Journal of Zoology. Print ISSN 0952-8369

Mortality parameters of the wolf in Italy: does the wolf keep himself from the door?

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Keywords
Canis lupus; survivorship; road kills; reproduction; population structure.

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Received 18 May 2006; accepted 14 August 2006

doi:10.1111/j.1469-7998.2006.00260.x

Abstract

Information on population parameters is rarely collected from carcasses. This method can be particularly useful – with limitations – when protected species are involved (e.g. the grey wolf *Canis lupus* in Italy). Local data on population structure, reproduction, survivorship and causes of mortality are necessary to build reliable conservation models to assess the state of a population and to predict its evolution. On the other hand, 'best guesses' or data from ecologically different areas have often been used to build population viability analysis and other conservation-oriented models. A sample of 154 wolf carcasses was found, collected and analysed from 1991 to 2001 in central-eastern Italy, the historic core of the wolf distribution range. Collision with a vehicle was the main cause of death in both sexes; however, road kills may be biased with a greater detectability, and we treated our data accordingly. Road kills were concentrated on the younger ($\leq$ 4 years old) age classes, whereas fully adult wolves died mainly because of poaching, intraspecific strife and pathologies. Cubs and subadults ($\leq$ 2 years old) showed a mortality peak in November/December, at the beginning of the dispersal period, whereas adults died mainly in January/February (mating season). The population structure of our sample of wolf carcasses appeared to be well balanced, although perinatal and cub mortality was underestimated. The sex ratio was 1:1 in the younger age classes and 1:0.7 in the older age classes. Only 20.7% of females, 2–6 years old, showed signs of reproduction; placental scar and embryo number varied from one to seven (mean, 4.4) per individual. Survivorship theoretical curves indicated a fair survival of cubs and subadults, but a steep decline as wolves approached maximum life span (9 years old). Our data and other published data on food habits and genetic features of the wolf in central-eastern Italy suggest that, despite ongoing heavy human-induced losses, this predator has fully recovered in the last 30 years from the brink of extinction.

Introduction

About 47% of the European population of grey wolves *Canis lupus* Linnaeus, 1758 (excluding those of the former Soviet Union) occurs in southern Europe (Schröder & Promberger, 1993). Wolf populations here are locally fragmented, sometimes comprising less than 500 individuals. In the Mediterranean area, the wolf is still seen as a nuisance, especially by shepherds and hunters; for example in the last few decades, intense illegal killing has occurred in Italy in spite of legal protection established in 1971 (Guberti & Francisci, 1991). Thus, the recent recovery of the wolf in southern Europe (e.g. Route & Aylsworth, 1999; Boitani, 2003) may not yet have removed the risk of local extinctions in areas of recent recolonization.

The main conservation problem lies with predation on domestic ungulates, which leads to extensive killing of wolves. The reintroduction of large wild herbivores has been advocated as a means to reduce attacks on livestock, but predation on the latter may remain high if domestic ungulates are locally abundant. A review of 15 studies (Meriggi & Lovari, 1996) on the food habits of the wolf in southern Europe has shown that ungulates are the main diet component overall. A significant inverse correlation was found between the absolute occurrence (%) of wild and domestic ungulates in the diet. Apparently, the presence of several wild ungulate species is necessary to reduce predation on livestock.

Surprisingly little information is available on wolf mortality, especially from environmental conditions comparable to those in southern Europe (see Fuller, Mech & Cochrane, 2003, for a review). A primary source of wolf mortality is interactions with humans. Wolves tend to survive where human density is low and the density of roads is $<0.6\,km/km^2$ (Thiel, 1985; Mech, 1989). In Italy, up to 15 years ago, the main causes of death included shooting, poisoning and road kills (Guberti & Francisci, 1991). A survey of the major causes of death and an assessment of the main demographic parameters could be used to suggest adequate conservation measures. Population viability analysis (PVA) models have been considered as a valid tool for conservation, if based on sound information. When sound information is lacking, 'best guesses' in combination with available estimates of biological features may help devise conservation measures (Ciucci & Boitani, 1991), but their reliability is strongly reduced. Local data on population structure, reproduction, survivorship and causes of mortality are necessary to build reliable models attempting to assess the state of a population and to predict its local evolution. This is particularly important for an adaptable species such as the wolf, which can readily survive from the Arctic to the tropics, from the tundra to the desert, to intensively human-used areas, shaping its biology to local conditions (Mech, 1970). In this paper, we deal with the main parameters relevant to mortality from a large sample of wolf carcasses found in central-eastern Italy, the area where the wolf has always maintained a viable population (Zimen & Boitani, 1975) and from which the recent recolonization of its former range seems to have started (Ciucci & Boitani, 2003).

A. S. analysed most data and participated in writing up all the drafts; R. F. carried out the necropsies and prepared the basic data records; C. S. worked out the data relevant to the survival functions; S. L. participated in data analyses and in the preparation of the paper, besides ideating and supervising most of the research work.

Study area

Our study area was located in central-eastern Italy and encompassed Abruzzo, Molise, as well as the southern part of Marche, East Latium and neighbouring areas. Boundaries were determined from the spatial distribution of wolf carcasses for a size estimate of total area of about 24 000 km^2 (nearly half of the Italian known range of the species). Altitude ranged from about 500 m to over 2000 m a.s.l. Intensively used areas, as well as protected areas, were included, for example three national parks, one regional park and several other protected areas for a total of about 7198 km^2. Deciduous forests and crops covered about 60% of the area, whereas urban settlements did not exceed 5%. Pastures (16%) and rocks (2%) were mainly distributed on the ridges of the Apennine mountains, while olive groves, orchards and vineyards (4%) were at the lowest altitudes or along valley bottoms. Climate ranged from Mediterranean near the sea coast, to meso-Mediterranean and sub-Mediterranean as the altitude increased. Urban areas and villages are mainly located at low altitudes and along valley bottoms. The area is characterized by a perhumid sub-alpine bioclimate (over 1800 mm of annual rainfall; mean annual temperature, about 3–5 °C). Winters are harsh and snowfall is abundant. The region is dominated by Mesozoic substrates: limestone, dolomite, marl, schist-marl and sandstone. The Alpine orogeny has been intense, resulting in steep, complex relieves. Karst systems (caves, dolines and gorges) are very frequent in the central Apennines.

The endemism rate of the main mountain massifs is between 10 and 20% of the total flora, increasing at higher elevations. More than 40 species of mammals are present, for example the brown bear *Ursus arctos*, a growing population of wild boar *Sus scrofa*, the Apennine chamois *Rupicapra pyrenaica ornata*, the roe deer *Capreolus capreolus* and the red deer *Cervus elaphus*. Human population is low, mainly in small villages or shepherd settlements.

Materials and methods

Between 1991 and 2001, 154 wolf carcasses were found and collected in central-eastern Italy by foresters, provincial rangers and park wardens during their routine activities. All specimens were sexed, weighed and measured at the Istituto Zooprofilattico Sperimentale (IZS) dell'Abruzzo e del Molise, Teramo, Italy. A detailed analysis of carcasses was performed to establish causes of death, pathologies, presence of toxicants (zinc phosphide, strychnine and pesticide compounds, e.g. chlorinated organic compounds (OCF) and organophosphate pesticides (OCL)) and reproductive status of females. Mortality causes were grouped into five categories:

(1) human induced (shooting, snaring, poisoning, etc.);
(2) intraspecific strife (wolves killed by other wolves or dogs);
(3) pathologies (disease and/or starvation to death);
(4) road kills (these are also 'human-induced' causes, but see further);
(5) unclassified.

Some wolf carcasses were putrescent when postmortem examinations were carried out. Thus, laboratory analyses to assess the presence of pathogenic microrganisms were sometimes difficult to make and hence disease as the cause of death may have been underestimated. If human-induced mortality, intraspecific strife and road killing could be discarded as the origin of death, and if appropriate analyses could not be carried out to detect pathogens, these cases were included in the 'unclassified' category.

Distribution of data on mortality causes was significantly different from normal (Kolmogorov–Smirnov test, two-tailed; $P = 0.003$); therefore, we used medians as representative values for our sample.

Age was assessed through the count of incremental lines of tooth cementum. A permanent tooth (lower premolar) was extracted and decalcified, and thin sections were prepared and interpreted (Jensen & Nielsen, 1968; Landon *et al.*, 1998). Results were then assessed in relation to the wolf reproductive cycle (assumed birth month in central and southern Italy: May; Boitani, 1981). Most of our analyses was based on biennial age classes: class 1: $\leq$ 24 months; class 2: 25–48 months; class 3: 49–72 months; class 4 $>$72 months. The first age class ($\leq$ 24 months) was divided into four 6-month periods to assess differences in the first months of growing, which include crucial phases, for example dispersion and sexual maturation.

A survival function, $l(x)$, for each sex was fitted with a theoretical model described in full elsewhere (Scala, 1990):

$$l(x) = [M(\log(\omega/x))^B/(M(\log(\omega/x))^B + 1]^N$$

where $\omega > 0$ is the oldest age in the population and $M > 0$, $B > 0$, $N > 0$ are real parameters. The maximum allowed age is reached when $x = \omega$. This survival model allows the calculation of standard demographic functions. The median, as all the quantiles, can be expressed in an explicit form. This is not the case for the arithmetic mean, which must be calculated via numerical methods. The model can be reduced to its truncated form $L(x) = 1-[1-l(x)]/[1-l(T)]$, where T is the maximum age observed in the sample, so that the parameter ω becomes an entity to be estimated, which may imply that $\omega > T$.

Results

Descriptive parameters

On average, 14 wolf carcasses (SD ± 4.9) were found and delivered to IZS every year. Apparently, collision with a vehicle was the main cause of death in both sexes (Fig. 1a). Poaching, predation by canids (intraspecific strife) and pathologies came next.

There was no significant relationship between sex and age classes in our sample of dead wolves (Kruskal–Wallis test; χ^2: 1.638; d.f. = 4; $P > 0.05$). We split our sample into road kills (n = 78) and other causes (n = 76), as presumably road kills were more likely to be found (because carcasses were located on or beside roads) than wolves dead because of 'other causes'. Road kills were concentrated on the younger biennial age classes (class 1 = 40%; 2 = 36.9%; 3 = 16.9%; 4 = 6.1%), whereas adults died mainly because of other causes (Fig. 1b). The lower age classes (<24 months, i.e. cubs to subadults) showed a mortality peak in November–December, whereas that of the upper age classes (>24 months, i.e. adults) occurred in January–February (Fig. 2).

Road kills and other causes were significantly correlated to biennial age classes (χ^2 test of association: 16.29; d.f. = 6; P = 0.012): percentage of deaths due to road kills declined significantly with the age of wolves, whereas percentage of other mortality causes increased with age. The largest difference between observed and expected values concerned age class 2 (χ^2 table: obs.–exp. = 6.1; in all other cases = 0–4.4), suggesting a strong association of this class with road mortality (Fig. 1b). The population structure of our sample of wolf carcasses was well balanced (Fig. 3). The sex ratio was 1:1 (n = 82) in the first two age classes, but biased to males (1:0.7; n = 38) in the upper age classes.

The cubs:subadults:adults ratio was 10:23:67. Hence, the cubs:(subadults + adults) ratio was 10:90 (Table 1).

One could assume that wolves involved in 'road kills' are in poorer body conditions than wolves dead because of other causes, because sick wolves may be slower than healthy ones in avoiding car collisions. If so, one could expect a smaller weight/body length ratio in road-killed wolves than in those dead because of other causes. We used the median ratio for the whole sample (road kills and other causes, pooled), 0.237 kg/cm, as the arbitrary threshold to assess health status (weight/length < M = poor body condition; weight/length > M = good body condition). Both road-killed wolves and those dead because of other causes were in similar, apparently good body conditions (road kills: $w/l < 0.237$ = 27, $w/l > 0.237$ = 25; other causes: $w/l < 0.237$ = 23, $w/l > 0.237$ = 25; Fisher exact probability test, not significant).

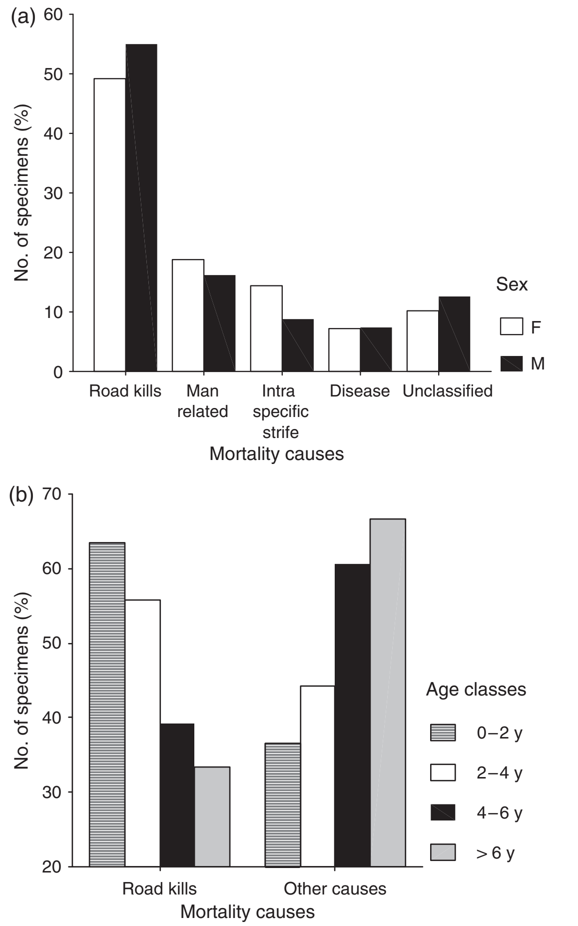

Figure 1 (a) Mortality causes of wolves (n = 154) in central-eastern Italy. F, females; M, males; (b) Main mortality causes within biennial age classes (n = 154); y, years old.

Reproductive status

The temporal distribution of reproductive data ranged from 1994 to 2001. Twelve females (20.67%) out of 58 showed signs of reproduction. Among the 10 females on whom ageing was carried out, reproduction occurred mainly in individuals between 2 and 6 years old (Fig. 4). Placental scar

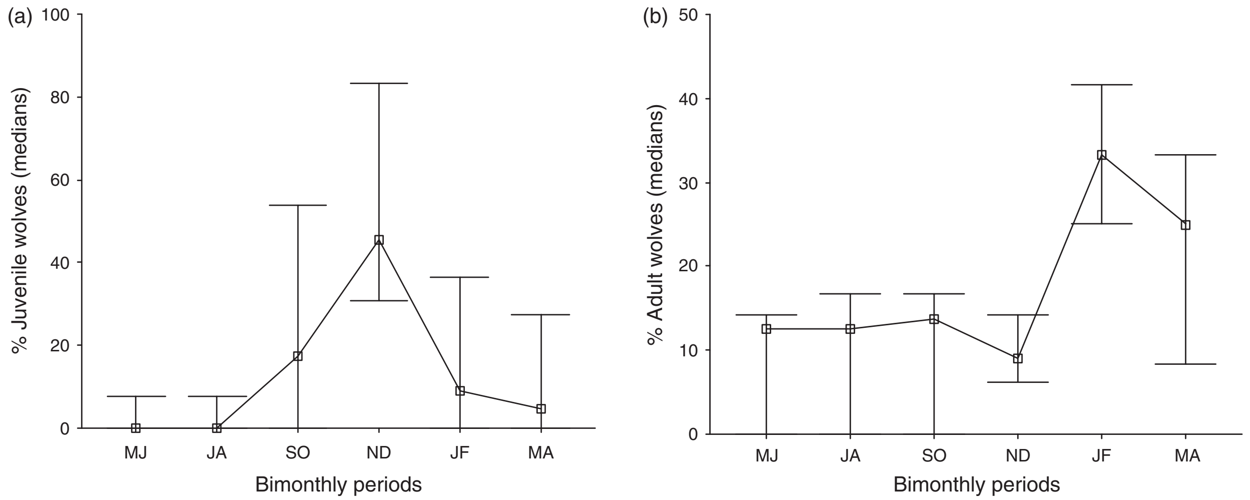

Figure 2 Bimonthly distribution of dead wolves. (a) Percentage of class 1 individuals within the first biennial age class; (b) Percentage of classes 2–3–4 individuals. Vertical bars represent range values. MJ, May–June; JA, June–August; SO, September–October; ND, November–December; JF, January–February; MA, March–April.

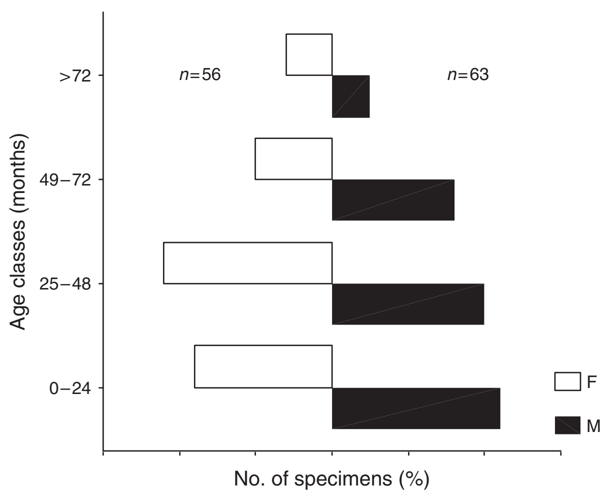

Figure 3 Population structure (biennial age classes; $n=120$). F, females; M, males.

and embryo number varied from one to seven ($n=9$; $\bar{x}=4.4$; SD $=2.41$). In only two cases ovarian follicles at different maturation stages were recorded. The presence of gravidic corpora lutea was recorded only once.

Disease

No acute pathology (potential cause of death) stood out as prevalent in our sample. Sarcoptic mange was present in two individuals only (out of 154), although their death could be ascribed respectively to intraspecific strife and septicaemia.

Survival curves

The empirical basis for the estimation of survival functions (males and females) has been set out in Table 2 as the arithmetic computation of the empirical survival function in its truncated (or incomplete) version [$L(x)$]. The maximum age recorded may not coincide with the actual maximum age in the population and the truncated survival function provides the basis for the estimation of parameters of the complete function. The maximum age at death (ω) is the most important parameter to estimate. The non-linear estimation method we used is that of Rosenbrock (1960; males: $M=0.4$, $\omega=11.3$, $B=2.6$, $N=1.0$; mean age at death, in the complete fitted survival function, is 3.1 years; females: $M=0.3$, $\omega=14.5$, $B=3.0$, $N=1.2$; mean age at death is 3.4 years). The theoretical survival curves are shown in Fig. 5. These curves indicate a fair survivorship of cubs and subadults and a steep decline as individuals approach maximum life span; however, one should be aware that perinatal and cub mortality was underrepresented in our sample, because of the little detectability of carcasses of these age classes.

Discussion

Our results on wolf survival appear to be the only one available for Eurasia, whereas comparable information may be found in Mech (1970) and Mech *et al.* (1998) for North America. It could be expected that mortality is enhanced by exploratory activities, such as pups wandering around a den or a rendezvous site, as well as dispersing movements of subadults in the autumn (Mech, 1970). On the other hand, during winter, especially in the case of heavy snowfalls, wolves tend to shift their movements to lower altitudes (Mech, 1970), where they are more likely to encroach on human activities, thus increasing the risk of being killed, which is consistent with the different mortality peaks in Fig. 4.

Our estimated maximum age at death of wolves (Fig. 2) is supported by the figures provided by Mech (1970, for a

Table 1 Pup–adult ratio in wolf populations under natural control (unexploited) versus exploited population (from Mech, 1970, modified)

	Natural control	*n*	Exploited populations	*n*	Source
Ontario	31:69	106	35:65	48	Pimlott, Shannon & Kolenosky (1969)
Northwest Territories	20:80	59	55:45	20	Fuller (1954); Fuller & Novakowsky (1955)
Northwest Territories	13:87	136–381	73:27	136	Kellsal (1968)
Alaska	–	–	45:56	4150	Raush (1967)
Russia	–	–	50:50	39	Makridin (1962)
Central-eastern Italy	10:90	154			This study

n is the sample size.

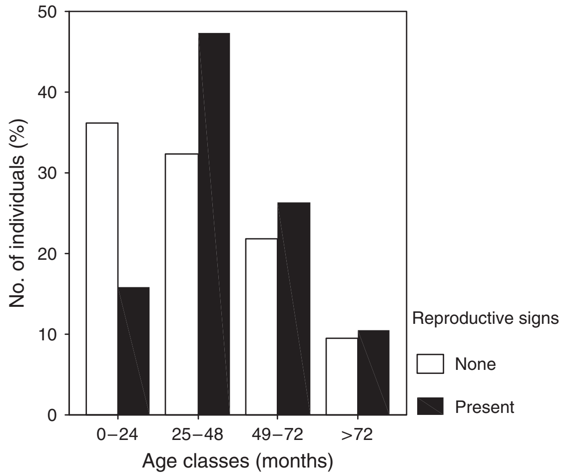

Figure 4 Presence (1) and absence (0) of reproduction signs in females of different age classes.

review) and Mech *et al.* (1998, for a sample of 94 live wolves in Denali National Park and Preserve, Alaska).

Mech (1970) summarized the pup–adult ratios of wolves in 'natural controlled' and 'exploited' populations. The former ranged from 13:87 to 31:69, whereas the latter varied from 35:65 to 73:27. Our sample showed a value (10:90) well within the range of 'natural controlled' populations. Although strictly protected by law, the wolf is still heavily poached in Italy. Our data have shown that a minimum of 14 wolves die every year in central-eastern Italy. Most likely, this figure is a gross underestimate, as most carcasses are unlikely to be found and the present distribution range of the wolf in Italy covers the central-southern part of Tuscany, all Apennines and the western part of the Italian Alps. Most of the causes of death are human induced. Nevertheless, human-induced killing is apparently not severe enough to make our wolf population fall among the 'exploited' ones (Table 1).

Under natural control as many as 40% of adult females may fail to breed, and those who breed bear fewer young (Mech, 1970). The relatively low number of reproductive females in our sample is not surprising, as only dominant individuals are likely to breed (e.g. Mech, 1970). In fact, the majority of younger she-wolves (i.e. up to 4 years old, thus presumably being subordinate) did not show any sign of reproduction, which fits Kreeger's (2003) finding that she-wolves usually do not begin to breed until 2–4 years old.

Sick wolves could fall victim to road accidents more often than prime ones. If so, one would expect road-killed wolves to be in poor health conditions. Our results do not confirm this assumption. On average, our sample of wolves did not show any sign of malnutrition, and an analysis of their digestive tracts showed that mammals were the staple of their diet (>65% in volume; Pezzo, Parigi & Fico, 2003). Our data are difficult to compare with the very few available in the literature because of widely different environmental features, for example wolf density, prey density, human density, wolf legal status and climatic conditions. In north-eastern Minnesota (USA), malnutrition (primarily involving pups) and intraspecific strife (the primary natural mortality factor for adults) accounted equally for 50% of the wolf mortality; human causes built up most of the remainder (Mech, 1977, 1994). The total known mortality of a radiotagged wolf sample ($n = 71$) monitored from 1979 to 1986 (Mech, 1989) was 69%. The main causes of mortality were human shooting (34.7%), other human-related causes (30.6%) and natural deaths (34.7%). A bigger wolf sample ($n = 129$), aerial-radiotracked from 1968 to 1976 (Mech, 1977), showed very different yearly mortality rates, with annual values ranging from 7 to 65%. About 58% of mortality was due to malnutrition and intraspecific strife (and, to a lesser extent, accidents and other unknown 'natural' causes), while about 42% was due to shot individuals (and, to a lesser extent, snared and road killed ones). In Croatia, where wolves have been actively persecuted, all causes of death were apparently human related in a sample of 92 dead wolves (Huber *et al.*, 2002). In Scandinavia, 51% of dead wolves had been shot, whereas road kills made up 26% and disease included about 12% of the sample ($n = 84$; Olsen, 2003). About 22% of Scandinavian wolves found dead were infected with sarcoptic mites (Olsen, 2003). In Italy, Guberti & Francisci (1991) reported that sarcoptic mange accounted for 8% of the overall mortality cases ($n = 60$), although a much greater impact (21.1%) was found for <1-year-old individuals ($n = 19$). We cannot confirm these figures for our sample, as just 8.3% of <1-year-old individuals ($n = 24$) were affected. This percentage becomes negligible (1.3%) in our overall sample. Guberti & Francisci (1991) did not provide details of the methods they used to assess causes of mortality. Apparently, they could always identify the origin of death, as no category

Table 2 Empirical basis for the estimation of survival functions

	Females						Males					
Age class	*n*	*CN*	*x*+	*F*(*x*+)	*x*–	*L*(*x*–)	*n*	*CN*	*x*+	*F*(*x*+)	*x*–	*L*(*x*–)
0–1	10	10	1	0.1786	0	1	13	13	1	0.2031	0	1.0000
1–2	8	18	2	0.3214	1	0.8214	9	22	2	0.3438	1	0.7969
2–3	6	24	3	0.4286	2	0.6786	15	37	3	0.5781	2	0.6563
3–4	16	40	4	0.7143	3	0.5714	5	42	4	0.6563	3	0.4219
4–5	4	44	5	0.7857	4	0.2857	10	52	5	0.8125	4	0.3438
5–6	6	50	6	0.8229	5	0.2143	6	58	6	0.9063	5	0.1875
6–7	1	51	7	0.9107	6	0.1071	3	61	7	0.9531	6	0.0938
7–8	2	53	8	0.9464	7	0.0893	1	62	8	0.9688	7	0.0469
8–9	3	56	9	1.0000	8	0.0536	2	64	9	1.0000	8	0.0313
	T=56				9	0.0000	*T*=64				9	0.0000

n is the number of dead individuals; *CN* is the cumulative number; *x*+ is the upper limit of each age class; *x*– is the lower limit of each age class; *T* is the total; *Fx*=*CN*/*T*; *L*(*x*–) is the truncated survival function, 1–*F*(*x*+). The theoretical definition *Lx*=1–*Fx* holds for perfectly continuous functions, in which the level *x* is unique. This is not the case for frequencies reported in classes whose upper and lower limits should be considered to warrant the correct definition of the functions involved.

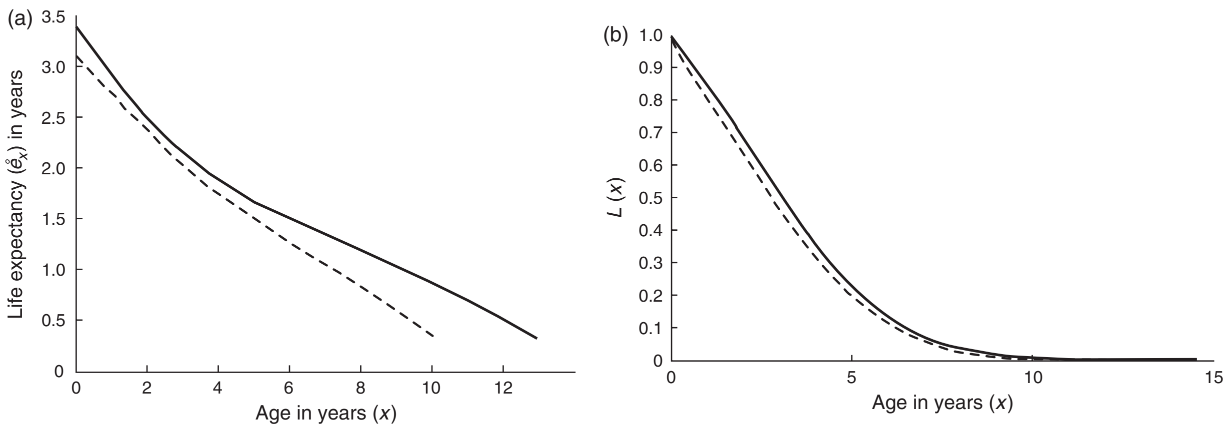

Figure 5 (a) Expectation of life, for female (solid line) and male (dotted line) wolves; (b) theoretical survival functions (complete models) for both sexes. M, males; F, females. Pups are underrepresented because they tend to move in the neighbourhoods of their dens and rendezvous sites (Mech, in press). Furthermore, their small size makes their carcasses hard to find in the field.

such as ‘other’ or ‘unknown’ was present in their study. These authors provided no clue on the way in which they could assess whether wolves in their sample died because of scabies, or just with scabies. Hence, their results and our results are hard to compare. On the other hand, the data reported in Guberti & Francisci (1991) may suggest that, in the 1980s, the first wave of sarcoptic mange hit the wolves of central Italy, thus determining a high mortality rate. In the 1990s, when our sample was collected, partial immunity could have developed in the wolf population (e.g. Pence & Ueckermann, 2002). Sarcoptic mange in dogs, red foxes and other wildlife species was not a rare event well before the 1980s in central Italy. It is unclear as to why it should suddenly develop in the wolf population in that decade.

The density of state and provincial roads was only available for the Abruzzo region, an important portion of our study area. The mean value of road density was 0.34 km/km^2. The density of state and provincial roads within the wolf range (determined by the recovery of dead specimens) was 0.32 km/km^2, while the value reached 0.42 km/km^2 outside the wolf range. Mech (1989) reports that an area could still support a viable wolf population even in the case of a road density exceeding 0.58 km/km^2, if it is close to extensive roadless areas.

Our results suggest that wolves in central-eastern Italy, that is the historic core of the wolf distribution range in the Italian peninsula, show a balanced population structure, a good life expectancy and fertility rate, and no acute pathology, although demographic data should be taken with caution because they are biased to the adult age classes, for example the natural mortality rate of pups can be up to 74% in the first year of life (Jędrzejewska *et al.*, 1996). Our information matches that reported by Pezzo *et al.* (2003), who documented a rich diet of this canid in that part of Italy, well within the parameters of wolf food habits in southern Europe (Meriggi & Lovari, 1996, for a review), as well as that on its recent and remarkable range expansion (Boitani, 2003). Even the steady, high figure of wolf carcasses ($n = 14$/year, on average, from 1991 to 2001) delivered to the IZS, in Teramo, may suggest indirectly a numerous population, granted that most likely many carcasses were not found because they were hidden or buried by poachers or just went lost in the forest. Legal protection does not prevent poaching efficiently and conservation campaigns (from 1970 onwards) have been effective mainly among town citizens, but no shepherd and just a few deer/wild boar hunters will actually respect a wolf. Although protection could have played an ancillary role in the recovery of the wolf, most likely the biological resilience of this species to quickly adapt to positive environmental changes, for example the comeback of forests (Apollonio, 1996) and the associated sharp increase of wild artiodactyls (the natural prey of the wolf) (Pedrotti *et al.*, 2001), has been the key factor promoting its increase in the last 30 years in Italy. Interestingly, even the feared reduction of genetic variability and/or hybridization with free-ranging dogs (Boitani, 1984) have not occurred or, alternatively, hybrids failed to pass on their genes to later generations (Randi, Lucchini & Francisci, 1993; Lorenzini & Fico, 1995; see also Vilà & Wayne, 1999). Among large mammals, the wolf can have a particularly large litter size (up to 8 cubs/litter; Jędrzejewska *et al.*, 1996), a wide spectrum of food resources (e.g. Meriggi & Lovari, 1996) and a social organization favouring dispersal (Mech & Boitani, 2003). Most likely, all these features will determine its rapid recovery, even in the presence of human-induced limiting factors, when basic ecological conditions are favourable. Presumably, anthropogenic limiting factors could be more active in areas of recent recolonization by the wolf. We suggest that conservation efforts and funding should be mainly concentrated there (or on other taxa presently at a much greater risk of local extinction than the wolf, e.g. in Italy: the Apennine chamois *Rupicapra pyrenaica ornata* and the brown bear *Ursus arctos marsicanus* cf. Bulgarini *et al.*, 1998). We also suggest that an extensive, routinely repeated 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. This information could be used in PVA and other conservation-oriented models when 'the lack of sound, objective and reliable data for the management of a wolf population makes it quite hard to plan appropriate conservation measures' (Ciucci & Boitani, 2004), as it happens in Italy (Genovesi, 2002).

Acknowledgements

We are greatly indebted to Lucia Burrini and Gabriella di Francesco for their technical help: the former performed the large majority of laboratory work to age wolves through incremental lines of tooth cementum, while the latter completed the analyses. Without their help this work could not have been carried out. We are also grateful to the officials of the Italian Department of State Forests, who collected the wolf carcasses from the field and sent them to the IZS 'G. Caporale', Teramo, for postmortem analyses. W. Jędrzejewski and B. Jędrzejewska, as well as P.G. Meneguz, read critically a first draft of our paper. L.D. Mech kindly helped with references and let us have a paper of his in press. The suggestions of two anonymous referees improved our final draft. K. Tustin kindly revised our English.

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