

Predation Risk Affects Reproductive Physiology and Demography of Elk

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Inducible defenses (changes in morphology or behavior in response to predation or herbivory) reduce an individual's vulnerability to predation but carry costs that select against their expression when predation risk is low. For plants and invertebrates, the costs of inducible defenses have important effects on demography and community structure (1). Elk (like most vertebrates) alter their behavior in response to predation risk, and these antipredator responses are analogous to inducible defenses in plants and aquatic invertebrates. Nonetheless, analyses of wolf-elk dynamics have focused on direct predation, ignoring the potential effects of antipredator behavior on dynamics (2–4). This is surprising, because the effect of changes in elk behavior on plant communities has been discussed extensively [e.g., (5)].

Elk behavior responds to the presence of wolves on a spatial scale of several kilometers and a time scale of minutes to days (6–8). Wolves were reintroduced to the Greater Yellowstone Ecosystem (GYE, United States) in 1995 and 1996, followed by rapid growth and geographic expansion of the wolf population and a concurrent decline in local elk numbers (9). In the Gallatin Canyon portion of the GYE (10), predation risk from wolves varies spatially and temporally (7), and elk respond to the presence of wolves by altering patterns of aggregation, habitat selection, vigilance, foraging, and sensitivity to environmental conditions (6–8). For all of these behaviors, females produce significantly stronger antipredator responses than males (7, 8), and females fall prey to wolves less often than males [in fig. S1, $\chi^2 = 194.8$, degrees of free-

dom (df) = 2, $N = 124$, and $P < 0.0001$]. Here, we show that these antipredator responses are associated with costs that can be measured by changes in reproductive physiology and demography.

In the GYE, elk populations mix in the summer but occupy discrete winter ranges with relatively little movement between populations (8). Elk-wolf ratios vary substantially across winter ranges (Fig. 1). Elk-wolf ratios are generally low in the center of the ecosystem and high at its edge, where wolf culling is common and wolf occupancy is sporadic. We assessed elk reproductive physiology by using enzyme-linked immunosorbent assay (ELISA) to measure progesterone concentrations for 1495 fecal samples from populations on five winter ranges, 2002–2006 (10). Across populations and years, mean fecal progesterone concentrations correlated strongly with elk-wolf ratios: Low progesterone values were associated with heavier predation pressure [in Fig. 1A, adjusted correlation (r^2_{adj}) = 0.54, $F_{1,13} = 17.6$, and $P = 0.0011$].

The recruitment of calves declined significantly in two of these populations since local recolonization by wolves (4, 8), and progesterone concentrations were correlated with calf recruitment in the subsequent year (in Fig. 1B, $r^2_{\text{adj}} = 0.32$, $F_{1,11} = 6.00$, and $P = 0.032$). The lowest observed progesterone concentration was associated with the lowest calf-cow ratio (8 calves per 100 cows), which was the lowest of 20 calf-cow ratios measured for that site over a period of 57 years. The highest progesterone concentrations were associated with calf-cow ratios above 30 (typical of growing populations) and with estimated preg-

nancy rates near 100% (10). Lastly, calf-cow ratios correlate directly with predation pressure (in Fig. 1C, $r^2_{\text{adj}} = 0.58$, $F_{1,11} = 12.95$, and $P = 0.004$).

Although correlative, these results suggest that wolf predation has indirect effects on elk dynamics, driven by costs of behavioral defenses that alter reproductive physiology and demography. Recent declines in calf recruitment (2–4, 8) are not well explained by density dependence, because these populations have recently been stable or declining. We have previously found that local winter severity is not a good predictor of recent shifts in elk demography and dynamics, and winters were locally mild over all years of this study (8). Lastly, data from radiotagged elk calves on the Gallatin Canyon site showed that none were killed by wolves in their first summer and fall ($N = 30$ calves, 13 mortalities). A larger sample of radiotagged calves on Northern Range of the GYE also showed little wolf predation on calves before their first winter (11): Together, these studies detected very low rates of direct wolf predation on calves before early-winter calf-cow estimates.

The benefit of antipredator behavior is a decreased risk of predation, and this is incorporated automatically into measures of the direct rate of predation. In contrast, most analyses of vertebrate predator-prey dynamics do not account for the costs of antipredator behavior. Without consideration of the indirect effects of predation, it is likely that decreased reproduction would be mistaken for bottom-up limitation by resources. Our data show that the reproductive costs of antipredator behavior can be large, with important consequences for prey dynamics.

References and Notes

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Supporting Online Material

www.sciencemag.org/cgi/content/full/315/5814/960/DC1
Materials and Methods

Fig. S1

References

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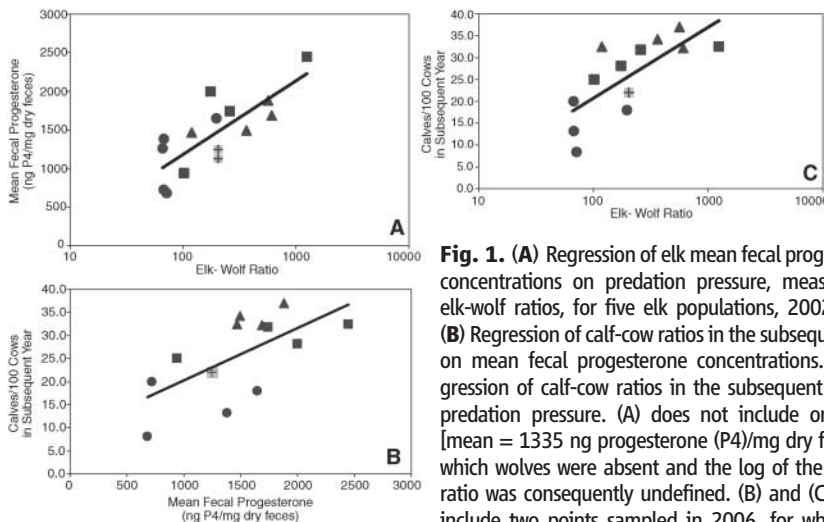


Fig. 1. (A) Regression of elk mean fecal progesterone concentrations on predation pressure, measured by elk-wolf ratios, for five elk populations, 2002–2006. (B) Regression of calf-cow ratios in the subsequent year on mean fecal progesterone concentrations. (C) Regression of calf-cow ratios in the subsequent year on predation pressure. (A) does not include one point [mean = 1335 ng progesterone (P4)/mg dry feces] for which wolves were absent and the log of the elk-wolf ratio was consequently undefined. (B) and (C) do not include two points sampled in 2006, for which subsequent calf-cow ratios are not known. Data point shapes denote different elk winter ranges within the GYE.