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ESTIMATING CAUSE-SPECIFIC MORTALITY RATES USING RECOVERED CARCASSES

Damien O. Joly,[1,5] Dennis M. Heisey,[2] Michael D. Samuel,[3] Christine A. Ribic,[3] Nancy J. Thomas,[2] Scott D. Wright,[2] and Irene E. Wright[4]

[1] Global Health Programs, Wildlife Conservation Society, 1008 Beverly Drive, Nanaimo, British Columbia, Canada, V9S 2S4
[2] US Geological Survey, National Wildlife Health Center, 6006 Schroeder Road, Madison, Wisconsin 53711, USA
[3] US Geological Survey, Wisconsin Cooperative Wildlife Research Unit, 204 Russell Laboratory, 1630 Linden Drive, University of Wisconsin, Madison, Wisconsin 53706, USA
[4] 4730 Toepfer Road, Middleton, Wisconsin 53562, USA
[5] Corresponding author (email: djoly@wcs.org)

ABSTRACT: Stranding networks, in which carcasses are recovered and sent to diagnostic laboratories for necropsy and determination of cause of death, have been developed to monitor the health of marine mammal and bird populations. These programs typically accumulate comprehensive, long-term datasets on causes of death that can be used to identify important sources of mortality or changes in mortality patterns that lead to management actions. However, the utility of these data in determining cause-specific mortality rates has not been explored. We present a maximum likelihood-based approach that partitions total mortality rate, estimated by independent sources, into cause-specific mortality rates. We also demonstrate how variance estimates are derived for these rates. We present examples of the method using mortality data for California sea otters (*Enhydra lutris nereis*) and Florida manatees (*Trichechus manatus latirostris*).

Key words: California sea otter, cause-specific mortality, *Enhydra lutris nereis*, Florida manatee, likelihood methods, marine mammals, necropsy data, *Trichechus manatus latirostris*.

INTRODUCTION

In many long-lived threatened and endangered mammals, variation in mortality is a principle determinant of population growth (e.g., Gaillard et al., 1998); therefore, describing the causes of mortality is an important component of conservation research and the initiation of conservation actions. Many methods have been developed to estimate cause-specific mortality rates; however, most require known fates of individuals tracked through mark–recapture methods or radiotelemetry (e.g., Heisey and Fuller, 1985; Schaub and Pradel, 2004). The expense and logistical complexities of these studies limit the sample size, scope, and study duration, particularly for species with long lifetimes.

For some marine mammals, such as the California sea otter (*Enhydra lutris nereis*) or the Florida manatee (*Trichechus manatus latirostris*), comprehensive networks have been developed to recover stranded individuals and conduct necropsies to determine the cause of death. For other species, long-term diagnostic databases have been developed in an ad hoc manner. Although these data have been valuable for evaluating the relative importance of different causes of mortality (Ackerman et al., 1995, Estes et al., 2003), determining the role of cause-specific mortality in population dynamics requires cause-specific mortality rates (Gerber et al., 2004). Herein, we show how necropsy data can be combined with independent estimates of total mortality rates to estimate crude cause-specific mortality rates (Heisey and Fuller, 1985). This approach has previously been applied in research on sea otter mortality patterns (Gerber et al., 2004); however, no derivation of these mortality rate estimators was provided. Here, we derive cause-specific mortality rate estimates and their variances based on maximum likelihood. We present examples of the method by using mortality data for two marine mammal species: California sea otters and Florida manatees.

MATERIALS AND METHODS

Cause-specific mortality rates can be estimated using two sources of information: 1) recovered carcasses where a cause of death was determined; and 2) population mortality rate estimates, $\hat{q}$, for the time interval in which carcasses were collected. Mortality rates can be estimated using mark–recapture, radiotelemetry, or life table approaches; essentially, any method by which mortality and its variance are estimated. The total mortality rate is partitioned among J causes of death, $j=1,\ldots, J$. We assume that carcass counts (y_j) are distributed in proportion to their corresponding mortality rates (q_j) for source j (we discuss implications of violating this assumption below). Let T be the time of death. Crude cause-specific mortality for the j-th source during an interval ending at time t is estimated by $q_j=\text{Prob}(T<t,J=j)$ (Heisey and Fuller, 1985), the probability of dying before t due to cause j. The term "crude" does not mean q_j suffers some flaw, but indicates that while all sources of mortality are considered in the estimate, these sources of mortality may not be acting independently and therefore, may not be additive. By the law of total probability, the total probability of death is $q=\sum_{j=1}^{J} q_j$. Let the total number of carcasses be $N=\sum_{j=1}^{J} y_j$. Then, the expected proportion of carcasses due to cause j is given as:

$$\frac{E[y_j]}{N}=\frac{q_j}{q} \tag{1}$$

where $E[y_j]$ is the expected number of deaths due to cause j, given N. Rearranging equation 1 yields the method-of-moments estimator for cause-specific mortality rates:

$$q_j=\frac{y_j}{N}q \tag{2}$$

where it is assumed that total mortality q is determined from other sources. This is the complement of equation 1 in Gerber et al. (2004). Note that because of the constraint $q_J=q-\sum_{j=1}^{J-1} q_j$, there are only J–1 free q_j parameters to estimate through the likelihood method (although an estimate for the final source can be made by subtraction). For most carcass recovery programs, a portion of the carcasses are assigned a cause of death of "undetermined," a reasonable category to exclude.

Alternatively, equation 2 can be derived by conditioning on the total number of carcasses N and assuming the carcasses are multinomially distributed among the J causes of death (within each age–sex class and year), and thus the kernel of the likelihood is proportional to:

$$L\approx\prod_{j=1}^{J}\left(\frac{q_j}{q}\right)^{y_j} \tag{3}$$

(Note that a likelihood could also be derived by allowing each y_j to follow a Poisson distribution and not conditioning on the total N.) Maximizing L with respect to q_j will yield Eq. 2, the maximum likelihood estimate. An implicit assumption of the multinomial distribution is that the probability of carcass recovery is similar for all causes of death. Further, each mortality source is assumed to be independent and mutually exclusive of other sources of mortality. Note that q_j is only maximum likelihood if the overall mortality rate q is maximum likelihood.

Up to this point, the total mortality q was treated as known, while it, too, is an estimate with an associated variance that needs to be reflected in the variance of the estimated cause-specific mortality. Let $\hat{q}$ be some consistent estimate of q with associated variance. Define $\hat{q}_j=(y_j/N)\hat{q}$. Variance estimates for the estimated cause-specific mortality rates, $\hat{q}_j$ are obtained as a variance of products (Seber, 2002):

$$V\left(\hat{q}_j\right)=V\left(\hat{p}_j\right)\hat{q}^2+V(\hat{q})\hat{p}_j^2 \tag{4}$$

where $\hat{p}_j=y_j/N$ and $V(\hat{p}_j)=\hat{p}_j(1-\hat{p}_j)/N$. This variance estimate is not a maximum likelihood estimate.

Example 1: Shark predation on adult male California sea otters

Since 1968, all California sea otter carcasses found on the shore in California are recovered and examined for cause of death (Pattison et al., 1997; Estes et al., 2003). Between 1992 and 1996, all otter carcasses found in sufficient condition received comprehensive necropsies at the USGS National Wildlife Health Center (NWHC; Thomas and Cole, 1996). As attacks by great white sharks (*Carcharodon carcharias*) are thought to be a substantial source of mortality for the California sea otter (Ames and Morejohn, 1980; Estes et al., 2003), we use this source of mortality to illustrate how to estimate cause-specific mortality rates from necropsy data. We focused on adult males (>3 years of age); this age–sex class was the most frequently recovered over the 5-yr period (73 of 245 necropsied carcasses). Adult male otters were classified as having died due to shark bite (12/73), "other" (54/73), and "un-

determined" (12/73). In order to meet the assumptions of the multinomial likelihood (as above), cause-specific mortality rate was not estimated for the undetermined category.

Ages are determined for most recovered otters by counting cementum annuli (Bodkin et al., 1997). We assumed a stable age structure and constant population growth and used likelihoods in Udevitz and Ballachey (1998) to estimate the annual mortality rate for adult males, $\hat{q}$, for the interval 1992–1996. The California sea otter population was growing at a fairly constant rate up to the mid-1990s (Estes et al., 2003), and thus, a stable age distribution appears reasonable. Likelihood maximization was conducted using nlm in R v. 1.9.0 (R Development Core Team, 2004), and the variance of $\hat{q}$, was estimated by inverting the numerically solved Hessian information matrix. Cause-specific mortality rates and associated variances were estimated using equations 2 and 4.

Example 2. Watercraft-related mortality in Florida manatees

As a long-lived mammal, the population dynamics of the Florida manatee are most sensitive to adult mortality (Marmontel et al., 1997). An estimated 25–30% of observed manatee deaths are attributed to watercraft collision (Ackerman et al., 1995; Wright et al., 1995), and a recent review of the status of the Florida manatee singled out watercraft collisions as a major threat to manatee recovery (Florida Marine Research Institute, 2002). A long-term database on causes of death in the Florida manatee was previously published (Ackerman et al., 1995), and the data are available online (http://research.myfwc.com/manatees/search_summary.asp).

Using previously published adult survival rates, we estimated the annual probability of mortality due to watercraft collision in the Florida manatee for the Northwest (1990–2000; Langtimm et al., 2004) and Southwest populations (1995–2000; Langtimm et al., 2004). We pooled annual data on causes of death from Florida Fish and Wildlife Conservation Commission, 2008 into three categories: watercraft-related mortalities, other causes of death, and undetermined (excluded to meet the assumptions of independent causes of mortality described above). We also excluded perinatal mortalities, as the published survival rate estimates were for adult manatees. Ideally, the cause-of-death data would be stratified by age and sex, as it is likely that causes of death would vary across different life stages (e.g., Siler, 1979); because these data were not available, we assumed similar cause-specific mortality rates across adult age and sex classes (juveniles were excluded). Although this assumption is most certainly violated, we felt it was a reasonable assumption, as we present this analysis as illustration only.

TABLE 1. Estimated annual watercraft-related mortality rates, $\hat{q}_j$, on the west coast of Florida (1990–2000). The Northwest and Southwest manatee populations are as defined in Langtimm et al. (2004).

	Population			
	Northwest		Southwest	
Year	$\hat{q}_j$	SE	$\hat{q}_j$	SE
1990	0.012	0.0023		
1991	0.010	0.0036		
1992	0.013	0.0033		
1993	0.020	0.0017		
1994	0.011	0.0021		
1995	0.000	0.0000	0.033	0.0011
1996	0.010	0.0019	0.010	0.0002
1997	0.020	0.0039	0.026	0.0008
1998	0.011	0.0028	0.039	0.0012
1999	0.012	0.0012	0.042	0.0010
2000			0.030	0.0008

RESULTS

The annual mortality rate, $\hat{q}$, for adult male sea otters (1992–1996) was estimated to be 0.16 (SE=0.022) with annual shark-related mortality estimated at 0.026 (SE=0.004) and "other" causes estimated at 0.119 (SE=0.016); the remaining mortality rate was associated with "undetermined" causes. The annual watercraft-related mortality rate in Florida manatees varied from 0 in 1995 in the Northwest population to 0.042 (SE=0.001) in 1998 in the Southwest population (Table 1).

DISCUSSION

As with any estimation procedure, violations of the assumptions can lead to biased estimates of cause-specific mortality rates. In our approach, cause-specific mortality rates are based on an independently derived total mortality rate (estimated by methods such as mark–recapture, radiotelemetry, or population simulation). Bias associated with estima-

tion of the total mortality rate will affect the cause-specific mortality rates. In general, potential biases may also arise from violation of the following assumptions: 1) carcasses have a multinomial distribution among independent causes of death; and 2) carcasses are recovered in proportion to the mortality risks faced by live animals. A discussion of violation of each assumption follows.

By using a multinomial likelihood, we assumed that animals die of one of a number of independent causes of death, an assumption made in most cause-specific survival analyses (e.g., Heisey and Fuller, 1985). Mortality can often be associated with multiple causes, wherein one factor increases the probability of dying from another factor. In addition, several incidental or insignificant conditions may be present. When assigning causes of death, the examiner must decide which insult was the most important factor causing death. This is often an educated decision based on available facts and can influence the outcome of the analysis presented here, particularly if cause of death is determined by multiple people or over a long period of time. There are several strategies to avoid potential bias of this type. First, the examiner may decide to focus on the ultimate or precipitating factor: "Which assault lead to inevitable death of the animal?" Second, the examiner may focus on the proximate cause of death: "What was the final assault that killed the animal?" Third, the examiner may attempt to choose cause-of-death categories that have as little overlap as possible. Finally, independent mortality syndromes could be established by expert opinion or analytically through a multivariate analysis (e.g., manatee cold stress syndrome; Bossart et al., 2003). The choice of strategy will alter the results, and so, should be applied systematically when evaluating causes of death—and documented in full so that the methods may be replicated, as in the case of the manatee data (Ackerman et al., 1995). Analytical methods are available to deal with nonindependent causes of death, but these require continuous measurement of the risk factors to which an animal is exposed prior to its death; information not typically available for free-ranging wildlife (see discussion of the interrelation between failure types in Kalbfleisch and Prentice, 2002). Further research in this area is necessary.

We also assumed that carcasses are distributed among the causes of death in proportion to the mortality risks. Cause-specific mortality estimates can be biased if the probabilities of an animal being recovered, or determining the cause of death, are not independent of the cause of mortality. There are several potential biases related to carcass recovery, handling, cause-of-death determination, and analysis of carcasses-derived data that could affect the accuracy of our cause-specific mortality estimates. For marine mammals, carcass recovery may be influenced by distance from shore at time of death, access for recovery based on land ownership patterns and coastline geography, cause of death (e.g., some causes of death, such as poaching, may make carcass recovery less likely), age and sex of animal (e.g., as a result of variation in size or behavior), ocean currents, weather events, and human activity and density. Spatial and cause of death-specific variation in time from death to carcass recovery could introduce bias, as decomposition decreases the likelihood that some causes of death can be determined. Finally, bias could be introduced through variation in interpretation of necropsy results among diagnostic pathologists and laboratories, as well as through the criteria by which carcasses are pooled into categories for analysis. Consequently, examination of the potential biases associated with carcass recovery is necessary to evaluate over- or underestimates for specific mortality risks.

Despite these potential limitations, this approach adds to our ability to assess the importance of various mortality factors in

the population ecology of threatened and endangered species. Necropsy data from salvaged carcasses are often collected for a variety of purposes, but until now, their use in activities such as population viability analysis has been limited. Population simulation could be used to assess the effect of variation in mortality rates on the population dynamics of these species (e.g., management actions to reduce watercraft–manatee collisions). Furthermore, patterns in cause-specific mortality rates can be assessed over time to identify changes in specific mortality rates that may require management action, something that may not be apparent when simply looking at numbers of carcasses. Finally, using carcass-derived data allows insight into mortality factors that limit species population growth over spatial and temporal scales that are beyond the reach of many mark–recapture or radiotelemetry studies.

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