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WHY PRAIRIE DOGS?

When I talk about my research, the most common question in almost every conversation or lecture is, "Why prairie dogs?" My response to this recurrent, incisive question seems like a good way to start the book that summarizes my 45 consecutive years of field research with the four species of prairie dogs that inhabit the western United States.

When I was a first-year graduate student with an interest in ecology and evolution at the University of Michigan in spring 1972, I collaborated with Paul Sherman to initiate research on why animals live in groups. For our study animals, we chose bank swallows, which are small birds that rear offspring in colonies that often contain hundreds of nests.[2171,2683] Our field study was the first to focus on the costs as well as the benefits of coloniality.[1320] In an attempt to better understand the generality of our conclusions for bank swallows, Sherman and I decided for our doctoral research that we wanted to study colonial, diurnal, herbivorous, medium-size or small *mammals* that lived in the United States. Sherman began long-term research with Belding's ground squirrels, and later with northern Idaho ground squirrels.[2516,2519,2520,2523,2526,2528] I initiated research in southwestern Wyoming with Wyoming ground squirrels, which were called Richardson's ground squirrels in 1973 when I first saw them.[512,896,897,1902,3093]

My research with Wyoming ground squirrels flopped immediately. The reason was simple: despite early reports,[511,512,1886,3075] those squirrels do not live in discrete colonies. How could I study costs and benefits of coloniality for an animal that does not live in colonies? Seeing my calamity and desperation, my wife (Judy Gaynier Hoogland) of 4 months instantly responded, "Why not study prairie dogs? *Everybody* knows that prairie dogs live in colonies." I listened, and I visited black-tailed prairie dogs (black-tails) soon thereafter in Fort Collins, Colorado, in late April 1974. I was mesmerized by the nonstop vocalizations, and by the chases, fights, and kisses that I was seeing everywhere. Moreover, the black-tails were living in a distinct colony. Instantly, my doctoral research took on a new life.

My early research with prairie dogs was an extension of Sherman's and my research with bank swallows—namely, what are the costs of prairie dog coloniality, and what are the benefits that override those costs? When compared to black-tails of smaller colonies, I learned that black-tails in large colonies (1) experienced higher competition for burrows, mates, and other resources; (2) harbored more fleas; and (3) were more conspicuous to predators. The only benefit of coloniality seemed to be a lower probability of predation for both adults and juveniles—because black-tails in large colonies detected predators, and then gave alarm calls, more quickly than black-tails in smaller colonies. For a compelling confirmation, I documented the same trends for a second species of prairie dog (white-tailed prairie dog, or white-tail) that lives in smaller, less densely populated colonies than black-tails (chapters 5 and 21).

So now you know how I got *started* on my research with prairie dogs in late April 1974. But why did I *continue* through 07 July 2018? The short answer is Prairie Dog Axiom #1: The more I learned about prairie dogs, the less I actually knew.

Following are brief summaries of the main issues in the behavioral ecology of prairie dogs that I explored after my early research with coloniality.

Alarm Calls Warned Both Close and More Distant Kin (Chapter 8)

An alarm call warns conspecifics (members of the same species) of danger, and alarm calling is a major reason why the probability of predation is lower in large versus smaller colonies of black-tails and white-tails. But why should an individual draw a predator's attention to itself by calling in order to save other prairie dogs with whom it competes? This question became my new focus as I was ending my research on the costs and benefits of prairie dog coloniality and starting to focus on territorial family groups of prairie dogs called *coteries* or *clans* (chapters 3, 9, and 10).

Seminal research with Belding's ground squirrels by my good friend and first collaborator (Paul Sherman) indicated that the most likely payoff for alarm calling is that the calls warn genetic relatives of danger (i.e., are *nepotistic*), and beneficiaries are most commonly juvenile offspring.[689,795,2516] The same was true for male and female alarm callers of all four species of prairie dogs that I studied. The alarm calls warned not only offspring, however, but also other close kin such as mothers, littermate siblings, and nonlittermate siblings as well. Further and more important, calls also warned more distant kin such as aunts, nieces, nephews, and first cousins. Moreover, beyond showing just nepotism, alarm calls of prairie dog females showed *discriminative nepotism*[31,33,34,2962,2969]: Females with close kin (offspring or mother) in the home territory were more likely to call than females with only more distant kin (e.g., nonlittermate siblings, nieces and nephews, full- and half-first cousins) in the home territory.

Some Prairie Dogs Were More Susceptible Than Others to Predation (Chapter 6)

The prairie dog defense against predators was consistently excellent, and captures at our colony-sites were rare (chapters 5 and 6). My research assistants and I had a special situation in 2005, however, when predations by a single red fox and one or more northern goshawks were unusually common at our colony-site of Utah prairie dogs (utahs). As for many other prey species, we were expecting that the most common adult victims of predation would be individuals with one or more of the following traits: old, young, sickly, or weak.[238,1389,1693,2313,2393,2298,2433] But the utahs surprised us, in three ways: (1) The largest, most aggressive, and most successful utah males were more susceptible than other males to predation during the 3 weeks of the mating season—because the former males were so committed to finding, inseminating, and then guarding sexually receptive females, with little concern for predators. (2) Further, for the third and fourth weeks after they copulated, utah females in late pregnancy were especially vulnerable—probably because they were overweight with as many as seven large fetuses, and therefore unable to run as fast as other females. (3) Last, adult immigrants were also easy targets soon after the arrival into a new colony-site—probably because they were less familiar than long-term residents with the best routes for escape in times of danger. For (1) through (3), my students and I appreciated the opportunity to demonstrate that certain types of adult prairie dogs were especially, and unexpectedly, vulnerable to predation during small windows of time.

Most Females Were Polyandrous (Chapter 19)

Colonies offer outstanding opportunities to maximize reproductive success. Like every other behavioral ecologist, I soon became obsessed with trying to figure out the mating system of the species I was studying. Black-tails offered my first challenge. Previous anecdotal research indicated that black-tails in South Dakota usually copulate in late February and early March.[1492,2178] Even though four research assistants and I watched every day for the entire time that black-tails were aboveground at my colony-site in South Dakota from mid-February through early March 1978, however, we did not see

a single aboveground copulation. Then something new and perplexing happened on 11 March 1978. Late in the day, female-62 was constantly being chased by, and getting attacked by, the single sexually mature male (male-17) in her home territory. Estrus (sexual receptivity), perhaps? The pair remained aboveground for more than 30 minutes after all other members of the colony-site had submerged for the night. But female-62 and male-17 never copulated aboveground.

Confused, I hyper-focused my watching of female-62 on the following morning of 12 March 1978. Her behavior was radically different from her actions of the previous day. She was now the aggressor in all interactions with male-17, and she also became aggressive with the other adult female in her home territory. And then female-62 began to take many mouthfuls of dry grass underground. Female-62 was acting like a female that had already copulated! Frustrated and bewildered, I was forced to concede that black-tails must copulate underground. And then discouragement set in. How could my assistants and I study the black-tail mating system if females copulate underground? Desperate, I could only think to fixate on females that acted like female-62 on 11 March 1978—and hope for the best. I got lucky. Over the next 2 weeks and the next several years, I identified eight diagnostic behaviors that enabled my teams and me to identify when a black-tail male and female were copulating underground. And we learned that, even though the black-tail mating system for the entire colony-site usually spanned about 4 weeks, each female—like female-62 on 11 March 1978—was in estrus and sexually receptive for only several hours on a single day of each year.

Once I figured out how to document underground copulations, I quickly realized a black-tail female often copulated with more than one male during the single day of her sexual receptivity. When I read about mating systems of other species, I learned that females of almost every sexual species that had been carefully studied—from hundreds of plant species through humans and other primates—commonly solicit sperm from two or more males.[275,1107,1454,1926,2551,2565,2659,2818,3173,3174] But why? A female almost always can obtain sufficient sperm to fertilize all her eggs from a single copulation, and additional copulations exacerbate the risks associated with copulation, such as diseases, parasites, and predation. This puzzle annoyed me for years, more so over time as I learned that polyandry (i.e., copulating with two or more males) was also common among Gunnison's prairie dogs (gunnisons), utahs, and white-tails. When I had accumulated information from more than 2700 copulations of 1751 estrous (sexually receptive) females over all four species, I seized the opportunity to compare annual reproductive success (ARS) versus a female's number of sexual partners. For gunnisons, utahs, and white-tails—but not black-tails—polyandrous females experienced at least one of three hefty benefits when compared to monandrous females: they were more likely to conceive, they weaned larger litters, or their offspring had higher survivorship in the first year after weaning. For three species of prairie dogs, at least, polyandry is no longer a mystery—with the implication that these same benefits might apply to the thousands of other less-studied species for which females frequently mate with more than one male.

Documenting the prevalence and significance of polyandry among prairie dogs was exciting and far-reaching—second only to the simultaneous horror and thrill of recording infanticides, as described later.

Prairie Dogs Dispersed to Avoid Incest (Chapter 22)

Incest, or *extreme inbreeding* (i.e., copulation with close kin, for which the coefficient of genetic relatedness, $r, \geq 0.2500$), commonly leads to offspring that do not live as long, or do not rear as many offspring, as offspring from copulations with nonkin (outbreeding).[901,2534,2657,3008] When colonies are isolated and individuals tend to mature and rear offspring near the natal site (i.e., are *philopatric*), the avoidance of inbreeding might be challenging, as for species such as American pikas, banded mongooses, hoary marmots, naked mole rats, and yellow-bellied marmots.[103,104,179,2071,2530,2592,3189]

Such avoidance is a potential problem for the four species of prairie dogs that I studied, but I discovered four different mechanisms that deter copulations with close kin such as parents, offspring, and littermate siblings: (1) Young males usually dispersed away from the mother and littermate sisters of the natal territory before reaching sexual maturity, but females usually remained in the natal territory for life. (2) Older males usually dispersed away from their daughters of the breeding territory before their stay-at-home daughters reached sexual maturity. When dispersal of young and old males did not separate close kin of the opposite sex, then (3) a female sometimes did not come into estrus, and thereby skipped an entire year of reproduction, or (4) she came into estrus but refused to copulate with a father or littermate brother of the natal territory. These four mechanisms helped to prevent copulations with close kin, but black-tails frequently copulated with more distant kin such as half-nieces and nephews, and full- and half-first and second cousins (chapter 22). Incest was thus rare for black-tails, but *moderate inbreeding* was common.

Prairie Dogs Also Dispersed for a Reason Unrelated to Incest (Chapter 23)

As just described, a female prairie dog of all four species usually remained in the home natal territory for life, but a male usually remained in the home natal territory only until he attained sexual maturity, and then he dispersed. But an unexpected surprise regarding dispersal occurred when—upon persistent persuasion from Judy Gaynier Hoogland and after almost four decades of completed research[3143]—I tried to figure out why usually philopatric females sometimes dispersed. Too rare, I thought—so why bother? To my astonishment, however, my investigation revealed that a female of all four species was more likely to disperse when all her close kin (mother, daughters, sons, and littermate siblings) within the home territory had died or dispersed—12.5 times more likely for black-tails, and 3.2 times more likely for gunnisons. This blockbuster pattern defies the long-accepted wisdom of two of ecology's superstars (William Hamilton and Robert May[1150]) that relatives tend to disperse to avoid competing with close relatives of the home territory. Similar dispersal in response to the *absence* of nearby close kin has been documented in only one other vertebrate species[113] even though dispersal is one of the most commonly and thoroughly studied issues in all of ecology.[334,1097,1527,1596,1606,2663,2916] Serendipity at its finest, thanks to Judy Hoogland.

Infanticide Was Common (Chapter 21)

Infanticide—the killing of conspecific juveniles—occurs in myriad colonial species, but usually occurs at a low frequency and does not involve kin.[1207,1720,2120,2520] For black-tails, however, both adult males and lactating females commonly killed and cannibalized a female's unweaned offspring, and this infanticide was the main cause of juvenile mortality in most years. Lactating black-tail females were especially likely to kill, and murdered most or all of the juveniles for a whopping 65 of 294 litters (22%) under surveillance by my students and me over several years. These 65 mass killings involved 38 different females, and, incredibly, the victims were the offspring of close kin in the killer's home territory in 62 of the 65 killings (95%). The most common victims were the offspring of the killer's mother (the killer's full- or half-siblings), the offspring of the killer's daughter (the killer's grandoffspring), or the offspring of the killer's littermate sister (the killer's nieces and nephews). Some black-tail lactating females were more likely to kill than others. One serial killer, for example, slew all juveniles of seven litters over 3 years, and some juveniles of one other litter. Another serial killer dispatched all juveniles of four litters over 3 years, and some juveniles of two other litters. Black-tail infanticides occurred underground and were so subtle that my teams and I watched marked black-tails for 7 consecutive years before we suspected they were occurring. Once we learned the diagnostic aboveground behaviors associated with underground infanticides, however, we documented the elimination

via infanticide of a minimum of four entire litters per year over the next 8 years.

Documenting black-tail kin-directed infanticides was the greatest challenge of my 4.5 decades of research. But documenting black-tail infanticides was also the most exhilarating task, because the stakes were so high when a female killed the offspring of her mother, her daughter, or her littermate sister. Nobody ever would have predicted that back in the 1970s.

In addition to the many infanticides within my black-tail colony-sites, my research assistants and I looked for infanticides at colony-sites of the other three species that I studied. Two of our most compelling results are that infanticide was absent for the species for which colony densities (and competition, presumably) were lowest (white-tails), and varied directly with colony density for black-tails, gunnisons, and utahs (chapter 21). These findings offer persuasive support for the argument in every previous study of infanticide that killing of conspecific juveniles ultimately results from competition for resources such as mates or territories.[235,828,1207,1719,2183,2520,2842]

Prairie Dog Females Commonly Nursed the Offspring of Other Females (Chapter 18)

Because the production of milk is costly,[557,1394] and because natural selection typically favors mothers that are especially concerned with their own offspring,[542,2962,3017] communal nursing (i.e., the nursing of another female's offspring), in theory, should be rare. When juvenile black-tails were about 6 weeks old and appeared aboveground from their natal nursery-burrows for the first time, however, mothers commonly suckled the offspring of close kin such as sisters, daughters, and nieces living in the home territory—the *same offspring* they had been trying to kill for the previous several weeks when infanticides were so common! Life for prairie dogs is all about balancing competition versus cooperation, but this sudden black-tail transition from the *killing* of the offspring of close kin to the *communal nursing* of the offspring of close kin was nonetheless extraordinary.

In addition to the many cases of communal nursing at my black-tail colony-site, communal nursing of foster offspring (i.e., offspring of a different mother) also occurred at my gunnison and utah colony-sites.

Demography, Population Dynamics, and Senescence (Chapters 11–14 and 24)

Demography is the study of factors that affect the survivorship and reproduction of individuals, and the dynamics of their populations.[1553,1916,2658] Demography was never a focus of my research with prairie dogs. However, my investigations of issues such as alarm calling, annual and lifetime reproductive success (ARS and LRS), and levels of inbreeding required the eartagging and marking of *every* resident at the colony-site each year via Catch 'em, Mark 'em, Watch 'em (see chapter 4). I was no dummy, and recognized that this comprehensive marking program provided fortuitous, outstanding opportunities to investigate several meaningful demographic topics that were relevant to behavioral ecology—such as body mass, immigration, life tables, senescence, sex ratios, and sexual dimorphism.

Prairie Dogs Sometimes Killed Ground Squirrels (Chapter 25)

Individuals of different species frequently compete with each other. African lions and spotted hyenas try to capture individuals of the same prey species,[462,2926] for example, as do Iberian lynxes and red foxes.[912,913] To reduce interspecific competition, natural selection sometimes favors divergence in behavior, ecology, morphology, or physiology.[397,1730,2457,2694] But natural selection has favored a different, unusual strategy for one species of prairie dog: white-tail adults sometimes kill, but do not consume, Wyoming ground squirrels (hereafter, simply "ground squirrels") encountered in a white-tail's home territory. Similar to white-tails in many ways but smaller, ground squirrels are gregarious (but not truly "colonial," as noted earlier), diurnal, burrowing rodents that

inhabit western North America. Further, ground squirrels eat *exactly the same plants* that white-tails also consume, at almost the same frequencies.[514,1315,1316] In addition, ground squirrel females frequently have their nursery-burrows within white-tail colony-sites.

My students and I discovered that interspecific killing (IK) of ground squirrels by white-tails was common, involving 47 different killers of both sexes. In 3 of 6 years, the number of IKs was higher than the number of ground squirrels killed by the *combined efforts* of *fifteen mammalian and avian predators* such as American badgers, coyotes, and Swainson's hawks. Incredible! In a typical IK, the white-tail chased and then captured the trespassing ground squirrel; repeatedly bit it in the neck or thorax over a period of 1–3 minutes; shook it several times until death; and then walked away with no consumption. "Catch it, bite it, shake it, kill it, and leave it."

Most killers (N = 28) slew a single ground squirrel, but 19 serial killers dispatched two or more ground squirrels. One white-tail female killed six ground squirrels over 5 years; another killed nine over 4 years; and a third killed seven ground squirrel juveniles from the same litter in a single day. My large sample size (N = 163 IKs, over 6 years) allowed Charles Brown and me to demonstrate that white-tail females that killed ground squirrels had significantly higher ARS and LRS than nonkillers (chapter 25). Documenting the existence and consequences of interspecific killing of ground squirrels by white-tails was one more electrifying finding of my research.

Conservation of Prairie Dogs (Chapter 27)

Prairie dogs of all four species have a profound impact on their grassland ecosystems, and are therefore *keystone species*.[650,668–670,673,674,1202,1544,1545,1803,1913,3167,3170] Their burrows change the landscape and soil chemistry, affect the cycling of water and nutrients, alter floral species composition, and provide shelter and nesting habitat for many other organisms such as burrowing owls, tiger salamanders, and hundreds of species of insects and spiders. Further, prairie dogs serve as prey for numerous predators such as American badgers, bald and golden eagles, black-footed ferrets, bobcats, coyotes, long-tailed weasels, northern goshawks, prairie falcons, and red foxes. If prairie dogs disappear, grassland ecosystems as we know them will vanish as well.

Despite their importance as keystone species, all four species of prairie dogs that I studied are now rare because of 200 years of plague, poisoning, recreational shooting, and destruction of habitat. The focus of my long-term research was never conservation, but many of my results can help us to save prairie dogs for future generations. One of my key findings, for example, has helped to dispel a century-old myth perpetuated by farmers and ranchers—namely, that prairie dogs are fast-breeding like mice and rats, and that they will take over grasslands unless they are exterminated. By contrast, I have documented that prairie dogs first captured as juveniles do not live long (usually only 1 or 2 years), that many females do not reproduce every year, and that successful females can only wean a small number of offspring (usually three or four), per year. If we want to save prairie dogs and their ecosystems, knowledge is power. My research has provided copious, crucial information on every aspect of the biology of prairie dogs. The battle to save prairie dogs is one we can win (chapter 27).

Definitions for Common Terms in This Book

Natural selection—or differential reproduction, the process by with some parents rear more reproductive offspring than other parents—leads directly to both evolution and adaptation.[978,1232,3007,3017] *Evolution* is a change in the frequency of *alleles*—i.e., variations of the same gene—over time.[1000,1829] An *adaptation* is some sort of anatomical, physiological, or behavioral trait shaped by natural selection to improve survivorship or reproduction.[680,2015; see also 3007,3010] The most common way to transmit alleles to the next generation is via offspring, and natural selection usually favors those individuals that produced the largest number of reproductive offspring. An individual's nondescendant genetic relatives also share many alleles identical by

descent, and close kin share more alleles than more distant kin. Consequently, natural selection also might favor individuals that help kin such as siblings, parents, and nieces and nephews to survive and reproduce.[696,943,1144,1232,1827,2969] Reproductive success via offspring is called *direct fitness*, and reproductive success via nondescendant kin is called *indirect fitness* via *indirect selection*.[390,764,1015,1464,1528,2065,3126] *Inclusive fitness*[1144,1484,1528,2962,3192] measures an individual's reproductive success via both offspring and nondescendant kin, and thus is a sum of both direct and indirect fitness. *Kin selection* is natural selection for characteristics that favor the survival of close relatives such as offspring, siblings, and nieces and nephews.[1827; see also 696,1144,2962]

Altruism involves a cost with no overriding benefit to self to confer a benefit to another individual (usually a conspecific); *reciprocal altruism* (*reciprocity*) is an exchange of actions that yields an overall benefit to both interacting individuals—i.e., cooperation involving reciprocating partners.[2561,2797,2800,2998] *Spite* involves a cost to both interacting individuals—i.e., an individual incurs personal harm in order to harm another individual, with no overriding benefits to either individual.[1016,1147,2961] I looked, but detected no clear evidence of altruism, reciprocal altruism, or spite for any of the four species of prairie dogs that I studied.

A *colony* is a group of conspecifics living together, often at a single colony-site but other times with regular movement. A few other genus-specific or species-specific names for colony include band, bevy, community, flock, gaggle, herd, mob, pack, swarm, and troop. Individuals of a *different* species sometimes predictably live at colony-sites of a species—e.g., ground squirrels at colony-sites of white-tails (chapter 25). Some biologists have used the name *town* for an aggregation of prairie dogs,[593,594,930,1562,2087,2446] and others have used the term *village*.[600,603,1139,1268,1658,2445; cited in 2758,2884] Prairie dog colony-sites often have subcolony-sites called *wards* (chapters 3 and 11). A group of distinct colony-sites in the same geographic area is called a prairie dog *complex*.[134,647,1521,1785] A forb is a nonwoody plant that is not a grass.

Mammalian females usually copulate only during a brief period of sexual receptivity called *estrus*, *heat*, or *season*.[63,216,364,999,1346,2368,2611] *Ovulation* is the release of eggs from the ovary, so that *fertilization* of eggs by sperm can occur.[216,364,421,432,2368] *Copulation* is the coupling of male and female genitalia, and *insemination* is the deposition of sperm into a female's reproductive tract.[835] Copulation does not always involve insemination, and insemination does not always lead to fertilization of a female's ova.[721,835] I scored a successful copulation for prairie dogs when a sexually mature male spent ≥5 minutes underground with an estrous female, or when a sexually mature male copulated for ≥2 minutes aboveground with an estrous female (chapter 15). *Cuckoldry* occurred when a juvenile born within a resident prairie dog male's home territory was sired by a male from a different territory.

Monandry occurred when a female copulated with a single male only, and *polyandry* occurred when a female copulated with two or more males (chapter 19). *Monogyny* occurred when a male copulated with a single female only, and *polygyny* occurred when a male copulated with two or more females (chapter 20).

A *juvenile* prairie dog first emerged from the natal nursery-burrow ≤6 months before the time of observations. An *unweaned juvenile* had not yet appeared aboveground, and *emergent juveniles* had appeared aboveground after first emerging from the natal nursery-burrow. Juvenile prairie dogs sometimes continued to nurse from their own and other mothers after first emergence from the natal nursery-burrow (chapters 17 and 18). With this understanding, I often refer in this book to *weaning* as the date of first emergence from the natal nursery-burrow, and to offspring at first emergence as *weanlings* (chapters 11–14).

An *adult* prairie dog (including 1-year-olds, or *yearlings*) first emerged from the natal nursery-burrow ≥9 months ago. *Yearlings* were young adults that emerged from the natal nursery-burrow ≥9 months ago, but ≤20 months ago; with only a few exceptions that are clearly noted, the term "adult" includes both yearlings and older individuals. A *resident male* was a sexually mature male within a territory (chapters 4, 9, and 10).

Immigration occurred when an individual (an immigrant) entered a local population from far

away, and was unequivocal evidence of successful long-distance dispersal.[738,852]

Additional definitions for terms related to dispersal and level of inbreeding are listed in table 22.1.

What's New in This Book?

I have published 60+ articles in peer-reviewed journals, and two books, about different aspects of my long-term research with prairie dogs. Readers might therefore wonder, "What's new in this book?" Good question, which I will try to answer here:

- Many of the chapters in this book focus on topics for which I have published no information for either gunnisons, or utahs, or white-tails. Some of those topics include ARS and LRS for males and females, communal nursing, demography, dispersal in groups, infanticide, mating calls, polygyny, senescence, and sex ratios.
- I published much of my information for black-tails in my first two books,[1294,1304] but I have reanalyzed many of those data for this book for comparisons with the other three species. These reanalyses have yielded new results and several new conclusions. The merging of black-tail information with information from the other three species into a single book seemed like a valuable objective—better and more useful than a separate book for each species.
- For all four species of prairie dogs that inhabit the western United States, my book includes short stories about confessions, disappointments, dreams, failures, mistakes, successes, and surprises. It includes compelling results that support some of my hypotheses, but it also includes findings that offer only tepid support—or no support whatsoever—for other hypotheses. My book also offers recommendations and encouragement for future behavioral ecologists who want to increase our knowledge and understanding of the amusing, captivating, provocative, and puzzling keystone species that I was able to study for 45 consecutive years.

Order of Chapters, Interspecific Differences, and Scientific Names

The chapters in this book are all related. A clear understanding of demography and population dynamics of prairie dogs (chapter 11), for example, requires information about infanticide (chapter 21), predation (chapters 5 and 6), and reproductive senescence (chapter 12). Similarly, a thorough appreciation of polyandry, polygyny, and reproductive success (chapters 13, 19, and 20) depends on my discoveries about estrus, copulations, and mating calls (chapters 15 and 16). Logical, satisfactory ordering of chapters was therefore challenging. In an attempt to mitigate this problem, I have included a comprehensive index.

For issues such as alarm calling and mating calls, the four species of prairie dogs were remarkably similar. For other topics such as polyandry and infanticide, the species were radically different. My first draft included a discussion of interspecific similarities and differences for each chapter. In response to an astute referee, this book now condenses comparisons of interspecific similarities and differences into a single chapter (chapter 26).

Common and scientific names for all organisms mentioned in this book are listed in the appendix, which includes page numbers for information about each species.

Summary

In the chapters that follow, I describe in more detail the discoveries summarized in this chapter, and other sweeping findings as well. As in several other studies,[104,246,384,452,534,535,1212,1455,1485,1487,1617,2155,2320,2345,2486,2643,3172,3225] my findings nicely show the copious rewards of careful long-term research. Prairie dogs are charming and cute—but they also can be nasty serial killers.

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