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Creel S, Christianson D and Winnie JA 2011. A survey of the effects of wolf predation risk on pregnancy rates and calf recruitment in elk. Ecological Applications 21: 2847–2853
http://dx.doi.org/10.1890/11-0768.1

Ecological Applications, 21(8), 2011, pp. 2847–2853

A survey of the effects of wolf predation risk on pregnancy rates and calf recruitment in elk

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Abstract. We have previously found that the behavioral responses of elk to the risk of predation by wolves are correlated with changes in habitat selection, altered diets, reduced food intake, decreased fecal progesterone concentrations, and decreased calf recruitment. P. J. White et al. recently questioned these results, concluding that "multiple lines of evidence and/or strong validation should be brought to bear before relying on indirect measures of how predators affect pregnancy rates." Here, we systematically surveyed available data and found that five studies (with data from 10 widely distributed populations) have directly detected decreases of 24–43% in elk pregnancy rates in response to increased predation risk. This survey includes data not discussed by White et al. from their own research, which reveal a 32% decrease in pregnancy rates following wolf recolonization in central Yellowstone. Following the survey of available data, we discuss several methodological and statistical problems in White et al.'s study that would be expected to mask the effects of predation risk. While other factors also clearly affect elk recruitment, multiple lines of evidence using a broad array of methods have detected an association between predation risk and reduced reproduction in elk.

Key words: behaviorally mediated effect; Canis lupus; Cervus elaphus; *elk; population dynamics; predation; pregnancy; progesterone; reproduction; risk effect; wolf.*

BEHAVIORAL AND ECOLOGICAL RESPONSES OF ELK TO THE RISK OF PREDATION BY WOLVES

Predators can limit prey by direct predation or through risk effects, which are the costs of antipredator responses. Behavioral responses to predation risk include changes in habitat use (Werner and Peacor 2003, Creel et al. 2005, Heithaus and Dill 2006), vigilance (Lima and Dill 1990, Armitage 2004), foraging (Lima and Bednekoff 1999, Brown and Kotler 2004), aggregation (Boesch 1991, Krause and Ruxton 2002, Caro 2005), movement patterns (Sih 1980, Sih and McCarthy 2002, Fortin et al. 2005), and sensitivity to environmental conditions (Winnie et al. 2006). The benefit of antipredator behavior is a reduction in the risk of direct predation, and these benefits are automatically incorporated into measurements of the predation rate. In contrast, the costs of antipredator responses are often ignored by studies of predation as a limiting factor. Risk effects can be manifest by reduced survival, growth, or reproduction (Peckarsky et al. 1993, 2008, Creel et al. 2007, Pangle et al. 2007, Creel and Christianson 2008). Experiments allow risk effects to be clearly identified and quantified (Schmitz et al. 1997, 2008), but this task is more difficult in field studies (Creel and Christianson 2008). With many traditional designs for field studies, these costs are simply aggregated with bottom-up limitation through competition for resources. Recent empirical research has shown that risk effects on prey dynamics can be as large as direct effects, or even larger (Schmitz et al. 1997, Nelson et al. 2004, Preisser et al. 2005, Pangle et al. 2007). Nonetheless, many analyses of predation as a limiting factor still consider only direct offtake, particularly in studies focusing on conservation and management, and particularly in studies of large vertebrates.

Elk (*Cervus elaphus*) alter many aspects of their behavior in response to spatial and temporal variation in the risk of predation by wolves (*Canis lupus*), although these antipredator responses vary in a manner that depends on attributes of their herd, the risk that they face, and the environment in which they encounter predators (Liley and Creel 2008). The behavioral responses of elk to wolves include moving out of preferred grassland foraging habitat into wooded areas (Creel et al. 2005, Fortin et al. 2005), increased vigilance and reduced foraging (Childress and Lung 2003, Winnie and Creel 2007, Creel et al. 2008, Liley and Creel 2008), changes in herd size (Hebblewhite and Pletscher 2002, Creel and Winnie 2005), and changes in their responses

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Manuscript received 6 May 2011; revised 25 July 2011; accepted 5 August 2011.

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to environmental constraints such as snow accumulation (Winnie et al. 2006). Parallel to these behavioral responses, physiological data have revealed a decrease in the quantity of food obtained by elk in the presence of wolves and changes in the composition of their diet that exacerbate nutritional deficits in winter (Christianson and Creel 2008, 2010).

Several elk populations have declined significantly following recolonization by wolves, in some cases to less than one-third of their size immediately prior to wolf recolonization (Creel and Christianson 2008, White 2008, Garrott et al. 2009, Christianson and Creel 2010), and decreased calf recruitment has generally accompanied decreases in population size (Zager et al. 2005, Creel et al. 2007, Creel and Christianson 2008, Garrott et al. 2009, Stephenson 2010). While factors other than predation undoubtedly have important effects on calf recruitment and elk dynamics, predation risk from wolves has been consistently correlated with recent declines in elk recruitment (Creel et al. 2007, Creel and Christianson 2008, Garrott et al. 2009). Collectively, these data suggest a hypothesis that risk effects may have contributed to declining elk numbers in the Greater Yellowstone Ecosystem, in part by affecting calf recruitment.

Considering only data on calf-to-cow ratios from population surveys, changes in calf recruitment in the presence of wolves could have two primary causes (which are not mutually exclusive). First, wolves might prey heavily on elk calves between the annual birth pulse (in late May to early June) and the time of population composition surveys. Composition counts are commonly conducted in early winter, about 6 months after the birth pulse. Testing the hypothesis that early-winter calf recruitment has declined due to neonatal wolf predation requires data on cause-specific mortality for elk calves that are radio tagged immediately after birth and monitored until the time that population surveys are conducted. We radio-tagged 30 newborn elk in our study of risk effects on elk calf recruitment, and detected no predation by wolves in the first six months of life (Creel et al. 2007). Two subsequent studies including a study on Yellowstone's northern range (Barber-Meyer et al. 2008) and a collaborative analysis of data from 1999 calves in 12 populations (Griffin et al. 2011) have confirmed that the rate of predation on calves by wolves is typically low (see Plate 1). In the exceptionally large and broad sample considered by Griffin et al., mortality due to wolves was only 0.04 ± 0.01 (mean ± SE) over the first three months of life, much too low to account for observed declines in calf-to-cow ratios. Griffin et al. also found that "calf survival was lower in systems that contained wolves, despite the fact that these systems had low wolf mortality rates," as predicted by the hypothesis of risk effects.

If direct predation rates are too low to account for decreased calf-to-cow ratios, this further suggests that reproduction might be affected by wolf recolonization. Among elk herds that have declined since wolf colonization, calf-to-cow ratios have declined not only in early-winter surveys, but also in surveys conducted soon after the birth pulse. For example, calf-to-cow ratios in summer counts declined significantly after wolf recolonization in the Gallatin Canyon, from 45 ± 23 calves per 100 cows (mean ± SE, pre-wolf) to 27 ± 3.2 calves per 100 cows (post-wolf; Creel and Christianson 2008).

Based on these patterns, we hypothesized that the antipredator responses of elk entail physiological costs that can alter reproductive physiology and calf recruitment. We tested this hypothesis by collecting 1495 fecal samples from five elk populations in the Yellowstone region over six years. We used the same methods of collection and analysis for all populations, and selected populations to represent winter ranges with a broad range of wolf-to-elk ratios within one ecosystem (with one out-group), sampled in the same span of years. All of the samples used in this analysis were collected after 15 March, because preliminary analyses revealed that progesterone concentrations of pregnant females were not as reliably elevated prior to the third trimester of gestation. Sampling was systematically stratified at two-week intervals until the end of gestation. Sampling in late winter has the advantage of detecting risk effects on reproduction at any stage from conception through parturition. Samples collected earlier would not detect losses that occur late in winter, when the energetic costs of gestation are at their peak and female condition is at its nadir. We emphasize that comparison of samples from different periods of winter would not be valid, a point is relevant to our discussion of White et al.'s methods (see *Methodological and statistical problems in White et al.'s critique*). We used previously published methods to extract steroid metabolites and measure fecal progesterone concentrations, and tested for correlations between wolf-elk ratios, fecal progesterone concentrations, and calf-to-cow ratios. We found that third-trimester fecal progesterone concentrations were correlated with wolf-to-elk ratios, and that mean fecal progesterone concentrations in the gestation period strongly predicted the subsequent calf-to-cow ratio (Creel et al. 2007). We concluded that "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."

White et al. (2011) recently questioned our conclusions, using data from one herd in the Northern Range of Yellowstone National Park. First, they failed to detect changes in the mean pregnancy rate in a comparison of data from 1962–1968 (wolves absent) and 2000–2006 (after wolf reintroduction). Second, they failed to detect a change in body fat within this herd between the two periods. Finally, they suggested that body fat was higher in Northern Range elk than in several other populations (White et al. 2011). However, each of these results suffers from methodological and statistical flaws that would be expected to mask risk effects. When these issues are corrected, the original data show that wolf predation risk is associated with reduced elk pregnancy rates in the Northern Range, as in all other studies of which we are aware. We explain these issues below, after summarizing

PLATE. 1. Newborn elk calves are hidden by their mothers for several days after birth. Hidden calves can be located by observing the mother from a distance until she reveals the location of the calf. Because hidden calves do not flee when approached, they can be radio-tagged to determine survival rates and causes of death. Several studies of radio-tagged calves have found that the rate of predation by wolves in the first months of life is too low to explain observed declines in calf : cow ratios since wolf recolonization. Photo credit: D. A. Christianson.

recent data that confirm a repeated pattern of declining pregnancy rates in elk with wolf recolonization.

DECREASED ELK PREGNANCY RATES SINCE WOLF RECOLONIZATION IN RECENT STUDIES

Garrott et al. (2009) presented data on pregnancy rates of elk in Central Yellowstone based on measurements of serum pregnancy specific protein B (PSPB), serum progesterone, and fecal progesterone. All of these methods detected a large decline in pregnancy rates since wolf recolonization. After wolf recolonization (data from 2002–2007), Garrott et al. (2009) reported a pregnancy rate of 54% based on 39 determinations of serum PSPB, and the same rate based on 48 determinations of serum progesterone. Garrott et al. (2009) reported pregnancy rates of 81% (serum progesterone, 27 samples) and 77% (serum PSPB, 61 samples) for a span of years from 1991–2001, prior to wolf establishment. Thus, their data showed that pregnancy rates declined by 32% with wolf recolonization. This decrease in the pregnancy rate was threefold to 30-fold larger than the decrease in female survival rates in the same population. It is difficult to understand why White and Garrott failed to mention these data while arguing that there is little evidence that pregnancy rates have decreased and that "it is imperative that multiple lines of evidence and/or strong validation be brought to bear when assessing the effects of antipredator responses on elk demographic rates" (White et al. 2011).

Counts by the Wyoming Department of Game and Fish show that calf-to-cow ratios have declined significantly in August–September counts of elk that migrate between Yellowstone's Northern Range and the Crandall/Sunlight Basin region to the east. For nine years prior to wolf recolonization, calf-to-cow ratios for this herd were stable (or slightly increasing) at 30–45 calves/100 cows (with one year below 30), then declined significantly at the time of wolf recolonization to <15 calves per 100 cows (data from Wyoming Department of Game and Fish; Stephenson 2010). As wolf numbers in the area stabilized, calf-to-cow ratios remained significantly below pre-wolf levels for more than a decade. During the same period, calf-to-cow ratios in an immediately adjacent nonmigratory herd with little wolf predation remained high (data from Wyoming Department of Game and Fish). Decreased calf recruitment with wolf recolonization in the Crandall/Sunlight herd was associated with decreased pregnancy rates. Summarizing four years of post-wolf data from serum PSPB, Stephenson (2010) stated that "the average rate of pregnancy in the migratory herd was 68% while the average rate of pregnancy for the nonmigratory herd was 89%."

Based on reproductive tract inspections, Greer (1965) and Peek (1967) summarized pregnancy in 148 prime-aged (2.5–9.5 years) female elk harvested in January of 1965 and 1967 in the Upper Gallatin Canyon portion of the Greater Yellowstone Ecosystem. They reported a pregnancy rate of 96.7% (Greer 1965, Peek 1967), similar to the 95.3% pregnancy rate in their data from 763 prime-aged female elk (primarily 3.5–8.5 year-olds) from the Northern Range of Yellowstone (Greer and Howe 1964, Greer 1966, 1967). Fewer data exist for post-wolf pregnancy rates in the Gallatin, but data from mandatory hunter check stations on 32 prime-aged female elk harvested in January of 2001–2004 yielded a pregnancy rate of 71.9% (Montana Fish, Wildlife and Parks, *unpublished data*). For the Gallatin Canyon, these data reveal a 26% decrease in the pregnancy rate in post-wolf samples relative to pre-wolf samples. While this result is as predicted by the hypothesis that predation risk affects elk reproduction, we caution that the data are rather indirect, the post-wolf sample is small, and alternative explanations may exist.

In a report by the Idaho Department of Fish and Game examining recent elk population declines, Zager et al. (2005) concluded that "cows exhibit generally lower than expected pregnancy rates." In this study, they implemented experimental changes in policy in 1999 that promoted predator increases on one site (South Fork), and decreases on another site (Lochsa/North Fork). Pregnancy rates (measured by fecal progesterone) were comparable at the beginning of the experiment (South Fork = 80%, Lochsa/North Fork = 76%). Pregnancy rates decreased by 43% under the "high predation" policy, and after two years pregnancy rates were significantly lower ($\chi^2 = 7.04$, $P = 0.008$) on the South Fork (46% of 181 elk) than on the Lochsa/North Fork (73% of 169 elk; data from 2001–2004 in Table 4 of Zager et al. [2005]).

The data above are mainly from sources that are difficult to obtain, such as job completion reports. We have compiled PDF files, links, or direct quotes for all of these data in the Appendix.

To summarize, there are substantial data from several elk populations that allow tests of the hypothesis that elk reproduction is affected by predation risk. Elk calf-to-cow ratios have declined in many populations since wolf recolonization. These declines in recruitment are substantially larger than reported decreases in adult survival rates. Calf-to-cow ratios have declined for counts conducted at all times of the year, including green-up counts conducted shortly after the birth pulse. Studies of radio-tagged elk calves in several populations have not detected sufficient predation by wolves to account for the observed changes in early-winter calf-to-cow ratios. The effect of wolves on calf-to-cow ratios is detected in tests that control for variation in bear numbers and snow conditions, and model selection gives more support to wolf effects than to other limiting factors such as snow accumulation, rainfall, drought indices or bear density (Creel and Christianson 2008, Hamlin and Cunningham 2009). Data from five studies of ten populations have directly detected decreases of 24–43% in pregnancy rates in response to increased predation risk. As with data on calf-to-cow ratios, these decreases in pregnancy rates are larger than reported decreases in adult survival rates. While other limiting factors are also important, multiple tests with data of several types support the hypothesis that responses to wolves affect the reproductive physiology and demography of elk, with important consequences for population dynamics.

METHODOLOGICAL AND STATISTICAL PROBLEMS IN WHITE ET AL.'S CRITIQUE

The results just discussed provide consistent support for the hypothesis that the pregnancy rate of elk has declined in sites with high wolf-elk ratios. Still, it remains to be explained why this pattern was not apparent in the analysis of White et al. (2011). While differences among populations in the strength of risk effects are expected, several aspects of their methods would be expected to obscure any effect of predation risk on pregnancy rates.

Different methods for pre-wolf and post-wolf data.—A basic premise of inferences based on statistical comparison of two samples is that the two samples should be collected in the same manner. All of the analyses in White et al. (2011) compare samples collected in the 1960s with one set of methods to samples collected with different methods after wolf reintroduction. Their data on body fat from the 1960s come from measurements of kidney fat deposition in dead elk, while their data from 2000s come from ultrasound estimation of rump fat in live elk. Their data on pregnancy rates from the 1960s come from examination of reproductive tracts of dead elk, while their data from the 2000s are based on serum PSPB in live elk. These methodological inconsistencies should be considered when interpreting the study's failure to detect risk effects (for example, PSPB can remain elevated after pregnancy loss [Romano and Larson 2010]). With White et al.'s design, any effect of wolves is fully confounded with changes in methodology, and both of these effects are fully confounded with changes in other ecological conditions that might have altered body condition or pregnancy rate between the 1960s and 2000s (*Comparison of samples from mild and severe winters*). With this degree of confounding, it would not be surprising if their analysis failed to detect one or more real effects.

Comparison across ecosystems of samples from different times of winter.—White et al. stated that body fat measurements for elk in the Northern Range of Yellowstone were "among the highest recorded in a comparative study of 19 elk herds." This statement was based on inspection of their Fig. 1, which was reproduced with large but unexplained modifications from Cook et al. (2010). In White et al. (2011, their Fig. 1), predicted ingesta-free body fat values for 19 herds fall mainly between 3% and 6%. In the original study by Cook et al. (2010, their Fig. 7), none of the values for these same 19 herds is less than 7.5%, although the two studies state that they have used the same index of body fat (i.e., scaledLIVINDEX).

Leaving this inconsistency aside, a flaw in the basic inference only emerges upon reading the original study from which White et al.'s data were reproduced: samples from Yellowstone were collected substantially earlier in the winter than samples from the other populations to which they were compared. The exact dates of collection cannot be ascertained for all samples, but the Yellowstone data came from the first weeks of February and mid-March, while Cook et al. (2010) state that the other populations were sampled in March and April. As winter progresses, elk steadily lose body mass and fat. Greer and Howe (1964) measured the change in eviscerated body mass for the same prime-aged female elk in White et al.'s (2011) pre-wolf sample, and reported a rate of mass loss of 0.28 ± 0.06 kg/d (mean ± SD). With this rate of loss, sampling the Yellowstone herd approximately 30 days earlier than the other herds would be expected to produce a difference of 8.4 kg in body mass, mostly due to changes in body fat content (Greer and Howe 1964). Consequently, had Yellowstone elk in the post-wolf sample been collected as late in winter as the other herds, we would expect predicted ingesta-free body fat to have been approximately 5% lower than White et al. reported, which would be lower than any other herd in White et al.'s (2011) analysis. The effect of this error is to obscure any effect of predation risk on fat stores. This problem is particularly relevant because it is compounded by the point that follows.

Comparison of samples from mild and severe winters.—Winter conditions during the 1962–1968 pre-wolf sample were substantially more severe than conditions during the post-wolf sample, an effect that, when ignored, is expected to mask any effects of predation risk on mass dynamics. The post-wolf data reported by White et al. came from a period of mild winters, as they have noted previously: "The index of winter severity for the Lamar Valley during the winter months immediately preceding each of our elk captures was 0.18, 0.71, and 2.56 for 2000, 2001, and 2002, respectively (0 = average, <0 = harsher than average, and >0 = milder than average with respect to precipitation and temperature)" (Cook et al. 2004). The same index of winter severity tabulated for their pre-wolf period (1962–1968) included two "very severe" winters and two "severe" winters, including the most severe winter in 53 years of weather records from the Northern Range (data from U.S. Geological Survey, Northern Rocky Mountain Science Center). Snow accumulation in 1962–1968 (mean = 108.6 mm snow water equivalent) was double that of 2000–2005 (mean = 50.2 mm snow water equivalent), and winter temperatures averaged 4.5 C lower (Farnes and Hansen 2005; data from Mammoth weather station WY 9905).

Treating predictions from regression models as if they were data.—To compare measurements of kidney fat in dead elk (pre-wolf) to rump fat in live elk (post-wolf), White et al. used a sequence of models. First, they used regression to convert measurements of chest circumference to an alternative measure of chest circumference. They used these predicted chest circumferences as the input for a second regression that predicted body mass. Finally, using different regression equations for the pre-wolf and post-wolf data, they obtained predictions of "ingesta-free body fat" for the two time periods. In their primary analysis, White et al. treat these predicted values as empirical data, ignoring the prediction errors generated by this sequence of models. Specific values predicted by a regression model are not data, they are predictions with an associated uncertainty. It is not valid to discard prediction errors and simply treat $\hat{y}$ values from a sequence of regressions as though they were empirical data. The prediction limits for each $\hat{y}$ are substantially larger than the confidence limits for the regression model itself, and the effect of prediction error is to obscure potential differences in body fat between the two periods.

Underestimation of the change in pregnancy rate from prior data for Northern Range elk.—For their estimate of the pregnancy rate of Northern Range elk in the 1960s, White et al. cited a subset of data originally reported by Greer (Greer 1965, 1966, 1967). White et al. reported pregnancy rates of 91% for prime-aged elk and 64% for elk >9 years old, with a sample size of 387 from Greer's data. In the original data, we found a higher pregnancy rate of 95.3% from a larger sample of 763 prime-aged elk (Greer 1965, 1966, 1967). We could not determine what subset of the original data was excluded by White et al. (2011). Greer primarily examined prime-aged elk between the ages of 3.5 and 8.5 years, but his 1966 sample of 108 elk included some elk <2.5 years or >9 years. Following the methods in White et al. (2011), we calculated Wald's 95% confidence interval on the complete, original data reported by Greer and found a 95% CI of 93.5–96.6%. This pre-wolf pregnancy rate is significantly higher than the 87% pregnancy rate reported by White et al. for prime-aged elk following wolf recolonization (Yates continuity-corrected $\chi^2 = 6.0738$, $P = 0.014$). Thus, when all of Greer's original data from the 1960s are considered, there is evidence that pregnancy rates have declined in Northern Yellowstone elk since wolf recolonization, as in other populations.

Clarifications of the Original Study

Data on pregnancy rates, calf survival, and calf-to-cow ratios in several elk populations support the hypothesis that predation risk affects elk reproduction. Nonetheless, we would like to correct several points about our original study (Creel et al. 2007).

White et al. stated that: "Creel et al. (2007) inferred pregnancy rates from ratios of calves per 100 cows in the subsequent year, which is a tenuous assumption as low recruitment could be related to low calf survival." We did not make this assumption. Our exact statement was that "progesterone concentrations were correlated with calf recruitment in the subsequent year." We believe that the discussion above makes it clear that we have carefully considered changes in calf survival. For example, see Fig. I of Box 2 in Creel and Christianson (2008), which addressed this point directly by examining pre-wolf/post-wolf changes in the calf-to-cow ratio just after parturition, relative to changes in the calf-to-cow ratio after 6 months of life.

White et al. argued that our results might be "biased by collecting a variable and unknown proportion of samples deposited by immature or male elk." It is true that we collected samples from herds of elk rather than directly from single individuals. To account for this, we gathered data on the structure of the herds that we sampled, and tested whether this variation affected our inferences. As stated in the original study, "we controlled for variation among sites in population structure by dividing the mean progesterone concentration by the proportion of the population that was composed of adult females. This value was calculated separately for each site in each year using aerial count data, and ranged from 0.69 to 0.83. All reported P values were <0.01 with or without this adjustment." Finally, note that the proportion of calves was lower in herds with low progesterone concentrations; because progesterone secretion is low in calves, imperfect correction for herd composition would clearly be expected to produce a bias opposite to the effect that we detected.

White et al. argued that the correlations between fecal progesterone or calf-to-cow ratio and the wolf elk ratio that we detected were driven mainly by differences between winter ranges, rather than differences within winter ranges. In all ecological disciplines, inferences are routinely drawn by comparisons among populations (for example, White et al.'s comparison of body fat among populations). For every population in our analysis, the slope of the relationship between fecal progesterone or calf-to-cow ratio and the wolf elk ratio had the same sign as the overall regression.

White et al. suggest that "there is some unexplained failure of the fecal hormone assays for progesterone under certain circumstances … we urge caution in using the fecal progesterone technique until further work resolves inconsistencies." This statement is based on data from Madison headwaters elk not included in their paper or our original study. Our enzyme immunoassay of these samples revealed a substantial drop in mean fecal progesterone concentrations, coincident with the 32% decrease in pregnancy rates reported by Garrott et al. (2009), and coincident with a decrease in the calf-to-cow ratio to <1 calf per 100 cows: (Garrott et al. 2009). Thus, we detected low fecal progesterone values for this herd during a period with the lowest pregnancy rate (based on serum samples), the lowest calf-to-cow ratio and the highest wolf-elk ratios yet observed in the Greater Yellowstone Ecosystem. A threshold of 830 ng immunoreactive P4/mg dry feces caused pregnancy diagnosis via fecal progesterone assay to agree closely with pregnancy diagnosis via serum PSPB (see the supplemental online methods of Creel et al. [2007]). Nonetheless, Garrott et al. (2009) estimated pregnancy rates for the Madison headwaters herd using a higher threshold derived from a different assay (Garrott et al. 2009). The resulting underestimates of pregnancy rates are the "unexplained failure" discussed by White et al., but we emphasize that had we included these data in the correlation of fecal progesterone on wolf-elk ratios reported in Creel et al. (2007), the relationship would only have been stronger.

Finally, the fecal progesterone assay was procedurally validated by standard tests of specificity, accuracy, and precision, and was biologically validated as described in the original study: "We compared pregnancy diagnosis via fecal ELISA (with threshold = 830 ng P4/mg dry feces) with diagnosis via serum pregnancy-specific protein B (PSPB) for 30 samples collected from the same individual on the same day. This comparison yielded 93.3% sample-concordance, with identical pregnancy rates (80%). We also compared pregnancy diagnosis by ELISA to results from a previously validated progesterone RIA, with 94.3% sample-concordance and $r^2 = 0.95$ for 35 samples."

The strength of risk effects is likely to vary among species and populations, so we encourage future research with elk to complement results emerging for many other species (Peckarsky et al. 2008). For now, multiple lines of evidence show that the presence of wolves provokes behavioral and ecological responses by elk. Other studies have detected changes in diet and nutrition that are predicted by the observed behavioral responses. Five studies with data from 10 populations have detected changes in pregnancy rate and calf recruitment associated with population declines during wolf recolonization. These responses have been detected in several regions, with a variety of methods. While other factors also affect elk nutrition, reproduction, and calf recruitment, substantial data support the hypothesis that predation risk decreases pregnancy rates in elk, with important effects on population dynamics (Creel et al. 2007).

ACKNOWLEDGMENTS

This research was supported by NSF award IOS-0642393. We thank Stewart Liley for excellent field and lab work in our original study of risk and progesterone concentrations in elk and the authors of the agency reports that we summarized for this survey.

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APPENDIX

Data sources for elk pregnancy rates (*Ecological Archives* A021-129-A1).