exceptions occur when lactating females defend small areas centered around burrow entrances containing young. Thus it seems unlikely that there could be food sources within the home coterie territory that could not be easily located by independent solitary foragers.

Third, even though the location of bonanzas might require colonial foraging, it does not necessarily require colonial living (Hoogland and Sherman 1976). All that matters is that individuals live close enough to be able to find each other easily every day. If Black-tail coloniality depends mainly on the finding of bonanzas, then, because of the costs of coloniality, individuals should form groups only during warm daylight hours when all foraging occurs and should spread out at other times. By contrast, rather than single individuals using single burrow systems, Black-tails regularly form underground groups containing 2–15 individuals during the two periods when no foraging occurs: during inclement daylight weather and, during all seasons of the year, at nighttime (King 1955, J. L. Hoogland 1980 and personal observation); to a lesser degree, the same is true for White-tails (J. L. Hoogland 1977 and personal observation). These patterns again suggest that prairie dog coloniality is unrelated to the finding of food bonanzas.

The farming hypothesis.—Black-tails commonly expose subsoil during the excavation of burrow systems and the maintenance of burrow mounds. Further, as noted above, individuals sometimes clip or uproot certain species of plants before these plants are able to reach maturity. King (1955, 1959) pointed out that, because of such “agricultural” activities (herein referred to collectively as farming), the vegetation within a Black-tail ward usually differs markedly from that of the surrounding habitat:

Another analogy to human farming methods is offered by the cultivation of the soil by the boring of the prairiedogs. Subsoil is thrown out on the surface of the ground and is exposed to invasion by forbs, which, on the topsoil, cannot compete with the grasses. The earth exposed about the burrows frequently is covered by plants not found abundantly in the region. Fetid marigold (Bobera paposa), scarlet mallow (Sphaeralcea coccinea), black nightshade (Solanum nigrum), and pigweed (Amaranthus retroflexus), for example, are species which occur exclusively on the subsoils about a prairiedog burrow. These plants, which have been more or less ‘cultivated’ by the prairiedogs, are often eaten and at times appear to be important food items. (King 1955: 12–16; emphasis is mine).

It follows from King’s (1955) observation that farming of plants by individual Black-tails may constitute an important benefit of coloniality. That is: if various Black-tail activities, such as the excavation of burrows, “fallowing,” (King 1955:12), and the clipping and uprooting of vegetation, effect more favorable and/or more abundant growth of vegetation than would otherwise occur, and if groups can somehow farm more efficiently than can single individuals, then perhaps Black-tail coloniality is maintained in this context.

One way to test the farming hypothesis would be to examine the effect of ward size on the quality and quantity of vegetation. A major difficulty here would be to determine the quality of each plant species to the Black-tails; simply comparing the energy content of different plant species by bomb calorimetry would not remove this difficulty, since available energy is not the only factor that determines the suitability and quality of a particular food item (Thorsteinson 1960, Pulliam 1975). Another way to test the farming hypothesis might be to examine the effect of ward size on adult body mass and juvenile growth rate, on the assumption that these variables correlate positively with the quality and quantity of available food. The problem
here is that factors other than the quality and quantity of food also affect adult body mass and juvenile growth rate; for example, adults in large wards might be heavier than adults in smaller wards simply because the former have proportionately more time to feed (see below).

If Black-tails fed and farmed throughout the entire physical areas of their wards and colonies, then the farming hypothesis might explain the maintenance of Black-tail coloniality. However, as noted above, Black-tails spend over 99% of their time in the home coterie territory. Thus the farming hypothesis might explain the maintenance of Black-tail coteries, but it cannot explain the maintenance of Black-tail wards and colonies. That is, the farming hypothesis cannot explain why coteries are invariably grouped together to form wards and colonies. An important assumption in this interpretation is that farming limited to one coterie territory does not significantly enhance the quality or quantity of vegetation within adjacent coterie territories (through dispersal of seeds, for example); unfortunately, verification of this assumption would be difficult.

**Group-defense of foraging grounds.**—Coloniality might also be maintained in the context of group-defense of foraging grounds, against members of either the same or different species (Brown and Orians 1970, see also Bertram 1978). That is, a cooperating group of individuals might be more efficient than a solitary individual at defending an important feeding site. For Black-tails, the crucial point here is that coterie members do not defend just any section in the home ward, but only the home coterie territory. Thus for reasons that parallel those presented above for farming, group-defense of foraging grounds might explain the maintenance of Black-tail coteries, but it cannot explain the grouping of coteries into wards and colonies.

**Explanation number 3:** reduced predation?

Finally, coloniality might evolve if individuals within groups are somehow better protected from predators than are solitary individuals. Such increased protection can result in numerous ways (e.g., see Bertram 1978). For prairie dogs in this context, there are at least four benefits that might account for the evolution or maintenance of coloniality: (a) increased awareness of predators, (b) decreased individual alertness, (c) increased “selfish herd” effects (Hamilton 1971), and (d) increased density of burrow entrances.

**Increased awareness of predators.**—A predator is usually more likely to be detected while approaching a group than while approaching a solitary individual. With the former, numerous individuals’ detection systems must be eluded, while only one individual’s detection system must be eluded with the latter. If individuals within a group give some sort of intentional or unintentional alarm signal after detecting a predator, it follows that one possible benefit of coloniality is an increased ability to detect predators. That is, individuals within a group can sometimes benefit by using the responses of other group members to predators, and are thereby less likely than solitary individuals to be captured by a predator. This simple point was made by Galton (1883) almost 100 yr ago, and has since been elaborated by numerous investigators (e.g., Lack 1968, Goss-Custard 1970, Pulliam 1973, Treisman 1975a, b, Lazarus 1978, and references therein). It is therefore surprising that the crucial observations from natural populations exist for only a handful of species, including wintering shorebirds (Page and Whitacre 1975), Laughing Doves (Streptopelia senegalensis) (Siegfried and Underhill 1975), and Bank Swallows (Hoogland and Sherman 1976).

At the outset of my study, I had hoped to compare predatory success with prairie dog ward size. However, I observed only six successful predations, all involving juvenile prairie dogs, during the course of the 6-yr study (see also below), even though I saw numerous (N > 200) apparent attempts by predators such as coyotes, badgers, bobcats (Lynx rufus), Golden Eagles (Aquila chrysaetos), Prairie Falcons (Falco mexicanus), and Buteo hawks (Buteo spp.). That is, the White-tail and Black-tail defense systems were consistently successful (see also King 1955, Smith 1958, Clark 1977). By using stuffed specimens of a badger and weasel and by recording alarm signals (visual alarms and alarm calls), I was indirectly able to compare antipredator defenses with ward size.

When a prairie dog detects a predator, it immediately either runs to a burrow mound or assumes one of numerous “alert postures,” and thereby provides a visual alarm to other ward residents (King 1955, Tileston and Lechleitner 1966, Smith et al. 1973, Clark 1977); a visual alarm usually offers the first sign of danger during a predatory attack (Hoogland 1977). The primary function of a visual alarm is probably not to warn conspecifics of danger, but rather to protect better the individual that gives it (e.g., by making it easier to see the predator, by decreasing conspicuousness of self, or by allowing a retreat to a safer position); valuable information is nonetheless transmitted to conspecifics, and individuals within a ward gain by being able to use the visual alarms of others. Individuals seem constantly to watch close neighbors for visual alarms, and respond quickly when one is given; in general, individuals do not respond to visual alarms of distant neighbors (>~20 m away). Clark (1977) pointed out that visual alarms are probably especially important under those conditions when hearing of alarm calls is impaired, as it may be on windy days. Visual alarms indicate suspected as well as real danger (Hoogland 1979b), and commonly turn out to be false alarms. After detecting a predator and giving a visual alarm, a prairie dog sometimes then gives a series of vocal alarms, or alarm calls (King 1955, Smith 1958, Tileston...
FIG. 2. The effect of ward rank on the antipredator defense systems of (a) White-tails and (b) Black-tails. All data are from experimental runs with the stuffed badger. Data were analyzed by the Kendall rank correlation test; the number above each SE line indicates the number of experimental runs. Rank 1 is the smallest ward.

and Lechleitner 1966, Waring 1970, Clark 1977, Hoogland 1980). Other individuals usually join the first alarm caller, and a chorus of alarm calls typically results during a predatory attack. Prairie dogs do not give alarm calls in response to any animal that approaches a ward, but only in response to their known predators (Hoogland 1977). Coyotes, badgers, Golden Eagles, and Prairie Falcons inevitably elicit alarm calls, whereas nonpredators such as rabbits (Lepori-
FIG. 3. Interspecific comparison of the first visual and the first alarm call in response to (a) the stuffed badger and (b) the stuffed weasel. Data were analyzed by the Mann-Whitney U test; the numbers above each bar indicate the number of experimental runs and the number of different wards observed, respectively.

runs at four wards). For these same experimental runs, contrary to expectation, the first visual alarm occurred significantly earlier ($P = .007$, MW) in the White-tail wards ($x \pm sd = 2.05 \pm 3.13$ min) than in the Black-tail wards ($x \pm sd = 3.23 \pm 2.75$ min). The reason for this unexpected result is not clear, but may be related to interspecific differences in the structure of burrow mounds (Clark 1977, Hoogland 1977), such that a 1-m mound for one species is not equivalent to a 1-m mound for the other species. For (b), the first visual alarm ($P < .001$, MW) and the first alarm call ($P < .050$, MW) in response to the badger both occurred earlier in Black-tail wards than in White-tail wards (Fig. 3a). For experiments with the weasel (c), Black-tails again had access to the first visual alarm ($P = .029$, MW) and the first alarm call ($P < .001$, MW) sooner than did White-tails (Fig. 3b). These latter data, along with those of Fig. 3a, indicate that Black-tails probably have more time to reach safety during a predatory attack than do White-tails.

Safety from an attacking predator probably also increases directly with the absolute number of visual alarmers during a predatory attack for (a) White-tails and (b) Black-tails. During each experimental run with the badger or weasel, I made several counts of the number of visual alarmers: from these counts, I determined the mean number and the maximum number of visual alarmers for each experimental run. For both White-tails and Black-tails, the mean and maximum numbers of visual alarmers elicited by the badger and weasel did not differ ($P > .10$ for both for each species), and the data from responses to badger and weasel were therefore combined. Data were analyzed by the Kendall rank correlation test; the number above the SE line of each maximum number indicates the number of experimental runs, and this number is the same for mean numbers.

FIG. 4. The effect of ward rank (1 is smallest) on the number of visual alarmers during a predatory attack for (a) White-tails and (b) Black-tails. During each experimental run with the badger or weasel, I made several counts of the number of visual alarmers: from these counts, I determined the mean number and the maximum number of visual alarmers for each experimental run. For both White-tails and Black-tails, the mean and maximum numbers of visual alarmers elicited by the badger and weasel did not differ ($P > .10$ for both for each species), and the data from responses to badger and weasel were therefore combined. Data were analyzed by the Kendall rank correlation test; the number above the SE line of each maximum number indicates the number of experimental runs, and this number is the same for mean numbers.
alarmers and alarm callers, at least up to some asymptotic point, for at least three reasons. First, the probability that an individual prairie dog will see or hear an alarm signal in time to escape probably varies directly with the absolute number of alarm signallers. This consideration might be especially important under conditions of poor visibility (as in most White-tail wards; see below) or poor audibility (as on windy days). Second, the probability that a collection of alarm signallers conveys a false alarm probably varies inversely with the absolute number of signallers (see also Lazars 1979). That is, whereas small numbers of visual alarmers and, rarely, small numbers of alarm callers are sometimes evident during times of apparent safety (King 1955, Smith 1958, Waring 1970, Hoogland 1977), large numbers of alarm signallers are restricted almost entirely to times of real danger. It follows that individuals in small wards, where maximum numbers of alarm signallers during a predatory attack are relatively small (Figs. 4 and 5), might sometimes find it difficult to distinguish between times of safety and times of danger. Third, the probability of deterring certain predators might vary directly with the number of alarm signallers. For example, large numbers of alert, alarm-calling prairie dogs might distract or confuse certain predators better than do smaller numbers. Perhaps other predators interpret a large number of alarm signallers within a large ward as a sign that few residents in that ward will still be unaware, and are thereby encouraged to look elsewhere for food.

For White-tails, I recorded the number of visual alarmers at 12 wards during experimental runs with the badger and weasel (Fig. 4a), and I recorded the number of alarm callers at three wards during experiments with the badger (Fig. 5); data were collected in July of 1975 and June–July of 1976. The number of visual alarmers and the number of alarm callers in response to the simulated predators both varied directly with ward size (P < .001 for both, KRC). That is, White-tails in large wards evidently can see more visual alarmers and can hear more alarm callers during a predatory attack than can White-tails in smaller wards. For Black-tails, I recorded visual alarmers at six wards during experimental runs with the badger and weasel in August of 1975 and July–August of 1976 (Fig. 4b). The number of visual alarmers again varied directly with ward size (P < .001, KRC). I was unable to record the number of Black-tail alarm callers during experiments with the badger or weasel, mainly because alarm-calling Black-tails are extremely difficult to identify since there is almost no movement of the mouthparts (Waring 1970). Thus a comparison of Black-tail ward size with the number of alarm callers and the appropriate interspecific comparison could not be made. In an interspecific comparison of the number of visual alarmers, Black-tail wards had significantly more visual alarmers than did White-tail wards (P = .005, MW) (Table 1).

**Decreased individual alertness.**—When an individual’s awareness of predators is higher in groups because of the vigilance and alarm signals of other group members, and when risks of predation within groups are further lowered because of selfish herd effects (see below), it follows that individuals of large groups should be able to reduce their own alertness and still be safer from predators than individuals of smaller groups. Even though each individual’s contribution of time devoted to scanning for predators might be small in large groups, the collective amount of time can be high. Thus the amount of time that can be devoted to feeding and other activities should vary directly with group size (Lack 1968, Pulliam 1973). For similar reasons, individuals in densely populated groups should be able to be less watchful than individuals in sparsely populated groups. Empirical support for these arguments comes from studies of numerous species, in

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**Table 1. Interspecific comparison of the number of visual alarmers during a predatory attack.** Mean and maximum numbers were computed as described in Fig. 4. Data were analyzed by the Mann-Whitney U test.

<table>
<thead>
<tr>
<th>Ward rank</th>
<th>Mean number of visual alarmers</th>
<th>Maximum number of visual alarmers</th>
</tr>
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<tbody>
<tr>
<td>White-tails</td>
<td>(N = 44 trials from 12 wards)</td>
<td>24.8 ± 12.9</td>
</tr>
<tr>
<td>Black-tails</td>
<td>(N = 33 trials from 7 wards)</td>
<td>36.8 ± 17.8</td>
</tr>
<tr>
<td>Significance of interspecific difference</td>
<td><em>P</em> = .005</td>
<td><em>P</em> = .002</td>
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Increased selfish herd effects.—For at least two reasons, a solitary individual that is subjected to a predator’s attack is probably more vulnerable to capture than is an individual within a group when that group is attacked. (a) First, this is true because of simple probability: assuming that the predator can capture only one individual at a time, the chance that any particular individual will be the victim varies inversely with group size. Bertram (1978) called this “protection by dilution.” (b) Second, an individual within a group sometimes has the opportunity to make other individuals more vulnerable than himself to the predator, mainly by carefully positioning himself within the group center. “Selfish herd” effects (Hamilton 1971) such as (a) and (b) could lead to coloniality even in the absence of any form of active group defense (such as mobbing, which would presumably further contribute to an individual’s safety). Though they are probably important to individuals within groups, selfish herd effects are difficult to demonstrate in natural populations.

If selfish herd effects are important, then individuals at the best positions within a group (usually the central positions) should fare better than those individuals at poorer positions (usually the peripheral positions). This effect is often intensified by (and, in an empirical sense, confounded by) the tendency of older, stronger, and more experienced individuals to acquire the best positions within a group (e.g., Coulson 1968, Coulson and Horobin 1976). Evidence that central nesters rear more offspring than peripheral nesters, directly because of reduced predation or for other reasons that may be indirectly related to reduced predation, is available for numerous bird species, including Black-headed Gulls (Larus ridibundus) (Kruuk 1964, Patter-
son 1965), Piñon Jays (*Gymnorhynchus cyaniceps*) (Balda and Bateman 1972), White Pelicans (*Pelecanus erythrorhynchos*) (Schaller 1964), and Brewer’s Blackbirds (Horn 1968).

For prairie dogs, I was unable to compare reproductive successes of central and peripheral ward residents. For Black-tails, however, I was able to examine center-edge differences in individual alertness (Hoogland 1979b); comparable White-tail data were not available. For approximately 30 min, an assistant and I simultaneously observed a central and a peripheral Black-tail of the same ward (*N* = 21 pairs from 10 wards; adults and yearlings only were observed); edges of Black-tail wards can be identified by the tall vegetation there (see below), and peripheral individuals were near such edges while central individuals were distant from the edges. For 16 of the 21 center-edge comparisons, the peripheral individual was more watchful (i.e., devoted more time to scanning for predators) than was the central individual (*P* = .005, Wilcoxon matched-pairs signed-ranks test). These data indicate that selfish herd effects might be important to prairie dogs. Similar center-edge differences in individual alertness have been observed in yellow-bellied marmots (Armitage 1962), and, anecdotally, also in Rooks (Fear et al. 1974), and Adelie Penguins (*Pygoscelis adeliae*) (Tenaza 1971).

Breeding synchronization is another expected outcome if selfish herd effects are important, for at least two reasons. First, in the late stages of the breeding season, parents that started to breed too soon may have to work harder than later, more synchronized parents in order to defend their young appropriately, because the former will be closer than the latter to completing the rearing of their young (Hoogland and Sherman 1976). That is, late in the breeding season, the probability of successfully rearing young (and, incidentally, cumulative parental investment) will be higher for those parents that started too early, and such early parents may be forced to take more risks than synchronized parents in order to protect their young. On the other hand, late parents may be able to exploit the predator defenses of early and synchronized parents during most of the breeding season, but these parents will probably suffer grave consequences at the end of the breeding season for the reason given below. Second and more important, the young of parents that start to breed too early will be especially vulnerable to predation early in the breeding season, simply because there will be so few other young available as prey (Kruuk 1964, Patterson 1965, Hamilton 1971). That is, early in the breeding season, young of early breeders will have few other young with which to form a selfish herd. Similarly, late in the breeding season when young of early and synchronized breeders have already dispersed or are better able to defend themselves, young of late breeders will have little access to selfish herd effects and will therefore be especially vulnerable. Empirical support for these arguments is available for numerous bird species, including Puffins (*Fratercula arctica*) (Nettleship 1972), Red-winged Blackbirds (*Agelaius phoeniceus*) (Robertson 1973), Bank Swallows (Emlen and DeSeng 1975), and three species of gulls (*Larus*) (Patterson 1965, Brown 1967, Parsons 1971). Hoogland and Sherman (1976) emphasized that, although breeding synchronization is consistent with selfish herd effects, it is also consistent with other possible benefits of coloniality: for example, breeding synchronization is expected to accompany either group hunting (see Bertram 1975, for an example with lions) or the location of large, scattered food supplies (see Ward and Zahavi 1973, for possible examples with birds).

Approximately 4 wk after birth, weaned White-tail and Black-tail young with masses of 80–200 g emerge from their natal burrows for the first time and begin to eat vegetation (King 1955, Tileston and Lechleitner 1966, Clark 1977). In both species, young from one litter begin to mingle within days after their first emergence with young from other litters (Hoogland 1979a). As a result, it is difficult to monitor the emergence of different litters without the color-marking of young as they first emerge, and a comparison of intraward and interward breeding synchronization, similar to those made for numerous bird species; see references in Hoogland and Sherman 1976) is therefore difficult to make. For White-tails, I have no data bearing on this issue. For Black-tails, to one degree or another, intraward breeding synchronization based on emergence dates seemed to be more pronounced than interward breeding synchronization for 5 consecutive yr while I was at Wind Cave National Park, from 1975 through 1979 (J. L. Hoogland 1977 and personal observation). Only in 1979, however, was I able to quantify this impression (Fig. 7). In that year, I had data available from three wards: at two of these wards, all the young from each litter were color-marked as they first emerged from their natal burrow entrances; the third ward was small enough that, even though there was no color-marking of young, new litters could be accurately scored as they first began to emerge. Two of the wards were separated by 1 km, while the third ward was approximately 7 km away. Even with this small sample size, the mean emergence times at the three wards were significantly different (*P* < .001, Kruskal-Wallis ANOVA); further, all three pairwise comparisons produced significant results (*P* ≤ .028 for all three, MW). In addition to this level of synchronization, there is evidence for nearest-neighbor breeding synchronization within Black-tail wards (J. L. Hoogland 1977 and personal observation), similar to that observed within colonies of numerous bird species (see references in Hoogland and Sherman 1976). Even though the first emergences of litters may extend over 20–30 d within a large Black-tail ward as a whole (e.g., see Fig. 7), the litters within a single
and those badgers that attempt to dig out a prairie dog
from different burrow entrances during a predatory attack and
periods of inclement weather is inconsistent with
analyzed by the Kruskal-Wallis ANOVA; all three pairwise
comparisons were also significant (P < .028, Mann-Whitney
U test). Equivalent White-tail data were not available.

Data were synchronized in Black-tails. Lower RRS and RR are 1 km
apart, and Monte is approximately 7 km away. Data were
determined for 1 or more yr (see above references). With these small sample sizes, a mean-
ningful comparison of ward size with the density of bur-
trances, involving counts of all burrow entrances
within each colony examined, are available for both
White-tails and Black-tails (King 1955, Tileston and
Lechleitner 1966, Stromberg 1975, Clark 1977, J. L.
Hoogland 1977 and personal observation, Martin and
Schroeder 1978, Campbell and Clark 1981, M. Garrett,
personal communication). The observed ranges are
incredible: the number of burrow entrances per hect-
are ranges from 3 to 223 for White-tails (N = 191 ex-
amined colonies) and from 11 to 245 for Black-tails
(N = 24 colonies). With these ranges, it is not sur-
prising that there is no interspecific difference in the
density of burrow entrances (P > .100, MW, using
all available data). For each species, there are only
four wards for which both the number of adult and
yearling residents and the density of burrow entrances
have been determined for 1 or more yr (see above references). With these small sample sizes, a mean-
ful comparison of ward size with the density of bur-
row entrances cannot be made for either species. To
summarize: evidence to this point does not indicate
that an increased density of burrow entrances repres-
ents a benefit of prairie dog coloniality.

Why the interspecific differences
in coloniality?

Why are ward sizes larger and ward densities higher
for Black-tails than for White-tails? That is, why are
Black-tails more colonial than are White-tails? This is
a difficult question for which there are numerous pos-
sible answers. I will consider three likely possibilities:
(a) interspecific differences in the costs of coloniality,
(b) interspecific differences in predation, and (c) in-
terspecific differences in the density of protective cov-
er.

Interspecific differences in
the costs of coloniality

As noted above, prairie dog coloniality involves cer-
tain costs such as increased aggression and increased
ectoparasitism. It may be that certain costs of co-
loniality would be intolerable to individuals if White-
tails were more colonial. For example, though less co-
lonial, White-tails seem to fight and chase almost as much as Black-tails on a per-individual basis (Hoogland 1979a): if White-tails were to become more colonial, then perhaps the costs associated with the increased fighting and chasing that would presumably result would be extremely high and would outweigh any possible benefits, unless there were concomitant major changes in social organization. However, there is no reason to believe that White-tails are less able than Black-tails to evolve mechanisms (such as the Black-tail coterie system?) to circumvent partially the costs of coloniality. Thus, it seems unlikely that interspecific differences in the costs of coloniality could ultimately explain why White-tails are less colonial than Black-tails.

**Interspecific differences in predation**

Data in this report indicate that individual prairie dogs in large wards are better protected from predators than are individuals in smaller wards; the same is probably true for individuals in densely populated (vs. sparsely populated) wards. It follows that increased predation might ultimately lead to increases in the degree of coloniality. More specifically, as also suggested by Clark (1973a:192), perhaps Black-tails are more colonial than White-tails because they consistently have been subjected to more predation over evolutionary time.

All predators known or suspected to prey on Black-tails are also known or suspected to prey on White-tails. That is, White-tail and Black-tail predators are probably qualitatively the same, at least today, but it would be almost impossible to compare quantitatively the predators of the two species. A comment is warranted for the black-footed ferret, a specialized carnivore which can easily enter prairie dog burrow systems and which may subist almost entirely on these rodents (e.g., Lechleitner 1969, Sheets et al. 1971). A review of the literature might suggest that ferrets are limited exclusively to Black-tail colonies (e.g., Cahalane 1954, Hillman 1968, Sheets et al. 1971, R. L. Lindner, personal communication). But this is not true, since ferrets have also been observed near White-tail colonies (Clark 1973b, Torres 1973, Yannone 1973). In 1978–1979, for example, an examination of 268 White-tail colonies in Wyoming yielded seven ferret skulls (T. Clark and S. Martin, personal communication); comparable data are not presently available for Black-tails, but a search for ferret skulls at Black-tail colonies in Wyoming is planned for 1980–1981 (S. Martin, personal communication). The larger number of sightings of live ferrets at or near Black-tail colonies may result simply because Black-tail colonies are larger, more numerous, and more conspicuous than are White-tail colonies, and are therefore more likely to attract the attention that is necessary for the detection of a predator as secretive (e.g., Hillman 1968) as the ferret. Thus, the greater coloniality of Black-tails cannot be easily explained as an adaptation to a predator unique to that species. Further, the small amount of available information (Hillman 1968, Henderson et al. 1974) suggests that a significant proportion of predation by ferrets occurs at night. It is not clear how nocturnal predation by ferrets might ultimately affect the ward sizes and ward densities of diurnal animals such as prairie dogs. Defenses that have evolved against certain predators may leave individuals especially vulnerable to other predators (Hamilton 1971). Specifically, prairie dog coloniality may have evolved in response to diurnal predators such as coyotes, badgers, raptors, etc., with the result that individuals are especially vulnerable to nocturnal, burrow-entering ferrets. More research is obviously needed to determine if the black-footed ferret, or any other predator, is (has been) more dangerous for Black-tails than for White-tails.

**Interspecific differences in the density of protective cover**

Of the numerous possible antipredator defenses (e.g., see Harvey and Greenwood 1978), two are especially common: one defense involves hiding or crypt sis (i.e., the avoiding of detection by the predator), while the other involves detecting the attacking predator soon enough to allow for escape. Although there are some exceptions (e.g., see examples in Wickler 1968), hiding from predators is usually only possible for single individuals and small groups. Further, animals that depend on hiding for survival usually live in habitats where there is extensive protective cover. On the other hand, the ability to detect predators usually increases directly with group size, and prey animals depending mainly on the quick detection of predators usually form large groups and live in habitats with little protective cover. Empirical support for these arguments comes mainly from comparative studies of ungulates (e.g., Jarman 1974, Hirth and McCullough 1977), primates (e.g., Clutton-Brock and Harvey 1977, Alexander et al. 1979), and kangaroos (Macropodidae) (e.g., Kaufmann 1974). I attempted to determine if the interspecific differences in coloniality between White-tails and Black-tails might be partially explained by interspecific differences in the density of protective cover.

Except when protective cover occurs in large clumps, hiding behind a particular piece of cover is usually only possible for single individuals and small groups. When protective cover is present but limited, it follows that effective hiding for an individual may be consistently possible only when the number and density of nearby conspecifics is low, such that there is sufficient protective cover per individual. Perhaps White-tail habitats contain a limited amount of protective cover that allows hiding of individuals and small groups. If White-tails were to become more colonial, then there might be too much competition for the lim-
ited protective cover, such that individuals might too often be exposed at the wrong times. On the other hand, perhaps Black-tail habitats contain little or no protective cover, and Black-tails have been selected to form larger, denser colonies than White-tails in order to capitalize on the quick detection of predators and selfish herd effects. In other words, the greater density of protective cover in White-tail wards may ultimately explain why White-tails are less colonial than are Black-tails.

Tileston and Lechleitner (1966) and Clark (1977) both suggested that White-tail habitats contain more protective cover than do Black-tail habitats. In my study, I found that White-tail habitats in the Walden and Laramie areas regularly contain large numbers of at least three species of woody shrubs that could presumably serve as adequate protective cover for prairie dogs: rabbit brush (Chrysothamnus sp.), greasewood (Sarcobatus sp.), and some sort of woody sage (Artemisia sp.). On the other hand, Black-tail habitats in the Wind Cave and Fort Collins areas rarely seemed to contain comparable protective cover. I attempted to quantify these differences in two ways. First, I measured plants along transects (Hoogland 1977). White-tail wards (N = 11) contained more, taller plants per metre of transect than did Black-tail wards (N = 15) (P < .050, MW). Second, I examined proportions of foraging prairie dogs that are visible. Foraging prairie dogs sometimes move behind protective cover and thereby become difficult for an observer to see. If White-tail wards contain more protective cover than do Black-tail wards, then the proportion of above-ground, foraging individuals that is visible to an observer (and presumably also to predators) under undisturbed conditions should be lower for White-tails; if there are no interspecific differences in the density of protective cover, then proportions of visible White-tail and Black-tail foragers should be equal. As shown in Table 3, the proportion of visible foragers was significantly lower for White-tails (P = .008, MW). Proportions of randomly thrown, prairie-dog sized cans that were visible to an observer from 64 m away further indicated that White-tail wards contain more protective cover than do Black-tail wards (Hoogland 1977).

In colonial species that depend mainly on the quick detection of predators and have little available protective cover, there might be selective pressure on animals to remove what little protective cover is present. Such removal would lead to a slightly increased conspicuousness of the group to predators (Tinbergen 1952, Hoogland 1979a), but this disadvantage would presumably be offset by the increased ability of individuals to detect predators and visual alarms of conspecifics (Hoogland 1979b). Removal of protective cover probably only works to the prey’s, rather than the predator’s, advantage when the prey animals are group-living, so that the increased range of vision for

| Table 3. Interspecific comparison of the proportion of foraging prairie dogs that was visible under undisturbed conditions. Foraging prairie dogs sometimes move behind protective cover and consequently become difficult for an observer to see. Before each experimental run with the badger or weasel, the number of visible foragers was recorded under undisturbed conditions. This number was then compared to the maximum number of prairie dogs observed during the experimental run (= the total number of aboveground individuals that were foraging before the predator), and the appropriate proportion was calculated. These data indicate that White-tail wards contain more protective cover than do Black-tail wards. Data were analyzed by the Mann-Whitney U test. |
|---|---|
| **Proportion of foraging prairie dogs that was visible under undisturbed conditions** |  |
| White-tails | .436 ± .184 |
| (N = 62 trials from 12 wards) |  |
| Black-tails | .539 ± .142 |
| (N = 27 trials from 6 wards) |  |
| **Significance of interspecific difference** | P = .008 |

the collective group outweighs the cost of increased conspicuousness. If the White-tail defense system involves an element of hiding while the Black-tail defense system does not, then perhaps White-tails and Black-tails should respond differently to the presence of protective cover. Specifically, White-tails should retain protective cover to promote hiding, whereas Black-tails should remove such protective cover. I investigated this prediction in two ways: (a) by comparing the density of protective cover at ward centers and edges, and (b) by making experimental transplants of protective cover. Regarding (a), if prairie dogs are selected to retain protective cover, then the density of protective cover at central ward positions (where individuals of both species commonly forage and are exposed to predation) should be approximately equal to the density at outermost peripheral ward positions (where individuals of both species only rarely forage). On the other hand, if prairie dogs are selected to remove protective cover, then central ward positions should contain less protective cover than should outermost peripheral ward positions. Available protective cover at centers and edges was estimated by weighing plant biomass collected in a 61.0 × 0.51 m (31-m²) area by means of a conventional lawn mower (Fig. 8). Central ward cuttings were made at approximate ward centers; ward edges were determined by locating outermost peripheral burrow entrances, and peripheral cuttings were made just inside boundaries defined by such burrow entrances. Center-edge comparisons were based on the masses of cuttings, with the assumption that these masses varied directly with the density of protective cover; White-tail and Black-tail
FIG. 8. Density of protective cover at centers and edges of White-tail and Black-tail wards. Data were analyzed by the Wilcoxon matched-pairs signed-ranks test; the number above each ward center bar indicates the number of wards at which one central and one peripheral estimate of the density of protective cover was made. Plant species that formed protective cover were similar at different wards of the same species, but were totally different between species; thus, an interspecific comparison of grams per square metre of protective cover was not possible.

cuttings were both made in August 1975. Whereas there was no significant difference between White-tail centers and edges, Black-tail centers contained strikingly less protective cover per square metre than did edges $(P = .687, P < .001$, respectively, Wilcoxon matched-pairs signed-ranks test). Evidently Black-tail activities significantly reduce the density of protective cover within wards, whereas White-tail activities have little effect on protective cover (see also Tileston and Lechleitner 1966:301–302). The assumption that the masses of cuttings varied directly with the density of protective cover was probably valid for intraspecific comparisons, since different wards of the same species tended to have the same species of plants. However, White-tail plant species were totally different from Black-tail plant species, so an interspecific comparison of the density of protective cover on the basis of the masses of cuttings was not possible.

Regarding (b), I uprooted 40–60 cm high plants from just inside or just outside ward boundaries and transplanted them, single file, into a 1 m long shallow trench that was 1 m from an active burrow entrance (Table 4). The fate of all transplants was followed for at least 15 d. White-tail transplants were made in June–July of 1975; Black-tail transplants were made in April–May and August of 1975 and June of 1976. Whereas White-tails usually did not disturb transplants of protective cover, Black-tails almost invariably clipped or uprooted most or all of each transplant within a few days $(P < .001, \chi^2)$. To verify that Black-tail transplants were removed by the prairie dogs themselves, and not by sympatric herbivores such as rabbits, pronghorn antelope, buffalo, elk (Cervus canadensis), mule deer (Odocoileus hemionus), or thirteen-lined ground squirrels (S. tridecemlineatus), I placed five “control” transplants just outside two of the wards that contained experimental transplants: none of the five transplants was ever noticeably disturbed at the end of 15 d. The data of Table 4 again indicate that White-tails retain protective cover and that Black-tails remove such cover. It is possible that the differences of Fig. 8 and Table 4 resulted because of greater competition for food among Black-tails, such that individual Black-tails were forced to eat plants that would otherwise have served as protective cover. However, on several occasions Black-tails clipped or uprooted entire experimental transplants while eating few or none of the plants therein, and this suggests that factors other than voracious feeding by Black-tails accounted for the observed differences; King (1955), Koford (1958), and Tileston and Lechleitner (1966) also observed clipping of vegetation without eating. It is also possible that the differences of Fig. 8 and Table 4 resulted because potential protective cover in Black-tail wards is usually herbaceous and probably easy for prairie dogs to remove, whereas potential protective

<table>
<thead>
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<th></th>
<th>No uprooting or clipping of transplant (transplant untouched)</th>
<th>Uprooting or clipping of less than one-half of transplant</th>
<th>Uprooting or clipping of more than one-half, but not all, of transplant</th>
<th>Uprooting or clipping of entire transplant</th>
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<tbody>
<tr>
<td>White-tails</td>
<td>6</td>
<td>3</td>
<td>0</td>
<td>17</td>
</tr>
<tr>
<td>(N = 10 transplants from 7 wards)</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Black-tails</td>
<td>0</td>
<td>1</td>
<td>3</td>
<td>10</td>
</tr>
<tr>
<td>(N = 14 transplants from 6 wards)</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Significance: $P &lt; .001$</td>
<td></td>
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</tr>
</tbody>
</table>
cover in White-tail wards is often tough and woody and probably difficult for prairie dogs to remove. Even though White-tails are probably physically able to uproot or clip woody shrubs such as rabbit brush, greasewood, and certain sages, the time and energy that would be required may not outweigh possible gains in increased range of vision.

To summarize, the interspecific differences in the density of protective cover may ultimately explain why White-tails form only small, sparsely populated wards and Black-tails form large, densely populated wards. Although the quick detection of predators and selfish herd effects are probably also important (e.g., see Fig. 2a), White-tails seem to depend to some extent on hiding from predators behind available protective cover. On the other hand, Black-tail habitats contain little protective cover, and individuals seem to make no effort to conceal themselves; instead, Black-tails seem to depend almost entirely on the quick detection of predators and selfish herd effects.

**DISCUSSION**

In this report, I have examined various hypotheses that might explain the evolution or maintenance of coloniality in White-tailed and Black-tailed Prairie Dogs. I have not attempted to examine every hypothesis that has ever been formulated as a possible explanation for group-living. For example, Cody (1971, 1974) proposed that avian flocking might sometimes evolve because individuals can forage more efficiently in an area if they forage over it as a single large flock, because flock members can then easily avoid moving into areas that have recently been stripped of food. I have not seriously considered Cody’s (1971, 1974) hypothesis simply because it does not easily lead to an evolutionarily stable strategy; there will always be selection for individuals that forage alone (and thereby avoid competition with other flock members) but can somehow monitor the movements of the flock (and thereby avoid stripped areas). As a result, stable groups will not easily evolve in this context. For a second example, several investigators have argued that “social stimulation” or “social facilitation of breeding” (the “Fraser Darling Effect”) might sometimes lead to the evolution of coloniality (e.g., Darling 1938, Snapp 1976, Coulson and Dixon 1979). However, such stimulatory effects can only be secondary consequences, and never causes, of coloniality (Orians 1961, Hoogland and Sherman 1976). For a third example, mobbing of predators is a common form of group-defense in colonial bird species that leads to increased safety of offspring (e.g., Kruuk 1964, Horn 1968, Burger 1974, Hoogland and Sherman 1976). Benefits of mobbing may sometimes be primarily responsible for the evolution of coloniality. I have not considered the possible importance of mobbing in the evolution of prairie dog coloniality simply because White-tails and Black-tails do not mob their predators (Hoogland 1977, where possible exceptions are noted). For a fourth example, an increased ability of individuals to conserve body heat while within a group may sometimes be primarily responsible for the evolution or maintenance of groups (Sealander 1952, Muul 1968, Trune and Slobodchikoff 1976). As noted above, both White-tails and Black-tails sleep in underground groups during periods of cold weather, and reduced loss of heat by individuals is probably one effect of such communal sleeping. However, an increased ability to conserve body heat probably has not been important in the evolution or maintenance of prairie dog coloniality for at least two reasons. First, unlike groups of southern flying squirrels (*Glaucomys volans*) (Muul 1968), for example, colonies of both White-tails and Black-tails persist during periods of warm weather (i.e., during late spring and summer), when an improved ability to thermoregulate by grouping would presumably be of relatively little advantage. Second, White-tails and Black-tails never cluster together inside burrows in groups of more than 7–8 or 10–15, respectively, during cold weather. Thus, small groups of prairie dogs could conceivably be maintained by attempts of individuals to reduce the loss of body heat during cold weather, but large colonies containing scores and hundreds of individuals could not be maintained in this context. Finally, benefits such as an increased individual ability to swim or fly while within a group because of either resistance due to drag (Weihs 1973, Gould and Heppner 1974) or the pooling of information (Hamilton 1968) might rarely be responsible for the evolution or maintenance of groups (Alexander 1974, Bertram 1978). I have not considered these and similar possibilities simply because they are not relevant for prairie dog coloniality (Hoogland 1977).

Certain benefits of group-living can probably only evolve if groups are already present for some other reason. That is, certain benefits can be responsible for the *maintenance* of coloniality, but probably cannot be responsible for the *evolutionary origin* of coloniality. For example, group-defense of foraging grounds (Brown and Orians 1970), complex behaviors of a frightened, fleeing group that might confuse a predator (see Jarman 1974, and Neill and Cullen 1974, for possible examples), “farming” of the soil (see above), the location of large, scattered food supplies (Ward 1965), and groups serving as “information centers” (Ward and Zahavi 1973) can probably only be secondary consequences of coloniality that has evolved for some other reason. I agree with Alexander (1974, 1975) that most groups probably first evolve because of either (a) an increased safety from predators due to group-defense, selfish herd effects, or an increased awareness of predators, (b) an increased quantity or quality of food per individual resulting from group-hunting of large or elusive prey that is only rarely available to solitary foragers, or (c) the use of clumped resources such as sleeping sites or breeding habitats.
The last 200 yr have been responsible for drastic reductions in population sizes of both White-tails and Black-tails (Linder and Hillman 1973, Clark 1979). Black-tails, for example, presently occupy <10% of their former range. I assume that my results and conclusions do not apply merely to today’s reduced populations of prairie dogs, but testing this assumption would be difficult. That is, it would be almost impossible to assess how recent decimations of the described sort have affected the costs and benefits of coloniality that evolved over millions of years. By studying White-tails on a national wildlife refuge and Black-tails on a national park, I attempted to minimize the effect of human disturbance during my period of study.

I have argued that the White-tail antipredator defense system involves an element of hiding behind protective cover from predators and that the Black-tail defense system depends mainly on the quick detection of predators and selfish herd effects with no hiding. I have suggested that part of this interspecific difference in coloniality and antipredator defense system results because White-tail habitats contain numerous woody shrubs that can serve as protective cover, whereas Black-tail habitats contain almost no protective cover. A good test of this hypothesis would be to compare White-tail and Black-tail ward sizes and ward densities in areas where the two species are sympatric or nearly so. If my hypothesis is correct, then White-tail and Black-tail ward sizes and ward densities should be more similar in areas of sympatry (where interspecific differences in the nature and density of protective cover are presumably minimized) than in areas of allopatry. Unfortunately, testing this hypothesis would be difficult since there are few protected populations of prairie dogs in Montana and Wyoming (Hall and Kelson 1959, T. W. Clark 1973a, personal communication) where White-tails and Black-tails are sympatric or nearly so.

If reduced predation is an important benefit of coloniality, then the rate of predation (i.e., the predation per individual per unit time) should vary inversely with colony size. Such an inverse relationship has been observed in numerous species, including Black-headed Gulls (Patterson 1965), Red-winged Blackbirds (Roberson 1973), Common Eiders (Somateria mollissima) (Munro and Bedard 1977), monarch butterflies (Danaus plexippus) (Calvert et al. 1979), and possibly White Wagtails (Motacilla alba) (Zahavi 1971). From data in this report, I conclude that reduced predation is the most important, and perhaps the only, benefit of prairie dog coloniality (see also King 1955, and Smith et al. 1973). Direct evidence for this conclusion would be difficult to obtain, even though predators commonly attack at wards, simply because predation on prairie dogs is so rarely observed. For example, during over 10,000 h of watching prairie dogs in 1974–1979, field assistants and I observed only six predators. Further, predators usually do not leave behind any evidence for their successes and failures at prairie dog wards. Until the comparison between ward size and predation rate can somehow be made directly, the conclusion that prairie dog coloniality ultimately depends on reduced predation must remain tentative.

Acknowledgments

This report is dedicated to my wife, Judy Gaynier Hoogland, who single-handedly persuaded me to do a comparative study that involved Black-tails in addition to White-tails. Judy’s ability to devise and repair just about anything, her development of the system for holding and marking prairie dogs, and her constant understanding and encouragement were as fundamental as the prairie dogs themselves for the completion of this project.

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