tain their position for years, producing several generations of offspring. Even following the death of one or both breeders, a pack can persist through survival of remaining offspring and/ or accepting stepparents into the pack. Turnover from generation to generation can result in the same family occupying an area for years—and hence the well-known packs in places such as Yellowstone and Denali National Parks.

Exactly how and why wolves evolved this type of social system is the subject of tremendous interest and debate among scientists. What is well established, though, is that the stable, cooperative nature of wolf packs provides advantages to the individuals within them. The presence of litters of different ages enhances the survival of newborn pups. Offspring that remain in their natal, or birth, pack into adulthood

All in the Family:

by JUSTIN H. BOHLING

Perhaps no word is more associated with wolves than the term "pack." The pack is one of the defining characteristics of wolf biology and stirs fascination in scientists and the public. Decades of research have opened a window into the inner workings of these social groups.

In wild populations the typical wolf pack is a hierarchical family unit composed of a dominant breeding pair and its offspring, cooperating to hunt prey, raise pups and defend territory. It can be remarkably stable; breeders can mainhave higher survival rates than those that disperse. Research on red wolves in North Carolina suggests that male wolves that hang around the pack for a few years before moving on (a phenomenon called delayed dispersal) are more likely to survive and father offspring than those that take off immediately upon becoming adults.

On the flip side, studies of wild wolf populations have revealed the effects of breeder loss and social disturbance. Packs that experience the loss of a breeder and fail to accept a new breeder are more likely to dissolve, meaning the individuals move apart and no longer act as a cohesive group. Loss of breeders makes a pack more susceptible to takeover from neighboring packs, too. If the pack does manage to persist following the loss of the primary breeders, it often does so at a smaller size, and if the remaining wolves manage to produce any offspring those pups are less likely to survive into

Pack Disruption and Social Stability

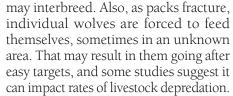
adulthood. In populations experiencing high mortality and breeder loss, packs become composed of increasingly unrelated individuals instead of the typical related family group.

As one could probably guess, breeder loss can be amplified by human-caused mortality. To be clear, wolf populations free from human impact do lose breeders and experience turnover. However, the yearly rate of breeder loss is higher for populations that experience consistent pressure from humans. Further, the patterns of breeder loss are different. Normally breeders lose their position once they ascend in age and their vitality declines. Human-inflicted death, though, can hit vibrant wolves at their peak.

Now, there is a novel aspect of this phenomenon. Research from around the globe has shown that wolf populations can tolerate moderate levels of mortality every year, often up to 30 percent. In other words, in many areas one-third of the wolf population can be removed each year, and yet the total population can remain stable from year to year. However, while the *number* of wolves in a population may be stable, individual packs can be in dramatic flux. Therefore the composition of the entire population changes.

So, how do these populations stay stable? Even with the annual loss, the wolves that do breed manage to produce enough pups to replace those individuals that move away or die. Even more importantly, the dissolution of territorial The typical wolf pack is a hierarchical family unit composed of a dominant breeding pair and its offspring, cooperating to hunt prey, raise pups and defend territory. Packs can be remarkably stable. On the flip side, studies have revealed the effects of breeder loss and social disturbance. packs allows an influx of dispersers from neighboring regions, maintaining the number of wolves in a given area. Also, breeding wolves comprise such a small portion of a population (generally 15 to 33 percent during fall hunting seasons) that often relatively few are taken.

This quirk in wolf biology masks the impact of breeder loss. Even with moderate levels of human exploitation, a wolf population can still hit and even exceed management targets. However, the nature of these populations fluctuates. In heavily exploited populations, the social dynamics are altered, which has consequences on how wolves behave and move about the landscape. For eastern wolves in southeastern Ontario and red wolves in North Carolina. breeder loss is believed to facilitate interbreeding with coyotes. The thought is that the sudden loss of a breeder can cause its mate or another pack member to quickly look for a mate. If the only individuals available nearby are coyotes, then they



This phenomenon is not unique to wolves: other carnivores display similar social reactions to hunting. Research on cougars in the Pacific Northwest has shown that trophy hunting tends to remove older males that rule over expansive territories containing the home ranges of multiple females. These males defend this territory from younger males searching for their own place to settle. When these older males are removed, younger males rush in. They enter territory already occupied by females, some of which may have offspring from the previous male. A new young male may view these offspring as competition—not only for him, but for his potential offspring. Areas with heavy hunting of cougars often see higher levels of infanticide. Females will then adjust their behavior to avoid these younger males, sometimes selecting poorer quality habitats.

The presence of more young males also leads to more territorial overlap. When these territories overlap in humanoccupied areas, it can lead to more human-cougar conflict. Heavy hunting of cougars results in more livestock predation, not less. Similar patterns have been observed for other carnivores such as bears and big cats, and other species with complex social systems such as African elephants.

The question then becomes how to address this issue from a wildlife management perspective. Wildlife managers are trained to use a host of information to understand animal populations. Typically it comes down to the numbers. Data such as births, deaths, immigration, emigration, recruitment, habitat availability and quality, and other variables feed mathematical models that estimate the number of individuals standing at the end of the year. That is how hunting quotas are set; managers use those data to estimate how many individuals can be harvested and still keep a population within a given target. Targets are based on a variety of factors such as

maintaining population viability, minimizing human-wildlife conflict, preventing overabundance, meeting legal requirements and others.

Adding social dynamics to the mix introduces another layer of complexity. Individuals can no longer be seen as mere numbers; the presence and death of certain individuals, such as pack breeders, has a disproportionate effect on the population. Individuals targeted by hunters, such as the breeding male, the tom cougar or the bull elephant are important to maintaining stable social dynamics.

Incorporating social dynamics also raises the question of what constitutes successful population management. Is the goal based solely on numbers, or do the characteristics of the population matter? There is an increasing emphasis in conservation circles on the concept of "ecologically relevant" recovery. This means that the recovery of depleted species is defined not only by its abundance, but also its return to its ecological niche and impact on the ecosystem. A companion concept may be centered on the idea of social recovery, meaning that successful management facilitates the expression of natural social dynamics. For wolves, this could mean fostering an environment where packs can ebb and flow, with minimal disturbance from humans, in environments such as national parks, wilderness areas and protected zones.

Creating such environments would require a shift in approach to setting hunting regulations and responding to depredation issues. Such an experiment is being carried out in the state of Washington with cougar management. Wildlife managers have adopted regulations and hunting quotas designed to limit mortalities of older male cougars and to target young males instead.

Science has provided fascinating insights into the social systems of wolves, including the impact of pack disruption on wolf behavior and social dynamics. There is always more to learn, but the real challenge for the future will be incorporating a more complex view of wolf social biology into our management of this highly scrutinized species.



References

- Borg, B. L., Brainerd, S. M., Meier, T. J., & Prugh, L. R. (2015). Impacts of breeder loss on social structure, reproduction and population growth in a social canid. *Journal of Animal Ecology, 84, 177–187.*
- Brainerd, S. M., Andrén, H., Bangs, E. E., Bradley, E. H., Fontaine, J. A., Hall, W., ... Wydeven, A. P. (2008). The effects of breeder loss on wolves. *Journal of Wildlife Management, 72*(1), 89–98.
- Rutledge, L. Y., Patterson, B. R., Mills, K. J., Loveless, K. M., Murray, D. L., & White, B. N. (2010). Protection from harvesting restores the natural social structure of eastern wolf packs. *Biological Conservation*, 143(2), 332–339.

Justin Bohling is a conservation biologist with a B.S. from SUNY College of Environmental Science and Forestry, and a Ph.D. from the University of Idaho. His dissertation focused on the endangered red wolf in North Carolina. He has published research articles on wolves and assisted the U.S. Fish and Wildlife Service with red wolf recovery efforts. Currently he is a conservation geneticist at Abernathy Fish Technology Center in Longview, WA.