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Authors: Korner-Nievergelt, Fränzi, Korner-Nievergelt, Pius, Behr, Oliver, Niermann, Ivo, Brinkmann, Robert, et al.

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**Original article**

# A new method to determine bird and bat fatality at wind energy turbines from carcass searches

**Fränzi Korner-Nievergelt, Pius Korner-Nievergelt, Oliver Behr, Ivo Niermann, Robert Brinkmann & Barbara Hellriegel**

Wind energy is of increasing importance for a sustainable energy supply worldwide. At the same time, concerns about the number of birds and bats being killed at wind turbines have been growing. In this situation, methods for a reliable estimation of bird and bat fatality numbers are needed. To obtain an unbiased estimate of the number of fatalities from fatality searches, the probability to detect the carcass of an animal being killed at a turbine has to be assessed by considering carcass persistence rate, searcher efficiency and the probability that a killed animal falls into a searched area. Here, we describe a new formula to determine the detection probability of birds or bats that are killed at wind turbines and which can estimate the number of fatalities from the number of carcasses found. The formula was developed to analyse a large data set of bats killed at wind turbines in Germany. In simulations, we compared it to three other formulas used in this context. Our new formula seems to have unbiased results when searcher efficiency and carcass removal rate are constant over time. When searcher efficiency or carcass removal rate varied with time, all four formulas showed a similar bias. These comparative results can be used to choose between methods depending on the quality of information available. Our estimator can, for instance, be adapted to different situations including temporal changes of searcher efficiency or carcass removal rate because it is based on an explicit process model.

*Key words: bats, birds, carcass searches, collision risk, detection probability, estimator, formula, wind energy turbine*

***Please note that supplementary information, including Figures S1-2 mentioned in this article, is available in the online verison of this article, which can be viewed at www.wildlifebiology.com***

*Fränzi Korner-Nievergelt & Pius Korner-Nievergelt, oikostat GmbH, Ausserdorf 43, CH-6218 Ettiswil, Switzerland, and Swiss Ornithological Institute, Seerose 1, CH-6204 Sempach, Switzerland - e-mail addresses: fraenzi.korner@oikostat.ch (Fränzi Korner-Nievergelt); pius.korner@oikostat.ch (Pius Korner-Nievergelt)*
*Oliver Behr, Friedrich-Alexander-Universität Erlangen-Nürnberg, Institut für Tierphysiologie, 91054 Erlangen, Germany - e-mail: obehr@biologie.uni-erlangen.de*
*Ivo Niermann, Leibniz University Hannover, Institute of Environmental Planning, Herrenhäuser Strasse 2, D-30167 Hannover, Germany - e-mail: niermann@umwelt.uni-hannover.de*
*Robert Brinkmann, Leibniz University Hannover, Institute of Environmental Planning, Herrenhäuser Strasse 2, D-30167 Hannover, Germany, and Freiburg Institute of Applied Animal Ecology, Habsburger Strasse 41, D-79104 Freiburg, Germany - e-mail: brinkmann@frinat.de*
*Barbara Hellriegel, Anthropological Institute and Museum, University of Zurich, Winterthurerstrasse 190, CH-8057 Zurich, Switzerland - e-mail: barhell@aim.uzh.ch*

*Corresponding author: Fränzi Korner-Nievergelt*

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Wind energy is showing a rapid growth and can help to avoid the ecological and health problems of fossil and nuclear energy production (Holdren & Smith 2000). At the same time, concerns about birds and bats being killed at wind energy facilities and possible ecological (e.g. de Lucas et al. 2007, Arnett et al. 2008) and economic (Boyles et al. 2011) consequences have been growing. In this situation, methods for a reliable estimation of bird and bat fatality numbers that are simple enough to qualify for general use are needed. In order to reliably estimate the number of fatalities at wind turbines from the number of carcasses detected, one has to correct for imperfect detection ('searcher efficiency'), for carcass removal, and, if necessary, for incompletely searched area. To do so, a model that reflects the important steps of the actual processes as well as possible sources of imprecision is needed.

The key parameter in estimating bird and bat fatalities is the probability that an animal being killed is found by a searcher (detection probability p). On the one hand, this probability depends on the distribution of the carcasses in the area beneath a wind turbine and on the fraction of this area that can be searched, i.e. the proportion of carcasses lying in the area searched (a). On the other hand, detection probability p is influenced by the carcass persistence probability (s), i.e. the probability that a carcass does not disappear within 24 hours (due to removal e.g. by scavengers), and the searcher efficiency (f), i.e. the probability that a carcass that has fallen in the area searched and has not been removed is found by a searcher. Thus, the probability that an animal killed is also found can be determined as the product of a and a function g which depends on s and f : $a*g(s,f)$. For simplicity, we will assume here that 100% of the area beneath a wind turbine is searched ($a=1$), so that the detection probability is $p=g(s,f)$. A simple example for function g is the product of carcass persistence probability and searcher efficiency, $p = f*s$. While this equation includes two very important factors, it does not take into account that carcasses that have been overlooked may be found during a later search. Consequently, the number of fatalities will be overestimated particularly when searcher efficiency is low and persistence time is high. More sophisticated estimators have been developed to account for repeated searches (e.g. Erickson et al. 2004, Huso 2010). In an extensive simulation study, Huso (2010) showed that her estimator is more reliable than two commonly used estimators (Johnson et al. 2003, Kerns & Kerlinger 2004). These simulations also showed that her estimator works well for North American cases where carcass persistence times normally are long (on average 32 days; Arnett et al. 2009) and usually search intervals of > 14 days are used. However, for central European cases with short persistence times (mean 4.2 days; Niermann et al. 2011) and short search intervals (usually 1-7 days) her estimator tends to overestimate the number of fatalities (Huso 2010). Therefore, we have developed a new formula to estimate the detection probability that allows for a detection of carcasses during repeated searches, and which is also reliable for central European cases. Our estimator is based on a conceptually different model than the one used by Johnson et al. (2003), Erickson et al. (2004) and Kerns & Kerlinger (2004) or the one used by Huso (2010). Our estimator is a more general formulation of the conceptual model used by Baerwald & Barclay (2009; see Methods).

An important advantage of our approach is that the formula can be adapted to different distributions of searcher efficiency or carcass removal rates, because it is based on an explicit model of the carcass removal and search processes. Searcher efficiency depends on the ability of a searcher to detect a carcass. This efficiency can be assumed to be approximately constant over time (i.e. with the number of searches) on uniform and bare ground. However, on structured ground some carcasses might be much more difficult to detect than others (Arnett 2006). As a result, carcasses that are easy to detect are more likely to be found during the first search, whereas hidden carcasses will be more likely to remain on the plot. Searcher efficiency for a cohort of carcasses will, hence, decrease in repeated searches. A modification of our formula accounts for such a decreasing searcher efficiency in repeated searches.

We assessed the bias and precision of our new formula for the estimation of bat or bird fatalities in a simulation study. We compared the results obtained with our formula to that of three different approaches to model carcass detection. The other approaches were 1) the above-mentioned simple formula $p = f*s^*$, where $s^*$ is the remaining proportion of carcasses of animals that were killed during one search interval (see below), 2) the formula of Erickson et al. (2004) that is one of the latest versions of the earlier estimators before the publication of Huso (2010), and 3) the formula of Huso (2010).

Simulation results were also compared with the uncorrected raw number of carcasses found (C). Using the carcass count as an estimate for the number of animals killed ($\hat{N}$) i.e. $\hat{N} = C$, or just correcting it in a simple way, e.g. $\hat{N}=C/(f*s^*)$ is still common practice despite the obvious shortcomings (Smallwood & Karas 2009, Dulac 2010).

In summary, we suggest a new formula to estimate bat or bird mortality at wind turbines and we analyse the differences in bias and precision between this new and four existing methods for different scenarios. The new estimator is based on an explicit model of the processes and can be adapted to specific situations when needed. Our goal is to help in deciding which method should advantageously be used in which context.

## Methods

### The formula

The formula we have developed is based on an explicit model of two processes: the removal by scavengers or decay, and the carcass search. The basic formula assumes that a mean number of $\bar{m}$ individuals are killed per day, that the carcasses of these killed animals are removed (e.g. by scavengers or decay) at a constant probability (1-s; i.e. s = daily persistence probability) and that the searcher efficiency is constant over time and similar for all carcasses. Variations of the formula can account for non-constancy in persistence time and/or searcher efficiency (see below). Searches are conducted at regular intervals of d days. During each search carcasses are found with searcher efficiency f and are removed from the plot. Based on these assumptions, the number of carcasses found can be calculated (see Appendix I and Table 1):

$$C = \bar{m} f \left( s \frac{1\text{-}s^{d}}{1\text{-}s} \right) \left( \sum_{i=0}^{n\text{-}1} (n\text{-}i) \left( (1\text{-}f) s^{d} \right)^{i} \right).$$

C is the total number of carcasses found during n searches conducted at intervals of d days, given an average number of $\bar{m}$ animals killed per night, a searcher efficiency f and a carcass persistence rate s. If we divide the number of detected carcasses by the total number of animals killed ($\bar{m}nd$), we obtain an estimate for the probability $\hat{p}$ of finding an animal that is killed at a wind energy turbine:

$$\hat{p} = \frac{C}{\bar{m}nd}$$

If the above formula for C is inserted in this formula, $\bar{m}$ cancels out. This makes the detection probability $\hat{p}$ independent of the number of killed animals:

$$\hat{p} = \frac{f \left( s \frac{1\text{-}s^{d}}{1\text{-}s} \right) \left( \sum_{i=0}^{n\text{-}1} (n\text{-}i) \left( (1\text{-}f) s^{d} \right)^{i} \right)}{nd} \qquad (1).$$

The formula assumes that f and s are constant over time (see results of the simulation study) and that these two parameters do not differ between individual carcasses (see Discussion).

Baerwald & Barclay (2009) used a similar formula as the one presented here. In their formula a carcass that is not found during the first search can also be found during the second search, but not thereafter. In contrast, our formula allows that such a carcass can be found at any subsequent search. Our formula may, therefore, be seen as a generalisation of the method proposed by Baerwald & Barclay (2009).

### Simulation study to assess the performance of the new formula in comparison with other formulas

To assess the performance of the new formula, we simulated data sets and subsequently used five different estimators for the number of animals killed.

Table 1. Definitions of important parameters used.

| Parameter | Definition |
|---|---|
| d | Search interval, i.e. number of days between two searches |
| n | Number of searches in the study |
| s | Daily persistence probability of a carcass, i.e. proportion of killed bats/birds which do not disappear (e.g. due to decay or scavangers) in 24 hours |
| $\bar{t}$ | Average persistence time of a carcass |
| f | Searcher efficiency, i.e. the proportion of bats/birds killed and not removed that are found during one search |
| I | Length of study period (days); I = n*d |
| N | Number of bats/birds which were killed during the study period I (unknown parameter of interest) |
| $N_t$ | Number of bats/birds which were killed during day t |
| $\bar{m}$ | Average number of bats/birds killed during one day |
| $c_i$ | Number of carcasses counted during search i |
| C | The total number of counted carcasses $\sum_{i=1}^{n} c_i$ |
| p | Probability that a bat/bird, which is killed during the study period I, is found |

The simplest estimator used the number of carcasses found as a measure of mortality:

$$\hat{N} = \sum_{i=1}^{n} c_i,$$

where $c_i$ equals the number of carcasses found during the ith search. All other estimators include a formula to estimate the probability p to detect a killed animal. For simplicity, we here divide the number of found carcasses by $\hat{p}$ to obtain an estimate of the number of killed animals:

$$\hat{N} = \frac{\sum_{i=1}^{n} c_i}{\hat{p}}.$$

In Appendix II, we present a method to obtain a credible interval for this estimate.

The four formulas for the detection probability were:

1) The simple formula $\hat{p} = f\, s^*$, where

$$s^* = \frac{1}{d}\sum_{i=1}^{d} s^{(d-i+1)}$$

is the proportion of carcasses that died in the time interval ]t-d, t] and remained until the search at time t, and f is the searcher efficiency, i.e. the proportion of carcasses present during the search that are found by the searcher. This formula ignores carcasses that were overlooked by the searchers, i.e. it assumes that all remaining carcasses have a probability of zero to be detected during further searches.

2) Our formula in two versions, namely in its basic version as presented above (1), as well as in an adapted version that accounts for decreasing searcher efficiency with the number of searches:

$$\hat{p} = \left\{Af + \sum_{x=1}^{n} Af\left(1 + ks^{d}(1\text{-}f) + \sum_{j=1}^{x\text{-}1}\left(k^{x\text{-}j}s^{(x\text{-}j)d}\prod_{i=0}^{x\text{-}j\text{-}1}(1\text{-}fk^{i})\right)\right)\right\}\Big/ nd \qquad (2),$$

where

$$A = s\frac{1\text{-}s^{d}}{1\text{-}s}$$

and k is the factor by which the searcher efficiency decreases with each search.

3) The formula suggested by Erickson et al. (2004):

$$\hat{p} = \frac{\bar{t}f}{d}\left(\frac{e^{d/\bar{t}}\text{-}1}{e^{d/\bar{t}}\text{-}1 + f}\right),$$

where $\bar{t}$ is the mean persistence time of a carcass. This parameter is related to the persistence probability s with

$$\bar{t} = \frac{1}{\text{-}\ln(s)}.$$

4) A formula recently developed by Huso (2010) and applied by Arnett et al. (2009):

$$\hat{p} = f\,k\,r = f\,k\frac{\bar{t}(1\text{-}e^{\text{-}d^{*}/\bar{t}})}{d^{*}}$$

where f is the searcher efficiency, $d^* = \min(d, \tilde{d})$, $\tilde{d}$ =-log(0.01)* $\bar{t}$ and $k = \min(1, \tilde{d}/d)$. Here, r is the proportion of animals killed during d nights which are still there at the end of the investigation period. k is either 1 or the ratio between the time until 99% of the carcasses have disappeared and d.

We simulated data given different scenarios (see below) and applied the five estimators to obtain an estimate of the number of killed animals from the number of carcasses found. The simulation study, i.e. the settings of true parameter values, was inspired by studies on bat collisions in Germany (Brinkmann et al. 2011) and North America (Arnett et al. 2009). For every simulated data set, we calculated the relative error of the estimates by dividing the difference between estimated and true number of animals killed by the true number: relative error of estimate = $(\hat{N}\text{-}N)/N$.

The following protocol was used to simulate data:

1) For n*d days, the true number of killed animals per day $m_t$ was drawn from a Poisson distribution with expected value $\bar{m}$. $\bar{m}$ was either held constant or was proportional to empirical acoustic bat activity data taken from Behr et al. (2011).
2) The number of carcasses that have not been removed during the first day ($N_1$) was drawn from a binomial distribution $N_1 \sim \text{binom}(m_1, s)$.
3) The number of carcasses present ($N_t$) at day $t = 2$ to $t = I$ was simulated autoregressively as the sum of two binomial processes: those animals that were killed before day t and have not been removed ($l_t$) and those that were killed during day t and were not removed during that day ($k_t$):

$N_t = l_t + k_t$ with $l_t \sim \text{binom}(N_{t-1}, s)$ and $k_t \sim \text{binom}(m_t, s)$.

4) At intervals of d days virtual searches were performed. For each search day, we subtracted the number of carcasses found and removed by a searcher from $N_t$: $N_t^* = N_t - c_i$ with $c_i \sim \text{binom}(N_t, f)$. $N_t$ was then replaced by $N_t^*$.
5) Steps 3 and 4 were repeated until t reached the end of the investigation period ($t = I$).

For scenarios with variable persistence probabilities s or variable searcher efficiencies f, we kept track of the individual cohorts (animals killed on the same day) during step 2 to 5. In all simulations, the number of carcasses was zero at the beginning of the study in order to exclude effects of the initial number of carcasses on the bias estimates. In field studies, this effect can be reduced by clean-out searches at the beginning of the study and by discarding old carcasses during the first days of the study.

We simulated data in order to estimate the bias in the different formulas and to assess their robustness against violations of the assumptions. First, the bias of the five estimators was assessed for data that met all assumptions made by our new basic formula (1), i.e. constant persistence probability as well as constant and independent searcher efficiency. Based on these assumptions, we simulated 12 different scenarios by using constant or variable mortality rates (for the constant case: $\bar{m} = 0.01$, for the variable case: $m_t$ proportional to empirical acoustic bat activity with an average of 0.01), short or high average carcass persistence times ($\bar{t} = 3$ days or $\bar{t} = 30$ days) and three different search intervals ($d = 1$, 7 and 14 days). We set searcher efficiency f to 0.8 and the study period to $I = 100$ days. Secondly, we assessed the robustness of the basic formula against violation of the assumption of constant persistence probability. The little empirical data available on carcass persistence times suggest that persistence time might generally increase with exposure time of carcasses (e.g. American crows *Corvus brachyrhynchos* and house sparrows *Passer domesticus* in North America; Ward et al. 2006, guillemots *Uria aagle* in Alaska; Van Pelt & Piatt 1995, bats Chiroptera spp. and brown mice *Mus musculus*; Fig. S2). Though, our own data (see Fig. S2) and those of Erickson et al. (2004) show that this increase in persistence time with exposure time might be negligible. To account for the scarce knowledge about temporal variability in carcass persistence times, we simulated data once with decreasing and once with increasing persistence probabilities over time for the six scenarios described above with constant $m_t$. Virtual carcass persistence times were simulated as random draws from a Weibull distribution with $\bar{t} = 3$ or 30 days and shape parameter 0.7 for increasing and 1.3 for decreasing persistence probability (Fig. S1). Third, we tested robustness against variation of searcher efficiency using nine scenarios: we set the average persistence time to 4.5 days, the search interval was $d = 1$, 7 or 14 days, and searcher efficiency was constant $f = 0.5$, 0.8, or decreased per carcass with the number of searches i: $f(i) = 0.8 * 0.25^{(i-1)}$. For these simulations, we also used our adapted formula (2) that takes a decrease in searcher efficiency into account.

Finally, we carried out a last set of simulations to assess the maximally possible precision that can be obtained when estimating the number of fatalities based on carcass searches. Here, we assumed that all parameters are constant in time. In different simulation runs, we varied average mortality rates ($\bar{m}$ from 0.01 to 1) and searcher efficiency (f from 0.05 to 0.95). Hundred scenarios that differed in the number of carcasses found and in the detection probability for carcasses were produced. For each scenario, we used the standard deviation of the relative error from 1,000 replicates as a measure for minimal uncertainty (i.e. maximal precision).

In field data, several additional factors will increase uncertainty, such as a clumped temporal distribution of fatalities (i.e. a non-constant mortality rate) or an uncertainty in the estimated searcher efficiency and persistence probability. The latter two were assumed to be known in our simulations, but actually have to be estimated from separate experiments using specific methods. Therefore, the standard deviations presented here have to be interpreted as a minimal possible uncertainty given the number of carcasses found and the specific detection probability.

Due to the large variety in methods applied to estimate searcher efficiency and carcass removal rates, the exploration of bias and precision in these estimates is beyond the topic of our paper. However, we present a worked example in Appendix II that shows how to combine the uncertainty of the estimated searcher efficiency and carcass persistence probability with the uncertainty that is inherent to the observation process.

The simulations were done in R 2.12.0 (R Development Core Team 2010). The R-code for the simulations can be obtained from the authors upon request.

## Results

The data simulation generally showed that the proportion of simulated data sets with zero carcasses found (i.e. no single carcass was found during the whole study period) reached up to 40% when assuming a true average of 10 animals killed during the 100 days of the virtual study period (Fig. 1). The proportion increased with increasing search interval, with decreasing persistence time, and when mortality rate varied over time. The 95% range of the relative errors strongly correlated with the proportion of zero counts among the data sets and they were similar between the different estimators.

The uncorrected count consistently underestimated the number of fatalities in all scenarios (see Figs. 1 and 2). The simple formula produced an overestimation with searcher efficiency kept constant over time for short search intervals (d = 1) and with long persistence times (see Fig. 1). When searcher efficiency decreased with the number of searches, the simple formula appeared to perform well, at least for an average persistence time of 4.5 days and search intervals of 1, 7 or 14 days (Fig. 2, right panel).

The new formula presented here appeared to be unbiased for all scenarios with constant parameters and robust towards a decrease of removal probability with time (see Fig. 1). When removal probability increased over time the formula produced an underestimation of the number of fatalities, especially with short persistence times and long search intervals. The size of this underestimation was similar to the underestimation by the other three formulas. When searcher efficiency decreased over time the basic version of our new formula produced a slight underestimation for short search intervals (see Fig. 2). However, this bias was reduced when the adapted formula was used (see Fig. 2).

The formula of Erickson et al. (2004) slightly underestimated the number of fatalities when persistence times were short (see Fig. 1), but appeared to produce unbiased results for long persistence times. This formula was rather robust towards temporal variation in removal probabili-

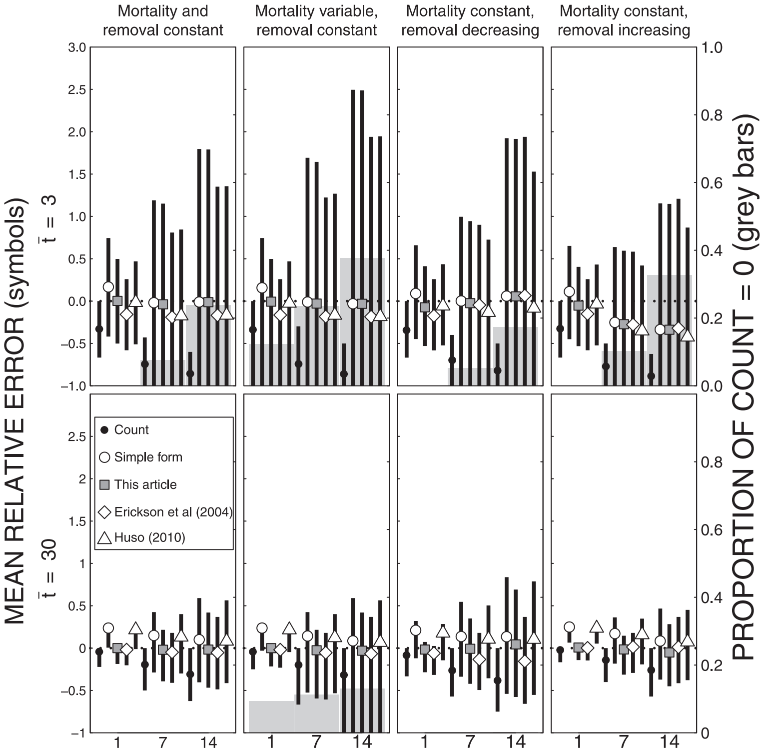

Figure 1. Relative errors of five different estimators for the number of fatalities in 1,000 simulated data sets for eight different scenarios (symbols = means, bars = range of 95% of the relative errors). In the upper row, data were simulated with a high carcass removal rate (short average persistence time $\bar{t}$ = 3 days). In the lower row, a long persistence time of 30 days was assumed. In the first column, mortality and removal rates were constant over time. In the second column, mortality rate was proportional to empirical acoustic bat activity (i.e. mortality rate varied from day to day; own data), simulating a natural distribution of bat fatalities. In the last two columns, removal rate decreased (third column) or increased (fourth column) with time. See text for details of the five different estimators. Constant parameters: searcher efficiency f = 0.8, mean mortality rate per night $\bar{m}$ = 0.1, study period I = 100 days. Wide grey bars (right axes): proportion of simulated data sets with zero carcasses found.

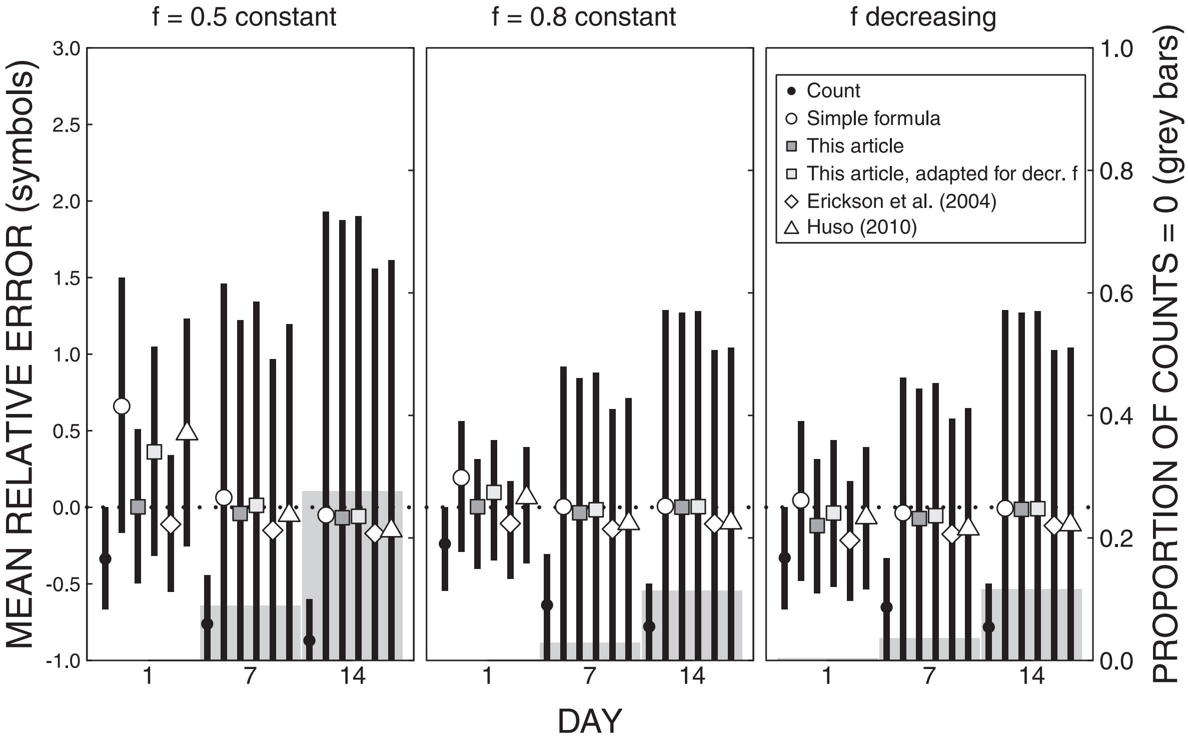

Figure 2. Relative errors of six different estimators for the number of fatalities in 1,000 simulated data sets for three different scenarios (symbols=means, bars=range of 95% of the relative errors). The first and second plots show the relative errors if searcher efficiency f is low or high, respectively, and constant over time. In the third plot, searcher efficiency was 0.8 during the first search and then decreased by the factor 0.25 for each subsequent search to simulate carcasses missed at the search. In addition to the five estimators presented in Figure 1, the adaptation of our formula that allows for a decrease in searcher efficiency (see formula 2 in the text) is shown. Grey bars as in Fig. 1.

ties. However, for short average persistence times and increasing removal probabilities, this formula produced an underestimation, too.

The formula of Huso (2010) tended to overestimate the number of fatalities for short search intervals and long persistence times and constant low searcher efficiency (see Figs. 1 and 2). This formula was quite robust when removal probabilities decreased over time and it showed a similar negative bias as our formula when persistence times were short, removal probability increased and search interval was large. The Huso (2010) formula seemed to be robust against decreasing searcher efficiency (see Fig. 2).

The standard deviations of the relative error (hereafter called 'uncertainty') were substantially smaller when the uncorrected counts were used as estimator than when a formula that accounted for detection probability was used. However, uncorrected counts were strongly negatively biased. Therefore, we do not show the uncertainty of this method here. The uncertainty and its correlation with the number of carcasses found and with the detection probability did not differ substantially between the four formulas (the simple formula, the new formula presented here, Erickson et al. 2004 and Huso 2010). Therefore, we present only the results for our formula. The uncertainty decreased with the number of carcasses found and with increasing detection probability (Fig. 3). When $< 10$ carcasses were found, the uncertainty increased dramatically, especially when detection probability was low.

## Discussion

We present a new estimator for the number of bats or birds killed at wind turbines from the number of carcasses found in fatality searches. Similar to previously published approaches, our new method accounts for the bias resulting from carcass removal by predators or decay and from imperfect detection. In a simulation study, we compared our estimator

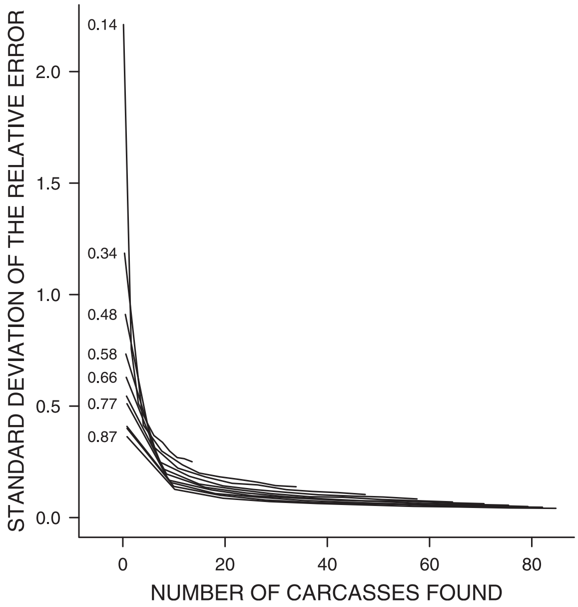

Figure 3. Highest possible precision given the number of carcasses found and the detection probability. Shown are the standard deviations of the relative errors (estimated fatalities minus true fatalities divided by true fatalities) for different numbers of carcasses found (x-axis) and for different detection probabilities (numbers), based on simulated data (see text). Only results for our formula are presented as the formulas of Huso (2010) or Erickson et al. (2004) showed similar results. For data simulation, average persistence time was set to 30 days, searcher efficiency varied from 0.05 to 0.95, mean number of fatalities per night varied from 0.01 to 1, search interval was set to seven days and total time sampled to 100 days. Note that the standard deviations in this figure only show the uncertainty induced by the variation of the Poisson distribution of the simulated fatalities and by random effects in the search process. In field data, several additional factors will increase uncertainty, such as a clumped distribution of the fatalities or the uncertainty in the estimated searcher efficiency and persistence probability (both were assumed to be known in our simulations).

with four existing ones. All five estimators assume that 100% of the area beneath a wind turbine is being searched. When only parts of the area can be searched, a correction is necessary that takes into account the distribution of carcasses beneath a turbine (Arnett et al. 2009, Hull & Muir 2010, Niermann et al. 2011).

The five estimators we compared differed with respect to bias. If the number of carcasses found was used directly as an estimator of the number of fatalities, this number was, of course, consistently underestimated. This method works best with high detection probabilities. It has the advantage of being cheap and fast, because no experiments to assess searcher efficiency (f) and carcass persistence probability (s) are necessary. However, it only gives a minimum number of dead animals and, under most conditions, the estimated number of fatalities will only be very weakly correlated with the real number of animals being killed.

Not surprisingly, the number of fatalities can be estimated more accurately when the detection probability is accounted for. Even using the simple formula $p = f*s^*$ reduced the bias considerably. However, this method overestimated the number of fatalities when search intervals were short or carcass persistence rates were high (see Figs. 1 and 2) because the formula ignores the carcasses that were missed in a search. When searcher efficiency decreases with the number of searches, the simple formula can produce fairly reliable results. Many studies on bat and bird mortality at wind turbines have used this simple formula, e.g. to estimate bird mortality with a mean search interval of 17 to > 90 days (Smallwood & Karas 2009) or to assess bat mortality with weekly searches (Dulac 2010).

When comparing the performance of the three more complex formulas (Erickson et al. 2004, Huso 2010 and our formula) none can be identified to be consistently superior to the others according to our simulations. The formula of Erickson et al. (2004) generally showed a slight underestimation. Our formula produced, on average, the smallest bias. When searcher efficiency decreased with the number of searches, our formula could be adapted, whereas the formula of Huso (2010) appeared to be robust towards decreasing searcher efficiency. This formula was designed to be robust when detectability is heterogeneous, as is the case when searcher efficiency decreases (see Huso 2010). It overestimated, however, the number of fatalities when searcher efficiency was low and independent of previous searches, and when the search interval was short (see Fig. 2). All three formulas similarly underestimated the actual number of fatalities when removal probability was high and when it increased over time.

If the strength of the increase or decrease of the removal probability over time is known (or estimated from experimental data), it is possible to adapt our new formula to account for the temporal variation in removal probability. This is possible because our estimator is based on an explicit model of the removal and search process. Empirical data from bats and mice carcasses (see Fig. S2, Erickson et al. 2004) or bird carcasses (Van Pelt & Piatt 1995, Ward et al. 2006) suggested that removal probabilities were either constant or slightly decreasing over time. Removal rates may decrease with time because those carcasses most easily detected by scavengers are removed first, leaving only those more difficult to detect on the plot. For the same reason, searcher efficiency is often assumed to decrease with persistence time.

A further issue that has to be addressed in real cases is that removal probability might be lower for the first day than during subsequent days because the exposure time is on average shorter than 24 hours for the day the animal is killed. In this case, it might be necessary to include a separate persistence probability for the first day in the formula. However, for bats in central Europe, it seems reasonable to assume similar carcass persistence probabilities s for the first and subsequent days: most of the bats are likely to be killed during the first half of the night (as inferred from acoustic activity measurements; Behr et al. 2011) and activity of the most common predator, the red fox *Vulpes vulpes*, peaks in the second half of the night (Ott 2009).

All formulas presented here assume a constant search interval. In the field, searches may be performed at irregular time intervals. Different search interval patterns will affect the fatality estimate each in its own way. Therefore, it is important to agree on a realistic schedule and to stick to it as closely as possible. Alternatively, the effect of a specific search interval pattern can be assessed based on simulated data.

When the animals killed include a variety of species with different body sizes (e.g. from hummingbirds to eagles), persistence time and detectability may differ substantially between individual carcasses. Such heterogeneity in persistence time and in detectability can produce a bias in the estimated number of fatalities, as it has been described for mark-recapture models used to estimate population size (Carothers 1973, Nichols et al. 1982, Pollock & Raveling 1982). Species-specific heterogeneity in persistence time and detectability can be reduced by analysing groups of similar species separately.

The distribution and the mean of carcass persistence times will also most likely differ substantially between different study sites because of differences in e.g. predator behaviour, temperature and humidity. Within Germany, we found carcass persistence times that varied between 1.3 and 24.5 days at 30 different wind turbines (with a mean of 4.2 days; Niermann et al. 2011). Arnett et al. (2009) report a mean persistence time of 32 days in North America. Furthermore, vegetation cover and other ground parameters (e.g. stones) differ between study sites producing heterogeneity in carcass detectability to different degrees. The search interval and study period also differ between studies depending on the time and funding available. These differences have to be accounted for when estimating fatality rates. Therefore, and based on our simulation results, we suggest that there may not be a universal formula that is applicable in all situations. For each study, the most appropriate method should be chosen and our simulation study can provide an orientation for this decision.

We found a strong correlation of the precision of the estimated number of fatalities with both the number of carcasses found and with the detection probability; if $< 10$ carcasses were found, the (highest possible) precision in our simulation was low, suggesting that conclusions from studies where only few dead animals are detected will be very uncertain. This implies that at some sites a big search effort may be necessary to obtain estimates with acceptable precision. The number of carcasses found can be increased e.g. with shorter search intervals, a longer study period, a larger proportion of area searched, an improved visibility in the area searched and by increasing the number of turbines included in the study. However, optimising the visibility in the area searched should be done with care, because it might affect the number of fatalities by altering the habitat use by the animals.

Data from different turbines and estimated searcher efficiencies from different searchers can be combined in different ways. Jones et al. (2009) suggested generalised linear models. In our extensive study, we used weighted averages of searcher efficiencies per turbine with weights proportional to three visibility classes in the area searched and to the number of searches per person (Niermann et al. 2011).

Once the searcher efficiency and removal probabilities have been estimated for a specific study, one of the formulas discussed in this article can be applied to obtain an estimate for the number of fatalities. To obtain an uncertainty measure for this estimate, several sources of uncertainties have to be included: 1) the randomness produced by the count process, 2) the uncertainty in the estimated removal probability, 3) the uncertainty in the estimate for searcher efficiency and 4) if $< 100\%$ of the area beneath a wind turbine is searched, the uncertainty of the estimated proportion of killed animals that fall into a searched area. The uncertainties 2) to 4) were not included in our simulation studies in this article. The uncertainty in actual field data would therefore be considerably higher than in the simulated data presented here. We provide one possibility to combine the sources of uncertainty mentioned above for real data in a worked example in Appendix II.

To summarise, our formula appears to provide an unbiased estimate of the number of animals killed when searcher efficiency and removal probability are constant in time. The robustness of our formula with respect to temporal variation in the removal probability or searcher efficiency is similar to that of other formulas published. However, in contrast to other approaches, our formula is based on an explicit carcass search process model that can be adapted to the specific circumstances of a field study.

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# Appendices

## Appendix I. Derivation of the new formula to estimate carcass detection probability

The table below contains the expected number of killed bats and birds that are present below a wind turbine for each day (1 to I) of the study period, if an average of $\bar{m}$ animals are killed per day. For each search the expected number of carcasses found is given in the last column. The last row gives the sum of the expected number of animals killed and the sum of the carcasses found during all searches.

| Search | Night/day | Expected number of killed animals present | Expected number of killed animals found |
|---|---|---|---|
| | 1 | $\bar{m}$ s | |
| | 2 | $\bar{m}$ (s + $s^2$) | |
| 1st search | d | $\bar{m}$ (s + $s^2$ + .. + $s^d$) = $\bar{m}$ s$\frac{1\text{-}s^d}{1\text{-}s}$ = $\bar{m}$ A<br>with A = s$\frac{1\text{-}s^d}{1\text{-}s}$ | $\bar{m}$ Af |
| | d + 1 | $\bar{m}$ (A(1-f)s + s) | |
| | d + 2 | $\bar{m}$ (A(1-f)$s^2$ + s + $s^2$) | |
| | .. | | |
| 2nd search | 2d | $\bar{m}$ (A(1-f)$s^d$ + s + $s^2$ + .. + $s^d$) = $\bar{m}$ (A(1-f)$s^d$ + A) = $\bar{m}$ A((1-f)$s^d$+1) | $\bar{m}$ A((1-f)$s^d$+1)f |
| | 2d + 1 | $\bar{m}$ (A((1-f)$s^d$ + 1)(1-f)s + s) | |
| | 2d + 2 | $\bar{m}$ (A((1-f)$s^d$ + 1)(1-f)$s^2$ + s + $s^2$) | |
| | .. | | |
| 3rd search | 3d | $\bar{m}$ (A((1-f)$s^d$ + 1)(1-f)$s^d$ + A) = $\bar{m}$ (A(x+1)x + A) = $\bar{m}$ A((x+1)x+1) = $\bar{m}$ A($x^2$ + x + 1) with x = (1-f)$s^d$ | $\bar{m}$ A($x^2$ + x + 1)f |
| | 3d + 1 | $\bar{m}$ (A($x^2$ + x + 1)(1-f)s + s) | |
| | 3d + 2 | $\bar{m}$ (A($x^2$ + x + 1)(1-f)$s^2$ + s + $s^2$) | |
| | .. | | |
| 4th search | 4d | $\bar{m}$ (A($x^2$ + x + 1)(1-f)$s^d$ + A) = $\bar{m}$ A($x^3$+ $x^2$ + x + 1) | $\bar{m}$ A($x^3$+ $x^2$ + x + 1)f |
| nth search | nd = I | $\bar{m}$ A($x^{(n\text{-}1)}$ + $x^{(n\text{-}2)}$ + .. + x + 1) | $\bar{m}$ A($x^{(n\text{-}1)}$ + $x^{(n\text{-}2)}$ + .. + x + 1)f |
| Sum of n searches | I | $\bar{m}$ A(1 + (1 +x) + (1 + x + $x^2$) + .. + (1 + x + .. + $x^{(n\text{-}1)}$)) = $\bar{m}$ A(n + (n-1)x + (n-2)$x^2$ + .. + (n-n)$x^n$) = $\bar{m}$ A $\sum_{i=0}^{n-1}$(n-i)$x^i$ | $\bar{m}$ Af $\sum_{i=0}^{n-1}$(n-i)$x^i$, where A = s$\frac{1\text{-}s^d}{1\text{-}s}$ and x = (1-f)$s^d$ |

## Appendix II. Worked example of fatility estimation

Here, we present a worked example using the statistical software R (R Development Core Team 2010) to obtain a fatality estimate based on an empirical carcass count. It assumes that both searcher efficiency and removal probability are experimentally assessed. By providing this example, we show one possible way to obtain an estimate together with an uncertainty measure (here a 95% credible interval).

To obtain an uncertainty measure for the estimated number of fatalities, the following sources of uncertainties have to be combined: 1) the randomness of the count process (e.g. two searches will result in different numbers of carcasses found even if detection probability and the true number of carcasses are the same), 2) the uncertainty in the estimate for removal probability and 3) the uncertainty in the estimate for searcher efficiency. The uncertainty of the fatality estimate which is due to the randomness of the count process is calculated with the help of Bayes' theorem. This gives a posterior distribution of the number of fatalities based on the carcasses counted and the (known) probability of detecting a carcass. To include the uncertainty in the detection probability (that is based on the estimated searcher efficiency and the estimated carcass removal probability) into this posterior distribution, we apply a Monte Carlo simulation.

Note that the credible interval presented here shows the uncertainty in the fatality estimate for the actual sample (the specific study period and study location) only, and it is only reliable for short search intervals. This is because it does not take the temporal or spatial distribution of the fatalities into account. If the aim of the study is to predict fatality in future or for different turbines or if search intervals are large, a model of the collision process (and presumably additional data providing information about the temporal and spatial distribution of the animals) is needed in addition to the search process model presented here to obtain a reliable uncertainty measure (see Korner-Nievergelt et al. 2011 for an example).

### Example study description

Carcass searches were performed every second day during a 200 days study period (100 searches). For simplicity, we assume that 100% of the area beneath a wind turbine is searched. If only a part of the area is searched, the probability that a killed animal falls into the searched area (a) has to be estimated (see Niermann et al. 2011). Then, the probability that a killed animal is detected by a researcher is p' = p* a, and the uncertainty in the estimate of a can be included in the uncertainty measure for p' by Monte Carlo methods in the same way as shown here for the uncertainties in the estimates for searcher efficiency and carcass persistence probability.

### Example data

Number of carcasses found C = 12, searcher efficiency f = 0.72 (95% CI: 0.62-0.81 from experiments), i.e. the probability that a carcass that is lying on the ground at the time of the search is found by the searcher, carcass persistence s = 0.84 (95% CI: 0.64-0.94 from experiments), i.e. the probability that a carcass is not removed during 24 hours. As CI, credible or confidence intervals can be used.

### Estimating the number of fatalities with a credible interval

#### *Step 1*

Describe the uncertainty in the estimates for searcher efficiency and carcass persistence probability by a beta distribution, i.e. transform the 95% CI into the shape parameters of the beta distributions.

```
f <- 0.72; f.lower <- 0.62; f.upper <- 0.81
s <- 0.84; s.lower <- 0.64; s.upper <- 0.94
# - - - - - - - - - - - - - - - - - - - - - - - - - - - - - - - - - - - - - - - -
# function to transform the 95% CI into shape parameters of a
# beta distribution
shapeparameter <- function (m, lwr, upr){
# m = estimate
# lwr, upr = lower and upper limit of the 95% credible or
# confidence interval
# - - - - - - - - - - - - - - - - - - - - - - - - - - - - - - - - - - - - - - - -
ci <- upr - lwr
sigma2 <- (ci/4)^2
a <- m*(m*(1-m)/sigma2-1)
b <- (1-m)*(m*(1-m)/sigma2-1)
list (a=a,b=b)
}
# end of function shape parameter # - - - - - - - - - - - - - - - - - - - - -
f.a <- shapeparameter(f, f.lower, f.upper)$a
f.b <- shapeparameter(f, f.lower, f.upper)$b
s.a <- shapeparameter(s, s.lower, s.upper)$a
s.b <- shapeparameter(s, s.lower, s.upper)$b
```

#### *Step 2*

Define the parameters of the simulations and prepare the vector for the resulting posterior distribution of the number of fatalities. Define a function to obtain the detection probability from searcher efficiency, persistence probability and search interval. Here, we use the new formula presented in this article. Define a function to obtain the posterior distribution of the number of fatalities based on the number of observed carcasses and the detection probability. This formula is based on the theorem of Bayes. Start the loop over step 3 and step 4.

```
maxn <- 500 # define a maximum for the number of fatalities
nsim <- 1000 # number of Monte Carlo simulations
# prepare a vector for the posterior density distribution
# of the estimated number of fatalities:
Npostdist <- numeric(maxn+1)
# - - - - - - - - - - - - - - - - - - - - - - - - - - - - - - - - - - - - - - - -
# function to obtain the probability of detecting a carcass
# given the searcher efficiency (f), persistence probability
# (s), search interval (d) and the total number of searches
# (n).
pcarcass <- function (s, f, d, n){
# s = probability that a carcass remains 24 hours
# f = probability that a carcass is detected by a
# searcher during a search given it persisted to the search
# d = (average) number of days between two searches
# n = number of searches (n * d = length of study period)
# - - - - - - - - - - - - - - - - - - - - - - - - - - - - - - - - - - - - - - - -
x <- (1-f)*s^d
A <- s*(1-s^d)/(1-s)
summep <- numeric(n)
for (k in 0: (n-1)) summep[k+1] <- (n-k)*x^k
p <- A*f*sum (summep)/(d*n)
p
```

```
}
# end of function pcarcass # ---------------------------
# -------------------------------------------
# function to obtain the posterior density distribution of the
# number of fatalities based on a (known) probability that a
# carcass is detected (p) and the number of observed carcasses
#(nf)
posterior.N <- function(p, nf=0, maxN=50, ci.int=0.95, plot=TRUE, dist=FALSE){
# p = probability that a killed animal is detected by a seacher
# nf = number of carcasses found
# maxN = maximal possible number of fatalities
# ci.int = size of the credible interval that should be calculated
# plot: posterior distribution is plotted if TRUE
# dist: posterior distribution is given if TRUE
# -------------------------------------------
N <- nf:maxN
if (nf==0) pN <- p*(1-p)^(N-nf)
if (nf>0) {
denom <- sum (choose(N, nf) * (1-p)^(N-nf))
pN <- choose (N, nf) * (1-p)^(N-nf)/denom
pN <- c (rep(0, nf), pN)
N <- c (rep(0, nf), N)
}
if(plot) plot(N, pN, type="h", lwd=5, lend="butt", xlab="Number of fatalities", ylab="Posterior density")
index <- cumsum(pN) < ci.int
indexLower <- cumsum(pN) < (1-ci.int)/2
indexUpper <- cumsum(pN) < 1-(1-ci.int)/2
if (nf==0) interval <- c(nf, min(N[!index]))
if (nf>0) interval <- c(min(N[!indexLower]), min(N[!indexUpper]))
if (interval [2]==Inf) cat("Upper limit of CI larger than maxN! -> increase maxN\n")
expected <- min(N[!cumsum(pN)<0.5])
results <- list (interval=interval, expected=expected)
if (dist==TRUE) results <- list (interval=interval, expected=expected, pN=pN)
results
}
# end of function posterior.N # -------------------------
for (i in 1:nsim){
```

### Step 3

Draw a searcher efficiency f at random from the beta distribution defined by f.a and f.b.

```
fr <- rbeta(1, f.a, f.b)
```

Draw a persistence probability s at random from the beta distribution defined by s.a and s.b.

```
sr <- rbeta(1, s.a, s.b)
```

Calculate the detection probability given sr, fr, search interval d = 2 and number of searches n = 100.

```
pr <- pcarcass(sr, fr, d=2, n=100)
```

### Step 4

Compute the posterior density distribution of the number of fatalities based on pr and the observed number of carcasses (number found = 12) using the function posterior.N.

```
postNtemp <- posterior.N(nf=12, p=pr, maxN=maxn, plot=FALSE, dist=TRUE)
```

Sum the posterior densities over all nsim simulations.

```
Npostdist <- Npostdist + postNtemp$pN
} # close loop i
```

### Step 5

Scale the summed posterior distribution and extract median and 95% credible interval.

```
Npostdist.sc <- Npostdist/nsim
indexLower <- cumsum(Npostdist.sc) < 0.025
indexMedian <- cumsum(Npostdist.sc) < 0.5
indexUpper <- cumsum(Npostdist.sc) < 0.975
lower <- min(c(0:maxn)[!indexLower])
estimate <- min(c(0:maxn)[!indexMedian])
upper <- min(c(0:maxn)[!indexUpper])
lower; estimate; upper
```

As a result we receive an estimate of 17 fatalities with a 95% credible interval of 12-31 fatalities.

The posterior distribution of the number of fatalities is plotted:

```
plot (0:maxn, Npostdist.sc , type="h", lwd=5, lend="butt", xlab="Number of fatalities", ylab="Posterior density", xlim=c(0,50))
```