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RESPONSE

A wolf in the hand is worth two in the bush: a response to Ciucci *et al.* (2007)

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The use of carcasses in demographic studies of mammals is not a new issue (e.g. Englund, 1980, for the red fox *Vulpes vulpes*; Sidorovich *et al*., 2007, for the grey wolf *Canis lupus*; Gonzalez & Crampe, 2001, for the Pyrenean chamois *Rupicapra pyrenaica*), but the reliability of these studies varies with the origin and quality of the samples. Ciucci *et al*. (2007) maintain that 'opportunistic or convenience sampling is not acceptable and should not be encouraged' in demographic studies. They generalize from the data reported in a recent paper of ours (Lovari *et al*., 2007) on mortality parameters of the Apennine wolf *Canis lupus italicus* Altobello (1921), in Central-eastern Italy, based on 154 wolf carcasses, over an 11-year period.

We agree with Ciucci *et al*. (2007) that sound data on the live population, with adequate sampling, are definitely preferable to data from carcasses. However, demographic data can be quite hard to collect from the live population of elusive species, for example the wolf. The first peer-reviewed paper on the biology of the wolf in Italy was published 32 years ago (Zimen & Boitani, 1975). Since then, studies on wolves in Italy have been carried out by several research teams across most of the wolf distribution range (e.g. Meriggi *et al*., 1991; Boitani, 1992; Meriggi *et al*., 1996; Ciucci *et al*., 1997; Ciucci & Boitani, 1999; Gazzola *et al*., 2002; Apollonio *et al*., 2004). In spite of these research efforts, only food habits (for a review: Meriggi & Lovari, 1996), some aspects of genetics (Randi, Lucchini & Francisci, 1993; Lorenzini & Fico, 1995; Randi *et al*., 2000; Scandura, Apollonio & Mattioli, 2001; Scandura, 2005; Scandura *et al*., 2006; Fabbri *et al*., 2007) and several predator/prey interactions (Meriggi *et al*., 1996; Mattioli *et al*., 2004; Gazzola *et al*., 2005) have been relatively well assessed. In the absence of information on demography, data from large samples of carcasses can be useful as a source of information to help formulate conservation models, but with appropriate cautionary interpretation.

We also agree that 'proper methodology and acknowledgement of potential sources of bias should be common practice' (Ciucci *et al*., 2007). This was why we repeatedly emphasized the limits of our sample of dead wolves in our paper (Lovari *et al*., 2007). Ciucci *et al*. (2007) also mentioned the theoretical qualities that a sample of dead animals should have to reflect the live population structure. Because these qualities are quite hard to meet in field conditions, their conclusion was that the use of dead animals found in the wild should not be encouraged. If data on the live population are missing (as it is very often the case for larger Mammals), when demographic information is required (e.g. for population modelling), educated guesses become the most likely alternative. The question is whether such guesses are better than using information from carcasses even though this may contain biases. We think that, when data are needed for elusive or rare species, the soundest approach is to test demographic models on real data from the wild, even from carcasses, if information on the live population is lacking or very hard to obtain. Variation in carcass recovery effort is a potentially important source of bias but, in our study, the 'recovery effort' was approximately constant throughout the study period. Carcasses were recovered mainly (no <98%) by rangers of the State Forestry Service, whose units were evenly distributed in our study area, that is the historic core of the wolf distribution in Italy. By law (Ministry of Agriculture and Forestry, doc. n. 30668, 24th October 1991), all dead wolves recovered had to be delivered to a single agency, where one of us (R. F.) performed necropsies, thus ensuring a consistent evaluation (Lovari *et al*., 2007).

Several passages of our paper have possibly been misinterpreted by Ciucci *et al.* (2007). For example, the sentence 'our sample of wolves did not show any sign of malnutrition' (Lovari *et al.*, 2007: in our paper, the above statement was preceded by 'On average', not quoted by Ciucci *et al.*, 2007, because obviously not all wolves were healthy) was referring to the hypothesis that a greater incidence of road kills could have been related to poor health conditions. Our statement was based on the lack of any evidence supporting the above hypothesis, which did not mean that we found no wolf carcass in poor body conditions. As to year-to-year fluctuations of population parameters and mortality, in 1991–2001, we provided a measure of variation (SD $\pm$ 4.9) in the mean number of wolf carcasses recovered annually ($n = 14$), with an approximately constant collecting effort (Lovari *et al.*, 2007). This measure of variation – although crude – did not provide any grounds to suspect die-offs or basic year-to-year differences as suggested by Ciucci *et al.* (2007).

We found a pup:subadult:adult ratio of 10:23:67 and a pup-adult ratio of 10:90 in our sample, falling within the ratio of naturally controlled populations of wolves, as compared with exploited populations (Lovari *et al.*, 2007). Ciucci *et al.* (2007) were sceptical about the reliability of these data, especially when used in population modelling in an applied perspective. We think that data, when their limitations are recognized, are preferable to guesses or unrealistic assumptions, for example the estimated age ratio of 33:33:33, used in a population viability analysis for the wolf in Italy (Ciucci & Boitani, 1991), may appear less credible than our ratio.

Another source of criticism from Ciucci *et al.* (2007) was the effect of the extent of carcass decomposition and the consequential reliability of necropsies. The creation of the 'unclassified' category among mortality causes helps to avoid misleading interpretations of data and it explains some variation of sample size in analysing different aspects. We were careful to include it in our paper (Lovari *et al.*, 2007).

We used data from wolf carcasses found in the wild to estimate age- and sex-specific survivorship, as well as maximum age at death (Lovari *et al.*, 2007). The criticism raised by Ciucci *et al.* (2007) on all aspects relevant to the statistical evaluation of these data can be rejected on the basis of the rationale of the model used to deal with our data. The age at death x for a subject belonging to a wildlife population is summarized by the survival 'law' $L(x) = f(x, A, B)$, where A and B are *fixed* parameters and $0 < x <$ omega (maximum age at death). The distribution of ages at death is $D(x, A, B) = -\mathrm{d}/\mathrm{d}x\ [L(x, A, B)]$ and may be used to build the function $L(x, A, B)$ only if the population is stable in the period $0 < x <$ omega and the sample distribution is Bernoullian. If these conditions are not met, the results are unreliable. Similar problems are often encountered in other fields (e.g. economics, medicine, insurance, geophysics). Treating the parameters A and B as *stochastic variables* that have their own densities is a way to overcome this difficulty. For example, the distribution of the stochastic variable A is $g(A, a1, a2)$ where $a1$ and $a2$ are parameters; the same could be said for B, with a density $h(B, b1, b2)$, and $b1$ and $b2$ are again parameters. As a consequence, the original basic (or '*primary*') 'law' $L(x, A, B)$ is transformed into a new 'law' $L^{\circ}(x, a1, a2, b1, b2)$ (with the functions $g(\cdot)$ and $h(\cdot)$ called '*mixing*' *densities*). L° is an infinite mixture of the basic L 'law', with infinitely changing parameters A and B. From the phenomenological point of view, it is the same to say that an L° survival function is a linear combination of infinitely many survival functions with infinitely many different parameters and the field data can be thought as drawn from infinitely many sources (fluctuations, if any, included). L° is a kind of functional average. This is the widely accepted framework (McDonald & Butler, 1987) to model samples from heterogeneous populations and this is the rationale of the model used to deal with our data. It is a mixture (an infinite mixture, in fact, for one parameter only) of the basic (or '*primary*') 'law' $L(x, A, B)$, which has in turn its own biological meaning (discussed in Scala, 1990). The randomization of heterogeneity means that the changing – *spatial and temporal* – environment is embedded in our model. As our model is a classic mixture, the criticism of Ciucci *et al.* (2007) is not relevant to our treatment of field data and it reduces their Table 1 to an arithmetic exercise (Ciucci *et al.*, 2007).

We were careful not to make any categorical claim throughout our paper (Lovari *et al.*, 2007) in order to reflect our level of uncertainty of interpretation. We are happy if our conclusions can be disproved or modified by providing demographic data from the live population, but for now they are probably the best that can be achieved.

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