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Territoriality and Inter-Pack Aggression in Gray Wolves: Shaping a Social Carnivore's Life History

Rudyard Kipling's Law of the Jungle Meets Yellowstone's Law of the Mountains

Kira A. Cassidy, Douglas W. Smith, L. David Mech, Daniel R. MacNulty, Daniel R. Stahler, & Matthew C. Metz

When Rudyard Kipling wrote *The Jungle Book* in 1894 and included the famous line "For the strength of the Wolf is the Pack, and the strength of the Pack is the Wolf," he would have had no idea that over a century later, scientific research would back up his poetic phrase. Recent studies in Yellowstone have found that both the individual wolf and the collective pack rely on each other and play important roles in territoriality. At a time when most fairy tales and fables were portraying wolves as demonic killers or, at best, slapstick gluttons, Kipling seemed to have a respect or even reverence for the wolf. Wolves in *The Jungle Book* raise and mentor the main character Mowgli, with the pack's leader eventually dying to save the "man-cub" from a pack of wolves. Kipling may have extended intra-pack benevolence to a human boy for literary sake, but he was clearly enthralled with how pack members treat each other. As wolf packs are almost always family units, most commonly comprised of a breeding pair and their offspring from several years, amiable behavior within the pack is unsurprising. By contrast, wolf packs are fiercely intolerant of their neighbors, their rivals. And this competition is proving to be an important facet in the life of a wolf and its pack.

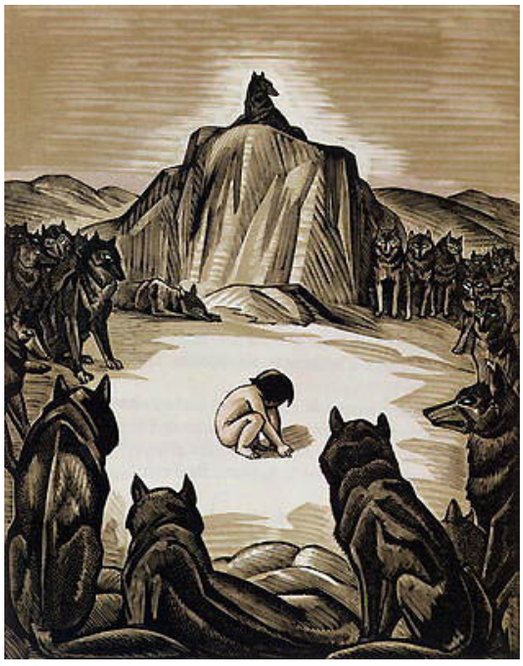

Illustration by Charles Maurice Detmold from *The Jungle Book* by Rudyard Kipling, Macmillan & Co., London, UK, 1894.

Although many animals live in groups, only some are considered territorial (willing to fight other groups or invading individuals to protect their territory). African lions, meerkats, chimpanzees, and mongooses regularly attack and even kill non-group members (Heinsohn and Packer 1995, Doolan and MacDonald 1996, Wilson et al. 2001, Cant et al. 2002). Even nomadic hunter-gatherer human groups fought; the often lethal conflicts ranged from primitive to complex warfare (Wrangham and Glowacki 2012). For this behavior to evolve, it must afford group members a survival advantage. Wolves likely evolved to be territorial because it benefits them in several ways: repelling intruders makes it easier to protect vulnerable pups at the pack's den, and securing territory with abundant prey ensures an uncontested

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The Agate Creek pack, led by several adult females, chases the Oxbow Creek pack (out of frame). Within a few minutes, the Agate Creek pack caught and killed a female from the Oxbow pack, effectively reducing that pack to only two wolves.

food source (Kittle et al. 2015). Success in both these aspects of life—reproducing and eating—perpetuates the genes of high-performing individuals. And in the case of the wolf, the ones best at reproducing and eating are aggressive with their rivals. In fact, of all the dead wolves recovered in Yellowstone, intraspecific (wolf vs. wolf) strife accounts for two-thirds of natural mortality (figure 1).

Although inter-pack conflict is not rare, wolves display a variety of nonaggressive territorial behaviors that di-

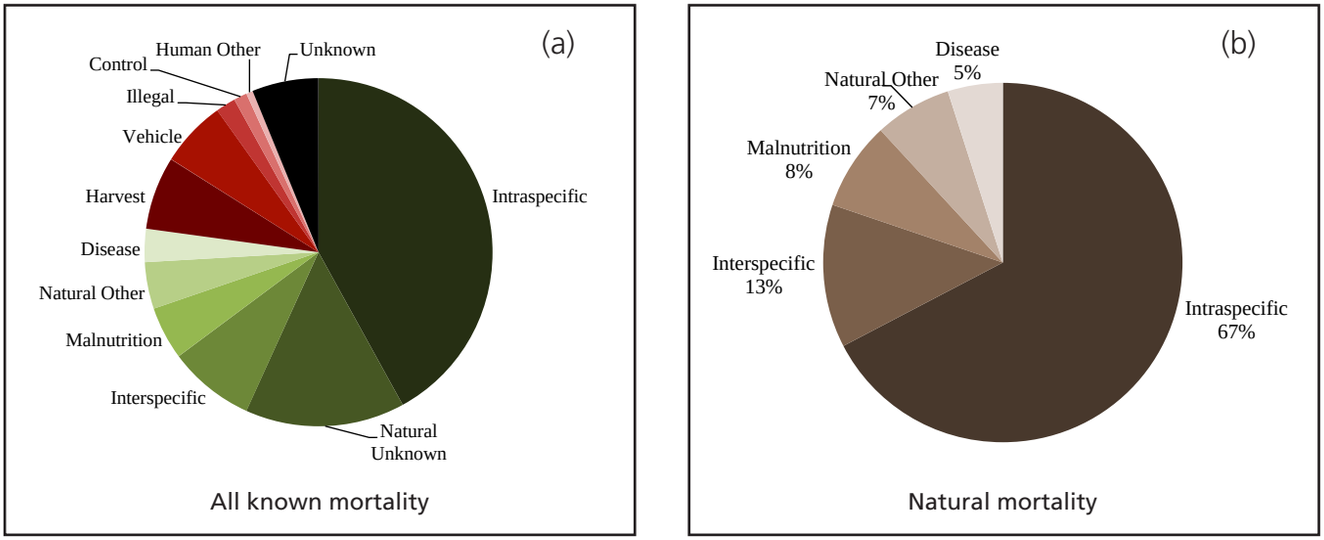

Figure 1. Causes of mortality for Yellowstone National Park collared wolves (1995-2015). (a) All causes of mortality; (b) Natural, known causes of mortality.

minish the risk of confrontation. They scent-mark within territories and along boundaries, and these scents can be detected by other wolves for 2-3 weeks(Peters and Mech 1975). They also howl, to signal their location and strength to neighboring packs (Harrington and Mech 1983). When these behaviors fail to separate neighboring packs or one pack decides to engage another, the ensuing confrontations are almost always aggressive. In these cases, each pack tries to displace the other and, if possible, catch and kill an adversary.

But what makes one pack better or more successful at aggressive encounters with another group? Is it simply a numbers game? Does the larger pack always win? If so, that would fit well with the first line of Kipling's writings: "The strength of the Wolf is the Pack." Using data gathered during direct observations of 121 aggressive encounters between packs from 1995-2011, we were able to test these questions. As expected, pack size was important to successful conflicts. The larger group was more likely to win (Cassidy et al. 2015), as seen in groups of African lions, chimpanzees, and hyenas (Mosser and Packer 2009, Wilson et al. 2002, Benson-Amram et al. 2011). And just one wolf can make quite a difference; a pack with one more wolf than its opponent has 140% higher odds of winning (or 2.4 to 1). If a pack of 10 fought a pack of nine 100 times, the pack of 10 would win about 71 of the encounters.

If the strength of the wolf is the pack, it makes sense that wolves have evolved to live in large groups. Between 1995 and 2015, Yellowstone packs averaged 9.8 wolves and frequently grew to 20, with the largest pack recorded at 37 members. But living in such a large family isn't always beneficial to other aspects of wolf life. The most efficient pack size for successful elk hunting is only four wolves (MacNulty et al. 2012) and eight for reproduction (Stahler et al. 2013). Living in a large group often means each individual wolf gets less to eat (Schmidt and Mech 1997). The largest packs tend to exhibit more fission-fusion behavior (Metz et al. 2011), much like chimpanzees and hyenas (Lehmann and Boesch 2004, Smith et al. 2008). They may be able to get away with being less cohesive because when they break into smaller groups, each wolf gets more food; and as long as each group is larger than its neighbor's full size, it is still likely to win in a territorial contest.

Wolves do several things to indicate that on some level, they might realize pack numbers give them an advantage. They will often disperse in same-sex cohorts. These pack mates, typically siblings, look to join an opposite sex individual or, even better, a cohort of opposite sex wolves. Most packs in Yellowstone have formed this way. Becoming an immediately-sizeable pack is critical to establishment and persistence on the wolf-dense northern range (wolf density in Yellowstone's northern range has ranged from 20.1 to 98.5 wolves/1000km^2 and averages 52.9, almost double the average wolf density in northeastern Minnesota and 10 times higher than Denali National Park [Fuller et al. 2003]). While each year new wolf pairs form, since 1995 only two simple packs—packs made up of one male and one female—have successfully raised pups and established a territory in the hyper-competitive northern range (Leopold, which formed early on in 1996; and Swan Lake, which formed at the western edge of high-wolf density territories).

Although infanticide, the killing of pups, has been recorded in gray wolves (Latham and Boutin 2012, Smith et al. 2015), it is less common than in bears and wild felids, and occurs when one pack attacks the wolves at the den site of another pack. Spring is the most effective time for one pack to impact another; den-attacks are more likely to result in adult and pup mortality, sometimes even wiping out an entire litter (Smith et al. 2015). Unlike wolves, female bears and felids become sexually receptive after they stop lactating, thus motivating males to kill nursing juveniles and mate with the female, replacing a rival's offspring with their own (Hausfater and Hrdy 2008). By contrast, female wolves come into estrus only once per year for about a week (Asa et al. 1986). So although mating competition is intense for a short time, there is no immediate advantage for outside males to kill dependent young. In fact, the evidence suggests that newly established breeding males attend the pups as if they were their own. There are several cases of a new dominant male joining a pack, either when the dominant female is pregnant with the previous male's pups (e.g., the Lamar Canyon pack in 2015) or after the pups were born. This suggests the new male realizes the value in raising unrelated pups; it ensures his pack size increases and remains competitive against neighboring packs. He can then breed with the female the next mating season—an incredibly long-vision for individuals that, in Yellowstone, only live an average of 4.6 years (MacNulty et al. 2009a).

During 121 aggressive interactions recorded in Yellowstone, 71 escalated to a physical attack and 12 resulted in mortality. We also recorded seven cases of apparently altruistic behavior, where one wolf was being attacked by a rival pack and its pack mate disrupted the attack

by running close by or even jumping into the middle of the group of wolves. In four cases the victim escaped. Kipling penned a similar scenario wherein Mowgli was saved from a rival pack of wolves by his lead male wolf, who was injured and eventually died—effectively giving his life for his pseudo-offspring. The risky behavior exhibited by the altruist is difficult to explain; but if successful, it enjoys the benefits of maintaining a packmate, who usually shares its genes (kin selection [Hamilton 1964]) and may reciprocate or aid them in the future (reciprocal altruism [Trivers 1971]). Whether it is through rescuing a pack mate, raising unrelated offspring, or traveling in a large pack to defeat rivals, "The strength of the Wolf is the Pack" rings true.

But there is the second part: "The strength of the Pack is the Wolf." Could Kipling be right? Could there be some pack composition influence: that one individual has a disproportionate effect, maybe helping its pack beat an opponent in an aggressive encounter, even when outnumbered? While statistically holding pack size fixed, we tested for effects from all age and sex categories. We also tested to see if residents were more likely to defeat intruders. This home-field-advantage hypothesis was not supported; even intruders were likely to win if they were larger. But Kipling would be happy to know that some types of wolves have a significant and positive effect on their pack's success: adult males and old adults (6 years or older; Cassidy et al. 2015). Adult males are the most aggressive wolves in the pack, and having one more than a rival meant 65% higher odds of winning (1.65 to 1). Males are 20% larger and more muscular than females (Morris and Brandt 2014), though this actually hinders males during some stages of prey hunting, as their bulk makes them slower (MacNulty et al. 2009b). This sexual dimorphism probably evolved as an adaptive response to intense inter-pack competition and protection of the family unit through fighting. A male wolf's aggressiveness actually increases throughout his entire lifespan, even as hunting ability and body size diminish into old age (MacNulty et al. 2009a, b).

Perhaps related to the value of adult males to territoriality, we have recorded several cases of an unrelated male joining an already established pack as a subordinate member. Even though the new male could be viewed as competition for breeding rights with the females, he is accepted, perhaps for the positive influence he has on pack success when encountering a neighbor. Conversely, in 20 years we have never recorded an unrelated female joining an already-established group. Females did not have an effect on conflict success. Their

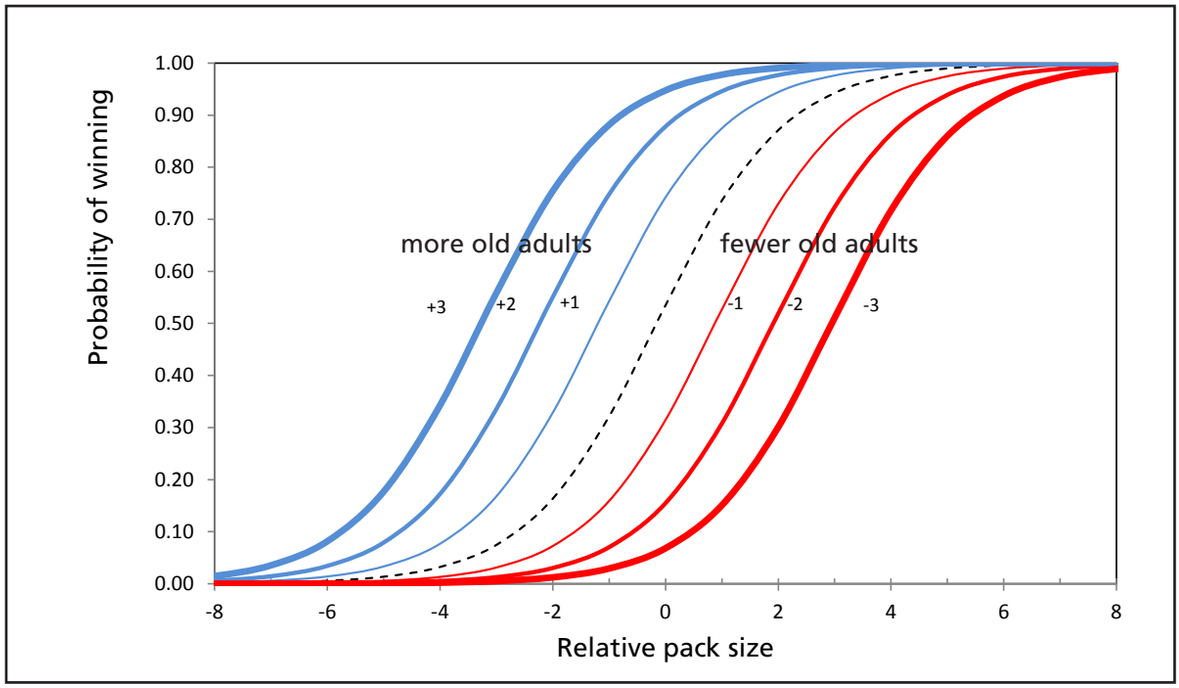

Figure 2. Predicted values for the probability of a wolf pack winning an aggressive inter-pack interaction based on relative pack size (RPS) and old adults. Red lines indicate probability of winning while having relatively fewer (-1, -2, -3) old adults than an opponent. Blue lines indicate probability of winning while having relatively more old adults than an opponent. Data collected from 1995-2011 in Yellowstone National Park.

aggression stays approximately constant throughout their entire lifespan and may drop slightly during their most reproductively-active years, likely a product of self-preservation.

But the most influential factor in whether or not a pack defeated an opponent was the presence of an old wolf. A pack with one old wolf more than the opposition has 150% greater odds of winning, making age more important than having a numerical advantage (figure 2). But why? Old wolves are past their physical prime, participating less and less in hunts as they age, instead relying on the younger, faster, stronger wolves to risk bison and elk hooves and antlers to provide food for the entire pack (MacNulty et al. 2009b). Even the lead wolf in *The Jungle Book* eventually became so old that he rarely left his lair yet was still the leader, as Kipling wrote in one of the last lines of wolf code or "The Law of the Jungle":

> ***"Because of his age and his cunning,***
> ***because of his grip and his paw,***
> ***in all that the law leaveth open,***
> ***the word of the head wolf is law."***

What old wolves possess is experience. They've encountered competitors many times, seen pack mates killed, participated in killing rivals. They may avoid a conflict they figure they can't win, upping their chance of survival. Having an experienced wolf allows a pack to draw from past knowledge, increasing the odds that even a small pack can defeat a larger pack.

As death by rival pack is by far the most common cause of natural mortality, the packs that can reduce this risk by being larger than their neighbors, having more adult males, or having old adult pack members are the ones most likely to acquire and maintain productive territory. Those territories include safe places to raise pups, lots of prey, and separation from humans and roads. One pack in Yellowstone, the Mollie's pack (originally called the Crystal Creek pack) has persisted for over 21 years, likely because it has traditionally been one of the largest packs with many adult males and long-term, old members. This pack has had only six dominant males and five dominant females in their entire history—reigns that help explain the pack's success and longevity.

The loss of an old adult or an adult male, through natural- or human-causes, reduces the competitive strength of the pack, likely affecting the remaining pack members' long-term survival, reproduction, ability to hold productive territory, and ultimately the entire pack's persistence. Over 100 years ago, when Kipling wrote "For the strength of the Wolf is the Pack, and the strength of the Pack is the Wolf," he couldn't know his creative writings would someday be interwoven with wolf research. But maybe that is why *The Jungle Book* is still such a classic; although Kipling's premise of wolves raising a human boy is obviously fictitious, the way he describes the heart of the wolf pack and the ways the pack treats its family versus rivals is based in truth and, now, supported with science.

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Kira Cassidy is a research associate with the Yellowstone Wolf Project. After graduating from Southern Illinois University in 2007, Kira started as a biological technician with the Wolf Project in 2008. For two years Kira worked on the Druid Road Management crew and participated in six winter studies, all but one following the famous Druid Peak pack. In 2013 she completed a MS degree at the University of Minnesota, advised by wolf biologist Dr. L. David Mech. Her projects focused on territoriality and aggression between wolf packs. In 2014 Kira accompanied a film crew to Ellesmere Island, Canada, to document arctic wolves. Living next to a wolf den for six weeks fostered Kira's desire to help communicate science through media, art, and writings for the public. Kira's current projects focus on wolf pack behavior and sociality. Results from some of these projects highlight the importance of old adults in a wolf pack and led Kira to consider connections to other social species, including humans. This was the topic of Kira's TEDx talk in Bozeman, Montana, in April 2016.

LEADING THE WAY:
Women in Science

Lisa Koitzsch, Kira Cassidy, Erin Stahler, & Brenna Cassidy

Early on, almost all people who studied wolves were men (with the notable exception of Lois Crisler who wrote *Arctic Wild* in the 1950s). Whether or not this influenced the science being done is debatable, and perhaps unknowable; but men and women often approach the same situation or problem differently. This may be especially evident in research concerning who was the "leader of the pack." Arguably, the very first wolf biologist, Adolph Murie, who studied wolves in Mount McKinley National Park (now Denali National Park and Preserve) in the 1930s and 40s set the stage for years to come in this area of behavioral study. Murie closely observed wolf behavior in the park and at one point in his book *The Wolves of Mount McKinley* wrote, "He [the alpha male] seemed more solemn than the others, but perhaps that was partly imagined by me, knowing as I did that many of the family cares rested on his shoulders." More recent research in Yellowstone and Ellesmere Island indicates it may be the alpha (now called the dominant breeder) female who runs the show.

- Doug Smith

Lisa Koitzsch currently works as a technician for the Yellowstone Wolf Project. She graduated from Johns Hopkins University with a BA in Humanities and French Literature and worked for several years in publishing and administration. During the two intensive months of winter study, her main focus is downloading location data from GPS-collared wolves, creating maps of clustered wolf locations, and coordinating searches of these clusters, which typically represent feeding and resting locations, in order to estimate wolf-pack predation rates. Lisa has worked with the wolf project every winter since 2008, when she and her husband, Ky, were hired as a two-person crew to conduct necropsies on wolf-killed prey. In addition to her current work with the Yellowstone Wolf Project, Lisa and Ky are working on a three-year noninvasive study estimating winter population size and vital statistics of moose in Yellowstone National Park's Northern Range.

Kira Cassidy (see page 42)

Erin Stahler (see page 54)

Brenna Cassidy is a Biological Technician with the Yellowstone Wolf Project. She graduated from University of Wisconsin-Stevens Point as a Wildlife Ecology major in 2012 and moved to Yellowstone National Park shortly after to participate in her first winter study. Since then, she has done six winter studies and has spent most of that time with the Junction Butte pack. Brenna has worked on a number of projects in Yellowstone including the Raptor Initiative, the Core Bird Program, and the Yellowstone Cougar Project. Studying multiple species has allowed Brenna to travel throughout the park by plane, foot, canoe, and skis. Seeing the park through the eyes of multiple species has shown her that each has a important role in the interconnected ecosystem of Yellowstone.