**Total-accounting method for reconstructing missing deaths of gray wolves (*Canis lupus*) in Wisconsin from wolf-year 1980 to 2012**

Our aim in using a total-accounting method was to reconstruct the causes of death for missing wolves from the unmonitored but collared subset (*methods and Materials*) and estimate the number of missing deaths in the non-radiocollared subset.

Had we estimated mortality patterns and rates from the actively monitored subset *only,* we would have estimated relative risk with a bias for older, female, territorial residents in core counties, which suffer differential hazard rates in other regions (Schmidt et al. 2015) and a bias against poached wolves whose transmitters were inactivated. An alternative approach is to estimate the number of missing wolves and then reconstruct their fates, a total accounting approach.

*Reconstructing the missing, radiocollared wolves*

Over the study period, 486 wolves were radiocollared by the State of Wisconsin, but 15 of those died in the *P* age class so we excluded them from consideration below (Eq. 1 first set of parentheses). Of the 471 in age class *A* that died, disappeared, or remained on the air, 251 (53%) deaths were recorded (noting that 28 Wisconsin-collared wolves died out of-state and 27 non-Wisconsin collared wolves died in-state, reflected in the second set of parentheses in Eq. 1 below; and see *Supporting information SD1, SD2*). Also 38 living wolves had actively monitored radiocollars (WDNR 2015 in ER report 143) and an unknown number of unmonitored but collared radiocollars were left on living wolves at the end of our study ($L_i$); these living wolves are represented in Eq. 1 by the third set of parentheses.

Eq. 1: $M_i = (486 - 15) - (251 + 27 - 28) - (38 + L_i) = 183 - L_i$

That left 183 - $L_i$ missing deaths in the unmonitored but collared subset for which we could not account. We estimated $L_i$, using the distribution of time-to-death, $T_m$, for radiocollared wolves with reported deaths (mean $631 \pm 674$ days, $n = 251$, *Supporting Information SD2*). The best-fit distribution for $T_m$ was the exponential (Akaike Information Criterion $AICc = 3977$ versus next-best fit $AICc = 4011$, SAS Corp. 2013). Thus $L_i$ was the sum of probabilities that each unmonitored but collared wolf of unknown fate might have survived to 14 April 2012 considering the expected value of $T_m$, the time elapsed between capture and disappearance, $T_{disappear}$, and the remaining time until the end of our study, $T_{end}$ . We began by estimating $Tc$ as the sum of two known times, using Eq. 2.

Eq. 2: $T_c = T_{disappear} + T_{end}$

where $T_{disappear}$ had an observed mean of $534 \pm 767$ days, $n = 179$ and $T_{end}$ $3878 \pm 2976$ days, $n = 179$ (*Supporting Information SD2*). The precision of dates of disappearance is unlikely to be better than $\pm 15$ days because of monthly aerial radio-telemetry flights. Then we estimated $Li$ by adding the probabilities that each missing wolf outlasted the expected survival time $Tm$ using Eq. 3.

Eq. 3: $L_i = \sum [e^{-(Tc \div Tm)}] \div T_m$

From Eq. 3, we estimated $L_i = 1.5 \pm 0.001$ unmonitored but collared wolves presumed alive by the end of our study period. This number was robust to relaxing the assumptions. For example, making the most liberal assumption that time on the air before disappearance did not count towards future survival time yielded $L_i = 2.6$ wolves. Thus $L_i$ gave us our final estimate for Eq. 1 of $M_i = 180–182$ missing deaths in the unmonitored but collared subset which we sought to reconstruct (Table 2).

*Migration.*—To reconstruct cause of death for $M_i$, we had to consider migration.

Migrants to and from Wisconsin died of similar causes as those that died in-state (*Results*),

therefore we assumed that missing deaths of migrants out-of-state resembled missing deaths in-

state and undertook no correction here to estimate $M_i$. Note that non-radiocollared wolves cannot

be treated the same way because neighboring states would not know these were originally

Wisconsin wolves hence reporting bias would affect estimates for all causes of death.

*Legal causes.*—We did not reconstruct any missing deaths from legal causes because the

missing, unmonitored but collared wolves had Wisconsin-labeled collars and legal causes were

perfectly reported in in the neighboring states (*Methods and Materials*).

*Nonhuman causes and collisions.*—Following the logic of detection bias in the *Methods*

*and Materials*, we assumed that nonhuman causes of death in the actively monitored subset

provided an unbiased estimate of relative risk of nonhuman causes of death in the unmonitored

but collared subset because the former was unaffected by detection bias. We also assumed

collisions in the actively monitored subset provided an unbiased estimate of the relative risk of

collisions in the unmonitored but collared subset. We assumed collisions only trigger reporting

bias in general because drivers would detect a collision but might not report it for various reasons

(*Methods and Materials*). Accordingly, we estimated relative risk for nonhuman causes or

collisions in the actively monitored subset by Eq. 4.

Eq. 4: $R_{a,cause} = O_{a,cause} \div O_a$

where $O_{a,cause}$ was the reported number of deaths for the given cause in the actively

monitored subset, and $O_a$ was the reported number of deaths from all causes n the entire actively

monitored subset. Note we estimated relative risk to reconstruct missing deaths – not mortality

hazard rate that would take into account the time exposed to a hazard. Eq. 4 assumed the same

real relative risk applied when a wolf was monitored or unmonitored. Departures from that

assumption for nonhuman causes of death would be most likely in the direction of higher human-

caused mortality, especially poaching (Liberg et al. 2012), rather than higher nonhuman causes,

because the unmonitored but collared subset was found more often in peripheral counties

(*Results*) where human-caused mortality predominated (Wydeven et al. 2001). Hence Eq. 4 was

an over-estimate for nonhuman causes and collisions and thereby conservative for estimating

poaching risk below.

By Eq. 4, the relative risk of nonhuman causes of death for the actively monitored subset

only was 30.4–40.2% (Table 2), where the lower bound omitted the unknown causes and the

upper bound treated unknown causes as nonhuman causes, which is an over-estimate. A relative

risk of 30.4–40.2%, was much higher than the 4% calculated for the unmonitored but collared

deaths reported in Table 2 ($O_{i,nonhuman}$), as expected when wolves were unmonitored. We also

calculated Eq. 4 for collisions, yielding 10.8% relative risk. With the above two estimates of

relative risk, we used a Monte Carlo simulation to estimate variation in the missing deaths from

nonhuman and collision causes among unmonitored but collared wolves (described below).

The reconstruction steps described above are conservative for estimating poaching risk

because poached wolves might die then have their collars inactivated, but we assumed

inactivation preceded death by estimating nonhuman causes and collisions before reconstructing

poaching.

*Reconstructing missing deaths from nonhuman causes and collisions.*—Because Eq. 4

provided no estimate of variability such as *SD*, we employed a Monte Carlo simulation with

5080 iterations for each of the upper and lower bounds to recreate the credible interval for

$M_{i,nonhuman}$ and $M_{i,collision}$ among the $M_i = 182$ missing deaths from Eq. 1. We chose to stop at

5080 iterations after the *SD* of nonhuman causes reached an asymptote. We used a uniform random number generator to reconstruct nonhuman causes and collisions. Legal causes were not reconstructed because none were missing (perfect reporting) for radiocollared wolves (*Materials and Method*s) and we did not need to reconstruct unknown causes because the missing deaths were by definition unknown. In the final step of the simulation, we assigned all remaining, missing deaths from $M_i$ as poached wolves. The output of the simulation was a lower bound and an upper bound on the number of deaths missing from the unmonitored but collared subset for nonhuman causes, collisions, and poaching (Table 2).

The averages of 5080 iterations for $M_{i,nonhuman}$ were $55.5 \pm 6.3$ for a lower bound and $84.1 \pm 7.0$ for an upper bound (Table 2). Note the upper bound reconstructs all observed unknown deaths as nonhuman causes, which was certainly an over-estimate. The range of values for $M_{i,nonhuman}$ provided an estimate for detection bias alone, by Eq. 5.

Eq. 5: $DETECTION_{nonhuman} = M_{i,nonhuman} \div (O_{nonhuman} + M_{i,nohuman})$

We estimated $DETECTION_{nonhuman}$ at $83 \pm 2\%$.

Recall that estimates of $M_i$ were subject only to one component of bias each; nonhuman causes were affected only by detection bias and collisions were affected only by reporting bias (*Materials and Methods*, Table 2).

As above, we reconstructed $19.5 \pm 4.3$ collisions among the missing deaths of unmonitored but collared wolves (Table 2). Using Eq. 5 for collisions instead of nonhuman causes, we estimated reporting bias alone at 58%. As predicted in *Methods and Materials*, reporting bias was lower (for collisions) than detection bias (for nonhuman causes of death).

*Poached.*—We were left with 77.9 to 105.5 missing deaths in the unmonitored but collared subset, which could not be assigned to any but the last remaining cause of death, which

was poaching. Hence $M_{i,poached}$ was simply calculated by Eq .6,

Eq. 6: $M_{i,poached} = 1 - M_{i,nonhuman} - M_{i,collision}$

not by recalculating Eq. 4 for poached wolves because the relative risk of being poached

for a wolf in the actively monitored subset required correction for both detection bias (accidental

poaching that led to undetected death) and reporting bias (cryptic poaching).

Because 'cryptic poachers' inactivated radiocollars after killing a wolf in our model, the

assumption that monitored and unmonitored wolves were equally likely to be poached was false

by definition – poaching ended monitoring sometimes (*Materials and Methods*). When we

calculated reporting bias for poached wolves that were unmonitored but collared, we used Eq. 5

again. That yielded 80–84% reporting bias, which represented the percentage of radiocollared

wolves that were poached but not reported and were either unmonitored at the time of death, or

had their transmitters inactivated after death. Alternately, we recalculated Eq. 5 including the

subset being actively monitored after death (yielding 46–54% reporting bias). That can be

interpreted as the percentage of unreported, poached wolves after radiotelemetry detected 30–

34% (the difference between the former and the latter estimates).

*Reconstructing the number of missing, non-radiocollared wolves*

The relative risk estimates presented in Table 3 for radiocollared wolf deaths combined (reported

and reconstructed) offered insight into the non-radiocollared subset. The non-radiocollared

subset experienced more detection bias we surmised. For example legal causes were 30.9% of

the reported deaths in the non-radiocollared subset compared to 6.3% in the reconstructed,

radiocollared subsets (Table 2), yet legal causes affected radiocollared and non-radiocollared

subsets equally (*Materials and Methods*). Therefore we knew a large number of non-

radiocollared wolf deaths were missing from the dataset (Table 2), which if reported would have reduced the relative risk of legal causes closer to 6%.

Furthermore the above difference of 24% allowed us to estimate the absolute number of unreported deaths among non-radiocollared wolves, for a total or $M_n = 1,986 \pm 3$ missing deaths in age class $A$ from wolf-year 1980–2012. Note the precision of this estimate reflects the low variation in the estimates of legal causes in the radiocollared subsets (Table 2).

We made no effort to reconstruct cause of death further among the non-radiocollared wolves because of the sampling biases that differentiated the radiocollared from the non-radiocollared subset (*Materials and Methods*).

*Annual unreported deaths.*—We apportioned the missing deaths by wolf-year with a single assumption. We assumed that missing deaths accumulated at an annual rate proportional to the population size. Thus we applied the logistic curve that fit the wolf population growth to allocate the missing deaths, given $M_n$ and $M_i$ from Table 2 and the minimum and maximum population estimates from Table 1. This assumption is consistent with the observation that disappearances of radiocollared wolves correlated closely to the wolf population estimates annually (Table 1–Pearson $r = 0.76$, $P < 0.01$).

By fitting the number of unreported deaths ($M_i + M_n$) to the population size each wolf-year, we estimated that 33–36% (*SD* 15%) of the estimated population died unreported annually (Table 1). Reported deaths comprised 10–11% (*SD* 4%) annually of the estimated population (*Results*) so only 31% of mortality was reported annually. Nor did the missing deaths correlate closely with reported deaths, when both were expressed as an annual percent of the minimum population estimate (Pearson $r = 0.16$), which suggests reporting was not a random process. That

finding is consistent with suggestions in Chapron and Treves 2016 that policy changes were

followed by changes in poaching that was more likely to be cryptic).

*Annual mortality hazard rates*.—We calculated *per capita* wolf mortality hazard rates, or

the average time to death for each radiocollared wolf of age class *A*, divided by its "time on the

air" exposed to mortality factors (Table 1, *Supporting information SD*2). We estimated the mean

mortality hazard rate at 18% ± 10% for monitored, radiocollared wolves. Treating

disappearances as deaths changed little (mean 19% ± 9%, *Supporting Information SD2*).

Computing the mortality hazard rate simply as the number of deaths in the actively monitored

subset divided by the number of radiocollared wolves annually from Table 1 also yielded an

annual average of 18% ± 12%, therefore calculating exposure or "time on the air" for each wolf

only improved the precision without changing the accuracy of the average. These estimates are

all consistent with official estimates (*Discussion*).

Next we compared the mortality hazard rate faced by the radiocollared subsets and the

non-radiocollared subset. Although the exposure time for non-radiocollared wolves was

unknown, the above result about precision of the estimate gave us confidence in assuming a full

year of exposure for each living wolf each wolf-year. This step assumed that the hazard posed by

exposure for non-radiocollared wolves was the same as the hazard posed by "time on the air" for

radiocollared wolves. Our assumption was conservative because radiocollared wolves tended to

have lower exposure to mortality hazards because they used areas with lower road density and

fewer people (*Results*).

Then, we divided the annual number of unmonitored wolves dying each wolf-year

(reported + missing, Table 1) by the annual number of unmonitored wolves estimated alive at the

start of the wolf-year (subtracting the number radiocollared from the minimum population

estimate, Table 1), to estimate the annual mortality hazard rate for all unmonitored wolves. Using he lower bound divided by the minimum population estimate and the upper bound divided by the maximum population estimate, we estimated a mean of 47% to 51% (*SD* 18 to 20%) annual mortality hazard rate for unmonitored wolves. That mean was 29–33% higher than for monitored, radiocollared wolves calculated in the same way (*Results)*.

We then added the number of wolves that were reported + reconstructed to have died each wolf-year and divided by all wolves alive at the start of that wolf-year (Table 1), to estimate the overall annual hazard rate as a weighted mean equaling 38 to 41% (*SD* 10%). That mean is an under-estimate because it assumed all wolves present at start were present the whole wolf-year.

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