

## EFFECTS OF HURRICANE LOTHAR ON THE POPULATION DYNAMICS OF EUROPEAN ROE DEER

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**Abstract:** Although extreme weather events—such as hurricanes—cause obvious changes in landscape and tree cover, the impact of such events on population dynamics of ungulates has not yet been measured accurately. We report a first quantification of the demographic consequences on roe deer (*Capreolus capreolus*) of the strongest hurricane (Lothar) that France has suffered in centuries. Based on long-term monitoring (>20 yr) of known-age individuals in 2 populations, we found that Lothar had no detectable negative effect on age- and sex-specific survival rates, except perhaps for old females. Likewise, although Lothar occurred during the time in the roe deer reproductive cycle when embryos are implanted, we found no evidence of a decrease in either the pregnancy rate or litter size. Our results show that roe deer populations are resistant to this kind of extreme weather event. The consequences for wildlife management are direct and important: (1) the hunting bag was low in 2000 due to restricted hunter access, and (2) the main effect of hurricane Lothar was to create openings within large forests that are good habitat for roe deer. We suggest that Lothar will paradoxically have a positive effect on roe deer population dynamics.

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In late December 1999, Hurricane Lothar, apparently the strongest hurricane in the region for at least 1,000 years, struck France, Switzerland, and Germany. This hurricane was very unusual in that it affected most parts of France, Switzerland, and Germany within a few hours. In France, 140,000,000 m<sup>3</sup> of trees fell, killing 92 people and disrupting power from the homes of 3,500,000 people. A deep trough of low pressure (960 hPa at the center) went from west to east at a mean speed of 100 km/hr (see <http://www.notre-planete.info/tempete.php> for further details). No rainfall was associated with Lothar. Within a few hours, however, 10 years worth of forest production fell, preventing access by foresters and hunters to most forests for a month, or more in many areas. As a consequence, hunting quotas of red deer (*Cervus elaphus*) and roe deer for the 1999–2000 season were only partly realized (e.g., 77.6% vs. an average of 91% in eastern France; Réseau de correspondants Cervidés-Sangliers, unpublished data). Two contrasting attitudes among wildlife managers emerged from this situation: many hunters requested a reduction of hunting quotas, whereas

many foresters requested an increase in quotas. The hunters were in favor of reduced hunting quotas in the following years on the basis that the hurricane must have killed many deer. On the other hand, foresters requested increases in hunting quotas, arguing that few deer had died and that the openings in the forests generated by the hurricane would greatly improve the food supply and thus increase reproductive rates of the deer in the future.

Reliable empirical information on the influence of this extreme weather event on deer population dynamics was therefore needed to clarify these management issues (Dale et al. 1998). Very few studies have addressed the impact of exceptional weather events on population dynamics of vertebrate populations (Meyers et al. 1996, Waide 1991, Swilling et al. 1998, Jones et al. 2001). Recently, Labisky et al. (1999) documented the impact of Hurricane Andrew, a storm with sustained winds of 242 km/hr, on a white-tailed deer (*Odocoileus virginianus*) population in Florida. They reported that adult survival of both sexes was not influenced by the hurricane, but production of fawns decreased, possibly due to the stress.

We quantified the impact of Hurricane Lothar on fitness components of roe deer from long-term monitoring (>20 yr) of 2 populations from forests located on the main trajectory of the hurricane. From data available for these 2 roe deer populations, we were indeed able to address whether Lothar negatively influenced survival rates (by age and sex classes), pregnancy rates, and/or litter sizes.

To assess the potential disruptive processes of Hurricane Lothar on roe deer, a brief overview of roe deer life history is warranted. Roe deer are small, temperate ungulates with male and female adult body mass of 23 and 25 kg, respectively (Andersen et al. 1998). Roe deer live mostly in forests and represent the main game species in Europe, with about 400,000 individuals harvested annually in France. Roe deer have a very unusual life cycle among temperate ungulates. The roe deer rut takes place between mid-July and mid-August, not in fall as in most temperate deer. Embryonic development stops at the blastocyst stage, soon after mating, and implantation is delayed until late December. The fetus grows fast after implantation, and fawns (usually 2) weigh an average of 1.6 kg at birth. Parturition occurs usually mid-May, with high synchrony (80% of births within <25 days; Gaillard et al. 1998b). Because Lothar occurred in late December, it therefore could have disrupted implantation.

Assuming that Lothar had a negative effect on survival and/or reproduction, we set the following research hypotheses: (1) survival of fawns and senescent adults would be affected more strongly than prime-age adults, (2) male survival would be more affected than female survival, and (3) Lothar would affect both pregnancy rates and litter sizes of primiparous and senescent females to a greater extent than prime-age does. We expected survival of fawns and senescent adults to be more affected by Lothar because prime-age survival has been shown to be highly resistant to environmental perturbations in ungulate populations (Gaillard et al. 2000). We expected males to be more affected than females because deer generally are both dimorphic in size and polygynous (Clutton-Brock et al. 1982). In such species, males allocate more energy to mating effort and thereby less energy to maintenance than females, making males more susceptible to environmental perturbations than females (Glucksman 1974). Roe deer are only slightly dimorphic (bucks about 10% heavier than adult does; Andersen et al. 1998), but we still expected males to be more

affected by Lothar than does because males become territorial at 3 years of age (Liberg et al. 1998), and therefore are less likely than does to leave their usual home range. Last, we expected both pregnancy rates and litter sizes of primiparous and senescent females to be more affected than prime-age does because implantation failure has been reported to be markedly age dependent in roe deer (Hewison and Gaillard 2001). Furthermore, research has established that litter size of ungulate females is also age dependent (Gaillard et al. 2000 for a review).

## STUDY AREAS

We conducted our study in 2 areas with different climates and contrasting demographic characteristics of the roe deer populations. Hunting was not permitted in either study site. Trois Fontaines (TF) is a 1,360-ha reserve situated in northeastern France (48°43'N, 2°61'W). The climate is continental, characterized by cold winters (mean daily temperature in Jan is 2 °C) and hot, but not dry summers (mean daily temperature in Jul is 19 °C; total rainfall in Jul–Aug is 130 mm). The overstory is dominated by oak (*Quercus* sp.; 63.5% of timber trees) and beech (*Fagus sylvatica*; 19.5%), whereas coppices are composed primarily of hornbeam (*Carpinus betulus*; 70%). The understory is dominated by ivy (*Hedera helix*) and brambles (*Rubus* sp.), which are principal and preferred foods of roe deer (Duncan et al. 1998). The soils at TF are fertile and the forests highly productive (long-term average of 5.92 m<sup>3</sup> of wood produced/ha/year; Inventaire National Forestier, unpublished data). On the basis of our current knowledge of roe deer food habits (Duncan et al. 1998), TF is considered good habitat.

The size of the TF roe deer population has been monitored since 1976. The roe deer population in TF was maintained from 1977 to 1999 through intensive culling, at 200–250 individuals >1 year old in March (Gaillard 1988). The population is highly productive, with all 2-year-old females breeding (Gaillard et al. 1998a). Annual survival rates averaged 0.82 and 0.93 for adult males and females, respectively (Gaillard et al. 1993), and the annual finite rate of increase ( $\lambda$ ) averaged 1.37 (Gaillard et al. 1992a), which is close to the maximum for roe deer (i.e.,  $r_{\max}$  sensu Caughley 1977).

Our second study site, Chizé (CH), is a 2,614-ha reserve located in southwestern France (46°05'N, 0°25'W). The climate is oceanic, with mild winters (mean daily temperature in Jan is 5.5 °C) and

hot, dry summers (mean daily temperature in Jul is 20.4 °C; total rainfall in Jul–Aug is 98 mm). The soils of CH are shallow, calcareous, and less fertile than those of TF. Three broad vegetation associations of varying quality for roe deer are found at CH (N. Pettorelli, unpublished data). The richest habitat for roe deer in CH is an oak forest with mainly hornbeam coppice (covering 1,046 ha). About a third of CH (815 ha) is poor roe deer habitat consisting of beech forest on limestone with virtually no coppice. The understory is dominated by woodfalse–brome (*Brachypodium* sp.), butcher’s broom (*Ruscus aculeatus*), ivy, wild madder (*Rubia peregrina*), and wood melick (*Melica uniflora*). Neither woodfalse–brome nor butcher’s broom is favored forage of roe deer. Ivy, which is highly selected by roe deer in winter, decreased following a peak in the size of the roe deer population in 1983–1984. The remainder of CH (758 ha) is a habitat of intermediate quality consisting of oak forest with mostly Montpellier maple (*Acer monspessulanum*) coppice. The productivity of the entire forest is quite low due principally to the summer droughts (long-term average of 3.77 m<sup>3</sup> of wood produced/ha/yr; Inventaire National Forestier, unpublished data).

The size of CH population has been monitored since 1978. In contrast to TF, the CH roe deer population fluctuated markedly during the monitoring period (1978–2000), increasing from 350 deer >1 year old in 1979 to about 550 in 1983, and then decreasing to <200 deer in 1993 (Gaillard et al. 1993). Since 1993, the population size has been maintained at about 200 roe deer >1 year old. The population increased because few roe deer were removed annually and decreased due both to high annual culling and density-dependent responses of population parameters. Without removals, the annual finite rate of increase ( $\lambda$ ) would have averaged 1.25 throughout the monitoring period (Gaillard et al. 1992a).

## METHODS

Both study populations were enclosed by a 2.5-m-high fence and managed by the Office National de la Chasse et de la Faune Sauvage. In each population, we marked >70% of individuals using numbered leather collars (Strandgaard 1967) and ear tags. This allowed us to estimate population size using capture–recapture models (Gaillard et al. 1986). We marked deer at each study area during drives conducted once or twice a week in January and February (see Gaillard et al. 1993 for further details). We weighed each deer

caught ( $\pm 0.5$  kg) and classified each as a fawn or a >1 year old. The fawns were easily identified on the basis of milk incisors and distinctive third premolars (Flerov 1952), or because they had been marked as newborns. The mortality rate induced by capture was low (0–3%; Van Laere and Boutin 1990). In addition, since 1985, a total of 755 newborn fawns (201 at CH and 554 at TH) have been caught and marked to assess neonatal survival (Gaillard et al. 1997).

We tested for the influence of Lothar on age- and sex-specific survival rates by using recent developments of capture–mark–recapture (CMR) methods (Lebreton et al. 1992). We first assessed whether the full time-dependent model fit our data sets by using program U-CARE (Choquet et al. 2001). We then assessed whether a “biological model” based on previous analyses of survival patterns in these populations was acceptable. The survival patterns of these roe deer populations have been studied in detail (e.g., Gaillard et al. 1993, 1997, 1998b; Loison et al. 1999). The age and sex structure of both populations is characterized by highly variable summer fawn survival (<0.10 to >0.90; shortly after birth to 8 months of age; Gaillard et al. 1997), but with nearly constant winter fawn survival (8–20 months of age), prime-age survival (2–7 yr of age), first senescent stage (8–12 yr of age), and second senescent stage ( $\geq 13$  yr of age; Gaillard et al. 1998b). Fawn survival, in both their first summer and their first winter, does not appear to differ between the sexes. For all other age classes, however, female survival is higher than male survival (Gaillard et al. 1993, 1997). We therefore pooled fawns of both sexes to estimate summer and winter fawn survival, but we estimated sex-specific survival for older age classes.

For both sites we retained a model for deer >1 year of age with 4 different capture probabilities (i.e., TF: 1977–1996, 1997–1999, 2000, and 2001; CH: 1979–1985, 1986–1999, 2000, and 2001; see Gaillard et al. 2003 for justification). For fawns, capture probabilities varied over time in both sites (Gaillard et al. 1997). Using this biological model, we built a general model of age- and sex-specific survival by considering 3 periods (the pre-hurricane years from the beginning of the monitoring to 1999 included, the hurricane year (from 1999 to 2000), and a post-hurricane year from 2000 to 2001). To test for an influence of Lothar on age- and sex-specific survival, we contrasted for each age and sex class a model including the 3 periods to a restricted model under which estimates during the hurricane year were

Table 1. Modeling the influence of Hurricane Lothar on survival probabilities of roe deer at Chizé, France, using survival ( $\Phi$ ) and capture probability ( $p$ ). The model selected for testing the influence of Lothar is the biological model (subscript b) involving time-dependent summer survival of fawns; 2 winter survivals of fawns (before and during the hurricane vs. post-hurricane); 2 sex-dependent survivals for deer 2–7 years old, 8–12 years old, and  $\geq 13$  years old (before and during the hurricane vs. post-hurricane); a time-dependent capture probability for fawns; and 4 constant capture probabilities for older roe deer between 1978 and 1985, between 1986 and 1999, in 2000, and in 2001. Models  $\Phi_{b1}$  to  $\Phi_{b5}$  correspond to models similar to  $\Phi_b$  but with 3 different survival probabilities (1 prior to Lothar, 1 in 2000 when Lothar hit France, and 1 after Lothar) for the indicated age–sex class.

Biological hypothesis	Models compared	Models		
		$\chi^2$	df	<i>P</i> -value
Effect of Lothar on winter fawn survival	$[\Phi_b p_b]$ vs. $[\Phi_{b1} p_b]$	0.022	1	0.882
Effect of Lothar on survival of males 2–7 yr old	$[\Phi_b p_b]$ vs. $[\Phi_{b2} p_b]$	0.408	1	0.523
Effect of Lothar on survival of males 8–12 yr old	$[\Phi_b p_b]$ vs. $[\Phi_{b3} p_b]$	0.207	1	0.649
Effect of Lothar on survival of females 2–7 yr old	$[\Phi_b p_b]$ vs. $[\Phi_{b4} p_b]$	0.532	1	0.466
Effect of Lothar on survival of females 8–12 yr old	$[\Phi_b p_b]$ vs. $[\Phi_{b5} p_b]$	2.586	1	0.108

the same as those during the pre-hurricane years. We did not test explicitly for an effect of Lothar on summer fawn survival because variations among years are strong in both sites, due to many confounding factors. Because too few roe deer lived over 12 years of age, we did not measure the effect of Lothar on very old adults of either sex. We compared the non-nested models (full time-dependent model and our biological model) by using Akaike's Information Criterion (AIC). To test our predictions about the possible influence of Lothar on survival, we used a standard hypothesis testing approach based on Likelihood ratio tests (Lebreton et al. 1992).

To assess whether Lothar influenced age-specific pregnancy rates and litter size, we used the long-term monitoring of does (1988 onward, anaesthetized with 0.4–0.5 ml of ZOLETIL) with an ultrasonic scanner (100LC Vet Pie Medical, Mode B and Mode M, using a linear probe, 6/8 Mhz) to determine whether each known-age doe captured after 15 January (i.e., when all fertilized does are assumed to have implanted their embryos; Gaillard et al. 1992b) was pregnant, and the number of embryos (Van Laere et al. 1997).

To test for an age-dependent influence of Lothar on female reproductive status, we considered 3 categories of does (Gaillard et al. 1998b): (1) 2-year-old does, (2) prime-age does from 3 to 12 years, and (3) senescent does >12 years. Because little

Table 2. Sex- and age-specific survival ( $\pm 1$  SE) of roe deer in the Chizé and Trois Fontaines Reserves, France, before and during Hurricane Lothar. Survival during the pre-hurricane period was averaged for 1978–1999 at Chizé and 1976–1999 at Trois Fontaines. Survival during Lothar corresponds to the survival between 1999 and 2000.

Age–sex class <sup>a</sup>	Period	
	Pre-hurricane	Hurricane
Chizé		
Fawns during winter	0.817 (0.030)	0.784 (0.251)
Prime females	0.953 (0.010)	1.000 (0.000)
Senescent females	0.891 (0.024)	0.508 (0.171)
Prime males	0.883 (0.015)	0.761 (0.137)
Senescent males	0.774 (0.049)	0.878 (0.326)
Trois Fontaines		
Fawns during winter	0.875 (0.025)	1.000 (0.000)
Prime females	0.920 (0.011)	1.000 (0.000)
Senescent females	0.788 (0.035)	0.634 (0.345)
Prime males	0.819 (0.018)	0.564 (0.188)
Senescent males	0.689 (0.067)	0.637 (0.479)

<sup>a</sup> Fawns during winter = survival between 8 and 20 months of age; prime = yearly survival between 2 and 7 years of age; senescent = yearly survival between 8 and 12 years of age.

variation existed among years in both pregnancy rates and litter size (Gaillard et al. 2003), we simply compared the age-dependent estimates of both components of reproductive output observed prior to Lothar (pre-hurricane estimates), just after Lothar (hurricane estimate in year 2000), and 1 year after Lothar (post-hurricane estimates) by using 2-way ANOVA and GLM models for litter size and the pregnancy rates, respectively.

## RESULTS

During the hurricane, the average wind speed was 148 km/hr at a weather station near TF and 151 km/hr at a weather station near CH. Peaks of >200 km/hr were recorded in both study sites.

### Influence of Lothar on Survival

*Chizé Population.*—The full time-dependent model fit the CMR data collected on known-age roe deer satisfactorily (male fawns marked as newborn:  $\chi^2 = 58.10$ , df = 49,  $P = 0.175$ ,  $n = 105$ ; female fawns marked as newborn:  $\chi^2 = 35.35$ , df = 42,  $P = 0.756$ ,  $n = 96$ ; male fawns marked as 8 months old:  $\chi^2 = 90.48$ , df = 82,  $P = 0.244$ ,  $n = 197$ ; female fawns marked as 8 months old:  $\chi^2 = 94.43$ , df = 83,  $P = 0.184$ ,  $n = 194$ ). As expected, the biological model described the variation in survival and capture probabilities observed at CH from 1978 to 2001 better than the time-dependent model (AIC = 4,439.6 vs. AIC = 4,603.9, respectively). We found no evidence that Lothar affected age- and sex-specific survival rates (Tables 1, 2)

although the influence of Lothar on survival of old females was not far from significance, suggesting that a larger proportion of old females may have died in the year of the hurricane.

*Trois Fontaines Population.*—The full time-dependent model fit the CMR data collected on known-age roe deer satisfactorily (male fawns marked as newborn:  $\chi^2 = 63.22$ ,  $df = 56$ ,  $P = 0.237$ ,  $n = 277$ ; female fawns marked as newborn:  $\chi^2 = 71.75$ ,  $df = 54$ ,  $P = 0.053$ ,  $n = 277$ ; male fawns marked as 8 months old:  $\chi^2 = 75.37$ ,  $df = 78$ ,  $P = 0.563$ ,  $n = 157$ ; female fawns marked as 8 months old:  $\chi^2 = 64.57$ ,  $df = 74$ ,  $P = 0.775$ ,  $n = 159$ ). The low  $P$ -value for females marked as newborn mainly was due to a poor fit for test 3 ( $\chi^2 = 34.38$ ,  $df = 15$ ,  $P = 0.003$ ) because of a marked difference in survivorship between newborn and 8-month-old fawns. The occurrence of differences in survival among age classes necessarily leads to a poor fit of the full time-dependent model. As expected, the biological model described the variation in survival and capture probabilities at TF from 1976 to 2001 better than the time-dependent model (AIC = 5,217.8 vs. AIC = 5,429.6, respectively). Again, we found no evidence that Lothar had an effect on age- and sex-specific survival rates (Tables 2, 3).

### Influence of Lothar on Pregnancy Rate and Litter Size of Roe Deer Does at Chizé

*Pregnancy Rates.*—We assessed the pregnancy status of 433 known-age females from 1988 to 2001. We found no interaction between the effect of period (pre-, during, post-hurricane) and that of age class on pregnancy rates ( $\chi^2 = 7.20$ ,  $df = 4$ ,  $P = 0.126$ ). As expected, the pregnancy rates differed among age classes ( $\chi^2 = 80.20$ ,  $df = 2$ ,  $P < 0.0001$ ), being highest for prime-age females ( $0.956 \pm 0.011$ ), slightly lower for primiparous ( $0.911 \pm 0.043$ ), and lowest for does >12 years ( $0.417 \pm 0.072$ ). We found no evidence for a lower pregnancy rate after the hurricane ( $\chi^2 = 0.80$ ,  $df = 2$ ,  $P = 0.670$ ; Table 4).

*Litter Size.*—We measured litter size from ultrasonography on 359 pregnant does. We also found no interaction between the effect of period (pre-, during, post-hurricane) and age of does ( $F = 1.923$ ;  $df = 3, 351$ ;  $P = 0.125$ ). However, litter size varied among age classes ( $F = 9.734$ ;  $df = 2, 354$ ;  $P < 0.0001$ ). Litter sizes were highest for primiparous females ( $1.842 \pm 0.060$ ), slightly lower for prime-age ( $1.797 \pm 0.023$ ), and lowest for does >12 years ( $1.400 \pm 0.112$ ). We did not find an influence of Lothar on litter size ( $F = 1.985$ ;  $df = 2, 354$ ;  $P =$

Table 3. Modeling the influence of Hurricane Lothar on survival probabilities at Trois Fontaines, France using survival ( $\Phi$ ) and capture probability ( $p$ ). The model selected for testing the influence of Lothar is the biological model (subscript b) involving time-dependent summer survival of fawns; 2 winter survivals of fawns (before and during the hurricane vs. post-hurricane); 2 sex-dependent survivals for deer 2–7 years old, 8–12 years old, and  $\geq 13$  years old (before and during the hurricane vs. post-hurricane); a time-dependent capture probability for fawns; and 4 constant capture probabilities for older roe deer between 1978 and 1985, between 1986 and 1999, in 2000, and in 2001. Models  $\Phi_{b1}$  to  $\Phi_{b5}$  correspond to models similar to  $\Phi_b$  but with 3 different survival probabilities (1 prior to Lothar, 1 in 2000 when Lothar hit France, and 1 after Lothar) for the indicated sex–age class.

Biological hypothesis	Models compared		$\chi^2$	df	P-value
Effect of Lothar on winter fawn survival	$[\Phi_b p_b]$ vs. $[\Phi_{b1} p_b]$		1.247	1	0.264
Effect of Lothar on survival of males 2–7 yr old	$[\Phi_b p_b]$ vs. $[\Phi_{b2} p_b]$		1.388	1	0.239
Effect of Lothar on survival of males 8–12 yr old	$[\Phi_b p_b]$ vs. $[\Phi_{b3} p_b]$		0.003	1	0.956
Effect of Lothar on survival of females 2–7 yr old	$[\Phi_b p_b]$ vs. $[\Phi_{b4} p_b]$		0.317	1	0.573
Effect of Lothar on survival of females 8–12 yr old	$[\Phi_b p_b]$ vs. $[\Phi_{b5} p_b]$		0.133	1	0.715

0.139). Contrary to what we expected, litter size tended to be higher in the year of the hurricane than prior to the hurricane (Table 4).

### DISCUSSION

We found no support for any of the 3 research hypotheses, indicating that Lothar had no detectable influence on the population dynamics of roe deer. Despite the strength of this hurricane, survival of both fawns and senescent adults was not affected by Lothar any more than for prime-age adults. Likewise, male survival did not decrease any more than female survival in the year of the hurricane. Last, Lothar did not influ-

Table 4. Age-specific pregnancy rates and litter size ( $n$ ) of roe deer in the Chizé Reserve, France, before (1978–1999), during (2000), and after (2001) Hurricane Lothar.

Age class <sup>a</sup>	Period		
	Pre-hurricane	Hurricane	Post-hurricane
<b>Pregnancy rates</b>			
Second year	0.900 (40)	1.000 (2)	1 (3)
Prime	0.951 (200)	0.947 (19)	1 (32)
Senescent	0.422 (45)	1.000 (1)	0 (2)
<b>Litter size</b>			
Second year	1.879 (33)	2.000 (2)	1.333 (3)
Prime	1.701 (253)	1.938 (16)	1.774 (31)
Senescent	1.368 (19)	2.000 (1)	0 (0)

<sup>a</sup> Second year = approx 20 months old; Prime = 3–12 yr old; and Senescent = >12 yr old.

ence either pregnancy rates or litter sizes, irrespective of the age class of the does.

Such resistance of roe deer population dynamics to an exceptional weather event such as Lothar is surprising at first sight, but this result is consistent with patterns previously identified in population dynamics of large herbivores, and of roe deer in particular. Increasing evidence exists that adult survival of female large herbivores is highly resistant to environmental perturbations (see Gaillard et al. 2000 for a review). That Lothar had no detectable influence on adult survival of roe deer does could therefore have been expected. However, males and old individuals often are more susceptible to environmental perturbation than prime-age females in most ungulate populations (e.g., mule deer [*Odocoileus hemionus*], Klein and Olson 1960; red deer, Clutton-Brock et al. 1982, Bonenfant et al. 2002; Kudu [*Tragelaphus strepsiceros*], Owen-Smith 1990; and Soay sheep [*Ovis aries*], Coulson et al. 2001), and we therefore expected the survival rates of males and old animals to be more strongly affected by Lothar. Likewise, juveniles in ungulate populations are highly sensitive to environmental variation (Gaillard et al. 2000). Our results showed that males, old animals, or fawns were not affected, but old females may have been. In addition, only 1 roe deer was found dead following Lothar at CH (none at TF). This small direct impact of Lothar on survival suggests, as previously noted by Labisky et al. (1999), that deer have timely escape behavior and are thus able to avoid injury from falling trees (Pimm et al. 1994).

Contrary to what Labisky et al. (1999) reported in their study of white-tailed deer, we found no evidence that Lothar affected reproductive output negatively, although the hurricane hit the deer at a critical stage of their breeding. On the contrary, virtually all females examined had implanted embryos just after the hurricane and were pregnant in January–February. This result supports previous findings on roe deer populations in England where implantation failure was found to be rather independent of environmental conditions (Hewison and Gaillard 2001). Although less marked, a similar pattern was found for litter size, and we found no evidence for a negative influence of Lothar on litter size, as for pregnancy rate.

## MANAGEMENT IMPLICATIONS

This work has quantified for the first time the overall effect of a major weather perturbation, the Hurricane Lothar, on roe deer population dynamics. Because the 2 populations we studied

had very different dynamics (see Gaillard et al. 1998b), we can conclude that such weather events have few, if any, numerical effects on roe deer populations. This conclusion will guide management in the future. In the next few years, roe deer populations likely will increase rather than decrease because the low rate of realization of hunting quotas was not counterbalanced by a negative impact from the hurricane on roe deer survival or reproduction. The main effect of the hurricane was to create openings within large forests that are good habitat for roe deer, thereby increasing the biomass of high-quality food plants. Managers therefore face a situation in which Lothar has had a positive impact on roe deer. This outcome, paradoxical for some, needs to be considered in future management plans for the deer.

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