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SOCIAL BEHAVIOR OF CAPTIVE BLACK-TAILED PRAIRIE DOGS (MAMMALIA, RODENTIA) WITH CHANGING NUMBER OF OBSERVERS

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Social Behavior of Captive Black-Tailed Prairie Dogs (Mammalia, Rodentia) with Changing Numbers of Observers. Eltorai A. E. M., Sussman R. W. — Black-tailed prairie dogs *Cynomys ludovicianus* (Ord, 1815) are diurnal rodents that live in intricate cities. Their social complexity rivals that of some primates, and, in some respects, resembles the behavior of humans. Due to the rich variety of readily-observable, sophisticated behaviors such as coloniality, infanticide, anti-predator behaviors, “kin recognition”, cooperation, conflict, and reproductive success, the black-tailed prairie dog is a wonderful model species for the study of behavior. Using a captive population, we were able to quantify the effects of observation on key social behaviors.

Key words: *Cynomys ludovicianus*, black-tailed prairie dogs, captive, social behavior, observation.

Социальное поведение чернохвостых луговых собачек (Mammalia, Rodentia) в неволе при сменяющемся количестве наблюдателей. Элторай А. Е. М., Сассман Р. В. — Чернохвостые луговые собачки — *Cynomys ludovicianus* (Ord, 1815) — дневные грызуны, которые обитают в малодоступных местах. Сложность их социального поведения соперничает с таковой у некоторых приматов и в некотором отношении сходна с поведением человека. Благодаря богатому разнообразию легко наблюдаемых особенностей поведения, таких как колониальность, детоубийство, защита от хищников, распознавание родичей, сотрудничество, конфликты и репродуктивная успешность — чернохвостые луговые собачки являются прекрасным модельным видом для изучения поведения. Используя популяцию, обитающую в неволе, мы смогли количественно измерить влияние наблюдения на ключевые особенности социального поведения.

Ключевые слова: *Cynomys ludovicianus*, луговые собачки, содержание в неволе, социальное поведение, наблюдение.

Introduction

“Prairie dogs have a complex social system, rivaling that of some primates and in some respects resembling the behavior of humans. Perhaps that is why prairie dog exhibits in zoos are very popular, with people sometimes spending hours watching the behavior of the animals” (Slobodchikoff et al., 2009: 43).

Black-tailed prairie dogs *Cynomys ludovicianus* (Ord, 1815) belong to the order of rodents and the squirrel family, Sciuridae. They are diurnal and live in socially-intricate colonies, when undisturbed, stretch for kilometers and can contain thousands of individuals (Hoogland, 1995).

As a social species, black-tailed prairie dogs frequently interact among themselves. Friendly interactions occur between individuals of the same family group, coterie. Examples of such friendly behaviors include: “play, allogrooming, and mouth-to-mouth contact that resemble kisses” (Hoogland, 1995: 2).

The “greet-kiss” (King, 1955), where the prairie dogs “open up their mouths, and press their tongues together for a brief period of time”, can occur between any combination of individuals (Slobodchikoff et al., 2009: 56). Steiner proposed the following self-explanatory hypotheses for why this kiss may occur: Food Information Hypothesis (1975), Individual Recognition Hypothesis (1974), and Dominance Maintenance

Hypothesis (1975). However “the picture is still not clear about the functions of a greet-kiss. Perhaps the behavior originated for any of the reasons given by the above hypotheses, and has persisted as a mechanism of social reassurance, somewhat like a human kiss» (Slobodchikoff et al., 2009: 57).

Allogrooming, or mutual grooming, occurs when one individual picks the fleas, lice, and ticks from another individual, consequently reducing the number of parasites on the groomed individual (Slobodchikoff et al., 2009).

Variations in how much time individual black-tailed prairie dogs spend doing particular behaviors have been studied. Individually-distinct use of time serves to suggest that black-tailed prairie dogs may have unique personalities, which effectively add to the nuanced prairie dog social system (Loughry, Lazari, 1994).

Less amicable behaviors are also observed. February through April, females are defensive of their nursery burrows and hostile interactions frequently occur. However, when the pups emerge from their subterranean burrows in May, friendly interactions are the coterie norm (Hoogland, 1995). The other form of hostile behavior occurs “when prairie dogs from different coteries meet, they engage in a flagrant territorial dispute that involves staring, tooth chattering, flaring of the tail, bluff charges, and reciprocal anal sniffing. Territorial disputes commonly persist for more than 30 minutes and sometimes include fights and chases as well” (Hoogland, 1995: 2).

From past studies of this North American ground squirrel, interesting observations have been reported regarding coloniality, infanticide, anti-predator behaviors, “kin recognition”, cooperation, conflict, and reproductive success. Prairie dogs are known to “have a sophisticated communication system that might out-strip monkeys and apes in its complexity, ” making them a compelling study subject (Slobodchikoff et al., 2009: 1). Readily observable examples prairie dog behaviors include: the “jump-yip display” (individual stretches vertically, throwing their body as they call), rapid scratching to remove fleas, burrow-mound enhancement, and nest-building by collecting leaves, grass and twigs in their mouths (Hoogland, 1995). Due to the rich variety of salient behaviors, the black-tailed prairie dog is a wonderful model species for the study of behavior.

Prairie dogs are even more fascinating study subjects considering the following observations: non-parental prairie dogs make antipredator calls to warn distant kin; lactating females commit infanticide against the offspring of close kin (sister, daughters)—resulting in the major source of pup death; mothers suckle the offspring of female kin (the same pups they tried to kill earlier); and prairie dogs avoid inbreeding with close kin while copulating with cousins (Hoogland, 1995).

Although the black-tailed prairie dog has been extensively studied in the wild, little literature exists regarding captive black-tailed prairie dogs (Smith et al., 1973 appears to be the only captive study). “Visitor effect” studies have focused primarily on primates (i. e. Hosey, 2005; Mitchell et al., 1992) while few studies have observed the black-tailed prairie dogs’ response to visitors. Our previous work (Eltorai and Sussman, 2010) appears to be the only study investigating black-tailed prairie dogs’ response to visitors.

In a study of captive black-tailed prairie dogs, Smith et al. (1973) found that summer months for captive black-tailed prairie dogs are characterized by “considerable disorganization but contained the seed of division into groups” (p. 213). Unlike in the wild, “individuals other than the dominant pair in each zoo coterie probably defend boundaries” (p. 214). These differences are most likely to be due to the relatively small amount of space in the enclosure, the high population density, and the inability to emigrate leading to a high density of individuals. Smith et al. also found that “the social behavior of the zoo prairie dogs is broadly comparable to that of their wild counterparts” (p. 214). Studying black-tailed prairie dogs in captivity offers a unique opportunity to research a popular study species in an uncommonly studied setting.

In this study, we investigated the relationship between human observer density and the prairie dogs’ social behaviors. Moreover, we looked at how observer density affected the behavior of the different-aged prairie dogs. Ultimately, we hope our findings will help to further our understanding of the broader question: How does density of observers affect social behavior?

Methods

Subjects. The Saint Louis Zoo is home to approximately 25 black-tailed prairie dogs. The zoo exhibit consists of mostly adult (determined by large size) prairie dogs and seven 1.5 month-old pups. The adults are likely to range from three to five years of age. The sex of the individuals was not able to be determined. The initial group of individuals was introduced to the exhibit in 1940. The present day zoo population is descendent from the original group.

Data collection. Instantaneous scan samples were taken every 5 minutes to determine the number of individuals that were participating in a given behavioral category at the time. Using this sampling method, we were able to observe the animals’ distribution within the enclosure at various points during the day; the number of individuals physically touching another individual at a given time; the percentage of time the group spends on a particular activity; and the visitor density at a given time. To account for normal changes in behavior due to time of day, samples were taken at various, evenly-distributed points throughout the day (9AM-7PM).

Focal scan samples of an adult and a pup were taken every 5 minutes to see if there were any activity and distributional differences with respect to age. Focal individuals were followed for as long as possible. When the focal individual disappeared into one of the holes, another focal individual, of the same category (adult, pup) was chosen to be followed. The replacement focal individual was chosen by being the most representative of the focal individual category at the time (i. e. resting adult in Region 4). Visitor number was found by averaging the number of visitors measured every five minutes. The number of physically touching prairie dogs is the sum of the every-five minute regional sampling measurements.

To further examine the focal individual categories, we used the all occurrence sampling method to focus on specific social behaviors. Using this sampling method, we observed the duration and frequency of specific behaviors of interest. When an individual went underground, the next focal categorized individual was chosen

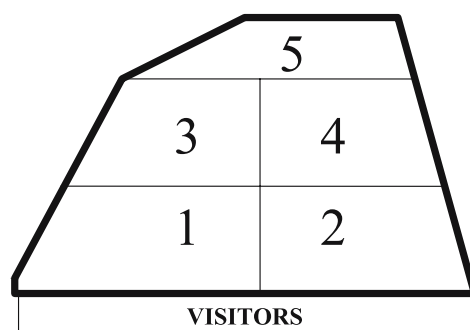


Fig. 1. Schematic map of enclosure showing how the space was divided into Regions 1–5 and where visitors observed the prairie dogs. This image was reproduced from Eltorai and Sussman, 2010.

Рис. 1. Схематическая карта огороженного участка, которая показывает, как пространство было разделено на площадки 1–5, и где посетители наблюдали за луговыми собачками.

by being the most representative of the current behavioral trends. The number of “socially close” individuals to the focal individual was determined by being within a radius of two feet from the focal individual.

A digital watch was utilized to properly record the activities to the minute. All eighty-one hours of observation were collected from June through August, 2009 and detailed by hand using an appropriate data sheet. All observations of the prairie dogs were above-ground and outside the burrows.

Enclosure. A map of the enclosure can be found in figure 1. The enclosure is approximately 75 × 40 feet. There are relatively uniformly distributed hole-openings throughout the enclosure; the most frequently used burrow entrances appear to be located in Regions 1 and 3. The ground is covered in wood chips. Food (generally: kale, Purina rat chow, sweet potatoes, and carrots; periodically: apples, bananas, and bamboo) is dispersed evenly throughout the enclosure each morning. The surrounding walls are textured rock; there is a climbing path on the back wall that allows for the animals to reach elevated vantage points. There are several logs of various shapes and sizes located in Regions 3, 4, and 5 that offer varied climbing, hiding and resting opportunities.

Statistics. Microsoft Excel was used to generate all of the plots and to determine the lines of best fit through linear regression. The regions where there are overlapping visitor numbers were used when comparing adults to pups on the same behaviors. To determine if adults vs. pups differed significantly ($p < 0.05$) from one another on the same behaviors with respect to increased visitor density, two-tailed, independent samples Student's *t*-tests were used for figures 2–5, 7, and 8. Within-subjects ANOVAs were used to see if there are significant differences for figure 6. Two-tailed probability values of the Pearson correlation coefficient *r* were found to determine, with respect to increased visitor density, the strength of the linear relationships. By plotting the behaviors vs. visitor density in a linear fashion, we understand that some of the nuanced changes will be overlooked. We justify plotting the relationships as linear for the following two reasons: 1) it simplifies the data to cleanly illustrate the major trends that are occurring; and 2) reduces the differences in the effects of the various types of observers/zoo-goers (i. e. 12 quiet photographers vs. 12 screaming, crying third graders).

Results

In figure 2, we show the percent of time adults and pups perform various social behaviors with respect to changing visitor density. With increasing visitor density, adults spend more time being alone. They spend less time being socially close to others. And when they are around others it involves increased touching. Pups, on the other hand, with increasing numbers of observers, spend less time being alone and more time being socially close to others without touching.

There is a significant difference between percent of each hour adults vs. pups spend being socially close to other prairie dogs without physically touching any others ($p = 0.0062$; $t(16) = 3.1488$) and the percent of each hour spent touching other prairie dogs ($p < 0.0001$; $t(16) = 5.5936$), but no significant difference for the percent of each hour spent being alone or being socially close to some and touching others.

In figure 3, we show adults' and pups' average duration of performing various social behaviors with respect to increasing visitor density. When adults are socially close to others, they do so for shorter periods of time with increasing number of observers. The bout duration of adults being alone and physically touching increase as the number of

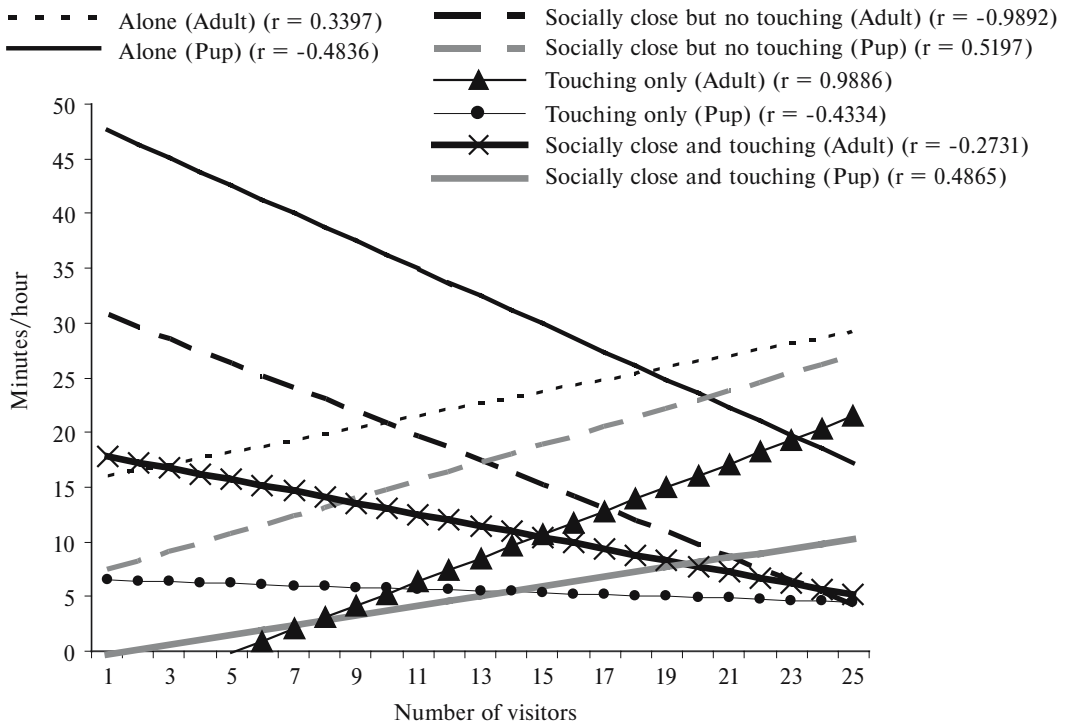


Fig. 2. Minutes per hour adults and pups perform various social behaviors with respect to increasing visitor density. Рис. 2. Время, в течение которого взрослые особи и детеныши демонстрировали разнообразное социальное поведение по отношению к возрастающему количеству посетителей.

visitors increases. The pups' average duration increased for all of the examined types of social behaviors with increased observer number.

There is a significant difference between the durations of adults vs. pups being alone ($p < 0.0001$; $t(88) = 9.3870$), being socially close but not touching ($p < 0.0001$; $t(36) = 16.8067$), but no significant difference for physically touching only nor for being socially close to some and physically touching others at the same time with increasing density of observers.

In figure 4, we show that the average number of other prairie dogs that adults and pups are socially close to mildly decreases as the number of visitors increases.

There is no significant difference between the average number of other prairie dogs adults vs. pups are socially close to with respect to increasing visitor density.

In figure 5, we show that as the number of visitors increases the number of other prairie dogs the focal adult physically touches remains constant, but the number of other prairie dogs the focal pup touches increases mildly. Moreover, when adults touch others, they are in contact with a greater number of individuals than pups.

There is a significant difference between the average number of other individuals adults vs. pups physically touch ($p = 0.0004$; $t(16) = 4.4241$).

In figure 6, we look at the number of physically touching prairie dogs in each region as the average number of visitors increases. With increasing visitor numbers the number of physically touching prairie dogs increases in Regions 1 and 3; and decreases in Regions 2, 4, and 5. As mentioned earlier, the main burrow entrances are located in Regions 1 and 3. Thus, it appears that with heavier observation, touching takes place closer to burrow entrances.

There is a significant difference between number of physically touching prairie dogs in Region 1 vs. 4 ($p = 0.040$; $F(15) = 5.113$), Region 1 vs. 5 ($p = 0.039$, $F(15) = 5.176$),

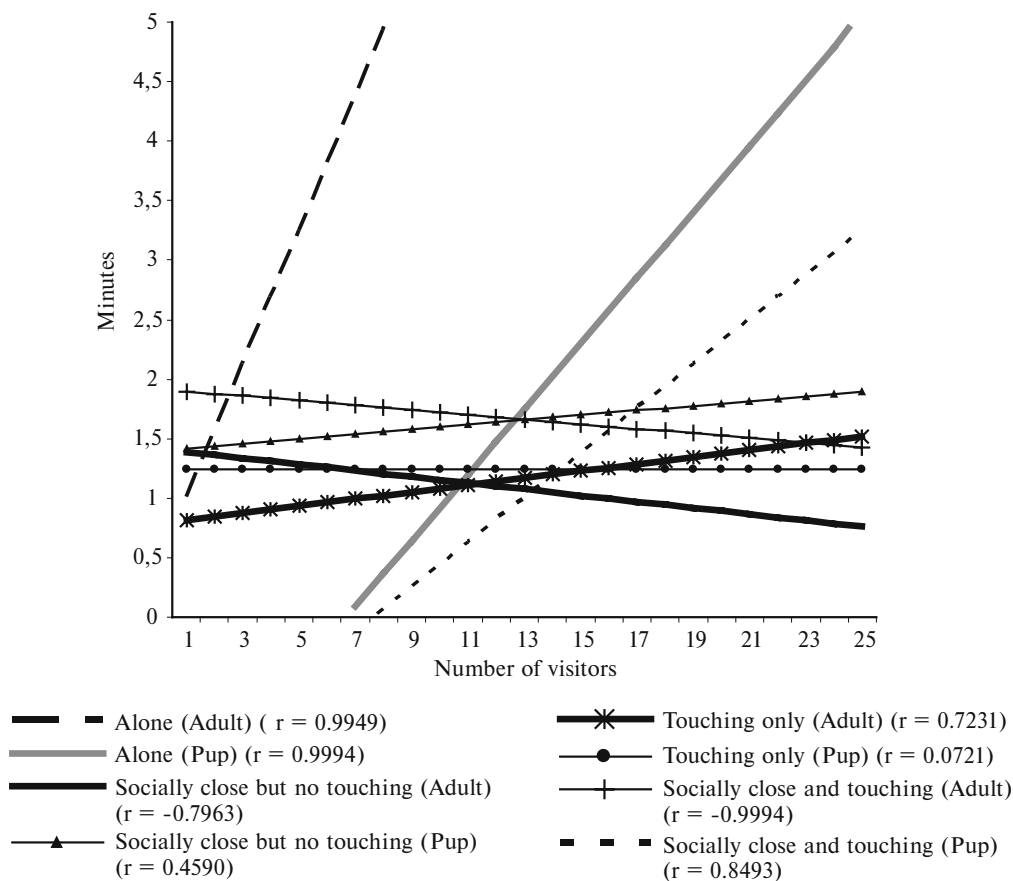


Fig. 3. The average duration of adults and pups performing various degrees of social behaviors with respect to increasing visitor density.

Рис. 3. Средняя продолжительность демонстрации разнообразного социального поведения взрослыми особями и детенышами в зависимости от возрастающей плотности посетителей.

Region 2 vs. 4 ($p = 0.004$; $F(15) = 11.967$), and Region 2 vs. 5 ($p = 0.004$, $F(15) = 11.594$). There are no significant differences between for the number of physically touching prairie dogs in each region for Region 1 vs. Region 2, Region 1 vs. region 3, Region 2 vs. Region 3, Region 3 vs. Region 4, Region 3 vs. Region 5, and Region 4 vs. Region 5. In sum, there is a significantly more physical touching occurring in the front regions vs. the more distant Regions 4 and 5.

Kissing and perianal sniffs are used both as greetings and a method for identification. In the wild, if an individual from another coterie is encountered a bout of agonistic behavior is likely to follow. In figure 7, we show that with increasing visitor density the adults' average number of mouth-to-mouth kisses per hour increases; the average number of perianal sniffs per hour decreases slightly; and the number of adult skirmishes decreases. The data are based on the number of recorded events in which adults were undoubtedly in dispute. The skirmish behavior was classified by any combination of the following: physical attacks, biting, wrestling, and teeth-bearing. On the other hand, with increasing visitor density, pups' average number of kisses and average number of perianal sniffs per hour decreases, and the number of occurrences of pup wrestling very modestly increases. Two important notes should be noted: 1) pup wrestling can either be viewed as agonistic or playful and 2) the total number of pup wrestling occurrences is quite a bit higher than the total number of adult skirmishes (43 vs. 12, respectively).

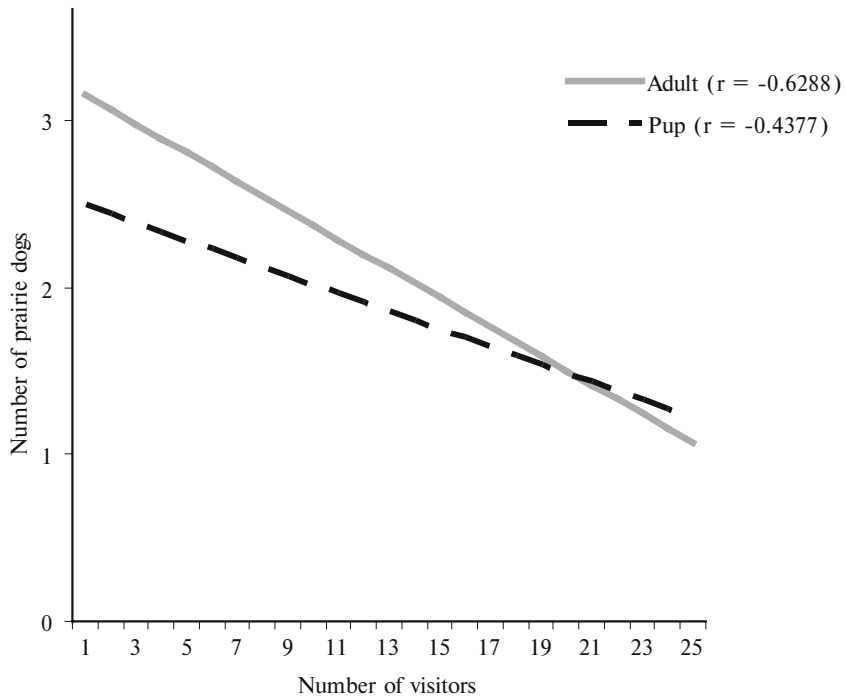


Fig. 4. The average number of other prairie dogs adults and pups are socially close to with respect to increasing visitor density.

Рис. 4. Среднее количество других особей близких к взрослым особям и детенышам луговых собачек в зависимости от возрастающей плотности посетителей.

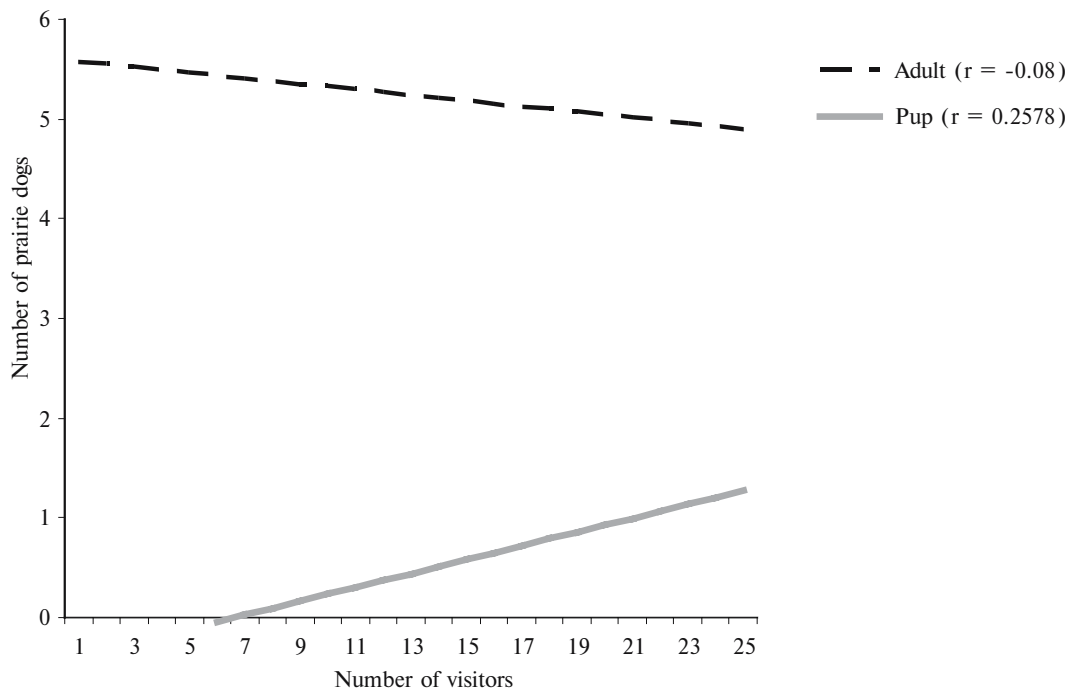


Fig. 5. The number of other individuals the focal adult and pup physically touches with respect to increasing visitor density.

Рис. 5. Количество физически соприкасающихся со взрослыми и детенышами из фокусной группы прочих особей в зависимости от возрастающей плотности посетителей.

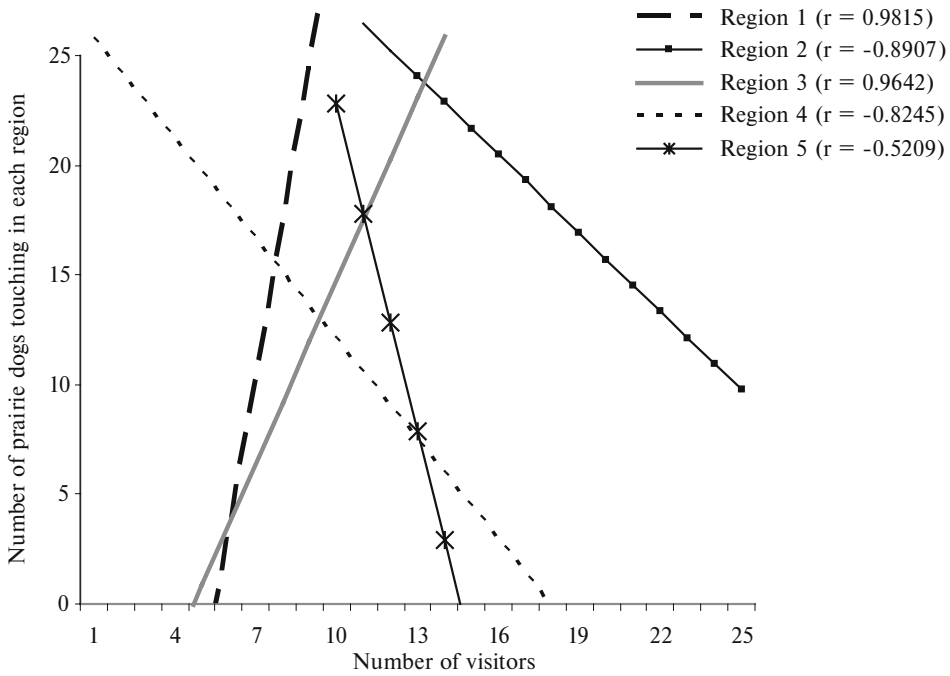


Fig. 6. The number of physically touching prairie dogs in each region with respect to increasing visitor density.
 Рис. 6. Количество физически соприкасающихся логовых собачек на каждом участке в зависимости от увеличивающейся плотности посетителей.

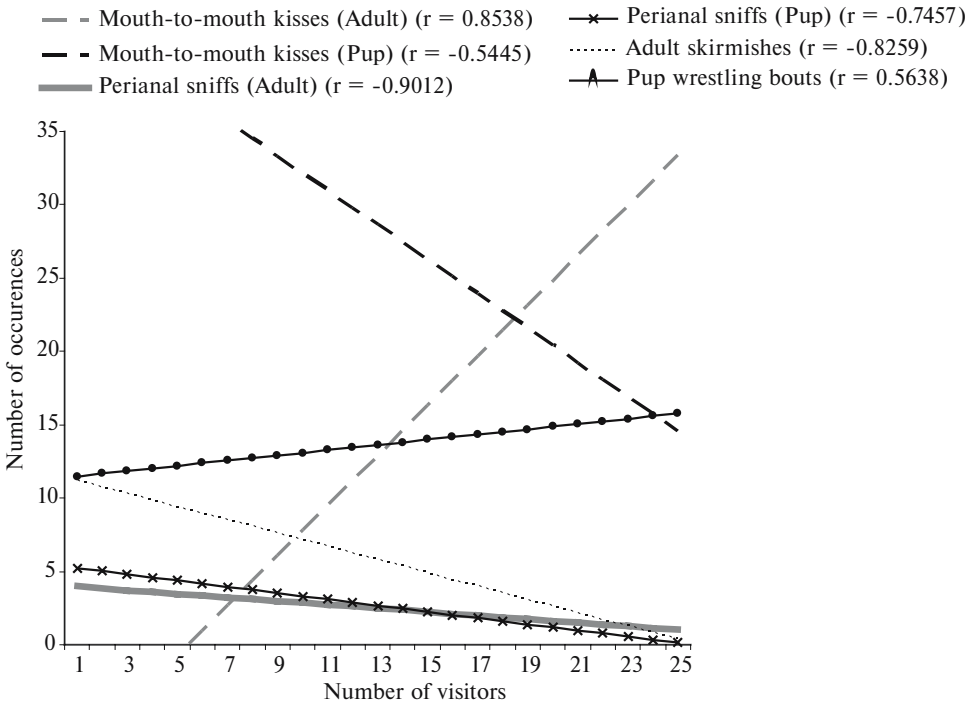


Fig. 7. With respect to increasing visitor density, the adults' and pups' average number of mouth-to-mouth kisses and number of perianal sniffs per hour; the number of adult skirmishes; and the number of pup wrestling bouts.

Рис. 7. Изменение особенностей поведения луговых собачек по отношению к увеличивающейся плотности посетителей в час.

There is a significant difference between number of adult skirmishes vs. number of pup wrestling bouts ($p < 0.0001$; $t(14) = 12.6557$) with adults being “more social.” There are no significant differences between average number of mouth-to-mouth kisses per hour or average number of perianal sniffs per hour adult vs. pup with respect to increasing visitor density.

Discussion

With increasing observation, adult prairie dogs touch a relatively constant absolute greater number of other individuals and more frequently than pups do. However, pups touch an increasingly greater number with more observers. Additionally, we showed that with increasing visitors the number of physically touching prairie dogs increases on the left side of the enclosure (Regions 1 and 3) and decreases on the right side (Regions 2, 4, and 5). We hypothesize that this may have to do with the main burrow entrances being located, in higher concentration, on the left side of the enclosure. Thus, the prairie dogs tend to touch more in the presence of increasing visitor numbers, but they do so close to home. This finding may indicate that touching relates to an altered state of vulnerability. Consequently, the prairie dogs adjust by situating themselves closer to escape routes.

Increases in visitor numbers appears to impact adults and pups differently. Adults spend more of their time being alone while pups spend more of their time being socially close to others. When adults are around other prairie dogs it involves increased touching. Duration of being alone or touching others increases for both adults and pups when visitor numbers increase. With increased observation, adults kiss more and fight less, whereas pups kiss less and fight more.

A comparison of pup to adult social behavior reveals different trends in each age category. We hypothesize that these differences are due to learning. In other words, the pups have not completely learned how to properly behave socially. To draw a broader conclusion from the data, it appears that pups demonstrate social behaviors immediately, but “proper” social behavior takes time and is consequently learned. To help to further investigate this question, data could be collected on intermediately-aged prairie dogs to see if their social behavior demonstrates a transitional phase between pups and adults.

If the act of observation changes behavior, then shouldn't all observational research findings be viewed with increased skepticism?

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