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CORRESPONDENCE

Estimation of mortality parameters from (biased) samples at death: are we getting the basics right in wildlife field studies? A response to Lovari *et al*. (2007)

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In a recent paper dealing with wolf mortality in Italy (Lovari *et al*., 2007), the authors used a sample of 154 dead wolves incidentally found during a 11-year period to infer population parameters (e.g. sex and age ratios, mortality patterns, survivorship) and to provide a way to assess population-scale responses to conservation strategies. In our comment, we offer explanations as to why Lovari *et al*.'s (2007) paper has basic methodological flaws (e.g. inferences at the population level from an opportunistic sample of age at death and the use of static life-tables under violation of basic assumptions) that weaken the results, so that its conclusions are not warranted and should be cautiously interpreted. Generalizing from this specific case, we hereby argue that the use of opportunistic or convenience sampling (in this case, of dead animals) is not acceptable and should not be encouraged, especially if the results are used in population modelling in an applied perspective as these authors do, as many sources of bias can distort sample statistics from population parameters.

Wildlife biologists working with endangered, low-density and elusive species such as large carnivores are constantly challenged to obtain robust and reliable population-scale datasets. These are needed to reliably assess the structure and dynamics of the populations, project their future trends and apply population models to conservation and management problems (Chapron *et al*., 2003). However, obtaining statistically, methodologically and biologically sound datasets at the population scale and for long time frames is not a trivial matter. Although researchers, especially dealing with endangered and threatened species, should strive to make the most out of any source of data, proper methodology and acknowledgment of potential sources of bias should be common practice 'to get the basics right in wildlife field studies' (Anderson, 2001) in order to provide 'reliable knowledge' (Romesburg, 1981).

In a recent paper on wolf mortality (Lovari *et al*., 2007), the authors address the important topic of estimation of critical population parameters (i.e. population structure, reproduction, survivorship and mortality) for the wolf *Canis lupus* in central Italy, relating these parameters to current conservation strategies. By analysing a sample of incidentally found wolf carcasses, they conclude that 'an extensive, routinely collection and analysis of wolf carcasses can be a relatively cheap but effective method to assess the state of a population, especially when data from the living population are missing' (Lovari *et al*., 2007). We definitively concur with these authors that theirs is a worthwhile effort, as the lack of information at the population level undermines any rational approach to wolf management and conservation in Italy, as well in other European countries where the species is currently expanding its range (Boitani, 2003). However, we firmly believe that the use of these data (i.e. incidentally found carcasses) to infer population parameters and trends should not be encouraged, especially if the potential sources of biases are not adequately addressed. Although the authors recognize some limitations of their dataset, their concerns fall short and do not seem to have been stressed enough in their analyses.

We believe that the major conclusions of the Lovari *et al*.'s paper are flawed by potential sources of bias that do not seem to have been adequately considered both in the results and discussion sections. In this letter, we explain why the basic nature of these flaws (e.g. inferences at the population level from an opportunistic sample of age at death, or the use of static life-tables under violation of basic assumptions) warrants some comments and criticism, in particular if the results are used in population modelling in an applied perspective (Chapron & Arlettaz, 2006).

(1) In a truly representative sample of dead animals, each wolf dying in the population has the same probability of being reported, irrespective of its sex, age, social status, location, proximity to humans and cause of deaths. The sample of 154 dead wolves, incidentally found in central Italy by different observers (foresters, game wardens, etc.)

during a period of 11 years, cannot be considered a representative sample of the living wolf population, nor of the age and sex distribution at deaths. This sample stems from what is called opportunistic or convenience sampling (Thompson, White & Gowan, 1998; Anderson, 2001), and many sources of bias can deviate the sample statistics from population parameters. First, some age and sex categories might have a higher chance of being found dead incidentally because of differences in behaviour, social interaction, spatial ecology and distribution in relation to anthropogenic features of the landscape and because of non-random human frequencies across all landscapes. Second, the causes of death may not have the same probability to be detected, that is a wolf killed in a vehicle collision is much more likely to be reported than a wolf dying of natural causes far from human settlements, and a wolf shot by poachers or hunters during a wild boar hunt can be hardly expected to be reported afterward. Although the authors recognize that their sample has limitations, and that 'most likely many carcasses were not found because they were hidden or buried by poachers or just went lost in the forest' (Lovari *et al*., 2007), they nevertheless present statistical analyses, results and final interpretations as if the sample originated from correct probability sampling, and they estimate mortality causes, age and sex associations with mortality causes, seasonal fluctuations in mortality, population age and sex ratios. When discussing mortality causes in wolf populations, the authors compare their findings based on the incidental sample of dead wolves with those of radio-tagged wolves in Minnesota (Mech, 1977, 1989, 1994): not surprisingly, mortality from starvation and other natural causes was higher in the latter, whereas 'our sample of wolves did not show any sign of malnutrition' (Lovari *et al*., 2007). Given the nature of Lovari *et al*.'s sample, what would have been the odds to incidentally find a wolf of any age and sex dead from starvation into the forest? In addition, based on the age ratio of their wolf carcasses, the authors estimate the population age structure (Lovari *et al*., 2007; fig. 3) and conclude that the Italian wolf population has a pup:subadult: adult ratio of 10:23:67, or a pup-adult ratio of 10:90, resembling naturally controlled as opposed to exploited wolf populations. In turn, they interpret this is as an indication that 'human-induced killing is apparently not severe enough to make our wolf population fall among the 'exploited' ones' (Lovari *et al*., 2007).

(2) By pooling together all the causalities from 1991 to 2001, the authors tacitly assume no year-to-year fluctuations in population parameters and mortality patterns. However, if the 11-year time frame is contrasted with the mean wolf generation time and the changes in wolf number, range and persecution that most likely occurred in Italy in this period, the no-fluctuation assumption seems quite unrealistic at best. To draw inferences for the entire period of study, and provided the sample of dead wolves was truly representative, the mean annual values (sex and age ratios, survivorship, etc.) and their sampling variability should have been used to avoid 'pooling fallacy' pitfalls (Schooley, 1994).

(3) It is not clear how differences in carcass age (i.e. time since death and extent of decomposition) affected the reliability of necropsies in assessing death causes and reproductive status. A more detailed illustration of post-mortem examination techniques would have been appreciated, also with regard to the reproductive assessment of adult females: as only 12 females out of 58 showed signs of reproductions, how were detection and counts of corpora lutea, placental scars and embryos affected by the extent of carcass decomposition and the month of the year in relation to reproductive physiology? In addition, it is not clear why only 10 out of the 12 reproducing females were aged if from previous results all 154 carcasses have been aged (Lovari *et al*., 2007; fig. 1b).

(4) The authors underline that their 'results on wolf survival appear to be the only one available for Eurasia' (Lovari *et al*., 2007). However, the empirical survival function that the authors used to estimate age – and sex-specific survivorship, as well as maximum age at death, is weakly supported and not suited to the dataset used. The truncated version of the survival function (Lovari *et al*., 2007; table 2) used to estimate the complete survival model equals a static life-table approach using the age distribution at death of an imaginary cohort of 56 (females) and 64 (males) wolves (Table 1; example provided for females only). As shown by Caughley (1977) using Dall sheep *Ovis dalli* skulls, the composite count of the dead animals across all age classes is assumed to represent an initial cohort, and the dead animals in each age class (d_x) are used to compute the number still surviving at the beginning of the next age class (n_{x+1}); l_x, the standardized survivorship with respect to the initial cohort is then computed, and from this the standardized mortality ($1-l_x$) is easily obtained. By comparing the l_x and $1-l_x$ columns in Table 1 with the F($x+$) and L($x-$) columns (Lovari *et al*., 2007; table 2), it is clear that the 'empirical survival function in its truncated form' turns out to be a simple static life-table. Notwithstanding how appropriate the estimation of the complete function from the truncated one is for this dataset (cf. Scala, 1990), we argue that the truncated function cannot escape the stringent

Table 1 Static life-table developed from the age distribution at death (Caughley, 1977) of 56 wolf carcasses (females only), incidentally found in Central Italy (data from Lovari *et al*., 2007; table 2)

Age class	n_x	d_x	l_x	$1-l_x$
0–1	56	10	1	0
1–2	46	8	0.8214	0.1786
2–3	38	6	0.6786	0.3214
3–4	32	16	0.5714	0.4286
4–5	16	4	0.2857	0.7143
5–6	12	6	0.2143	0.7857
6–7	6	1	0.1071	0.8929
7–8	5	2	0.0893	0.9107
8–9	3	3	0.0536	0.9464
9–10	0	0	0	1

Examples of l_x computations are given for the first two age classes: $0.8214 = 46/56$ and $0.6786 = 0.8214 \times 38/46$.

assumptions of the static life-table approach. As static life-tables are developed as an approximation to dynamic life-tables (where a real cohort is actually followed until the death of the last animal), the data used should not violate critical assumptions (Caughley, 1977; Krebs, 1999; Sinclair, Fryxell & Caughley, 2006). Among this set of assumptions, we believe that at least four are not met by Lovari *et al.*'s application: (1) the sample is representative of the population (false, by the nature of the data), (2) the population has reached a stable age distribution (false, due among other to poaching fluctuations), (3) the population growth rate is zero, or otherwise is constant but known (false), (4) age and age-classes should be determined without error [unlikely, as ageing methods are not detailed; the Jensen & Nielsen (1968) and Landon *et al.* (1998) references illustrate different methods]. Likely violations to this set of assumptions make the use of static life-table quite difficult and often unreasonable (Mills, 2007), and this is why few authors venture on these grounds, especially with biased samples in clearly unstable and persecuted populations.

In the introduction of their paper, the authors recognize that 'surprisingly little information is available on wolf mortality, especially from environmental conditions comparable to those in Southern Europe'. We concur with them, but we do not think they used reliable methods to address the issue and therefore failed to provide a significant contribution to our knowledge of wolf mortality, survivorship and population-scale responses to conservation strategies. Although we do agree that, not withstanding high levels of poaching, the wolf in Italy most probably 'keep himself from the door' because of its resilience, we nevertheless stress the need for sound and long-term field research projects on large carnivores in Europe so that we can manage their populations on a more rationale base by using more accurate methods and reliable results (Chapron & Arlettaz, 2006; Linnell, Salvatori & Boitani, 2007).

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