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AGGRESSION, ECTOPARASITISM, AND OTHER POSSIBLE COSTS OF PRAIRIE DOG (*SCIURIDAE*, *CYNOMYS* SPP.) COLONIALITY

by

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(With 4 Figures)
(Acc. 18-IX-1978)

INTRODUCTION

There are no automatic or universal benefits of coloniality. Two costs of coloniality, however, are probably inevitable: increased competition (for food, mates, nest sites, *etc.*) and increased transmission of diseases and ectoparasites (ALEXANDER, 1974). Other possible costs that are not automatic include increased probability of misdirected parental care resulting from either mixing of unrelated young, cuckoldry, or intraspecific brood parasitism; increased conspicuousness and increased attractiveness to predators; increased probability of indirect, deleterious consequences of nearby conspecific activity; and increased probability of having offspring killed or maimed by marauding conspecifics (HOOGLAND & SHERMAN, 1976).

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Previous investigations have concentrated on the benefits of coloniality, with little or no attention to the costs (but see HOOGLAND & SHERMAN, 1976). My purpose in this report is to examine possible costs of coloniality for two species of prairie dogs: loosely colonial White-tailed Prairie Dogs (*Cynomys leucurus*) and densely colonial Black-tailed Prairie Dogs (*C. ludovicianus*). Elsewhere I have examined possible benefits of prairie dog coloniality (HOOGLAND, 1978a, 1978b).

Prairie dogs are large, diurnal, colonial rodents of the squirrel family (Sciuridae). Five species, all of the genus *Cynomys*, are presently recognized (PIZZIMENTI, 1975), and all of them are probably in danger of extinction. The typical prairie dog colony is usually subdivided into two or more wards (KING, 1955), or subcolonies, by a small stream, a row of trees, a hill, *etc.* Residents of one ward can sometimes see or hear residents of an adjacent ward, but movements and communications between wards are uncommon. Some of my investigations involved wards, whereas others involved entire colonies. The following brief descriptions of White-tails and Black-tails are based mainly on reports by KING (1955), TILESTON & LECHLEITNER (1966), CLARK (1977), and HOOGLAND (1977, 1978a).

White-tailed Prairie Dogs live in medium to tall grass prairies at altitudes of 1900-2600 m, and are found only in parts of Colorado, Montana, Utah, and Wyoming. Ward densities from studies of marked individuals range from 1.47 to 5.65 adults per hectare (ha), with a mean \pm SD of 3.20 ± 1.40 (HOOGLAND, 1978a). Both males and females usually reach sexual maturity as yearlings, but only yearling females usually breed; males are considerably larger than females at all stages beyond weaning. White-tails hibernate during the winter months, and breed in March and April. The usual litter size is 5-7, and the first emergences of weaned juveniles from their natal burrows occur in May and June. At no time of the year are there identifiable White-tail harems.

Black-tailed Prairie Dogs live in short grass prairies at altitudes of 900-1600 m, and are found in a narrow western belt that extends from southern Canada to central Texas. Ward densities from studies of marked individuals range from 7.52 to 32.7 adults and yearlings per ha, with a mean \pm SD of 14.8 ± 9.67 (HOOGLAND, 1978a). Males and females of northern latitudes, at least, do not breed until at least two years old; adult males are only slightly larger than adult females. Black-tails do not hibernate, and breed in February and March. The usual litter size is 3-4, and the first emergences of weaned juveniles from their natal burrows occur in May and June. Black-tails are organized into harems known as coterie (KING, 1955): the typical coterie contains a single adult male and 1-4 adult females, along with nonbreeding

yearlings and young of the year. Coterie members defend a well-defined coterie territory from conspecifics, and restrict essentially all of their activities therein.

In addition to the higher Black-tail ward and colony densities, absolute sizes of wards and colonies with respect to both number of residents and physical area occupied are also higher for Black-tails than for White-tails. There is no indication that gross social structure varies with ward/colony density or absolute size for either species; for example, Black-tails are organized into coteries in wards/colonies of all densities and absolute sizes.

In the course of the 4-yr study, I never detected either a White-tail or a Black-tail living solitarily (HOOGLAND, 1978a). Thus, I was unable to compare noncolonial and colonial prairie dogs with respect to the costs of coloniality. I hypothesized that the costs 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 costs both intra- and inter-specifically. I realize, of course, that factors other than ward/colony density and absolute size affect the costs of prairie dog coloniality. Because such latter factors probably vary more between species than within species, I consider my intraspecific comparisons to be more valuable than my interspecific comparisons.

My investigations of the various costs of prairie dog coloniality are presented in the sections that follow. For additional references and a more detailed treatment of this subject, see HOOGLAND (1977, Chapter 1).

METHODS

Study sites.

White-tail study sites were in the vicinities of Laramie, Wyoming, and Walden, Colorado. The main study ward was located on the Arapaho National Wildlife Refuge, 5 km SW of Walden. The elevation there is 2500 m; the area has been described by TILESTON & LECHLEITNER (1966; see also CLARK, 1977). All the residents of the main study ward were ear-tagged and colour-marked in June of 1974, 1975, and 1976. This ward occupied 5.13 ha, and contained 1,145 burrow entrances (HOOGLAND, 1978a). Numbers of adult residents at the main study ward in June of 1974, 1975, and 1976 were 18, 21, and 29, respectively.

Black-tail study sites were in the vicinities of Fort Collins, Colorado, and Hot Springs, South Dakota. The main study ward, whose residents were all ear-tagged and colour-marked in 1975, 1976, and 1977, was located within Wind Cave National Park, 15 km N of Hot Springs. The elevation there is 1300 m; the area has been described by KING (1955), who also studied Black-tails at Wind Cave. The main study ward occupied 6.60 ha, and contained 1,591 burrow entrances (HOOGLAND, 1978a). Numbers of adult and yearling residents in April of 1975, 1976, and 1977 were 216, 121, and 143, respectively. Each year, Black-tails at the main study ward were organized into 24 coteries.

The main White-tail and Black-tail study wards were both protected from shooting, poisoning, and grazing by cattle and horses during the period of study.

Trapping, handling, and marking.

To capture adult prairie dogs, I used 15 cm × 15 cm × 60 cm National Double-door Live Traps (CLARK, 1977; FITZGERALD & LECHLEITNER, 1974) baited with whole oats (see PFEIFFER, 1972).

To capture young prairie dogs, I used 10 cm × 10 cm × 40 cm National Single-door Live Traps. I surrounded each natal burrow entrance with traps on the first day that young were seen emerging from that entrance, and also stuffed all nearby entrances that might have been connected to the surrounded entrance with towels, paper, *etc.* Thus, unmarked young were forced to enter one of the traps at the surrounded burrow entrance, and there was no mixing of young from different litters until all the young from each litter had been ear-tagged and color-marked (c.f. KING, 1955, and CLARK, 1977).

After capture, adults were transferred to a canvas, conical bag that could be unzipped from either end; openings at both ends of the bag were adjustable. Juveniles were usually handled directly with gloves. Each animal was weighed to the nearest gram with a spring balance, sexed, examined for ectoparasites and scars (see below), tagged in each ear with a numbered National "fingerling" ear-tag, and colour-marked with Nyanzol D fur dye. Pelages were dyed with numbers, spots, blotches, and combinations thereof, and retained markers only until the following molt (in spring or autumn; see SMITH, 1958).

Duration of study.

Results are based on data from the following research periods: 15 April-25 August, 1974; 20 January-19 August and 16-19 September, 1975; 3 March-2 August, 1976; 15 April-8 June, 1977. Assistants and I handled and marked 1,200 prairie dog adults and young, some of which were repeats from previous years.

Measurement of aggression.

To measure aggression, I distinguished five categories. *Fights* involved direct physical contact in the form of biting or kicking. A *chase* was scored when one prairie dog actively pursued another (fleeing) prairie dog. Sometimes one prairie dog approached another, and either ran away or caused the other prairie dog to run away, with no pursuit in either case: such an interaction was scored as a *runaway*. A *territorial dispute* was a ritualized form of aggression seen only in Black-tails that involved spreading of tail fur, baring of teeth, and exposure of anal glands (KING, 1955); such disputes usually occurred at the boundary between two adjacent coterie territories. Often fights, chases, runaways, and territorial disputes occurred in rapid succession. When any combination of these four occurred between the same two animals within a 1-2 min time period, without interruptions, that combination (*e.g.*, fight + chase) was scored as a single *aggressive encounter*.

During behavioural observations of unmarked animals, nonbreeding Black-tail yearlings cannot be distinguished from adults. In this report, the term "adult" includes both yearling and adult Black-tails.

Measurement of ectoparasitism.

Fleas (Siphonaptera), lice (Anoplura and Mallophaga), and ticks and mites (Acarina) were collected from the prairie dogs themselves during the process of colour-marking and fleas were also collected from burrow entrances, as described below (see also HOOGLAND, 1977). I made no attempt to identify any of the collected ectoparasites. A listing of the several species of fleas, ticks, and mites harbored by White-tails and Black-tails was provided by PIZZIMENTI (1975).

To determine the relative number of ectoparasites harbored by individuals, I examined each prairie dog during the process of ear-tagging and colour-marking. Further, I combed the back and sides of each individual 10 times with a fine-toothed comb (30 combs per individual). Visible lice on juveniles were sometimes so numerous that only estimates (of

either 25, 50, 75, or at most, 100) were made. I recorded all observed ectoparasites, including those fleas and lice that jumped or fell to a lightly coloured cloth below. In most cases, the counted ectoparasites probably represented a small proportion of those actually present, and I assumed that this proportion was constant. Prairie dogs were trapped at a small number ($N \leq 3$) of colonies and wards for each species, and intra-specific comparisons of animal counts with ward size were therefore unavailable. White-tail adults were examined for ectoparasites during breeding (March–April of 1976) and when young were first emerging from their natal burrows (June of 1975 and 1976). Black-tail adults were examined at comparable stages of the annual cycle (February–March of 1975 and May–June of 1975 and 1976). Young of both species were examined in 1975 and 1976 shortly after their first emergences from the natal burrows.

Ectoparasites were also collected from burrow entrances. The method involved a 46 cm \times 46 cm piece of white flannel attached by a spring clip to the end of a 2-m length of flexible plumber's cable. The cloth was inserted 2 m into the burrow entrance (when possible), was left there for 30 sec, and then was removed so that the ectoparasites clinging to it could be counted (c.f. LECHLEITNER *et al.*, 1968; BARNES *et al.*, 1972). Lice and mites were never observed on the flannel, and ticks were rare; fleas were common, and only these were used for comparisons. All burrow entrance counts were made between 1000 and 1800 hours. I randomized my selection of burrow entrances, and used only one active-looking entrance per mound. White-tail burrow entrance counts were made in July of 1974 and July and September of 1975. Black-tail burrow entrance counts were made near Fort Collins in late July and early August of 1974, and also at Wind Cave National Park in August of 1975. My method for burrow entrance counts permitted relatively quick collection of data from numerous colonies, and thereby allowed intra- as well as inter-specific comparisons. I assumed that the number of fleas on the white flannel cloth represented a constant proportion of the number of fleas actually present at the burrow entrance. Elsewhere I have examined possible biases of the burrow entrance method (colony age, burrow depth, *etc.*), and have shown that flea counts from burrow entrances positively correlate with counts from the animals themselves (HOOGLAND, 1977 and unpubl.).

Statistical analyses.

All data were analyzed by nonparametric statistical methods, since "The (nonparametric) method may be used on data with an ordinal scale of measurement." (CONOVER, 1971, p. 94). That is, nonparametric statistics can be legitimately used for those data that can be ranked on a relative (ordinal) scale, but not on an absolute scale. This was important: For each colony and ward, it would have been practically impossible to accurately determine the number of residents living there without colour-marking every prairie dog therein since individuals are active at different times of the day. I have used the terms "colony rank" and "ward rank" in this report to refer to colony and ward sizes, with respect to numbers of residents, relative to sizes of other colonies and wards. A ward with a rank of 2 contained more residents than did a ward with rank of 1, for example, but the magnitude of the differences could not be accurately determined. Colony and ward rankings were determined either (a) by colour-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 of the day, or (c) from calculations of physical areas occupied, on the assumption, supported by my own observations, that large areas contain more prairie dogs than smaller areas. 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/colonies included a proportion of small and large wards/colonies 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 shown in tables are means \pm SD (one standard deviation), numbers shown in figures are means \pm SE (one standard error), and numbers in figures above SE lines indicate sample sizes. I have used the abbreviation "KRC" in the text to refer to the Kendall rank correlation test.

THE COSTS OF PRAIRIE DOG COLONIALITY

COST #1: INCREASED AGGRESSION

Introduction.

Increased competition for various resources is probably a universal cost of coloniality. Aggression is one obvious indicator of competition, although not all competition involves aggression. Numerous studies have examined the effect of population density on aggression, but results have been inconsistent. Laboratory studies were reviewed by ARCHER (1970), who also reviewed some of the field studies.

Among squirrels, observable aggression seems ubiquitous. Fights, chases, territorial disputes, *etc.*, have been reported for chipmunks (*Tamias* and *Eutamias*) (*e.g.*, WOLFE, 1966), tree squirrels (*Sciurus* and *Tamiasciurus*) (*e.g.*, THOMPSON, 1977), marmots (*Marmota*) (*e.g.*, ARMITAGE, 1975), and ground squirrels (*Spermophilus*) (*e.g.*, MICHENER, 1973). Among prairie dogs, these sorts of interactions have been observed among Gunnisons (*C. gunnisoni*) (LONGHURST, 1944; FITZGERALD & LECHLEITNER, 1974; POTEKIN, 1976), White-tails (ERPINO, 1968; CLARK, 1977; this study), and Black-tails (KING, 1955; SMITH, 1958; LUND, 1974; SMITH *et al.*, 1973; this study). But attempts to correlate aggression among squirrels with population density have been limited to marmots. Using only approximate measures of population density and without carefully considering seasonal effects, BRONSON (1963) found no consistent correlation between density and aggression for Woodchucks (*M. monax*). For two Colorado colonies of Yellow-bellied Marmots (*M. flaviventris*), BARASH (1973) reported significantly more chases per individual per h at the large colony (8 adults, 8 young) than at the smaller colony (5 adults, 3 young). But ARMITAGE (1975) examined aggressive interactions at five Yellow-belly colonies for ten consecutive years, and found no consistent correlations with colony density (see also ARMITAGE, 1962, 1974, 1977). ARMITAGE concluded (1977, p. 585) that "Rates of (Yellow-belly) social behaviour are related to population density, the age-sex structure of the population, the individual behavioural characteristics of the residents and potential recruits, the way in which space is shared, and the number of years residents have lived together."

That intraspecific aggression among mammals can lead to serious injury

and even death has been documented by several investigators (*e.g.*, SCHALLER, 1972; WILKINSON & SHANK, 1976). Among squirrels, serious injury or death resulting from aggression has been reported for Red Squirrels (*T. hudsonicus*) (WALTON, 1903; SMITH, 1968), Belding's Ground Squirrels (*S. beldingi*) (SHERMAN, 1976), Columbian Ground Squirrels (*S. columbianus*) (STEINER, 1970, 1972), and Arctic Ground Squirrels (*S. parryii*) (MAYER, 1953; HOLMES, 1977). For prairie dogs, I never observed a death resulting directly from aggression. But at least three lines of evidence indicate that fights, chases, *etc.*, lead to decreases in individual fitness. (1) Injuries to both White-tails and Black-tails commonly result from fights. These injuries are accompanied by losses of fur and blood, and can hobble individuals for periods ranging from several hours to several weeks (KING, 1955; BAKKO & BROWN, 1967; CLARK, 1977; HOOGLAND, 1977 and unpubl.). (2) Aggressive interactions inevitably cause losses of time and energy. White-tail chases, for example, often involve 40-50 m of hard running (CLARK, 1977; HOOGLAND, unpubl.), and Black-tail territorial disputes can last for as long as 95 min ($\bar{x} \pm \text{SD} = 4.76 \pm 6.00$, range = .100-95.0, $N = 694$; see also KING, 1955). (3) Losers of both White-tail and Black-tail aggressive interactions are sometimes temporarily or permanently chased away from colony areas, where, away from burrows and other prairie dogs, they are probably easy prey (*e.g.*, KING, 1955, p. 37). For White-tails, I observed 3 permanent evictions; for Black-tails, I observed 8 permanent evictions and numerous (>20) temporary evictions.

By recording fights, chases, and other hostile interactions (see above), I investigated the effect of ward rank on aggression for both White-tails and Black-tails and possible interspecific differences. I assumed that increased aggression leads to decreased individual fitness. I did not investigate possible effects of variables other than aggression, nor did I determine the cause(s) of aggression for either species. I observed more aggression in both species during the breeding, pregnancy, and lactation stages of the annual cycles than at other stages, as did CLARK (1977) for White-tails and KING (1955) for Black-tails, and this suggests that mates and safe nesting burrows are probably important causes of prairie dog aggression (*i.e.*, are resources worth fighting for). Similar seasonal effects on aggression have been observed for several other squirrels (*e.g.*, CARL, 1971; FARENTINOS, 1972).

Results.

White-tail aggression.

I recorded White-tail aggressive interactions at five wards (from two colonies) of different sizes. Data were recorded during 1-2 h observation

TABLE 1
The effect of ward rank on White-tail aggression during the prebreeding, breeding, and pregnancy stages of the annual cycle

	Ward rank (No. days of observation)					Significance *
	1 (N = 17, 18, 16)	2 (N = 16, 14, 11)	3 (N = 7, 16, 13)	4 (N = 21, 18, 12)	5 (N = 16, 20, 17)	
Fights/individual/h						
(1) prebreeding	.04 ± .16	.28 ± .69	.05 ± .12	.09 ± .17	.17 ± .13	P < .001
(2) breeding	.02 ± .08	.23 ± .36	.13 ± .19	.43 ± .42	.19 ± .15	P = .001
(3) pregnancy	.08 ± .18	.07 ± .17	.13 ± .21	.20 ± .29	.06 ± .06	P = .050
Chases/individual/h						
(1) prebreeding	.17 ± .52	.20 ± .52	.57 ± .84	.23 ± .41	.47 ± .40	P = .002
(2) breeding	.23 ± .48	.68 ± 1.0	1.1 ± .79	1.5 ± .91	1.0 ± .79	P < .001
(2) pregnancy	.06 ± .25	.20 ± .39	.12 ± .23	.50 ± .64	.22 ± .16	P < .001
Runaways/individual/hour						
(1) prebreeding	.39 ± 1.2	.71 ± 1.6	1.5 ± 1.9	.75 ± .90	1.1 ± 1.3	P = .005
(2) breeding	.24 ± .44	.68 ± .95	.76 ± 1.2	1.0 ± 1.5	.74 ± .68	P = .003
(3) pregnancy	.07 ± .20	.19 ± .49	.13 ± .23	.18 ± .30	.08 ± .07	P = .013
Aggressive encounters/individual/h						
(1) prebreeding	.51 ± 1.4	.85 ± 1.8	1.5 ± 1.8	.82 ± 1.0	1.0 ± .75	P = .001
(2) breeding	.47 ± .69	1.3 ± 1.7	1.6 ± 1.2	2.2 ± 1.5	1.3 ± .94	P = .001
(3) pregnancy	.15 ± .35	.39 ± .56	.37 ± .49	.69 ± .62	.31 ± .14	P = .008

* All data were analyzed by the Kendall rank correlation test.

periods ($\bar{x} \pm SD = 1.55 \pm 1.48$ h) during three stages of the 1976 annual cycle: (a) prebreeding (2 March-1 April), when males were emerging from hibernation but most females were still hibernating, and when mean ward sizes at the five wards (based upon daily mean numbers of active prairie dogs observed) ranged from 1.24 to 4.79, (b) breeding (2 April-22 April), when females were emerging from hibernation and copulations were occurring, and when mean ward sizes ranged from 1.36 to 9.90, and (c) pregnancy (23 April-15 May), when inseminated females were building nests and preparing in other ways for their litters, and when mean ward sizes ranged from 2.22 to 12.2. Observations were made during periods of peak daily activity (usually 1100-1500 hours). Wards could not be monitored simultaneously, so I randomized the daily sequence with which the different wards were observed. At all three stages of the annual cycle, differences in daily mean numbers of active prairie dogs observed at the five wards were significant ($P < .001$, Kruskal-Wallis analysis of variance by ranks).

For all four measures of White-tail aggression during all three stages of the annual cycle, there was a significant positive correlation with ward rank ($P \leq .050$, KRC) (Table 1, Figure 1a). When all the data of Table 1 were considered together, without regard to stage, the positive correlation with ward rank for all measures was highly significant ($P < .001$, KRC).

If aggression per individual White-tail increases with ward size, it follows that aggression per individual within the same ward should increase when more individuals are active. This is so because increases in the number of active individuals (as opposed to nonactive individuals, which remain in their burrows) are equivalent to effective increases in ward size and ward density.

TABLE 2

The effect of intraward density on aggression for White-tails and Black-tails

	No. times this measure of intraward aggression correlates positively/correlates negatively with aboveground intraward density *	
	White-tails (N = 56 from 5 wards, 3 stages)	Black-tails (N = 15 from 3 wards, 1 stage)
Fights/individual/h	11/3	3/0
Chases/individual/h	10/4	3/0
Runaways/individual/h	13/1	3/0
Territorial disputes/individual/h	—	3/0
Aggressive encounters/individual/h	11/3	3/0
Totals	45/11	15/0

* All data were analyzed by the Kendall rank correlation test.

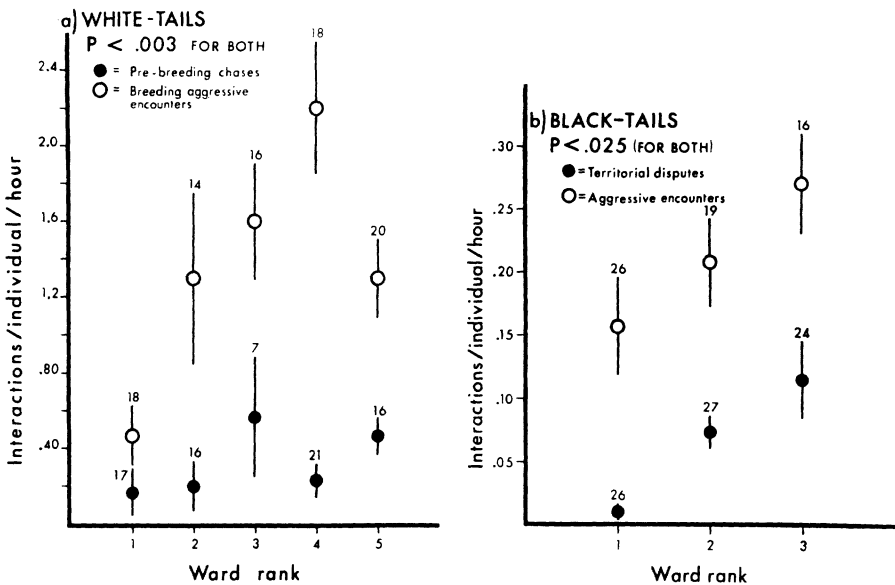


Fig. 1. The effect of ward rank on aggression for White-tails and Black-tails. Data were analyzed by the Kendall rank correlation test.

Within each of the five wards, I computed correlations for each stage of the annual cycle between daily levels of aggression and daily mean numbers of active prairie dogs (Table 2); data used for this analysis were the same as those of Table 1. Of 56 correlations (KRC), 45 were positive and 11 were negative. Further, whereas none of the negative correlations was significant, 15 of the positive correlations were significant ($P < .050$), thus indicating that aggression per individual White-tail increases with intraward aboveground density.

Black-tail aggression.

I recorded Black-tail aggressive interactions at three wards (from two colonies) of different sizes. Two assistants and I were able to simultaneously observe these wards in most cases (c.f. White-tails, above), for 1-2 h observation periods ($\bar{x} \pm SD = 1.88 \pm .262$ h; $\bar{x} \pm SD$ overlap of observation times was $.794 \pm .215$). Observations were made between 17 February and 25 March of 1975, during periods of peak daily activity (usually 1100-1500 hours). Because most Black-tail copulations occur underground, I could not determine the stage(s) of the annual cycle during which data were collected. By examining female reproductive tracts of Wind Cave Black-tails, PFEIFFER (1972, p. 41) concluded that Black-tail breeding within the Park "... begins

February 20 and may last until the end of March.”; thus, most of my observations were probably made just before and during the breeding stage. Mean ward sizes (based upon daily mean numbers of active prairie dogs observed) at the small, medium, and large wards during the period of observation were 5.29, 13.2, and 27.6, respectively, and differences in daily mean numbers of active prairie dogs at the three wards were significant ($P < .001$, Kruskal-Wallis analysis of variance by ranks). For all five measures of Black-tail aggression, there was a positive correlation with ward rank (Table 3 and Figure 1b), and four of the five correlations were significant ($P \leq .028$, KRC).

I also compared the daily levels of aggression within single Black-tail wards with daily mean numbers of active individuals observed at those same wards (Table 2); data used for this analysis were the same as those of Table 3. For all five measures of aggression at each of the three wards, there was a positive correlation (KRC) with daily numbers of active prairie dogs. That is, of 15 possible correlations, all 15 were positive, thus indicating a direct relationship between Black-tail aggression and intraward aboveground density. Five of these 15 correlations were significant ($P < .050$).

TABLE 3

The effect of ward rank on Black-tail aggression

	Ward rank (No. days of observation)			Significance *
	Small (N = 26)	Medium (N = 27)	Large (N = 24)	
Fights/individual/h	.050 \pm .073	.070 \pm .100	.085 \pm .070	P = .028
Chases/individual/h	.038 \pm .083	.163 \pm .165	.152 \pm .168	P = .001
Runaways/individual/h	.081 \pm .135	.062 \pm .089	.084 \pm .093	P = .116
Territorial disputes/ individual/h	.010 \pm .027	.073 \pm .066	.115 \pm .151	P < .001
Aggressive encounters/ individual/h	.157 \pm .199	.208 \pm .182	.270 \pm .194	P = .023 **

* All data were analyzed by the Kendall rank correlation test. ** Regarding aggressive encounters/individual/h (only), the N's for the small, medium, and large wards were 26, 19, and 16, respectively.

White-tail aggression vs Black-tail aggression.

Because absolute ward sizes are larger and ward densities are higher for Black-tails than for White-tails, I predicted that aggression should be more intense for the former species. Direct interspecific comparisons proved difficult, mainly because aggression in the two species was manifested differ-

ently. The problem was further complicated by my inability to rank fights, chases, runaways, territorial disputes, and aggressive encounters in terms of time and energy costs. Table 4 shows a comparison of White-tail and Black-tail aggression during three different stages of the annual cycles. Prebreeding and breeding data used for this analysis were the same as those of Tables 1 and 3; postbreeding data were collected in 1976 from single large wards only of each species, during the stages of pregnancy, lactation, and first emergences of juveniles from their natal burrows. $\bar{x} \pm \text{SD}$ observation times (h) for White-tails and Black-tails were 1.49 ± 1.41 and 2.25 ± 1.23 , respectively. Table 4 shows that certain measures of aggression (chases, runaways, and aggressive encounters) were generally more prevalent among White-tails, while others (fights and territorial disputes) were generally more prevalent among Black-tails. From these data, at least, it is not evident that aggression was more pronounced for densely colonial Black-tails than for loosely colonial White-tails.

TABLE 4

Interspecific comparison of aggression

White-tail rank/Black-tail rank (Significance * of these differences)

Stage of breeding cycle

(White-tail observation days, Black-tail observation days)

	Prebreeding (N = 79, 26)	Breeding (N = 86, 59)	Postbreeding (N = 36, 37)	All data (N = 265, 122)
Fights/individual/h	50/63 (P = .036)	75/70 (P = .428)	40/34 (P = .222)	187/210 (P = .039)
Chases/individual/h	51/59 (P = .196)	88/52 (P < .001)	48/26 (P = .001)	200/181 (P = .103)
Runaways/individual/h	52/56 (P = .573)	85/56 (P < .001)	44/30 (P = .001)	202/176 (P = .019)
Territorial disputes/ individual/h	48/70 (P < .001)	54/101 (P < .001)	19/55 (P < .001)	151/287 (P < .001)
Aggressive encounters/ individual/h	53/54 (P = .807)	88/49 (P < .001)	40/34 (P = .280)	202/175 (P = .024)

Numbers shown are ratios of those rank statistics derived from a Mann-Whitney U analysis (rank statistics should be equal if there are no differences; a higher rank indicates larger values). * All data were analyzed by the Mann-Whitney U test.

COST #2: INCREASED TRANSMISSION OF DISEASES AND ECTOPARASITES

Introduction.

Most mammalian diseases and ectoparasites are probably transmitted from one individual to another during periods of proximity or actual physical

contact (*e.g.*, STEFFERUD, 1956; BELL & CLIFFORD, 1964). Also, some ectoparasites (*e.g.* certain ticks) require repeated contacts with different host individuals for maximal reproductive output (CHENG, 1974; H. D. BLANKESPOOR, pers. comm.). Further, disease organisms and ectoparasites probably always gain by being able to select from a large rather than small number of available potential hosts. It follows that individuals of colonial species probably contract diseases and ectoparasites more often than do individuals of closely related solitary species, and that diseases and ectoparasites are probably more troublesome in large colonies than in smaller colonies.

Disease within squirrel populations is evidently common (*e.g.*, see reviews by DAVIS *et al.*, 1970, and DAVIS & ANDERSON, 1971). Among prairie dogs, disease and disease-related decimations have been repeatedly reported (*e.g.*, ESKEY & HAAS, 1940; POLLITZER & MEYER, 1961; LECHLEITNER *et al.*, 1968). Although tularemia might also be important (DAVIS, 1935), the most devastating disease for prairie dogs is almost surely sylvatic (bubonic, or wild rodent) plague: entire colonies of both White-tails (*e.g.*, CLARK, 1977) and Black-tails (*e.g.*, BARNES *et al.*, 1972) are sometimes eliminated after an initial introduction of plague.

It is unclear whether sylvatic plague is native to the United States or whether it was recently introduced by plague-infected, flea-bearing rats from foreign ships (POLLITZER, 1951; OLSEN, 1970). The causative organism is a bacterium, *Pasturella* (*Yersinia*) *pestis* (POLLITZER & MEYER, 1961). Transmission is achieved almost exclusively through fleas, but lice, ticks, and mites are other possible vectors (HIRST, 1953; POLLITZER, 1952). Direct transmission between individuals, without the intervention of a vector, probably seldom occurs (POLLITZER & MEYER, 1961). Among squirrels, prairie dogs seem to be especially susceptible to plague, perhaps because they are more densely colonial than any of the other squirrels. However, as noted by LECHLEITNER *et al.* (1968), it is unclear whether the seemingly extreme vulnerability of prairie dogs is real or merely an artifact that results because their large body size and colonial habits make their populations easier to census than those of other squirrels. I was unable to directly examine the transmission of sylvatic plague, or of any other disease. Data on prairie dog ectoparasites are indirectly relevant to this issue, and are discussed below.

For bats, UBELAKER (1970) summarized information which suggests that ectoparasitism by both bat flies (Diptera: Streblidae) and fleas correlates positively with colony size/density; PHILLIPS (1924) made a similar suggestion for nycteribiid (Diptera: Nycteribiidae) infestation of Ceylonese bats. For hibernating Townsend's Big-eared Bats (*Plecotus townsendii*), KUNZ (1976) reported that males within groups harbor significantly more bat flies

than do solitary males, and that bat fly infestation within groups of bats of both sexes correlates positively with density.

Essentially every species of mammal ever studied has been found to harbor a wide variety of fleas, lice, ticks, mites, *etc.* For squirrels, this can be verified from either reports on the squirrels themselves (*e.g.*, HOLDENREID *et al.*, 1951; HILTON & MAHRT, 1971; WHITAKER & SCHMELTZ, 1973) or various listings of ectoparasites (*e.g.*, KELLOGG & FERRIS, 1915; EWING & FOX, 1943; WHITAKER & WILSON, 1974). Prairie dog ectoparasites have been reported by numerous investigators (*e.g.*, WILCOMB, 1954; KING, 1955; LECHLEITNER *et al.*, 1968; PIZZIMENTI, 1975; this study), and PIZZIMENTI (1975) reported that most of them are shared by two or more host species of *Cynomys*. Regarding fleas, he reported that White-tails are potential hosts for at least eight species, and that Black-tails are potential hosts for at least four species.

That ectoparasites reduce fitnesses of their mammalian hosts has been reported by several investigators (*e.g.*, see reviews by SMITH, 1975, 1977). Among squirrels, such evidence exists for Eastern Chipmunks (*T. striatus*) (MCKINNEY & CHRISTIAN, 1970; BENNETT, 1973), Woodchucks (GRIZZELL, 1955; KO, 1972a, 1972b), and several other species (*e.g.*, see ESKEY & HAAS, 1940). For prairie dogs, I never observed serious injury or death directly attributable to ectoparasitism. But at least four lines of evidence indicate that reductions in individual fitness sometimes result from ectoparasitism. (1) Ectoparasites transmit diseases. (2) They remove blood from their hosts. (3) Their bites sometimes damage the skin and underlying tissues, producing wounds which may become infected. Especially with mites, I often detected open wounds at an ectoparasite's point of attachment. (4) Ectoparasites lead to increased amounts of time devoted to autogrooming (HOOGLAND, unpubl.), which can preoccupy individuals for as much as 5-10 min.

Using animal counts and burrow entrance counts (see above), I investigated both the effect of ward rank on flea infestation for both White-tails and Black-tails and possible interspecific differences. I assumed that increased numbers of ectoparasites lead to decreased individual fitness.

Results.

Avenues for transmission of prairie dog ectoparasites.

Increased transmission of diseases and ectoparasites within colonies presumably results because the extent of near and actual physical contact between individuals and between individuals and nonanimal sources of diseases and ectoparasites (such as nests and sleeping chambers) correlates positively with colony size and colony density. I investigated the possibility of such a correlation for prairie dogs, by examining the effect of ward size on the

frequency of various forms of aboveground contacts such as fights, allogrooming, play, *etc.* (HOOGLAND, 1977). I was unable to investigate underground contacts. For the most part, the data suggested that near or actual physical contacts (a) are more common in large wards than in smaller wards for both White-tails and Black-tails, and (b) are more common for Black-tails than for White-tails.

White-tail flea infestation.

I examined flea infestation for White-tails by collecting fleas from burrow entrances in July and September of 1975. Both times, fleas were collected from the same 10 colonies (approximately 50 burrow entrances per colony). I analyzed (a) the number of fleas *per* burrow entrance, (b) the proportion of entrances with at least one flea, and (c) the number of fleas per flea-infested entrance (*i.e.*, entrance with at least one flea); for (b), I assigned each burrow entrance a value of 0 or 1, depending on whether it contained 0 or ≥ 1 flea, and thereby had one data point for each entrance. For both July and September, both the number of fleas per burrow entrance (Fig. 2a) and the proportion of burrow entrances with at least one flea correlated positively with colony rank ($P \leq .007$, KRC; July data only are shown in Fig. 2a). There was no significant correlation in either July ($P = .700$, KRC) or September ($P = .084$, KRC) between colony rank and the number of fleas per flea-infested burrow entrance. Fig. 2a suggests that the effect of White-tail colony rank on flea numbers might have been asymptotic (*i.e.*, the effect of colony rank might have been insignificant beyond a certain rank, but this possibility was not rigorously investigated (*c.f.* HOOGLAND, 1978c, where September data are depicted).

Black-tail flea infestation.

I examined flea infestation for Black-tails by collecting fleas from burrow entrances at 9 colonies in August of 1975. Both the number of fleas per burrow entrance (Fig. 2b) and the proportion of burrow entrances containing at least one flea correlated positively with Black-tail colony rank ($P \leq .002$, KRC). Again, it seems that the effect of colony rank on flea numbers might have been asymptotic (*c.f.* HOOGLAND, 1978c). There was no significant correlation between Black-tail colony rank and the number of fleas per flea-infested burrow entrance ($P = .983$, KRC). Results similar to these were obtained from flea counts made at the same 9 Black-tail colonies in March-April of 1978 (HOOGLAND, 1978c).

Regarding Figs 2a and 2b, it might seem that the numbers of fleas per burrow entrance were simply too small to be of practical significance to

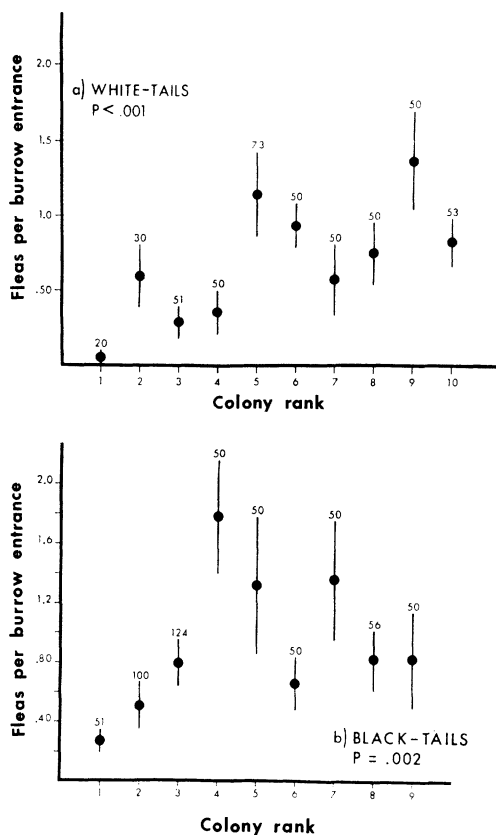


Fig. 2. The effect of colony rank on flea infestation of White-tail and Black-tail burrow entrances. Data were analyzed by the Kendall rank correlation test.

individual White-tails and Black-tails. Two points are relevant here. First, my technique for examining burrow entrances probably sampled only a small proportion of the fleas actually there (*e.g.*, see WILCOMB, 1954). Second, individuals of both species enter several, and sometimes even scores of, different burrows each day (KING, 1955; CLARK, 1977), and thus repeatedly expose themselves to those fleas at burrow entrances.

White-tail ectoparasitism vs Black-tail ectoparasitism.

For interspecific comparisons, I had data available from both burrow entrance counts and animal counts, as discussed below.

Burrow entrance counts.

By collecting fleas from burrow entrances of California Ground Squirrels (*S. beecheyi*), STEWART & EVANS (1941) detected striking seasonal differ-

TABLE 5

Interspecific comparison of flea infestation of burrow entrances

		Number of fleas per burrow entrance; Proportion of burrow entrances with at least one flea	Number of fleas per burrow entrance for those burrow entrances with at least one flea
Equivalent juvenile weight (20%-60% of adult weight)	White-tails (N = 335 from 10 colonies)	.821 ± 1.62 .397	2.17 ± 2.09
	Black-tails (N = 632 from 10 colonies)	.883 ± 2.06 .320	2.76 ± 2.85
	Significance * of these differences	P = .067** P = .016	P = .039
Equivalent juvenile age (3 months after first emergences)	White-tails (N = 464 from 10 colonies)	.358 ± .803 .233	1.54 ± .980
	Black-tails (N = 632 from 10 colonies)	.883 ± 2.06 .320	2.76 ± 2.85
	Significance * of these differences	P < .001 P = .002	P < .001
Same month of year (July)	White-tails (N = 355 from 10 colonies)	.834 ± 1.62 .400	2.08 ± 1.99
	Black-tails (N = 267 from 10 colonies)	3.30 ± 5.81 .581	5.69 ± 6.68
	Significance * of these differences	P < .001 P < .001	P < .001

* Absolute numbers of fleas were analyzed by the Mann-Whitney U test. Proportions of fleas were derived from the relevant chi-square analyses, which involved integers.

** The means for the number of fleas per burrow entrance for the "equivalent juvenile weight" comparison were misleading. Even though the Black-tail mean was slightly higher than the White-tail mean, flea infestation per burrow entrance was actually higher for White-tails than for Black-tails according to the Mann-Whitney U test (P = .067). Note that this case and the proportion of burrow entrances with at least one flea for the "equivalent juvenile weight" comparisons were the only ones that were inconsistent with theory. See text.

ences in flea densities. Similar seasonal variations at burrow entrances occurs for both White-tails and Black-tails (HOOGLAND, 1977 and unpubl.). Presumably, such variation could obfuscate interspecific differences resulting from differences in coloniality. In an attempt to reduce possible biases resulting from seasonal effects, I compared paired sets of White-tail and Black-tail burrow entrance counts. Data of each paired set were approximately equivalent regarding either juvenile weight, juvenile age, or month of year (Table 5). Except for two of the comparisons involving equivalent juvenile weight, Black-tail burrow entrances always contained significantly more fleas than White-tail burrow entrances ($P \leq .039$, Mann-Whitney U test or chi-square test).

TABLE 6

Interspecific comparison of ectoparasites found on adult prairie dogs

	Ectoparasites (number, proportion of individuals infested, sample size)			
	Fleas	Lice	Mites and ticks	All ectoparasites
White-tail adults, during breeding	8.47 \pm 16.6 .778 (N = 45)	.250 \pm .577 .188 (N = 16)	.022 \pm .149 .022 (N = 45)	8.58 \pm 16.5 .822 (N = 45)
Black-tail adults, during breeding	9.34 \pm 15.2 .875 (N = 128)	.171 \pm .811 .085 (N = 129)	.016 \pm .177 .008 (N = 128)	9.51 \pm 15.2 .883 (N = 128)
Significance * of these differences	P = .073 P = .117	P = .200 P = .192	P = .444 P = .437	P = .079 P = .303
White-tail adults, at first juvenile emergences	.951 \pm 1.60 .393 (N = 61)	.097 \pm .301 .097 (N = 31)	.105 \pm .344 .093 (N = 86)	1.81 \pm 1.97 .677 (N = 31)
Black-tail adults, at first juvenile emergences	1.36 \pm 2.01 .516 (N = 64)	5.52 \pm 7.67 .762 (N = 63)	.016 \pm .126 .016 (N = 63)	6.65 \pm 7.52 .903 (N = 62)
Significance * of these differences	P = .165 P = .170	P < .001 P < .001	P = .051** P = .051**	P < .001 P = .007

* Absolute numbers of ectoparasites were analyzed by the Mann-Whitney U test. Proportions of ectoparasites were derived from the relevant chi-square analyses, which involved integers. ** Almost all Black-tail adults that were examined for mites and ticks during first juvenile emergences were also examined one or more times during the previous 4-6 weeks when females were lactating; the same was not true for White-tails. Since many of the mites and ticks removed from Black-tails during lactation would probably have still been present during first juvenile emergences, Black-tail counts of mites and ticks during the latter stage were probably abnormally low; the same was probably not true for fleas and lice, which are more numerous and probably more mobile than mites and ticks (*e.g.*, see HOLDENREID *et al.* [1951] and LINSDALE [1946] regarding flea infestation of individual ground squirrels examined at different stages of the annual cycle). Thus, the significance levels with double asterisks (**) are probably misleading.

Animal counts.

As with burrow entrance counts, counts of ectoparasites from the animals themselves also vary seasonally for various species of squirrels (*e.g.*, STEWART & EVANS, 1941; HILTON & MAHRT, 1971; SHERMAN, 1976). The same is true for White-tails and Black-tails (Table 6 and HOOGLAND, unpubl.). Accordingly, interspecific comparisons involving adults (Table 6) and young (Table 7) were made only during comparable stages of the annual cycles. Regarding mites and ticks, none of the interspecific differences were significant ($P > .050$ for all, Mann-Whitney U test or chi-square test; but see footnote of Table 6). Regarding fleas and lice, Tables 6 and 7 generally support the prediction that Black-tails should harbor more ectoparasites than White-tails, and several of the observed differences were significant ($P < .050$, Mann-Whitney U test or chi-square test). ESKEY & HAAS (1940) also reported from animal counts that Black-tails harbored more fleas than White-tails (4.28 *vs* 1.24 [means]; $N = 128, 1,197$, respectively), but they did not consider seasonal effects.

TABLE 7

Interspecific comparison of ectoparasites found on juvenile prairie dogs

	Ectoparasites (number, proportion of individuals infested, sample size)			
	Fleas	Lice	Mites and ticks	All ectoparasites
White-tail young, at their first emergences	.469 \pm 1.40 .232 ($N = 177$)	3.35 \pm 5.83 .463 ($N = 82$)	.136 \pm .487 .093 ($N = 236$)	4.17 \pm 5.90 .683 ($N = 82$)
Black-tail young, at their first emergences	.930 \pm 2.18 .349 ($N = 86$)	80.7 \pm 33.6 .943 ($N = 88$)	.057 \pm .278 .045 ($N = 88$)	81.8 \pm 33.5 .965 ($N = 86$)
Significance * of these differences	$P = .030$ $P = .045$	$P < .001$ $P < .001$	$P = .157$ $P = .159$	$P < .001$ $P < .001$

* Absolute numbers of ectoparasites were analyzed by the Mann-Whitney U test. Proportions of ectoparasites were derived from the relevant chi-square analysis, which involved integers.

The role of immigration.

The identity of individuals contacted must also be important in the transmission of diseases and ectoparasites: contacting the same individual 10 times, for example, is probably never equivalent to single contacts with 10 different, previously unencountered individuals. FREELAND (1976) discussed the possible importance of extra-group contacts among several species of primates, and suggested several behaviours that might have evolved to reduce the probability of contracting diseases (and ectoparasites, presumably) through

such contacts. Further, FREELAND has shown, by fecal analysis, that primates within the same group harbor essentially identical intestinal flora and fauna, and that these differ significantly from those harbored by neighbouring groups (FREELAND, 1977). Thus, immigration into prairie dog wards is of special interest.

By ear-tagging and colour-marking every resident at my main study wards each year, I was able to confirm earlier findings which indicate that immigration into wards is more prevalent for White-tails than for Black-tails (KING, 1955; TILESTON & LECHLEITNER, 1966; CLARK, 1977). These interspecific differences might result, at least in part, because immigrating White-tails are often met with little or no resistance by the local residents, whereas immigrating Black-tails are invariably met with formidable resistance (fighting, chasing, *etc.*). I did not investigate possible intraspecific relationships between ward size/density and either immigration or response to immigrants.

To summarize, Black-tails evidently contact local conspecifics more often than do White-tails, but White-tails probably contact new conspecifics (immigrants) more often than do Black-tails. The relative importance of these factors for prairie dogs is not known.

COST #3: INCREASED PROBABILITY OF MISDIRECTED PARENTAL CARE RESULTING FROM THE MIXING OF UNRELATED YOUNG

Introduction.

Parents of solitary, ground-dwelling mammals must only rarely face the possibility of either mistaking another home burrow for their own, encountering unrelated young at the home burrow, or having their offspring wander into strange burrows containing unrelated young; but these are probably common accidents in colonial species. Possible consequences of such accidents include both the temporary or permanent loss of related offspring and the rearing of unrelated young: misdirected parental care resulting from the mixing of unrelated young is therefore another possible cost of prairie dog coloniality. The cost is not automatic, since it would be absent, for example, in most colonies of nonbreeding animals. Parent-offspring recognition represents an evolutionary response to this cost, and at the same time is evidence for its existence.

Temporary or permanent mixing of young from different litters shortly after their first emergences from natal burrows has been reported for several group-living squirrels (*e.g.*, MAYER, 1953; MCCARLEY, 1966; MICHENER, 1973; SLADE & BALPH, 1974; SHERMAN, 1976). Parent-offspring recognition shortly after first emergences has been reported for Richardson's Ground Squirrels (*S. richardsonii*) (YEATON, 1972; MICHENER, 1973), and has also

been suggested for Belding's Ground Squirrels (SHERMAN, 1976). Shortly after their first emergences, weaned or almost weaned White-tail and Black-tail young begin to interact (mix) with young from other litters (KING, 1955; CLARK, 1977; this study), and soon thereafter they regularly forage, play, allogroom, and sleep with these unrelated young. Once mixing has commenced, it seems that it would be difficult for parents to quickly locate their own offspring.

For both White-tails and Black-tails, I investigated both the mixing of unrelated young and the possibility of parent-offspring recognition. I assumed that parent-offspring recognition would evolve only if mixing of unrelated young were somehow deleterious to individual parents.

Results.

The time interval (days) between the first emergence of one or more young from each litter and the first interaction of one of these young with young from a different litter was determined by the colour-marking of entire litters followed by 1-2 h of daily observation. Because of trapping difficulties, observations in any one year were only made at single wards for each species. As predicted, Black-tail young first interacted (mixed) with unrelated young sooner than did White-tail young (Table 8), but the difference was not significant ($P = .142$, Mann-Whitney U test). Table 8 contains only those Black-tail data from coterie containing > 1 litter, and was thereby nonconservatively biased (see below).

One interesting consequence of the Black-tail coterie system is the restriction of juvenile mixing to litters within the coterie. Black-tail young quickly learn boundaries of their coterie territory and only rarely venture beyond (KING, 1955). A single parous female within a coterie presumably faces almost no possibility of costs associated with mixing of unrelated young. By

TABLE 8

Interspecific comparison of the onset of mixing of young from different litters

	Elapsed time (days) between first emergences of young from the natal burrow and first interaction (mixing) with young from another litter
White-tails (N = 16 from 1 ward)	11.9 ± 9.58
Black-tails (N = 31 from 2 wards)	6.55 ± 3.30
Significance * of these differences	$P = .142$

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

contrast, mixing of White-tail young is widespread and unrestricted to particular territories within the ward. Thus, even though first mixing probably occurs earlier for Black-tail young, the potential number of unrelated young with which to mix is usually higher for White-tail young. The relative importance of these factors for prairie dogs is not known.

In an attempt to determine if mixing of unrelated, recently emerged young is deleterious to prairie dog parents, I performed transfer experiments and watched for parent-offspring recognition. Single ear-tagged, colour-marked young were transferred as soon as possible after their first emergences from their natal burrows into same-stage litters that were distant (usually in different wards). Each foster litter was regularly checked until at least six days after the transfer. Of 6 White-tail transfers (5 males and 1 female from 2 different litters), 2 (both males) were never seen again, 1 remained with its foster litter for at least 2 days, and 3 remained for at least 6 days. White-tail young commonly disappear shortly after their first emergences, so the two transfers that disappeared were not necessarily the victims of parental discrimination. These preliminary data suggest that White-tail parents do not recognize their recently emerged young. Of 6 Black-tail transfers (2 males and 4 females from 3 different litters), all 6 remained with their foster litters until at least 9 days after transfer. Evidently, Black-tail parents also do not recognize their recently emerged young. Black-tail adults do, however, vigorously discriminate against unrelated juveniles about 6 weeks old or older that attempt to invade their coterie territory (see also KING, 1955). On the basis of my transfer experiments, I conclude that mixing of recently emerged young probably is not seriously deleterious for either White-tail or Black-tail parents.

COST #4: INCREASED CONSPICUOUSNESS TO PREDATORS

Introduction.

A colony of animals must almost always be more conspicuous to predators than is a single animal. By living in a colony, then, an individual might be subjected to certain notice, and possible subsequent attack, by predators that would otherwise be absent. It follows that increased exposure to predators is a possible cost of coloniality. The cost is not automatic, since there are some circumstances under which increased colonial conspicuousness might be favorable; this is probably the case, for example, for brightly coloured, poisonous caterpillars that remain in sibling groups (FISHER, 1958). For individuals of herbivorous, palatable prey species, though, increased conspicuousness of colonies to predators is probably always deleterious. Such a

cost has been suggested for several bird species (*e.g.* TINBERGEN, 1952, 1956; CULLEN, 1960; KRUUK, 1964). but the problem has never been investigated for any mammal,

I explored the possibility of costs associated with both increased vocal and increased visual conspicuousness of prairie dog colonies by measuring (a) the rate of territorial calling, (b) visibility of mounds, and (c) visibility of individual prairie dogs; for (b), data were only available for intraspecific comparisons. I also investigated the possible existence of adaptations aimed at reducing conspicuousness. Whereas I was able to examine aggression per individual and ectoparasites per individual, I was unable to examine conspicuousness on the same per-individual basis. This shortcoming seriously limits the significance of my findings (see below).

Results.

White-tail conspicuousness.

Rate of territorial calling.

A White-tail territorial call consists of 2-15 ($\bar{x} \pm SD = 5.17 \pm 2.03$; $N = 18$) identical sounds uttered in a rapid series, and probably functions in territorial defense (WARING, 1970 and pers. comm.; CLARK, 1977). In late June and early July of 1976, I recorded the number of territorial calls that I heard at three White-tail wards of different sizes (Fig. 3a). Under undisturbed conditions, counts were made for 30-40 min on several different days. June-July vocal conspicuousness (to me and presumably to predators) correlated positively with White-tail ward rank ($P < .001$, KRC).

Visibility of mounds.

In September of 1975, I chose good viewing sites at edges of six different White-tail wards, and therefrom recorded the number of mounds visible with binoculars. The number of mounds potentially visible to predators correlated positively with White-tail ward rank ($P < .001$, KRC).

Visibility of individual prairie dogs.

In June-July of both 1975 and 1976, I chose good viewing sites at edges of 12 White-tail wards, and therefrom recorded numbers of prairie dogs visible with binoculars under undisturbed conditions. Counts were repeated at least once on different days. Counts of White-tail adults and young visible to me, and presumably also to predators, correlated positively with ward rank ($P < .001$, KRC).

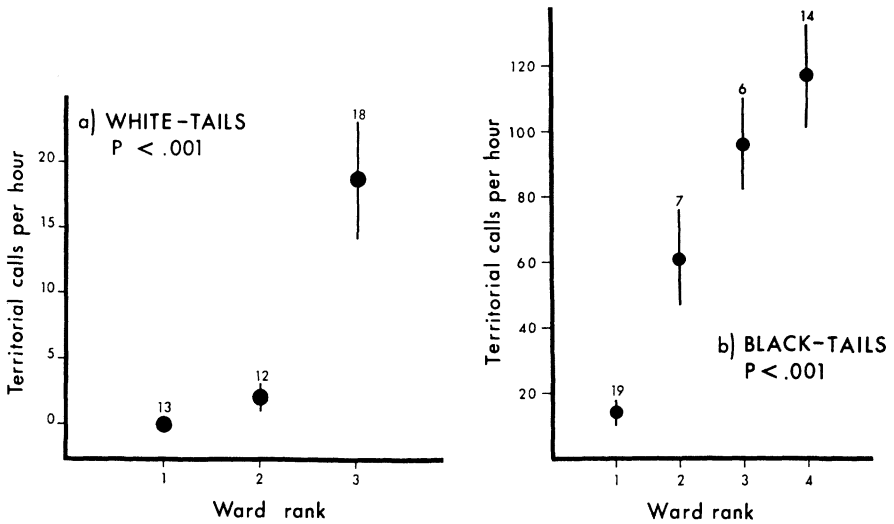


Fig. 3. The effect of ward rank on vocal conspicuousness to predators for White-tails and Black-tails. Data were analyzed by the Kendall rank correlation test.

Black-tail conspicuousness.

Rate of territorial calling.

A Black-tail territorial call contains two distinct, dissimilar syllables, is accompanied by a formalized upward leap, and functions in territorial defense as well as in other circumstances (KING, 1955; WARING, 1970; SMITH *et al.*, 1976). Using the methods described for White-tails, I recorded territorial calls at four Black-tail wards in July of 1976 (Fig. 3b). The vocal conspicuousness presumably available to predators correlated positively with Black-tail ward rank ($P < .001$, KRC).

Visibility of mounds.

Using the methods described for White-tails, I recorded the number of visible mounds at six Black-tail wards in July of 1976. The number of mounds potentially visible to predators correlated positively with Black-tail ward rank ($P < .001$, KRC).

Visibility of individual prairie dogs.

Using the methods described for White-tails, I recorded the number of visible prairie dogs at six Black-tail wards in August of 1975. Counts of Black-tail adults and young presumably visible to predators correlated positively with ward rank ($P < .001$, KRC).

White-tail conspicuousness vs Black-tail conspicuousness.

Rate of territorial calling.

For an interspecific comparison, I summarized the data of Figs 3a and 3b (Table 9). July Black-tail vocal conspicuousness to predators was significantly greater than June-July White-tail vocal conspicuousness ($P < .001$, Mann-Whitney U test). For this analysis, I assumed (a) equivalence of the stages of the White-tail and Black-tail annual cycles during which territorial calls were recorded, and (b) equal conspicuousness of White-tail and Black-tail territorial calls to predators' ears. Territorial calling in both White-tails and Black-tails seems to steadily decrease following breeding (CLARK, 1977; HOOGLAND, unpubl.), so any biases in (a) were probably conservative. White-tail territorial calls are usually longer and louder than Black-tail territorial calls (WARING, 1970), such that any biases in (b) were probably nonconservative.

TABLE 9

Interspecific comparison of vocal conspicuousness to predators

	Territorial calls per hour
White-tails (N = 43 counts from 3 wards)	8.41 ± 15.2
Black-tails (N = 46 counts from 4 wards)	63.1 ± 59.0
Significance* of these differences	$P < .001$

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

Visibility of individual prairie dogs.

For an interspecific comparison (Table 10), I summarized those White-tail and Black-tail data described above. Numbers of visible prairie dogs were significantly higher for Black-tails than for White-tails ($P < .001$, Mann-Whitney U test). There was no indication that this difference resulted because Black-tail behaviours somehow rendered them more conspicuous. Black-tail

TABLE 10

Interspecific comparison of the visual conspicuousness of individual prairie dogs to predators

	Number of visible prairie dogs (undisturbed conditions)
White-tails (N = 44 counts from 12 wards)	13.2 ± 7.37
Black-tails (N = 33 counts from 7 wards)	24.2 ± 10.5
Significance* of these differences	$P < .001$

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

wards did, however, contain significantly less protective cover behind which individuals could have concealed themselves, but this difference alone probably did not account for the significant difference in Table 10 (HOOGLAND, 1977, 1978a).

Significance of increased conspicuousness to predators.

Increased conspicuousness of a prairie dog colony to predators can probably only be seriously deleterious to the individual residents therein if new predators commonly move into the general vicinity of the colony. If all predators of prairie dogs are sedentary and know their home ranges well, then increased colonial conspicuousness probably only rarely exposes colony residents to predators that would otherwise remain ignorant. Initial exposure of a colony to an ignorant predator could have severe consequences for colony residents, since some predators return repeatedly to areas of high potential success. Too little is known about the hunting strategies of predators such as Golden Eagles (*Aquila chrysaetos*), Prairie Falcons (*Falco mexicanus*), Badgers (*Taxidea taxus*), Coyotes (*Canis latrans*), and Black-footed Ferrets (*Mustela nigripes*) to allow an accurate evaluation of the possible cost associated with increased conspicuousness.

If vocal conspicuousness, for example, is seriously deleterious, then individuals within large wards might be selected to be more quiet than individuals within smaller wards; such selection would presumably reduce the extreme vocal conspicuousness of large wards that would otherwise be expected. Thus, a negative correlation between territorial calls per individual per h and ward rank might be expected even in the face of the positive correlation between territorial calls per h and ward rank (Figs 3a and 3b). But territorial calls function in territorial defense, and territorial calls per individual per h might therefore be expected to correlate positively, as does aggression (Figs 1a and 1b), with ward rank. For both White-tails and Black-tails, the latter was true: territorial calls per individual per h correlated positively with ward rank ($P < .001$, KRC; data taken from Figs 3a and 3b, then transformed). Further, territorial calls per individual per h were significantly higher for Black-tails than for White-tails ($P = .001$, Mann-Whitney U test; data taken from Table 9, then transformed). Evidently, either increased vocal conspicuousness to predators was not seriously deleterious to individual ward residents or the importance of territorial calls in aggressive interactions outweighed the associated cost. Regarding increased visual conspicuousness, I observed no mechanism by which either White-tails or Black-tails attempted to reduce the visibility of either mounds or individual prairie dogs.

Large wards probably offer higher absolute numbers of obtainable prey than smaller wards, and the former might thereby be more attractive to predators. It follows that another possible cost of prairie dog coloniality, closely related to increased conspicuousness, is increased attractiveness to predators. This cost might be especially deleterious with respect to (a) those predators that return to sites where potential success is high, and, similarly, (b) those predators such as Long-tailed Weasels (*Mustela frenata*), Badgers, and Black-footed Ferrets that sometimes set up residence within or just outside ward boundaries (HILLMAN, 1968; HOOGLAND, 1977). I did not investigate the possibility of this cost for prairie dogs. As with increased conspicuousness, a rigorous analysis of increased attractiveness will require techniques that allow assessment of the cost on a per-individual basis.

COST #5: MISCELLANEOUS COSTS

Introduction and results.

In addition to the four costs discussed above, other costs of prairie dog coloniality, all nonautomatic, probably also exist. Likely possibilities, all of which are probably of relatively minor importance, include an increased probability of accidental collisions, increased deterioration of burrow entrances and mounds, increased probability of having nest materials stolen, and an increased probability of misdirected parental care resulting from intraspecific brood parasitism (HOOGLAND, 1977; see HOOGLAND & SHERMAN, 1976, for parallel arguments for Bank Swallows).

Another likely cost of prairie dog coloniality is misdirected parental care resulting from cuckoldry. I am currently investigating the possibility of such a cost for Black-tails.

Intraspecific killing or injuring of unrelated young is widespread among mammals (*e.g.*, see review by HRDY, 1977). Among squirrels, such behaviour has been reported for Yellow-bellied Marmots (ANDERSEN *et al.*, 1976) and seven species of ground squirrels (ALCORN, 1940; LINSDALE, 1946; BURNS, 1968; STEINER, 1970, 1972; QUANSTROM, 1971; SHERMAN, 1976). Parents of colonial species are probably more vulnerable than parents of solitary species to losing their offspring to marauding conspecifics, since there are presumably more potential marauders nearby for the former, and the increased probability of such loss represents another possible cost of coloniality. I detected no evidence of intraspecific infanticide under natural conditions for White-tails. For Black-tails, I observed several possible cases of intraspecific infanticide, and I am currently investigating this issue in this species.

DISCUSSION

ALEXANDER (1974) was the first to point out that costs, not benefits, are automatic and universal consequences of group-living. He noted (1974, p. 329) that: "It seems impossible to overstress the extent to which (this view) contrasts with those prevalent during the past century." Perhaps this explains why previous studies of coloniality have almost completely ignored the costs of grouping (but see HOOGLAND & SHERMAN, 1976).

Large wards contain more prairie dogs than smaller wards, and it seems that costs of coloniality should therefore increase directly with ward size. But this need not necessarily be the case. The number of fleas per burrow entrance, for example, might increase directly with ward size only up to a certain asymptotic point simply because there is probably a limit to the number of fleas that a burrow entrance can support. Also, it is possible that the 100 fleas per individual at a large ward (or within a densely colonial species) are effectively no more deleterious than the 75 fleas per individual at a smaller ward (within a loosely colonial species). Further, prairie dog strategies might change when a particular cost reaches a certain level. For example, when a ward reaches a certain size, it might be so conspicuous to predators that an individual's attempt at minimizing conspicuousness would be a waste of time and energy. Beyond the critical (threshold) size, alternatively, individuals might sometimes be selected to effect increased visual conspicuousness of

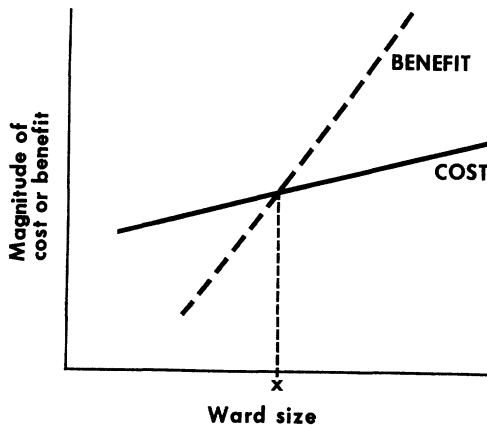


Fig. 4. Hypothetical relationship between ward size and both a single cost of coloniality and its complementary benefit. The magnitude of both the cost and the benefit increases directly with ward size, but the magnitude of the benefit increases more quickly (*i.e.*, its regression slope is steeper). At ward sizes below X , the cost exceeds the benefit. At ward sizes above X , the benefit outweighs the cost. The lines do not represent the only cost-benefit relationship: for another cost-benefit complementary pair, it may be the cost whose slope is steeper. See text.

themselves in exchange for better visibility of predators and visual alarms of conspecifics (which warn of predators). In other words, increased visibility and the resulting increased conspicuousness might work more to the prairie dogs', rather than the predators', advantage in large wards. This possibility seems especially likely for Black-tails (HOOGLAND, 1978a, 1978b). Finally, the significance of a particular cost will certainly vary with the magnitude of its complementary benefit(s) (Fig. 4). For example, both the cost of visual conspicuousness and the benefit resulting from "selfish herd" effects (HAMILTON, 1971) presumably increase directly with ward size. If the benefit here increases more quickly than the cost, then there may be a ward size (X in Fig. 4) beyond which selfish herd effects outweigh any cost associated with increased visual conspicuousness. In another case, it may be the cost that increases more quickly than its complementary benefit; depending on other cost-benefit relationships, the latter case could lead to an adaptive ceiling on ward size, beyond which costs would exceed benefits. In this study, I did not systematically investigate either asymptotic effects of ward size, responses of prairie dogs to threshold ward sizes, or regression slopes of complementary costs and benefits. I assumed that increases in my various estimates of costs (fights per individual, fleas per individual, *etc.*) corresponded to decreases in individual fitness.

Several studies have shown a positive correlation between group size (or group density) and either aggression (a measure of competition) or ectoparasitism. Several other studies have shown that either aggression or ectoparasitism can reduce individual fitnesses. But for either aggression, ectoparasitism, or any other possible cost of coloniality, no study has shown for any single animal both a positive correlation with group size and direct proof of reduced fitness. This study has come the closest: (a) for both White-tails and Black-tails, both aggression and flea infestation correlated positively with ward size, and (b) several lines of circumstantial evidence indicated that both aggression and fleas reduce prairie dog fitnesses, but direct evidence was lacking.

When faced with increased aggression and increased ectoparasitism, as well as other possible costs, why do prairie dogs live in colonies? Obviously, there must be benefits which outweigh the costs for every case of coloniality. ALEXANDER (1974) proposed that there are probably only three possible explanations for the evolution of coloniality: (1) there might be an extreme shortage of suitable habitat, (2) there might be benefits associated with social facilitation of foraging, or (3) there might be benefits associated with reduced predation. I have examined the benefits of prairie dog coloniality elsewhere (HOOGLAND, 1977, 1978a). I concluded that shortages of suitable

habitat and social facilitation of foraging are probably of little or no importance, and that increased protection from predators is probably the single benefit of prairie dog coloniality.

SUMMARY

In a 4-yr study, I investigated the costs of coloniality for two species of squirrels (Sciuridae): loosely colonial White-tailed Prairie Dogs (*Cynomys leucurus*) and densely colonial Black-tailed Prairie Dogs (*C. ludovicianus*). Study sites were in Wyoming and Colorado (White-tails) and Colorado and South Dakota (Black-tails). By an examination of both intra- and interspecific effects, four costs were investigated: (1) increased aggression, (2) increased transmission of diseases and ectoparasites, (3) increased probability of misdirected parental care resulting from the mixing of unrelated young, and (4) increased conspicuousness to predators. The possibility of various miscellaneous costs was also investigated. I hypothesized that the costs of coloniality should be greater (a) for individuals of large wards (subcolonies) than for individuals of smaller wards and (b) for Black-tails than for White-tails. Isolated individuals of either species were never observed.

To measure aggression, most of which was probably related to competition for mates and nesting burrows, I recorded fights, chases, and other hostile interactions. Three lines of circumstantial evidence indicated that this sort of aggression was deleterious to individual prairie dogs. For both White-tails and Black-tails, aggression per individual per h correlated positively with ward size. Aggression was not more pronounced for Black-tails than for White-tails, but interspecific comparisons were difficult because aggression in the two species was manifested differently.

White-tails and Black-tails are both extremely susceptible to sylvatic plague, but intra- or interspecific investigations of the transmission of this disease were not possible. I measured ectoparasitism by sampling for fleas at burrow entrances and by counting fleas and lice on the adults and young themselves. Four lines of circumstantial evidence indicated that ectoparasites were deleterious to their prairie dog hosts. For both White-tails and Black-tails, the number of fleas per burrow entrance correlated positively with ward size. Counts from burrow entrances and from the animals themselves both indicated that ectoparasitism was probably more costly for Black-tails than for White-tails.

Both White-tail and Black-tail young mingled regularly with young from different litters shortly after their first emergences from the natal burrows, with Black-tail young tending to mingle sooner. Experiments involving the transfer of colour-marked young into foster litters indicated that mixing of unrelated young, with the possible consequence of misdirected parental care, was probably not seriously deleterious for parents of either species.

Vocal conspicuousness was measured by recording the rate of territorial calling, and visual conspicuousness was measured by counting numbers of visible mounds and numbers of visible prairie dogs. Both vocal and visual conspicuousness correlated positively with ward size for both White-tails and Black-tails. Further, both types of conspicuousness were more pronounced for Black-tails than for White-tails. Neither vocal nor visual conspicuousness could be measured on a per-individual basis, and an assessment of associated costs was therefore difficult.

In summary, I conclude that there are probably several costs associated with prairie dog coloniality, that the severity of some of the costs correlates positively with colony or ward size for both White-tails and Black-tails, and that some of the costs are probably more pronounced for Black-tails than for White-tails.

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ZUSAMMENFASSUNG

Der Kostenaufwand des Zusammenlebens in Kolonien wurden in 4-jähriger Arbeit an zwei Hörnchenarten (Sciuridae) untersucht: lockersiedelnden weißgeschwänzten Prairiehunden (*Cynomys leucurus*) und dichtsiedelnden schwarzgeschwänzten Prairiehunden (*Cynomys ludovicianus*). Forschungsorte waren Wyoming und Colorado (für die Weißschwänze), und Colorado und Süddakota (für die Schwarzwänze). Vier verschiedene ungünstige Effekte wurden näher untersucht, entweder mit innerartlicher oder mit zwischenartlicher Wirkung: 1) zunehmende Aggression; 2) höhere Weitergabe von Krankheiten und Ektoparasiten; 3) zunehmende Möglichkeit von falsch angewandter elterlicher Pflege bei Mischung unverwandter Jungen; und 4) größere Auffälligkeit den Raubtieren gegenüber. Der mögliche Einfluß mehrerer anderer Faktoren wurde ebenfalls untersucht. Ich bildete mir die Hypothese, daß die Besiedelungsnachteile größer sein würden (a) bei Prairiehunden in größeren Siedlungen als bei denen in kleineren

Siedlungen, und (b) bei den Schwarzschnäuzen als bei den Weißschnäuzen. Einzelne lebende Tiere kamen nicht vor.

Um die Aggression, die wohl meist in Zusammenhang mit dem Wettbewerb um Weibchen und Bau zu beobachten war, zu messen, zeichnete ich Kämpfe, Jagden und andere feindliche Begegnungen auf. Der Indizienbeweis aus drei Richtungen hat darauf hingewiesen, daß diese Art Aggression dem einzelnen Prairiehund schädlich war. Bei den Weiß- sowie bei den Schwarzschnäuzen war eine Wechselbeziehung zwischen Aggression pro Tier pro Stunde und der Größe der Siedlung festzustellen. Die Aggression war nicht ausgeprägter bei den Schwarzschnäuzen als bei den Weißschnäuzen, aber Vergleiche zwischen den Arten waren schwer zu ziehen, weil die Aggression sich in den zwei Arten anders manifestierte.

Die Weißschnäuze wie auch die Schwarzschnäuze sind gegen die Beulenpest besonders empfindlich; aber es war unmöglich, Untersuchungen über die Weitergabe dieser Krankheit zu machen, weder innerhalb noch zwischen den Arten. Den Ektoparasitismus habe ich gemessen, indem ich von der Flöhezahl an Baueingängen Proben genommen, und die Flöhe und Läuse an den Tierkörpern selbst (bei Erwachsenen wie bei Jungen) gezählt habe. Der Indizienbeweis aus vier Richtungen hat darauf hingewiesen, daß Ektoparasiten dem Prairiehund schädlich sind. Bei den Weiß- wie auch bei den Schwarzschnäuzen war eine Wechselbeziehung zwischen der Flöhezahl am Baueingang und der Siedlungsgröße festzustellen. Die Flöhenmenge an Baueingängen und die Zahl der an den Tieren selbst gefundenen Flöhe haben darauf hingewiesen, daß der Ektoparasitismus den Schwarzschnäuzen wahrscheinlich schädlicher ist als den Weißschnäuzen.

Die Jungen der Weißschnäuze wie der Schwarzschnäuze mischten sich unter die Jungen anderer Würfe kurz nachdem sie aus dem Geburtsbau herausstiegen. Dabei waren die Schwarzschnäuze dazu geneigt, sich frühzeitiger als die Weißschnäuze zu mischen. Experimente, bei denen farbmarkierte Junge in Pflegewürfe umgesiedelt wurden, zeigten, daß die Mischung unverwandter Jungen und die daraus folgenden Möglichkeit falsch angewandter elterlicher Pflege den Eltern in beiden Arten wahrscheinlich nicht schädlich waren.

Die vokale Auffälligkeit der Prairiehunde wurde gemessen, indem das Vorkommen des territorialen Rufs aufgenommen wurde; die visuelle Auffälligkeit wurde gemessen, indem die sichtbaren Erdhügel und die Tiere selbst gezählt wurden. Bei beiden Arten stand die vokale wie auch die visuelle Auffälligkeit in einer positiven Wechselbeziehung mit der Siedlungsgröße. Darüber hinaus manifestierten sich die Schwarzschnäuze ausgeprägter als die Weißschnäuze. Weder die vokale noch die visuelle Auffälligkeit konnte gemessen werden für die einzelnen Tiere; deshalb waren auch mögliche Nebennachteile nur schwer einzuschätzen.

Zusammenfassend komme ich zu dem Schluß, daß das Zusammenleben in Kolonien bei dem Prairiehund wahrscheinlich mit mehrfachen Nachteilen verbunden ist, daß die Ausgeprägtheit einiger Nachteile bei den Weiß- sowie bei den Schwarzschnäuzen in positiver Wechselbeziehung mit der Siedlungsgröße steht, und daß einige Nachteile wahrscheinlich bei den Schwarzschnäuzen ausgeprägter sind als bei den Weißschnäuzen.