Motherhood of the Wolf

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"She is the creature of life, the giver of life, and the giver of abundant love, care, and protection. Such are the great qualities of a mother." – Ama H. Vanniarachchy, archeologist and scholar

For many of Yellowstone's species, spring's arrival not only brings relief from winter's challenges, but also resets the biological calendar that governs individuals' lives. As April's temperatures rise and its expanding daylight weakens the veneer of snow and ice, many animals enter a new phase of their life history through the process of birth. The female raven at her cliff ledge nest, a cow bison on the big sage flats, and a mother wolf down inside a boulder den—all share in the culmination of their reproductive efforts from the previous months. There are many challenges for animals of any sex and age to simply survive from one life stage to the next. For a mother charged with the great expense of gestation, birthing, lactation, and successful raising of offspring, the costs are extraordinary. Because of certain individual traits, or social and environmental conditions, some mothers are more successful than others. While awe and admiration is deserved for all who become mothers, a biologist studying animal reproduction is particularly interested in asking: What are the qualities of a great mother? What factors play most significantly in shaping success at this key life-history stage?

Individuals' life histories are the patterns of growth, reproduction, and survival over their lifetimes. Variation in growth rates, age of maturity, reproductive performance, and lifespan are the result of both species' evolutionary histories and the environments to which populations of individuals are exposed. For highly social species, social conditions can play a particularly influential role in individuals' life histories, even beyond that of prevailing ecological conditions. Wolves are a great example of the role sociality plays in this regard, as our scientific investigations on Yellowstone wolves effectively show. Through group hunting (MacNulty et al. 2012, 2014) and carcass use (Wilmers et al. 2003), pack defense of territory (Cassidy et al. 2015), advantages to the infirmed (Almberg et al. 2015), or the assistance of nonbreeding helpers in raising young (Stahler et al. 2013), individual wolf survival, and the ability of pups to survive, is often influenced by the qualities of the pack.

Reproduction is of great interest to biologists given its importance to population dynamics through recruitment, and to evolutionary processes through changes in heritable traits passed from parents to offspring over successive generations. Scientists studying a variety of species have demonstrated that reproduction in social organisms is shaped by numerous morphological, behavioral, and life-history traits, as well as environmental conditions faced by breeders (Clutton-Brock 1988). However, little is known about the relative influence of different traits, particularly in the context of environmental conditions that determine their value in adapting to changing environmental conditions. Interestingly, although wolves are among the most-studied mammals in the world (Mech and Boitani 2003), surprisingly little has previously been researched on which traits drive their reproduction. Here, we describe how our detailed monitoring of female breeders in Yellowstone has allowed us to better understand wolf reproduction. Using an impressive 14-year dataset (1996-2009) on individually known females' annual pup production, we were able to simultaneously evaluate and rank the effects of individual traits, pack size and composition, and ecological factors influencing female reproductive performance (Stahler 2011, Stahler et al. 2013).

For Yellowstone's wolf packs and the community of biologists and wolf enthusiasts who follow their lives, great excitement surrounds the arrival of pups each spring. Through this great maternal feat and the actions of the females' mates and pack members, much of our ecological and cultural perception of the wolf pack revolves around having and raising pups. But before describing our findings, a brief overview of wolf natural history will help place the importance of reproduction in context.

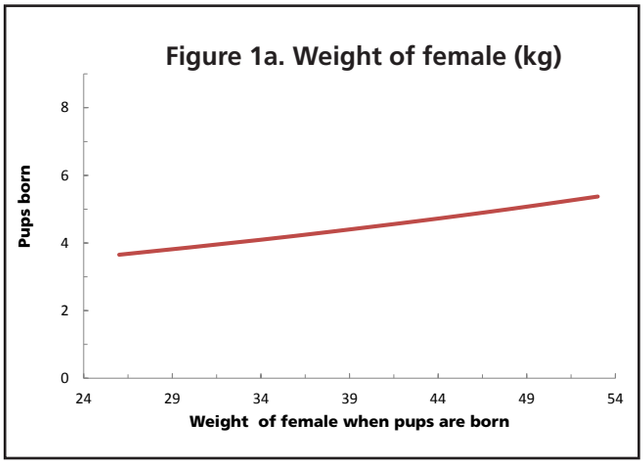
Wolves live in territorial family groups that cooperate to capture prey, raise young, and defend resources from

competitors (Mech 1970). Wolves have a brief life history relative to other large carnivores, including early first reproduction, high fecundity, rapid development, and relatively short lifespans. The basic social unit of wolf populations is the mated pair and their offspring (Mech 1970). Due to delayed dispersal, wolf packs typically consist of multiple age and sex class compositions. Wolves are true cooperative breeders, with the care of offspring performed by both parents, as well as by other pack members. Wolves are sexually dimorphic (males and females have different size ranges), with males about 16-24% larger than females (MacNulty et al. 2009a), and have a multi-year growth pattern (MacNulty et al. 2009a, Stahler et al. 2013). Differences in body size between males and females are presumably shaped by selection pressures related to their respective reproductive strategies and roles in hunting and territoriality.

In Yellowstone, as in most wolf systems, breeding occurs between January and March. Following a 61-63 day gestation period, offspring are born underground in dens by late April. With typically just the dominant male and female mating within a pack, wolves have long been classified as having a monogamous mating system (Mech 1970). However, sexual dimorphism, unbalanced reproductive success of both sexes, and occurrences of multiple litters produced by different females in a pack suggest the evolution of a more flexible mating system. In fact, we've documented about 25% of our packs each year exhibiting exceptions to monogamy, with both dominant and subordinate females and males participating in breeding activity. This phenomenon is believed to be influenced largely by Yellowstone's prey abundance, wolf density, and more complex pack structures containing multiple, unrelated, opposite-sex pack members (Stahler 2011).

Our research simultaneously assessed and ranked the strength of factors driving female reproductive success. Specifically, we evaluated how a mother's age, body size, coat color, genetic variability, and pack size and composition influenced litter size and pup survival. The role of environmental stressors such as competition and disease were also evaluated. By capturing, radio-collaring, weighing, and monitoring individuals through time, as well as applying molecular techniques, we were able to measure individual traits and reproductive performance for breeding females. We measured two components of reproductive performance for each female breeder: litter size (pups emerging from dens) and litter survival (pups surviving until their first winter). Early litter sizes averaged 4.7 pups, with one litter as large as 11. The number of pups surviving until independence averaged 3.1 per litter and ranged up to 9. Pups are generally weaned at 5-9 weeks of age, then fed by various pack members via meat regurgitation until the pups can accompany adults to carcasses by autumn. To evaluate the role of body mass, we used age-specific weights taken from a female growth model. Results showed females grow rapidly in their first year of life, then more moderately until reaching maximum body size just before three-years-old. This age corresponds to when females typically begin reproducing.

We first looked at what individual traits are characteristic of a successful mother. Reproductive performance improved with increasing body mass, with larger females having larger litters and better pup survival (figure 1a). This pattern is consistent with many other



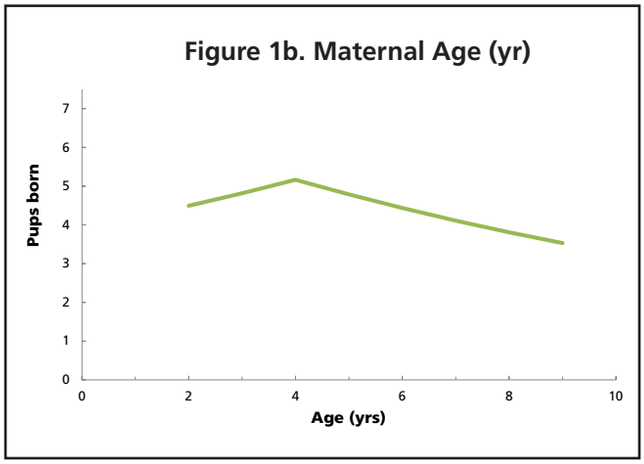


Figure 1. Effects of (a) body mass and (b) age on the number of pups first emerging from dens (pups born) in Yellowstone National Park, 1996-2009.

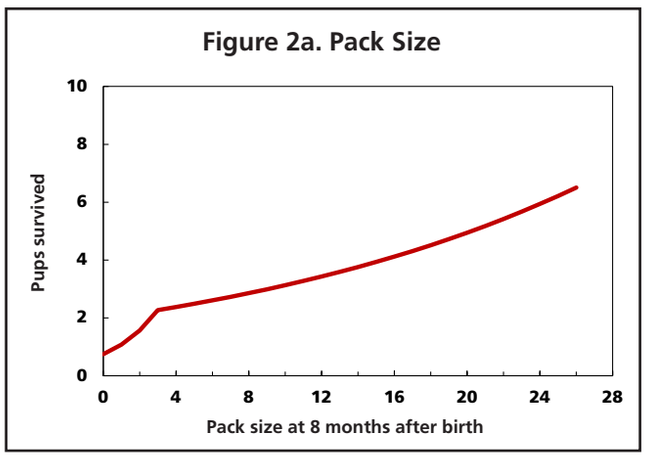
mammals, where larger body size indicates healthier individuals better able to invest resources towards reproduction. For wolves, the reproductive benefits of large size, combined with rapid growth and early age of first reproduction, indicate the first couple years of life are important to a female's lifetime reproductive success. As with other species, we found age-specific reproductive performance in wolves, a previously undetected pattern (figure 1b). Females showed no improved success following their first reproduction, but exhibited senescence (i.e., age-related deterioration in performance) around age five, which was the median lifespan for wolves during our study.

Although measures of individual genetic variation were not correlated with success, we found a surprising effect of coat color. Other work on Yellowstone wolves established that gray or black coat color is determined by the *K*-locus, a gene that is associated with immunity in other vertebrates (Anderson et al. 2009). Interestingly, gray females had a 25% greater litter survival than black females. While the mechanism for this effect is currently unclear, it is possibly due to how a female's color genotype influences physiological trade-offs important to reproduction and survival.

As in other cooperative breeding species, group size is an important predictor of a mother's success. Early litter sizes peaked when eight wolves were present, after which they decreased with additional pack members. This latter pattern may reflect costs on maternal condition incurred from intrapack competition for food or social stress during the breeding season. In contrast, pup survival was enhanced with increasing pack size (figure 2a). In addition to having more helpers to provision young, larger packs have numerical advantages during intergroup and intraguild competition for resources like food (Wilmers et al. 2003) and territory (Cassidy et al. 2015) which contribute to offspring survival. Importantly, the positive influence of helpers was strongest for small packs, indicating there is a threshold below which packmates are critical to breeder success.

However, it is not just a numbers game. Just as individuals vary in quality, we've learned so do packs. With variation in sex and age composition, group size alone fails to identify the true costs and benefits of pack members on a mother's success (Stahler 2011). For example, mothers benefited more from additional male helpers than female helpers. This makes sense in light of the demonstrated importance of males as more proficient hunters (MacNulty et al. 2009a) and aggressive defenders of territory (Cassidy et al. 2015). On the other hand, mothers experienced reduced litter survival in packs containing multiple breeding females. Cooperation presumably has its limits when mothers compete for resources needed to raise their own pups in a multi-littered pack. Regarding helpers' ages, mothers benefited the most in packs with more prime age wolves (2-5 years) than yearlings and older helpers, likely due to these individuals being higher quality foragers (MacNulty et al. 2009b).

Finally, besides a mother's and her family's qualities, her environmental surroundings can be important. We found higher wolf density (figure 2b) and disease outbreaks had significant negative effects on pup survival. Our finding of negative density-dependent effects is likely due to increased competition and strife with other packs under high wolf densities. Outbreaks of canine distemper virus were associated with pronounced pup



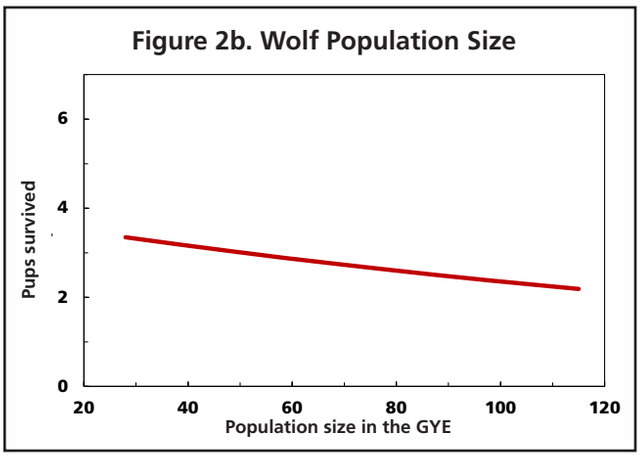


Figure 2. Effects of (a) pack size and (b) wolf population size (number of wolves/1000km^2 in the northern GYE) on the number of pups in a female's litter surviving until independence (pups survived) in Yellowstone National Park, December 1996-2009.

mortality. Although unpredictable, disease prevalence is a critical factor for female reproduction and may be a strong selective force in wolf systems, especially if linked to individual traits that offset its negative effects (e.g., coat color).

Having shown what the qualities of a successful mother wolf are, we then asked: What is the relative importance of different traits under varying environmental conditions? A sensitivity analysis, which allowed comparison of effects across a common scale, indicated body mass is most influential, followed by pack size. Reproductive gains due to larger body size and cooperative breeding appear to mitigate losses associated with population density and disease effects. These findings highlight the adaptive value of large body size and sociality for wolves, in promoting a mother's success in competitive environments.

Our work on Yellowstone wolves helps to clarify how life history, sociality, and ecological conditions interact in this cooperatively breeding carnivore, and ranks the adaptive value of different traits. Future work aims to explore how similar traits influence male reproduction, breeding strategies, and the link between food, territory, and reproduction. Knowledge about which traits promote fitness in the context of environmental challenges may help predict how wild populations will respond to global climate change, disease, habitat alteration, and human exploitation. Ultimately, we hope this knowledge serves the conservation of this controversial but charismatic and ecologically important carnivore. If decades of research and management around the world have taught us one thing, it is that wolves are resilient in the face of great challenges. Studies such as these from Yellowstone help explain why.

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