

Mismeasured mortality: correcting estimates of wolf poaching in the United States

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Three sentence summary: Poaching is not something happening only in distant regions, it is the most common cause of wolf mortality in every population where it has been measured accurately. During the period U.S. wolves were listed under the ESA, the relative importance of poaching was systematically and substantially under-estimated while the relative importance of legal causes of mortality was systematically over-estimated. We correct the algebraic errors and errors of inference that led to these biased estimates.

Abstract: Measuring rates and causes of mortalities are important in animal ecology and management. Observing the fates of known individuals is a common method of estimating life history variables, including mortality patterns. It has long been assumed that data lost when known animals disappear were unbiased. We test and reject this assumption under conditions common to most, if not all, studies using marked animals. We illustrate the bias for 4 endangered wolf populations in the United States by reanalyzing data and assumptions about the known and unknown fates of marked wolves to calculate the degree to which risks of different causes of death were mismeasured. We find that, when using traditional methods, the relative risk of mortality from legal killing measured as a proportion of all known fates was overestimated by 0.05–0.16 and the relative risk of poaching was underestimated by 0.17–0.44. We show that published government estimates are affected by these biases and, importantly, are underestimating the risk of poaching. The underestimates have obscured the magnitude of poaching as the major threat to endangered wolf populations. We offer methods to correct estimates of mortality risk for marked animals of any taxon and describe the conditions under which traditional methods produce more or less bias. We also show how correcting past and future estimates of mortality parameters can address uncertainty about wildlife populations and increase the predictability and sustainability of wildlife management interventions.

FAQs

How did mismeasurement of mortality risk escape notice for decades?

There are several ways to study the lives of wild animals. All methods have some uncertainty because wild animals go about their lives far from our scrutiny and may elude our efforts to detect them again. The ultimate cause of death for animals that elude monitoring is rarely known. Scientists call these marked animals unknown fates. Marking animals with radio-collars, as done with most wolves we studied, tends to have even more uncertainty because radio-telemetry technology required lots of human effort to detect marked animals again and because poachers can destroy radio-collars without too much difficulty.

The lead author became interested in what had happened to radio-collared wolves in Wisconsin where many eluded monitoring¹. The investigation spread to other populations because the authors found the same assumption had been used in other wolf populations. That assumption was the radio-collared wolves with known fates were a fair representation of all wolves. Our paper shows that assumption is misleading whenever people kill wolves legally – because no unknown fate wolves were killed legally. Had they been killed legally, wolves would have been reported and therefore had known fates. Because a sizeable proportion of wolves are killed legally each year during government culling or regulated hunting and trapping, the known fate sample of dead wolves is relatively full of such cases. But the unknown fate dead wolves never die from legal causes. When we set out to investigate what happened to unknown fates in Wisconsin, we did not expect to find a miscalculation that applied to all wolves.

¹ Treves, A., J. A. Langenberg, J. V. López-Bao, and M. F. Rabenhorst. 2017. Gray wolf mortality patterns in Wisconsin from 1979 to 2012. *Journal of Mammalogy* 98:17-32.

Last year, Treves and others notified experts on Northern Rocky Mountain wolves that the assumption was flawed² and in the ensuing year, the current team of authors investigated red wolves and Mexican wolves to confirm the same phenomenon applied. We now believe our finding applies to all studies of marked animals in which a perfectly reported cause of death occurs alongside imperfectly reported ones. Moreover, for populations with cryptic poaching – in which poachers conceal evidence – the biasing effect of the false assumption will be amplified.

Why does the article state that one error is a mathematical fact? Isn't this a dispute over interpretation of data?

We identified an error that is simply algebraic and an error of estimation that are separate issues. The algebraic mismeasurement is the over-estimation of the risk of legal killing. This should always be calculated as a proportion of all dead animals, not as a proportion of known fates because known fates over-represent legal causes of death by a known amount (Figures 1a,b below).

We also identified an error of inference about the other causes of death. After one corrects the calculation of risk of legal causes of death as above, then one has to confront what might have happened to the unknown fates. These unknown fates have been ignored traditionally, which discards useful information. We therefore presented a method to estimate what happened to those unknown fates. In the case of marked wolves, we show that poaching in particular has been under-estimated because cryptic poaching has not been accounted for properly. We presented two methods to account for cryptic poaching and one method that ignores cryptic poaching (Figures 2a,b below).

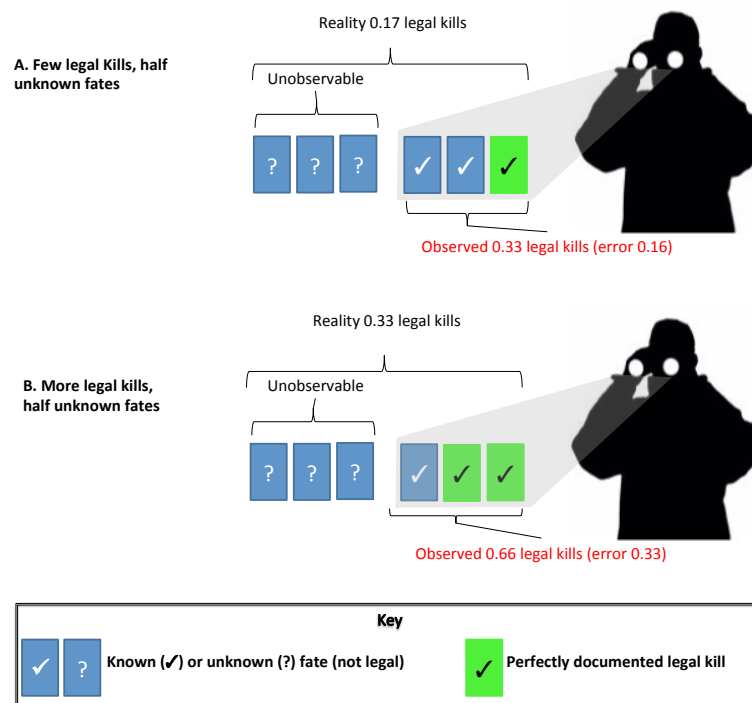


Fig. 1.—Systematic bias in calculating the risk of mortality from legal killing when some marked animals have unknown fates (unobservable with question marks ?) and causes of death vary in the accuracy of documentation. The green squares represent legal kills (perfectly documented) and the blue squares denote other causes of death (inaccurately documented). Observed (silhouette with binoculars) known fates (check marks ✓, and calculation in red text) alone would over-estimate the real risk of legal killing. **A:** Positive bias in estimating risk of legal killing is 0.16. **B:** Positive bias increases by 0.17 as the proportion of legal kills increases.

² Treves, A., M. Krofel, and J. V. Lopez-Bao. 2016. Missing wolves, misguided policy. Science (eLetter) 350:1473-1475.

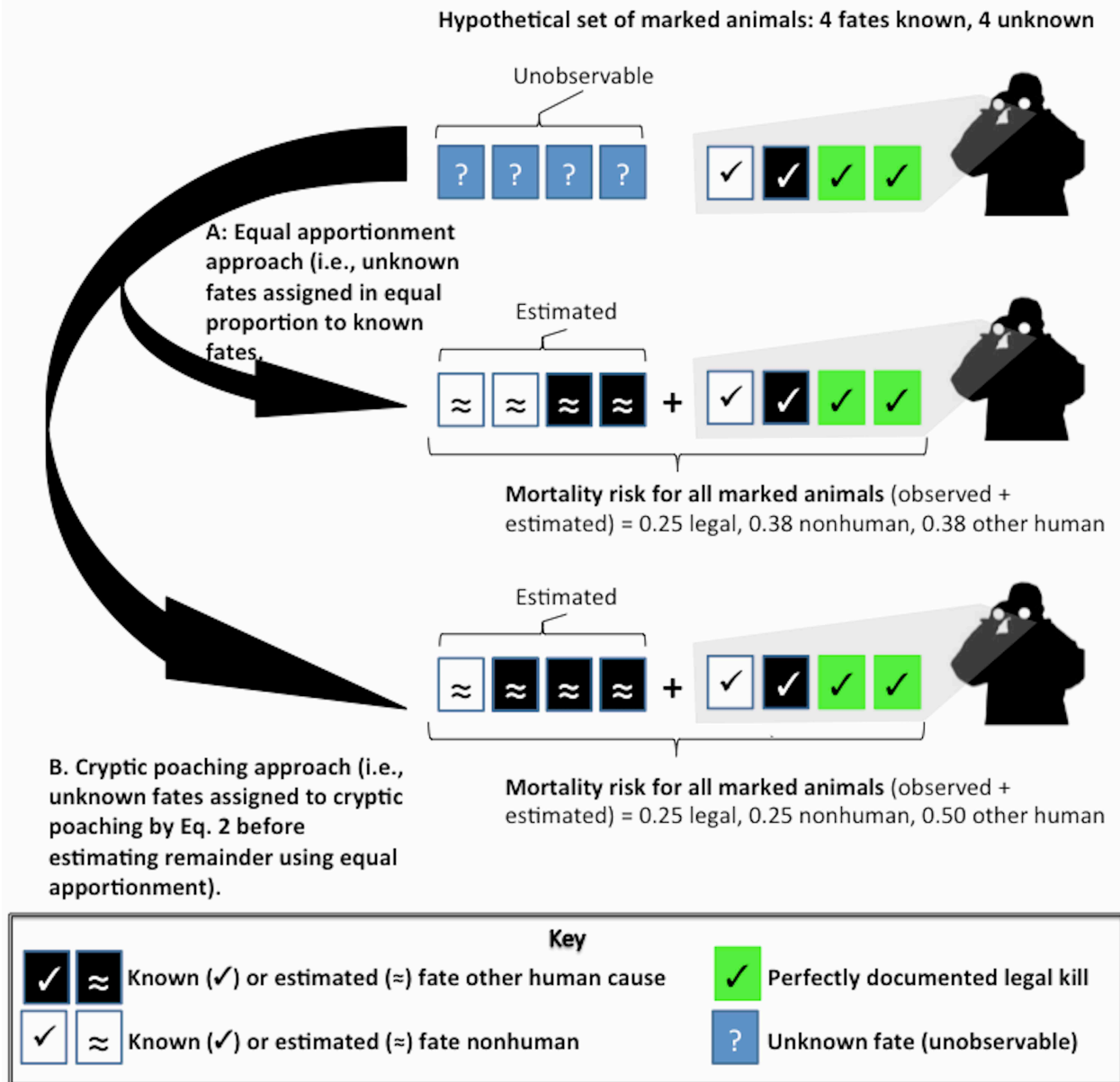


Fig. 2.— Systematic bias in estimating the risk of mortality when some marked animals have unknown fates (unobservable, question marks ?) and causes of death vary in the accuracy of documentation. Observed (silhouette with binoculars) known fates (check marks ✓) alone would under-estimate the inaccurately documented causes of death (unknown fates, white, black, and blue squares). Two approaches to estimating unknown fates produce lower and upper bounds on estimates of risk of mortality, using Eqs. 1a, b, and 2. A: The equal apportionment approach assumes that the observed ratio of known nonhuman causes of death (white squares with check marks) to known, other human causes of death (black squares with check marks) applies to the unknown fates (squares with approximately equal signs, ≈). B: The cryptic poaching approach with $C = 2$ from Eq. 2 assumes that for every one known-fate poached animal (black square with check mark) there will be two unknown-fate poached animals (black square with ≈), which must be accounted first before equal apportionment of the remainder adds one poached and one nonhuman cause of death (white square with ≈). This approach requires discrimination between poaching and vehicle collision or other unintentional human causes (see Supplementary Data S2).

What is the difference between mortality risk and mortality rate?

Mortality risk is the percentage of animals that die from a given cause; collectively all the mortality risks will sum to 100%. For instance, the risk of poaching is the number of dead wolves that died from poaching divided by all the dead wolves, expressed as a percentage or a proportion. Mortality rate by contrast is the number of animals that died in a given time period from an identified group of animals some of which remain alive at the end of the period. Mortality rate is often expressed as a proportion of all marked animals in a given time or as a per capita hazard rate (with a maximum of 1.0 therefore). The possible mix-up between mortality risk and per capita hazard rate can be one source of error and confusion our paper addresses. For example, if the mortality rate was 12 wolves per year in a population of 100 wolves, the per capita hazard rate can be expressed as 0.12 per year. Within that estimate, one can express the risk of different causes of death as a percentage of 0.12 wolves per year.

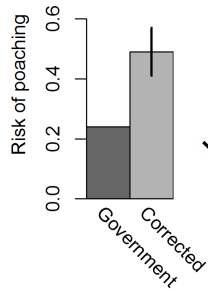
What implications does this study have for the viability of endangered wolf populations?

With the prior definitions in mind, mortality risk does not directly inform us about the mortality rate, because the risk estimate does not reveal how many marked animals were in the original pool or the time period under discussion. However, it is axiomatic in conservation that one abate the most severe threats to endangered species with high priority, so paying attention to mortality risk is common-sense.

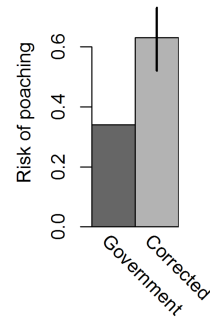
Also, our analysis revealed that marked animals that were monitored (known fates) experience different risks than animals that were not monitored (unknown fates). Because the vast majority of any population is unmonitored, we should be careful about assuming we understand viability when we base our conclusions on monitored animals (known fates) only, or even when we base our conclusions on marked animals (known and unknown fates) because unknown fates vastly outnumber known fates.

Furthermore, mortality rates are also likely to have been mismeasured in wolf populations. If one has under-estimated the major risk faced by marked wolves, one has likely also under-estimated the per capita hazard rate of all the other unmonitored animals simply because scientists and agencies extrapolate from the marked animals to the whole population. In the case of wolves, marked wolves actually experienced more poaching than scientists or government agency acknowledged. Also, we know from the Wisconsin mortality study¹ that poaching happens earlier in life than death from nonhuman causes or vehicle collisions on average. The same seems to be true for Northern Rocky Mountain wolves². Furthermore, per capita hazard rates of unknown fates differed from those of known fates in three wolf populations where both have been estimated. Because poaching is the major risk for all of the wolf populations we studied (Figure 3), we recommend re-evaluation of all policy interventions that increase mortality or choose not to address human-induced mortality, using our more accurate methods of estimation. We predict that wolf population viability and their resilience to human-induced mortality is not as rosy as U.S. governments have predicted.

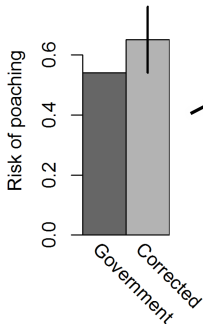
Northern Rocky Mountain Gray Wolf



Wisconsin Gray Wolf



Mexican Gray Wolf



Red Wolf

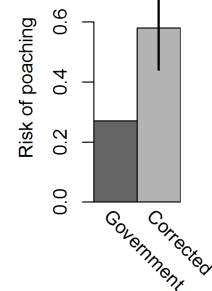


Fig. 3.—Endangered wolves (gray: *Canis lupus*, Mexican gray: *C. l. baileyi*, and red: *C. rufus*) and risk of mortality from poaching as a proportion of all deaths. Approximate geographic locations are shown for 4 populations in the United States. The relative risks of mortality from poaching by government estimates (dark gray bars, no uncertainty estimates available) are paired with the same estimates from this study (light gray bars; error bars: lower bound derived from the equal apportionment approach and upper bound derived from the Scandinavian estimate of cryptic poaching $C = 2$). See Supplementary Data S2 for poaching values separated from other human causes.

How did this happen?

The propagation of errors and their widespread publication and dissemination represents a systemic problem in which evidence is not handled with sufficient care before policies are made. Government agencies are placed in a privileged position with regard to accessing data paid for by taxpayers and collected in the public interest. Yet agencies are not required to submit their findings to rigorous peer review by anonymous, independent experts in the field, as is required for scientific publication. The consequences of failing to subject government science to peer review are particularly obvious in the case of wolves that we have presented, but similar less stark errors are certainly missed because government evidence is not peer reviewed rigorously. We recommend the system be reformed to follow the academic sciences model. This recommendation should not be interpreted as uncritical endorsement of academic peer review, which has proven flaws also. Although academic peer review is not perfect, it is demonstrably superior to no peer review or lack of independence among peer reviewers hand-picked by government agencies. The next task after that is to strengthen academic peer review.