Greater Yellowstone elk suffer worse nutrition and lower birth rates due to wolves

July 15, 2009 -- By Tracy Ellig, MSU News Service

Bozeman -- Wolves have caused elk in the Greater Yellowstone Ecosystem to change their behavior and foraging habits so much so that herds are having fewer calves, mainly due to changes in their nutrition, according to a study published this week by Montana State University researchers.

During winter, nearly all elk in the Greater Yellowstone Ecosystem are losing weight, said Scott Creel, ecology professor at MSU, and lead author on the study which appears in the Proceedings of the National Academy of Sciences.

The decline in the Greater Yellowstone's elk population since the reintroduction of wolves in 1995 has been greater than was originally predicted. In the three winters prior to the reintroduction of wolves, elk on Yellowstone's northern range numbered roughly between 17,000 and 19,000. In the three winters prior to 2008, annual elk counts had declined to between 6,738 and 6,279. (Photo courtesy of John A. Winnie Jr.)

"Essentially, they are slowly starving," Creel said. "Despite grazing and browsing during the winter, elk suffer a net loss of weight. If winter continued, they would all die, because dormant plants provide limited protein and energy, and snow makes it more difficult to graze efficiently."

With the presence of wolves, elk browse more - eating woody shrubs or low tree branches in forested areas where they are safer - as opposed to grazing on grass in open meadows where they are more visible, and therefore more vulnerable to wolves.

Browsing provides food of good quality, but the change in foraging habits results in elk taking in 27 percent less food than their counterparts that live without wolves, the study estimates.

"Elk regularly hunted by wolves are essentially starving faster than those not hunted by wolves," said Creel, who shares authorship on the paper with his former doctoral students John Winnie, Jr., and David Christianson.

The decline in the Greater Yellowstone's elk population since the reintroduction of wolves in 1995 has been greater than was originally predicted. In the three winters prior to the reintroduction of wolves, elk on Yellowstone's northern range numbered roughly between 17,000 and 19,000. In the three winters prior to 2008, annual elk counts had declined to between 6,738 and 6,279.

Obviously, wolves kill elk, and direct predation is responsible for much of the decline in elk numbers, but the rate of direct killing is not great enough to account for the elk population declines observed since 1995 in the Northern Range, the Gallatin Canyon, and the Madison-Firehole herds, all well-colonized by Yellowstone wolves. In addition to direct predation, the decline is due to low calving rates, which are a subtle but important effect of the wolves' presence, Creel said.

Two studies following radio-collared elk calves found that during the calves' first six months of life, relatively few of them were killed by wolves, Creel said.

"We knew the presence of wolves caused lower calf-cow ratios, but we didn't know why," he said. "Radiocollaring calves revealed that calf numbers were low immediately after the birth pulse, suggesting that a decline in the birth rate was part of the population decline."

The birth pulse is that time in spring when most cow elk have their calves.

This suggestion was confirmed when the researchers found that elk facing high levels of predation risk had substantially decreased progesterone levels prior to the annual birth pulse. Progesterone is necessary to maintain pregnancy, but a question remained: what was responsible for the decrease in progesterone?

There were two competing theories: One suggested elk suffered from chronic stress due to the wolves' presence. In all mammals, stress causes the release of cortisol, a hormone that helps free up energy to either fight or flee. But too much cortisol from chronic stress can cause the immune and reproductive systems to shut down.

The other theory was that the elk weren't getting enough to eat because they were always on the run from the wolves and spending more time in the forest, where food is sparse compared to grassy meadows. For wintering elk that are already on the edge of starvation, anything compromising nutrition could also cause the reproductive system to shut down.

The MSU researchers did chemical analysis of 1,200 fecal samples collected over 4 years, as well as urine samples for the study. They did not find the elevated levels of cortisol that would support the chronic stress theory. However, they did find that those elk living in the presence of wolves had lower levels of progesterone, a hormone necessary to maintain pregnancy, than those elk that didn't live with wolves.

"The elk are trading reproduction for longevity," Creel said. "Elk are potentially long-lived, and many prior studies have shown that, in species like this, natural selection favors individuals who do not compromise their own survival for the sake of a single reproductive opportunity."

If predators commonly affect the reproduction of their prey, it will change the thinking about predator-prey dynamics, and might change how wildlife managers plan for the reintroduction of predators, Creel said.

"This research shows that the total effect of a predator on prey numbers can be larger than one would determine simply by looking at the number that are killed," he said.

Until now, it would have seemed obvious to conclude that a herd losing many of its number to predators would decline faster than a herd where predators were less successful, Creel said.

"However, now it is conceivable that the herd with the lower direct predation rate could decline faster, if it spends more of its time and energy avoiding being eaten and less on reproduction," Creel said.

Creel and his current doctoral student Paul Schuette are seeing if the theory holds up with other prey-predator populations, with a study of lions, spotted hyenas and a diverse array of prey animals on a Maasai Community Conservation Area in the South Rift of Kenya.

The study of Montana elk ruled out weather as the cause of poor calf production, because elk populations that were exposed to little or no wolf predation had good calf production during the study period, which was typified by winters with little snow accumulation -- ideal for elk.

The study also considered grizzly bears.

"It is true that grizzlies prey on elk calves, and grizzly numbers have increased in the region," Creel said. "However, the increase in total grizzly numbers has mainly been due to geographical expansion, rather than increases in the number of bears in places where they were already well-established at the time of wolf reintroduction."

The work by Creel, Winnie and Christianson was funded by the National Science Foundation.

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Glucocorticoid stress hormones and the effect of predation risk on elk reproduction

Scott Creel,[1], John A. Winnie, Jr. and David Christianson

+ Author Affiliations

Edited by Mark S. Boyce, University of Alberta, Edmonton, Canada, and accepted by the Editorial Board June 12, 2009 (received for review March 3, 2009)

Abstract

Predators affect prey demography through direct predation and through the costs of antipredator behavioral responses, or risk effects. Experiments have shown that risk effects can comprise a substantial proportion of a predator's total effect on prey dynamics, but we know little about their strength in wild populations, or the physiological mechanisms that mediate them. When wolves are present, elk alter their grouping patterns, vigilance, foraging behavior, habitat selection, and diet. These responses are associated with decreased progesterone levels, decreased calf production, and reduced population size [Creel S, Christianson D, Liley S, Winnie JA (2007) *Science* 315:960]. Two general mechanisms for the effect of predation risk on reproduction have been proposed: the predation stress hypothesis and the predator–sensitive–food hypothesis. Here, we used enzyme immunoassay to measure fecal glucocorticoid metabolite concentrations for 1,205 samples collected from 4 elk populations over 4 winters to test the hypothesis that the effect of predation risk on elk reproduction is mediated by chronic stress. Across populations and years, fecal glucocorticoid concentrations were not related to predator–prey ratios, progesterone concentrations or calf–cow ratios. Overall, the effect of wolf presence on elk reproduction is better explained by changes in foraging patterns that carry nutritional costs than by changes in glucocorticoid concentrations.

antipredator behavior | nonconsumptive effects | risk effect | wolf

Footnotes

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Author contributions: S.C., J.A.W., and D.C. designed research; S.C., J.A.W., and D.C. performed research; S.C., J.A.W., and D.C. analyzed data; and S.C. wrote the paper.

The authors declare no conflict of interest.

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Elk, wolf researchers probe wildlife battlefield

April 19, 2006 -- By Evelyn Boswell, MSU News Service

Scott Creel climbs a hill to look for more elk remains (MSU photo by Jay Thane).

BIG SKY -- Cawing ravens gave Dave Christianson his first clue that something was afoot in the animal kingdom between Big Sky and West Yellowstone.

One day earlier, Christianson had spotted elk on a hill and wolves on a nearby ridge. Now he saw only ravens and wondered if their presence signaled another back country battle in the Taylor Fork Drainage.

"Most of the time, we find kills because of ravens or magpies," said Christianson, a Montana State University graduate student from Glasgow.

"We're going to see if we can go find it," said Scott Creel, an MSU ecologist and Christianson's advisor.

Christianson and Creel are researching elk in the northwest part of the Yellowstone Ecosystem to see how they're affected by wolves. From previous years, they know that wolves cause elk to change herd sizes, behavior patterns and use of the landscape. Now, the researchers are trying to understand how these changes affect the elks' nutrition, reproduction and survival.

From January into spring, Christianson lives during the week in a one-room bunkhouse off U.S. 191. He spends his days doing things like spotting elk and wolves, inspecting tracks and scrutinizing videotapes of the animals. Creel generally drives down from Bozeman every Wednesday to join Christianson on his rounds.

Every two weeks, the researchers follow elk paths through the Porcupine, Taylor and Tepee/Daly drainages, recording where the elk have traveled and fed and what plants they have eaten. Sometimes, they drop a lead ball or pound the snow with an imitation hoof to see how hard the elk had to work to get through the snow to a meal. It's all to see how wolves affect how well the elk are feeding and how hard the elk have to work for a meal.

This day was somewhat different, though. With an unsolved mystery pulling them toward Cameron Draw, Christianson slipped into cross-country skis while Creel donned snowshoes. Both wearing backpacks, they trudged and glided across a field and up a ravine. They stopped to take photos. They pushed branches aside. They finally came upon blood splatters in the snow, stiff brown hair in a hole, rumen near a log and tracks on a hill.

It was a battle scene without a body, a combat zone without troops.

"This is odd that there isn't much here," Creel said.

Christianson added, "Usually the entire skeleton is here."

Looking for more clues and additional remains, Christianson headed up the ridge where he had seen the wolves the day before. Creel clambered up the opposite side.

"One of them sat here and ate a big chunk of it," Creel yelled. "I'm going to climb higher."

Several minutes later, the researchers returned, Creel with an elk hide and

Christianson with a pelvis, two femurs and part of a skull. It appeared, they said, that wolves had killed an eight-month old elk on the side of the hill. As the wolves fed on the calf, the carcass had slipped toward the ravine. The wolves retrieved it and hauled it up to the ridges, evidently still chewing on it the next day. When Creel reached the top of the hill, he found wolf tracks, drag marks and three freshly melted-out beds.

"I think they were up there eating away when we arrived or shortly before," Creel said.

Bone marrow revealed that the elk calf had been suffering even before the wolves attacked it, Christianson said as he cut through one of its bones. An elk with plenty of food has bone marrow that looks like thick Crisco, he said. This marrow was watery and deep red, indicating that the elk was slowly starving and starting to digest the fat in its marrow.

This was Christianson's fourth winter near Big Sky and his final season in the field. With results published recently in the journals Animal Behavior and Ecology, the researchers have found that the number of elk calves in their study area has declined, but not because they were eaten by wolves. Wolves, in fact, rarely kill elk in the first six months of the elks' lives.

"This year, bears were far and away the main predators in the first six months," Creel said. "That was a surprise to us, but it confirms what P.J. White and Doug Smith have also seen with wolves and elk in other parts of Yellowstone. If the calves are missing, but wolves are rarely killing them in the first six months, what's going on?"

It appears that one effect of changed behavior is lower pregnancy rates, Creel said. Preliminary data from the Gallatin Canyon, Yellowstone National Park, the Madison Valley, Paradise Valley and Elkhorn show that elk pregnancy rates have declined where wolves are most active. The elk -- especially females -- spend less time eating and more time watching for predators when wolves are around.

"They just say, ?Today the job is to avoid being killed,'" Creel said. "So they're probably not as efficient at foraging. That's what Dave (Christianson) is studying now."

Unsuccessful this time at staying alive, the elk remains they discovered represented the ninth wolf kill they'd seen in a month, the researchers said as they returned through U.S. Forest Service land to their vehicles. This area of the Taylor Fork contains approximately 250 elk.

A slideshow is located on the Web at
http://www.montana.edu/cpa/gallery/060417/pages/page_1.html

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MSU researcher builds better radio collar

July 28, 2004 -- By Jean Arthur, MSU News Service

BOZEMAN--He has worked with muggers and gunners and now Montana State University doctoral student John Winnie, Jr. has invented his own elk-tracking device to lower research costs and improve tracking success.

High-risk adventure and a quest for scientific knowledge drew Winnie, an award-winning photographer, to MSU from Kalispell to work on a doctorate in ecology. Adrenaline and necessity had him buzzing around in helicopters helping "mug," or capture elk. He buckled radio-collar tracking devices on the kicking, bucking, ungulates that weigh up to 900 pounds.

"We were net gunning the animals from a bubble helicopter," said Winnie, now in his last year of doctoral studies. "The gunner fires a net onto an elk. The net flares out over the animal, and then the mugger jumps out of the helicopter onto the tangled animal to restrain it."

A biologist then places a radio collar on the animal, takes blood and fecal samples, estimates the animal's age from its teeth and finally, untangles it from the net--all in about a half hour.

"Everyone gets kicked," said Winnie. "It is exciting stuff, but when you consider the cost involved in studying wild animals in rugged terrain, it's mind boggling."

For four years, Winnie has worked with MSU ecology professor Scott Creel studying wolf-elk interactions in the Porcupine, Taylor and Teepee/Daly drainages between Bozeman and West Yellowstone.

To study elk behavioral and spatial responses to wolves, they needed high-tech, global positioning system collars that offered hourly tracking in addition to traditional radio collars, which require a person to use hand-held telemetry to track each animal.

"We wanted to determine where the elk were moving every few hours and needed GPS collars, which were a formidable $3,500 each," Winnie said. "The purchase would not only consume much of the research dollars, but the available collars often failed. So I decided to build my own."

At first, Creel was skeptical. He knew they needed a better device because the commercial units did not collect data well. Some had faulty drop-off mechanisms, which meant that even if the collar had worked properly, it could not be retrieved to download the data.

"John said, 'Look, if someone can sell a tiny handheld GPS for $150 and make a profit, then the components have to cost far less,'" Creel said. "John wagered that it had to be possible to make a GPS collar for way less than $3,500."

Winnie constructed two prototypes on his own time and money.

"Fortunately, the components were inexpensive," he said. "These units could acquire a position in about a minute and store 5,000 fixes on board. Once I had working devices and showed it could be done, Scott came up with the money to work on refinements and go into production."

"After testing dozens of lightweight aluminum boxes, plastic sleeves and

exotic epoxy resins, John came up with a small, lightweight, self-contained package that we could simply
rivet to a regular radio collar," said Creel. "John tested trial versions by soaking them in buckets of water overnight, smashing them on the floor, and freezing them at minus forty degrees. When they stood up to that, we put them on the elk, and we've had 100 percent success."

They collected more than 20,000 locations from 18 elk over the last two winters and now know a great deal about the ways that elk respond to the risk of predation by wolves. They used traditional radio telemetry to find the wolves, which had radio collars too.

The researchers currently have nine GPS collars on elk and hope to complete their study next year. By then, Winnie can add "inventor" and "Ph.D." to his resume.

Note to editors: A related story, titled "MSU research: Bull elk oblivious to danger at dinner time" is available at http://www.montana.edu/commserv/csnews/nwview.php?article=1833

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Current Research**:**

General Areas of Interest: Behavioral ecology, population biology, conservation, behavioral endocrinology, evolutionary ecology. Virtually all of my research is based on field studies, generally using observational rather than experimental methods, and often following known individuals. Much of the work in my lab involves the integration of behavioral and demographic data from the field with physiological and genetic data from the lab. My lab is equipped for extraction and radioimmunoassay or enzyme immunoassays of steroid hormones, DNA extraction, and PCR.

My current research mainly examines responses of prey to the risk of predation. One part of this work examines the responses of elk to variation in the risk of predation by wolves. This work is based in four subsites within the Gallatin Canyon, bordering

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mwanzo on zebra kill

Yellowstone National Park on federal, state and private land. The goals of the project are:

(1) To quantify the responses of elk to variation in predation risk. These include responses in behavior, feeding ecology, distribution, and patterns of grouping.
(2) To determine the costs of these responses, physiologically and demographically
(3) To determine the impact of these costs on the population dynamics of both elk and wolves.

sam, patrick, mike and albert

A second part of this work is on the Shompole & Olkiramatian Maasai group ranches in the South Rift Valley of Kenya. Working with the local Maasai authorities & Dr. Jonah Western, we are examining interactions between lions, spotted hyenas and their prey, effects on small and medium-sized carnivores, and interactions with people and cattle inside and outside of a Community Conservation Area. This research is testing the generality of conclusions from the wolf-elk project, and identifying ramifications for ecosystem function, management and conservation in East Africa.

My students and I address these goals with a wide variety of methods, including behavioral observations, demographic & ecological monitoring, ground and aerial censuses, camera trapping, GPS and VHF radiotelemetry, RIA/EIA of fecal steroids to measure pregnancy rates and stress responses, measurements of abiotic factors such as weather and snow conditions, and assessments of diet quality by chemical and microhistological methods.

Teaching:

- Conservation Biology, BIOL 447 & BIOL 521, Fall semester
- Principles of Ecology, BIOL 303, Spring semester. I am currently revising this course, but it will cover aspects of demography/life history, single-species population dynamics, competition, predation, disease, community ecology, behavioral ecology and evolutionary ecology.
- Animal Physiology, Biol 411, Fall semester (not currently teaching this course)
- I also teach a one credit graduate seminar (BIOL 500) in Fall of most years. The emphasis is on discussion of papers, grant proposals and presentations of our own work.

Recent Publications:

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Creel S. 2010. Interactions between wolves and elk in the Yellowstone Ecosystem, pp 65 - 80 In: Knowing Yellowstone: Science in America's First National Park. J. Johnson (ed). Taylor Trade Publishing, Boulder, CO

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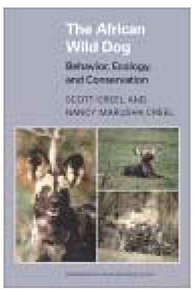

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Students

Here are some excellent general notes about preparing for the graduate qualifying exam, from Colleen Cassady St Clair at the Univesity of Alberta. Though they pertain to the exam at a different department & school, they apply well here.

I encourage my graduate students to participate fully in developing their research questions and to pursue independent funding.

Paul Schuette (PhD): NSF GRA. Paul is studying interactions between top carnivores (lions, spotted hyenas, leopards), their competitors, their prey and humans, working on the Olkiramation and Shompole Maasai group ranches. Paul is cosupervised by Dr. Jonah Western of the African Conservation Centre.
Leslie Frattaroli (MS): Leslie, co-advised by Dr. Chuck Schwartz, is using downloadable GPS collars to visit foraging sites of black bears soon after their use, to assess recreation impacts on habitat use and to assess the affects of grizzly bear range expansion on black bears. Her field work is with Steve Cain in Grand Teton National Park.
Tyler Coleman (PhD): Tyler, co-advised by Dr. Chuck Schwartz, is conducting an evaluation of the effectiveness of Yellowstone National Park's grizzly bear management policies, focussing on the closure or restriction of use in bear management areas. His field work is with Kerry Gunther of Yellowstone National Park.
Angela Brennan (PhD): Angela, co-advised by Dr. Paul Cross of USGS, is developing a project to examine the ecology and epidemiology of brucellosis in elk on Wyoming feedgrounds and the Yellowstone Ecosystem.
Tyler Creech (MS): Tyler co-advised by Dr. Paul Cross of USGS, is also developing a project to examine the ecology and epidemiology of brucellosis in elk on Wyoming feedgrounds and the Yellowstone Ecosystem.
Tiffany Holland (MS): Tiffany, co-advised by Dr. Marcel Huisjer of WTI, is examining factors that contribute to vehicle collisions with deer on US 93, specifically testing for reductions after mitigation measures.

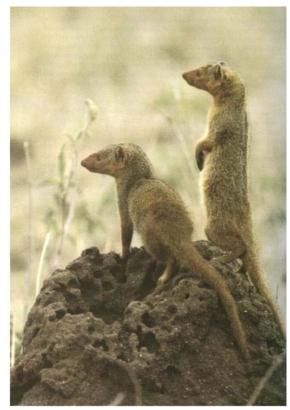
Recent graduate students are:

Dave Christianson (PhD): Dave is examined changes in elk foraging behavior in response to the presence of wolves, and the impacts of these changes on elk diets, nutrition, and demography. He went on to an EU Fellowship with Anne Loison's research group at the Université de Savoie, to examine interactions between predation and resource limitation on chamois nutrition and population dynamics.
Cecily Costello (PhD): Cecily studied black bear social organization and space use as they relate to population genetics and patterns of relatedness, using data from two populations in NM. Wildlife Conservation Society/Hornocker Wildlife Institute grants. Cecily went on to research with the Interagency Grizzly Bear Study Team on the genetic structure of N. Rockies populations of grizzly bears and issues to do with ESA protections.
Stewart Liley (MS): Stewart used model selection methods to test the relative strength of predator, prey and environmental characteristics in predicting antipredator responses of elk to the presence of wolves. Surprisingly little prior work has attempted to determine the relative importance of these three types of variables in determining the strength of antipredator responses. Dangerous places? The size or proximity of predator groups? Characteristics of the prey group itself? Answers are in his paper in Behavioral Ecology. Stewart is now the head elk biologist for the state of New Mexico.
John Winnie (PhD): John studied the effects of predation risk from wolves on elk behavior, grouping patterns and spatial distributions, producing wide ranging data that revealed strong responses by elk in almost every aspect of their behavior that we considered. He went on to a postdoc with Wayne Getz and Paul Cross, studying habitat selection by African buffalo, and then to work for WCS on the conservation of argali (Marco Polo sheep) in the Wakhan corridor of Afghanistan.
Aaron Wagner (PhD): Aaron studied striped hyenas on the Laikipia Plateau of Kenya, including aspects of behavior, ecology, endocrinology and genetics. He went on to a postdoc to continue his work on

striped hyenas in Kenya, with Kay Holekamp at Michigan State University (thereby keeping his career wholly within institutions called MSU).
Julia Nelson (MS), who studied the impacts of coyotes on the use of space and stress physiology of endangered San Joaquin kit foxes, working with Dr. Brian Cypher. She went on to do some world travelling, study languages and work in Belize for the Peace Corps.
Goran Spong (PhD), who studied population genetics and social evolution in African lions (in the Selous Game Reserve). Goran went on to a postdoc at Cambridge university with Dr. Tim Clutton Brock, studying meerkats, and then to a faculty position at the University of Umea.
Jennifer Sands (MS), who studied interactions between aggression, social status and glucocorticoid stress hormones in wolves (in Yellowstone National Park). Jennifer went on to become a secondary science teacher in Boulder.
Amanda Hardy (MS), who studied the impacts of winter recreation on elk and bison (in YNP). Amanda went to a job as a wildlife ecologist for the Western Transportation Institute, and then a PhD at CSU.

Other Research:

From 1984-1986, I studied behavioral and physiological mechanisms that mediate the effects of early experience on milk production in **Holstein dairy cattle**. I am consequently one of a relatively small set of people who know how to make cows urinate on demand. Really.



From 1987-1990, my wife Nancy and I studied evolutionary, behavioral and physiological aspects of cooperative breeding in **dwarf mongooses** (*Helogale parvula*) in Serengeti National Park, working with Dr. Peter Waser and Dr Jon Rood, for my PhD at Purdue. This work involved using demographic and molecular genetic data to calculate inclusive fitness costs and benefits, and using behavioral and endocrine data to identify the mechanisms responsible for reproductive suppression in socially subordinate adults.

Some of the primary results of this research are found in:

Creel & Creel 1991. Energetics, reproductive suppression and obligate communal breeding in carnivores. *Behavioral Ecology and Sociobiology* 28:263-270.
Creel et al. 1991. Spontaneous lactation is an adaptive result of pseudopregnancy. *Nature* 351:660-662.
Creel & Waser 1991. Failures of reproductive suppression in dwarf mongooses (Helogale parvula): accident or adaptation? *Behavioral Ecology* 2:7-15.
Creel et al 1992. Behavioural and endocrine mechanisms of reproductive suppression in Serengeti darf mongooses. *Animal Behaviour* 43: 231-245.
Creel & Waser 1994 Inclusive fitness and reproductive strategies in dwarf mongooses. *Behavioral Ecology* 5:339-348.
Creel S 2001. Social dominance and stress hormones. *Trends in Ecology and Evolution* 16: 491-497

From 1991-1996, Nancy and I studied **African wild dogs** (*Lycaon pictus*) in the Selous Game Reserve. At roughly 80,000 square kilometers, the Selous is one of the largest protected areas in the world, but its ecology is still little-studied. This project focused initially on simply assessing the size of the wild dog population in Selous (a formidable task in itself), and progressed to identifying the ecological factors that cause wild dogs to be endangered, attaining uniformly low densities in comparison to other large carnivores that are well-protected by Tanzania's system of parks and reserves. In this regard, interspecific competition

plays a major role in limiting wild dog numbers and distributions. We also used demographic data to make quantitative assessments of extinction risk, and collected a substantial data set on prey selection, predator-prey interactions and the costs/benefits of cooperative hunting. Finally we examined social evolution and behavioral and endocrine mechanisms of reproductive suppression in wild dogs, in a manner similar to our earlier work with dwarf mongooses.

Some of the major results of this work are found in:

Creel & Creel 1995. Communal hunting and pack size in African wild dogs, Lycaon pictus. *Animal Behaviour* 50:1325-1339.
Creel & Creel 1996. Limitation of African wild dogs by competition with larger carnivores. *Conservation Biology* 10:526-538.
Creel et al. 1996. Social stress and dominance. *Nature* 379: 212. (also see Morell, V 1996. Life at the top: animals pay the high price of dominance. *Science* 271: 292.)
Creel et al. 1997. Rank and reproduction in cooperatively breeding African wild dogs: behavioral and endocrine correlates. *Behavioral Ecology* 8:298-306.
Vucetich & Creel 1997. Ecological interactions, social organization and extinction risk in African wild dogs. *Conservation Biology* 13:1172-1182.
Creel & Creel 2002. *The African wild dog: behavior, ecology and conservation*. Princeton University Press.
Creel et al. 2004. *African wild dogs: demography and population dynamics of wild dogs in three crticial populations*. In: Biology and Conservation of Wild Canids, ed. by D.W. Macdonald & C Sillero-Zubiri, Oxford University Press.

Incidental to these studies, I've done some collaborative research on the behavioral ecology and evolution of **lions**, **leopards**, **banded mongooses** and **slender mongooses**, some of which is in the following:

Creel S & Creel NM 1997. Lion density and population structure in the Selous Game Reserve: evaluation of tourist hunting quotas and offtake. *African Journal of Ecology* 35:83-93
Spong G, Hellborg L & Creel S 2000. Sex ratio of leopards taken in trophy hunting: genetic data from Tanzania. *Conservation Genetics* 1: 169-171.
Spong G, Creel S, Stone J & Bjorklund M. 2002 Genetic structure of a population of lions (Panthera leo): implications for the evolution of sociality. *Journal of Evolutionary Biology* 15(6):945-953.
Spong G & Creel S 2004. Effects of kinship on territorial conflicts among groups of lions, Panthera leo. *Behavioral Ecology and Sociobiology*. 55: 325-331
Waser PM, Elliott L & Creel SR 1995. *Habitat variation and mongoose demography*. In: Serengeti II:

Dynamics, conservation and management of an ecosystem. pp. 421-447, Sinclair ARE & Arcese P (eds). University of Chicago Press, Chicago.

For questions or comments: screel@gemini.oscs.montana.edu

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