SUMMARY OF RESEARCH AND TEACHING FOR JOHN HOOGLAND

Why do animals live in groups? This deceptively simple question and its myriad spin-offs have maintained my interest in behavioral ecology and population biology since I was Richard Alexander's graduate student at The University of Michigan. My first effort, with Paul Sherman (then a first-year graduate student like me, now at Cornell University), was to investigate coloniality of bank swallows. We learned that ***increased competition and greater ectoparasitism are inevitable disadvantages of group-living***, and that enhanced safety from predators is probably the only advantage (*Ecological Monographs* 46:33-58). My doctoral research revealed the same costs and benefits of coloniality for prairie dogs (*Behaviour* 69:1-35; *Animal Behaviour* 27:394-407; *Ecology* 62:252-272; *Ecology* 63:1968-1969). More recently, students and I have begun to investigate the tradeoffs between increased ability of colonies to detect predators versus the increased susceptibility of colonies to pernicious diseases such as plague.

Bank Swallow or Sand Martin

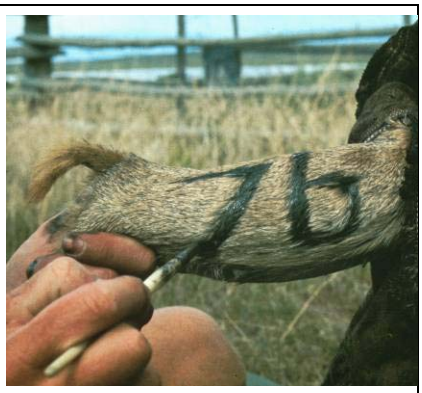
Paul Sherman and I studied the costs and benefits of coloniality of bank swallows.

Does male-biased sexual dimorphism ultimately result from intra- and inter-sexual competition for females? If so, then ***sexual dimorphism should vary directly with harem size***. Richard Alexander's and my review of the literature shows the predicted positive correlation for primates, and our collaborators found similar correlations for pinnipeds and ungulates (Pages 402-435 in *Evolutionary Biology and Human Social Behavior*). Sexual dimorphism does not, however, vary directly with harem size for different species of prairie dogs (*Journal of Mammalogy* 84:1254-1266).

Richard Alexander and I examined sexual dimorphism versus harem size for 22 species of primates. I also have investigated sexual dimorphism among 5 species of prairie dogs.

Why should an individual draw a predator's attention to itself by giving an alarm call? Calling by parents to nearby offspring is common, and such expressions of parental care are easily explicable in terms of natural selection. Prairie dogs also call to warn sons and daughters, but my research shows that they have gone one important step further: ***Nonparental individuals call to warn more distant kin such as nieces, nephews, and first and second cousins*** (*Animal Behaviour* 31:472-479; see also Chapter 37 of *Rodent Societies*).

Infanticide is one of the most intriguing, controversial, and misunderstood issues in behavioral ecology and population biology. How prevalent is infanticide, is it adaptive, and who are the victims? My longterm research has generated surprising answers. ***Infanticide accounts for the partial or total demise of 39% of prairie dog litters***, for example, and thus is the major cause of juvenile mortality. ***The most common killers are lactating females and, incredibly, the most common victims are the offspring of close kin***. Mothers probably kill



To mark prairie dogs, students and I use Nyanzol fur dye. Marked individuals, which also have eartags for permanent identification, are visible from 150 meters away.

to obtain sustenance via cannibalism during the stressful period of lactation, but convincing evidence for the adaptive significance of infanticide remains elusive (*Science* 230:1037-1040).

Male prairie dogs also kill juveniles. In the most bizarre cases, ***males kill and cannibalize the offspring of females with whom they mated*** (i.e., their own potential offspring). Females usually mate with more than one male, however, and multiple paternity within litters (same mother, different fathers) is common (*Journal of Mammalogy* 82:917-927; *Journal of Mammalogy* 84:1244-1253). Can infanticidal males discriminate between their own and other males' unweaned offspring? Via DNA-fingerprints, students and I are investigating this intriguing possibility.

How important is kinship in the evaluation of possible mates? Should individuals avoid both extreme and moderate inbreeding by maximizing outbreeding via long-distance dispersal? These questions have been the focus of many articles and several books, but nonetheless continue to vex psychologists, anthropologists, behavioral ecologists, and population biologists. Once again my longterm research, involving pedigrees as deep as six generations, is providing important insights. ***Prairie dogs have four separate mechanisms for avoiding extreme inbreeding with parents, offspring, and siblings. But individuals regularly engage in moderate inbreeding*** with more distant kin such as first and second cousins (*Science* 215:1639-1641; *Evolution* 37:273-281; *Behavioral Ecology and Sociobiology* 11:155-163). Despite large sample sizes, ***prairie dogs show no evidence for inbreeding depression*** (*American Naturalist* 139:591-602). Perhaps moderate inbreeding is a compromise between the benefits of extreme outbreeding versus the increased mortality associated with long-distance dispersal.

Can animals recognize genetic relatives with whom they never have associated previously, or are learning and familiarity necessary for the kin recognition that we often see in natural populations? This question befuddles behavioral ecologists and psychologists. For prairie dogs, ***learning to identify relatives during a critical period of four weeks after weaning is the key to kin recognition among older individuals***. Though it would be theoretically beneficial, individuals evidently cannot use mechanisms such as self-referential matching of phenotypes to recognize kin with whom they never have previously associated (*Animal Behaviour* 34:263-270).

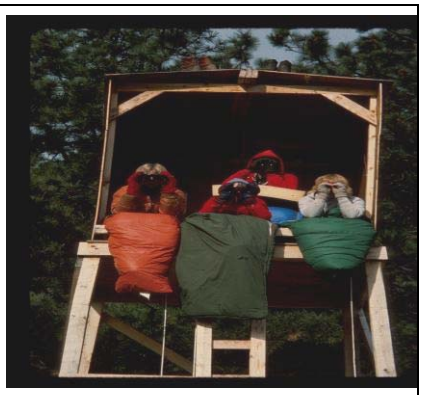
Experiments with radionuclides show that, in addition to nursing their own offspring, prairie dog mothers commonly nurse the offspring of other mothers. ***Specifically, 68% of juveniles receive milk from foster mothers via communal nursing*** (*Behavioral*

To elicit alarm calls from prairie dogs, we pull a stuffed specimen of an American badger across the study colony. Alarm calls warn not only offspring, but also more distant kin such as nieces, nephews, and first and second cousins.

To combat infestation by fleas, lice, and ticks, prairie dogs commonly groom one another. Ticks are rare, but we often find >100 fleas and >100 lice per individual during marking and eartagging. Fleas transmit plague.

Prairie dogs frequently use mounds at burrow entrances to scan for predators such as coyotes, American badgers, bobcats, golden eagles, and prairie falcons. Mounds also impede flooding of burrows and, via Bernoulli's Principle, promote underground ventilation.

Ecology and Sociobiology 24:91-95; see also *Behavioral Ecology and Sociobiology* 63:1621-1634). In proximate terms, communal nursing might result because prairie dog mothers seem unable to discriminate between their own and others' unweaned offspring. In ultimate terms, two factors probably have been important: (a) kin selection, because beneficiaries are usually juvenile nieces, nephews, and grandoffspring, and (b) increased safety of a foster mother's offspring, because juveniles in multi-litter groupings that form during communal nursing are better protected against predation.



From 4-meter high towers, students and I track matings, predations, infanticides, alarm calling, and communal nursing. Sleeping bags and handwarmers help us to survive when the prairie dogs are breeding in March. Many students use observations for a senior thesis.

Male reproductive success in most species increases directly with the number of inseminations. Natural selection for multiple mating by males is thus widespread and easily explicable. A female, however, usually can obtain enough sperm to fertilize her entire collection of eggs from a single insemination, and mating involves certain automatic costs such as increased exposure to diseases and parasites. Why, then, do females of so many species routinely mate with more than one male? My research documents two clear benefits for prairie dogs. ***First, multiply-mating females are more likely to conceive. Second, females directly increase litter size, and hence reproductive success, by mating with several males*** (*Animal Behaviour* 55:351-359; see also Chapter 37 of *Rodent Societies*).

Female-62 and male-13 on top of 1.5 meters of snow during the mating season. Because individuals are engrossed with sex and cannot run quickly in the snow, predation is high during the breeding season. Some females mate with only 1 male, but other females mate with as many as 5 males in rapid succession.

Of numerous demographic factors that enhance reproductive success, two are striking for prairie dogs: body mass and longevity. Large, heavy individuals of both sexes are more likely than smaller individuals (a) to survive until the next mating season, (b) to mate if they survive, and (c) to produce numerous offspring if they mate. With some males surviving for 6 years and some females persisting for 8 years***, longevity is the ultimate vehicle for improving lifetime reproductive success***.

Fight during mating season between male-9 and male-13. Winners secure mates. Losers incur serious injuries, and sometimes die.

Fisher's (1958) theory predicts that parents as a collective unit should invest approximately equally in male and female offspring. Natural selection nonetheless might favor individual parents that specialize in the production of only one sex. Factors that might bias the sex ratio within litters include sex ratio among adults, maternal age and condition, paternal reproductive success, local mate competition, and local resource enhancement. ***Despite large sample sizes, prairie dogs show little evidence for adaptive variation of the sex ratio at weaning*** (Chapter 15 in *The Black-tailed Prairie Dog*). These data do not negate the theories about juvenile sex ratios, but perhaps call into question the generality and feasibility of these theories for animals living under natural conditions.

The Black-tailed Prairie Dog (University of Chicago Press) summarizes longterm research with marked animals under natural

conditions. My book has been the focus of numerous enthusiastic reviews (e.g., *Science*, *Animal Behaviour*, *Journal of Animal Ecology*, *Journal of Wildlife Management*, *Mammalia*, *Zoo Biology*, and *Ethology, Ecology, and Evolution*). Island Press has recently published my second book, ***Conservation of the Black-tailed Prairie Dog: Saving North America's Western Grasslands***. In this treatise written for wildlife managers, politicians, and curious naturalists, other authors and I examine the precipitous decline of prairie dogs over the last 150 years, propose realistic solutions for conservation and management, and argue that, because it is a keystone species, the prairie dog is a linchpin for the survival of grassland ecosystems of western North America.

Male-13 giving mating call just before copulation. Mating calls attract females, but also intimidate other males. Old, heavy males are more likely than younger, lighter males to give mating calls.

To this point, I primarily have summarized my research with black-tailed prairie dogs (*Cynomys ludovicianus*). More recently, students and I have been studying the population biology and behavioral ecology of Gunnison's and Utah prairie dogs (*C. gunnisoni* and *C. parvidens*). Our longterm comparative research has uncovered numerous interspecific similarities, but also has defined several puzzling differences (Chapter 37 in *Rodent Societies*). Consider alarm calling, for example. As noted above, both male and female black-tailed prairie dogs call to warn both offspring and nondescendant kin within earshot. Female Utah prairie dogs also call to warn kin, ***but male Utah prairie dogs almost never call—even though they are consistently surrounded by adult and juvenile offspring***. And consider levels of inbreeding. As noted above, black-tailed prairie dogs use 4 different mechanisms to avoid extreme inbreeding. ***Utah prairie dogs, by contrast, regularly mate incestuously with siblings, parents, and offspring***. For a third example that illustrates the merits of comparative research, consider infanticide. For black-tailed prairie dogs, the percentage of litters affected by infanticide is 39%, and both males and females kill juveniles. For Utah prairie dogs, the percentage is 15%, and only males kill. ***For Gunnison's prairie dogs, however, students and I have not detected a single unequivocal case of infanticide during 7 years of observation***—nor have we found any circumstantial evidence for killings (e.g., aboveground carcasses with puncture wounds).

Perhaps to enhance protection for their own offspring, prairie dog mothers frequently accept foster offspring—so that numerous juveniles from $\geq$2 litters use the same nursery burrow. Communal nursing of foster offspring is common. Beneficiaries of communal nursing are usually juvenile nieces, nephews, and grandoffspring.

Because predators strike quickly and often avoid areas with humans, assessing patterns of predation under natural conditions is difficult. In my research with Utah prairie dogs in 2005, ***a high frequency of predation provided an unusual opportunity to examine vulnerability of five different types of individuals: juveniles, individuals at the periphery of a colony, immigrants,***

Heavy prairie dogs are more likely than lighter prairie dogs (a) to survive until the next breeding season, (b) to mate, and (c) to produce numerous offspring. Body mass is the best predictor of *annual* reproductive success, and longevity is the best predictor of *lifetime* reproductive success.

males during the short mating season, and pregnant females (*American Naturalist* 168:546-552). This fascinating tale has been featured in *ScienceNow* (the on-line complement of *Science*), *New Scientist*, and two radio programs (*Quirks and Quarks* and *Science Update*).

The National Science Foundation (NSF) has funded my research since I was a graduate student. Also important have been a Career Development Award from The Harry Frank Guggenheim Foundation, and grants from The Denver Zoological Foundation, Earthwatch, Environmental Defense, The National Geographic Society, The Turner Foundation, and The National Fish and Wildlife Foundation

I can teach courses in Animal Behavior, Conservation Biology, Field Ecology, Population Biology, and Wildlife Management. ***My favorite course is Field Ecology, in which students and I conduct weekly experiments in population biology and behavioral ecology***. Our study organisms include bumblebees, cabbage butterflies, Canada geese, eastern gray squirrels, eastern red-backed salamanders, field crickets, honeybees, mallards, Queen Anne's Laces, short-horned grasshoppers, and white pines. ***Field Ecology also entails collections of insects (90 families) and tree specimens (90 species)***.

Juvenile prairie dog at first emergence from natal burrow, when it is about 5.5 weeks old and weighs about 150 grams. Because females usually mate with >1 male, determination of paternity requires collection of blood samples (for DNA-fingerprints) from mothers, offspring, and putative fathers.

My research at national parks such as Wind Cave, Petrified Forest, and Bryce Canyon offers superb opportunities to involve students, many of them sponsored by NSF's REU Program (Research Experiences for Undergraduates). Students participate in *all* aspects of research—from livetrapping and collection of blood samples (for paternity) to statistical analysis and publication of results. Many students have applied their research under my direction toward a senior thesis (e.g., Brown, Davidson, Minnesota, Pennsylvania, Princeton, and Yale). Working with me in the field has helped other students to gain acceptance into graduate schools such as Auburn, Brown, Cornell, Michigan, Oklahoma, Oklahoma State, Penn State, Princeton, UC-Davis, UC-San Diego, Washington, and Yale.

Litter size at weaning ranges from 1-8. To capture complete litters, students and I surround the home nursery burrow with livetraps as soon as juveniles first appear aboveground. Females that mate with several males wean larger litters than females that mate with only 1 male.

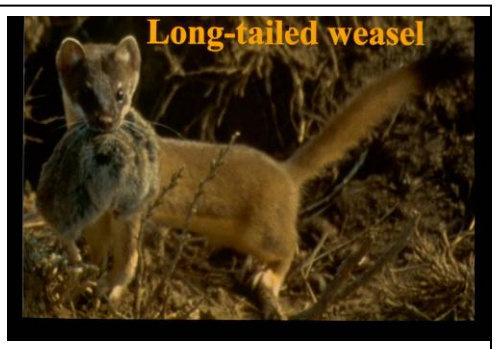
Competition, infanticide, and inbreeding are major issues in behavioral ecology and population biology that affect humans and other social animals. Consequently, ***my publications have generated 2,180 citations in 106 different journals***. Fifteen of my first-authored publications have generated >50 citations, and five have generated >100. The popular press also is curious about my latest results. Issues of *Audubon*, *National Geographic*, *BBC Wildlife* (N = 2), *National Wildlife* (N = 2), *New* Scientist, Ranger *Rick* (N = 3), *Science News* (N = 2), *ScienceNow*, *ScienceUpdate*, and *Terre Sauvage*, for example, have had articles that feature my research. Newspapers such as *The New York Times*, *Washington Post*, *Cleveland Plain Dealer*, *Chicago Sun Times*, *Detroit Free Press*, and *Le Generaliste* also have highlighted my discoveries. ***Eight television companies have filmed documentaries about my adventures***.

My longterm research under natural conditions has led to a better understanding of several pivotal issues in behavioral ecology and population biology. ***But many baffling, provocative questions remain***. Some individuals with nearby kin refuse to give alarm calls—so why do other individuals with no nearby kin sometimes call? Some females mate with only 1 male—so why do other females mate with as many as 5 males in rapid succession? Why is infanticide rampant in some years, but rare in other years? Certain females specialize in the killing of juvenile offspring of close kin—so why do other females specialize in the communal nursing of offspring of close kin? How do population/metapopulation dynamics affect vulnerability to ruinous diseases such as plague? ***By continuing to track the survivorship and reproductive success of marked individuals over time, students and I will investigate these and other compelling questions***.

To verify identification, prairie dogs frequently kiss. If close kin, the kissing individuals resume foraging. If unrelated, a fight or chase ensues. On a busy day, students and I record >1,000 kisses and >300 fights and chases.

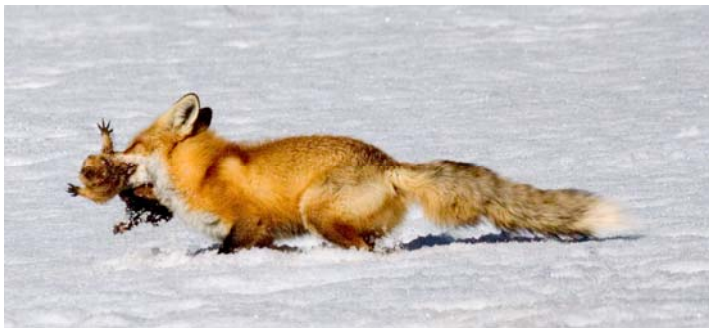
After mating with a female, male-05 tries to precludе matings with other males by sequestering the female in a burrow.

Factors such as sex ratio among adults, maternal condition, local mate competition, and local resource enhancement do not affect the sex ratio within litters. Consequently, each mother usually weans approximately equal numbers of male and female offspring.



In 2002, a *single* male long-tailed weasel killed the unweaned offspring of 18 complete litters. The cumulative number of juvenile victims was >80. Students and I were able to document this carnage because we knew the precise location of every nursery burrow.

After a predator has departed, male-08 jumps into the air and gives an "all-clear" call. Unlike alarm calls, all-clears seem unrelated to the kinship of other prairie dogs within earshot.



Individuals at the periphery of a prairie dog colony are especially vulnerable to predation. This red fox has just captured adult male-R12, who lived at periphery of my study colony. Photo by Elaine Miller Bond.

Because they are unfamiliar with the best routes for escape, prairie dogs that have just immigrated into a colony are especially susceptible to predation. This northern goshawk has just captured adult male-R44, who had immigrated into the study colony just 2 days earlier. Photo by Elaine Miller Bond.

The black-footed ferret, one of the rarest mammals in North America, feeds exclusively on prairie dogs. Burrowing owls and mountain plovers also depend on prairie dogs for survival, as do >150 other species of plants and animals of the western grassland ecosystem. The prairie dog is thus a keystone species that needs better conservation and management.

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