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Forest Ecology and Management 195 (2004) 237–242
Forest Ecology and Management
www.elsevier.com/locate/foreco

The effects of hurricane Lothar on habitat use of roe deer

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Received 14 January 2003; received in revised form 27 October 2003; accepted 27 February 2004

Abstract

Hurricanes profoundly modify the structure of forests, affecting the habitat quality of forest dwelling ungulates. For browsers in European forests the effects are expected to be positive in the short-term due to increased availability of browse, but the data to test this prediction are rarely available. In this study, data on home ranges and habitat use were collected both before and after the passage of the hurricane Lothar for six female roe deer. Deer switched from using both coppice- and timber stands to living almost only in timber stands, where most of the damage occurred. Sizes of their home ranges declined sharply (on average by >50%). These results suggest that the effect of this winter hurricane was short-term improvement in the quality of deer habitat.
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Keywords: *Capreolus capreolus*; Habitat use; Home range; Hurricane; Telemetry; France; Roe deer

1. Introduction

The effects of environmental disturbances such as hurricanes on mammalian populations are of considerable interest to population ecologists and wildlife managers. However, the impact of hurricanes is often measured after such events. It is rarely possible to evaluate the effects on animals directly, because data collected before the event are rarely available. The impact of hurricanes on the habitats of browsing species, like roe deer, is likely to be positive in the short term, by returning mature forests to early succession stages and by increasing cover. The impact could also be positive immediately following hurricanes if new food resources are made available.

In late December 1999, hurricane Lothar, which may have been a 1000-year storm event, caused widespread destruction to forests in France, Switzerland and Germany. Within 2 h, 30% of trees in some forests fell, representing some 10 years of forest production (see the website http://www.notre-planete.info/tempete.php for further details). In fact, more windfalls should be expected in the timber stand than in the shrub-coppice, because there are large trees that could be toppled by the storm. Access to most forests by foresters and hunters was prevented for over a month. However, neither increased mortality nor reduced fertility of roe deer were observed in the

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doi:10.1016/j.foreco.2004.02.021

study population (Gaillard et al., 2003). Perhaps the result of an improvement of the resource availability in the short-term.

Home range size is a function of habitat productivity and resource distribution, as well as individual energy requirements (Harestad and Bunnell, 1979) making home range size an indicator of habitat quality (Byford, 1969; Tufto et al., 1996). One of the few studies which has addressed the impact of a hurricane on deer was conducted on white-tailed deer in the Everglades before and after hurricane Andrew (Labisky et al., 1999). This study showed that the home ranges of the deer during the months following the hurricane (January–March) did not differ from those of pre-hurricane years, implying that the resources for the deer (food, cover) were not affected by the hurricane.

Lothar hit the site of a long term study of roe deer population ecology (Gaillard et al., 1993, 1997, 1998) and habitat use, including a radio telemetry study of home ranges (Widmer et al., 1998). Six radio-marked female roe deer were being monitored when Lothar struck, which created an opportunity to observe the effects of a severe hurricane on another population of ungulates for which baseline data existed. However, our predictions of the consequences of winter hurricanes for roe deer are different: one of the principal winter food plants of roe deer is ivy, *Hedera helix*. Large quantities of this plant grow in the tops of trees, so a consequence of hurricanes is to make this resource easily available to deer. We therefore expected that:

1. after Lothar, the animals would shift to areas with dense windthrow;
2. home range size would decline, as a result of increased food availability.

2. Study area

Six females were tracked in the *Territoire d'Etude et d'Expérimentations* of Trois-Fontaines (TF), a 1360 ha enclosed forest. TF is situated in northeastern France (48°43′N, 4°56′W) and has a continental climate, characterised by cold winters and hot summers. The forest overstory is dominated by oak (*Quercus* spp.) and beech (*Fagus sylvatica*), and hornbeam (*Carpinus betulus*). The soil is fertile and the forest highly productive (long-term average of 5.92 m^3 of wood produced/ha per year (Inventaire Forestier National). Based on our current knowledge of food habits of roe deer in France (Duncan et al., 1998), TF is good habitat. The weather in the winters of 1999 and 2000 was similar, with average temperatures of 8.5 °C. The number of frost days was 29 in 1999 and 33 in 2000 (data from Météo France station Saint Dizier).

In western Europe generally, ivy (*H. helix*) is normally of principal plant in the winter diet of roe deer (Tixier and Duncan, 1996; Duncan et al., 1998). At TF, ivy represents 9.8% of the winter diet (Denis, 1987).

The roe deer population in TF was approximately 200–250 individuals >1 year old in March (ca. 15 km^{-2}) from 1977 to 1999.

3. Materials and methods

Six female roe deer fitted with Televilt TXH-3 radio collars were tracked before and after the hurricane, in Winter (January–March) for both 1999 and 2000. The does were tracked by using a TONNA five-element antenna attached to Televilt RX 900 or Yaesu FT-290R receivers. One fix was obtained on each animal during the day every 5 days to obtain about 20 locations each animal per winter. Fixes were determined by triangulation (White and Garrott, 1990) and several bearings were taken with a compass to obtain locations accurate to a quarter of a hectare. The locations of the animals were considered to be independent for statistical analyses (see Powell, 2000).

3.1. Measurements of the impact of the hurricane

In Spring 2000, before the fallen trees had been removed, 25 m radius plots at the intersections of a 50 m grid were sampled within the ranges occupied by every female monitored in the winters of 1999 and 2000. In each plot, the type of habitat was noted (timber stand versus coppice; the latter was not damaged by the storm). The trees of all species whose circumference was >20 cm were counted, as was the number of windfalls. We calculated the relative proportion of timber stand habitat (timber stand/timber stand + coppice) in each female home range before and after the hurricane.

3.2. Spatial analyses

A geographical information system (GIS), ArcView 3.2, including the animal movement and both vector and raster modules (ArcView extension) (http://www.absc.usgs.gov/glba/gistools/index.htm) was used to measure the home ranges of the roe deer.

Home range sizes were estimated for each 3-month period, using fixed kernel estimators (Silverman, 1986; Worton, 1989). The kernel method is a robust probabilistic approach for estimating home range size (Seaman and Powell, 1996; Powell, 2000). Fixed kernels are non-parametric estimators of probability distribution and can estimate distributions of any shape (Silverman, 1986).

Fixed kernels, with an optimum smoothing factor (h) calculated using least-squares cross validation, give the best estimate of the home range and are used here (Seaman and Powell, 1996; see Silverman, 1986 for an extensive coverage of methods).

For the kernels, we applied 95 and 50% boundaries to represent the animal's home range (Worton, 1989). Silverman (1986) suggests that 19 observations give a reliable density estimate. We therefore only estimated home ranges for roe deer with at least 20 fixes in a 3-month period. Kernels were calculated with the GIS application ArcView 3.2 (Environmental Systems Research Institute Inc., Redlands, USA) using the animal movement extension (http://www.absc.usgs.gov/glba/gistools/index.htm) (Hooge and Eichenlaub, 1997). We created the cluster (Kenward, 1987) and included the information about number of windfall trees in the home range.

3.3. Statistical analyses

The effects of Lothar on home range size were analysed by analysis of variance (ANOVA), t-tests and the sign test for paired data. The statistical analysis system (SAS Institute, 1989, Cary, NC, USA) was used for parametric statistical analyses.

4. Results

Most of the windfall occurred in the timber stand habitat and, as predicted, the deer spent most of their time in timber stands in 2000 (96% compared to only 60% in 1999, $t = 14.679$,$P < 0.0001$; Table 1). The shrubwood habitat occupied half of the 50% kernel before storm (on average 53%), whereas after the storm 98% of the kernels were in timber. An example is given in Fig. 1.

Prior Lothar, home range size varied between 34 and 159 ha (95% kernel; median = 66.3 ha), whereas after Lothar between 9.9 and 48.5 ha (95% kernel; median = 24.3). All the females reduced their home range sizes between before and after Lothar ($P = 0.016$, sign test; mean = −58 ha; Fig. 2). The size of the 50% kernel showed the same trend: in five of the females its size declined, but the change was not significant ($P = 0.078$, sign test; mean = −11.2 ha;

Table 1
Characteristics of the radio-tracked females in Trois-Fontaines, and their use of habitat, the time spent in timber stands (where windfall occurred) and the percentage of the home ranges situated in timber stands

	Female roe deer					
	1	2	3	4	5	6
Age (years)	5	10	7	10	6	6
Weight (kg)	20	24	24	25	24.5	23
Percentage of timber stand in home range						
Before hurricane (kernel 95%)	85	90	90	45	55	55
After hurricane (kernel 95%)	90	80	100	80	85	80
Before hurricane (kernel 50%)	90	75	70	1	50	30
After hurricane (kernel 50%)	100	100	100	100	85	100
Spent time in timber stand (%)						
Winter before hurricane (1999)	84	85	84	37	53	42
Winter after hurricane (2000)	95	95	100	95	95	95

Fig. 1. Female 4 home range before and after the hurricane. Home range size (the bold line corresponds to the 95% kernel and the fine line to the 50% kernel) decreased, as in the other does. The core of the home shifted to the windfall areas (areas in grey are timber stands; white areas are shrubwoods).

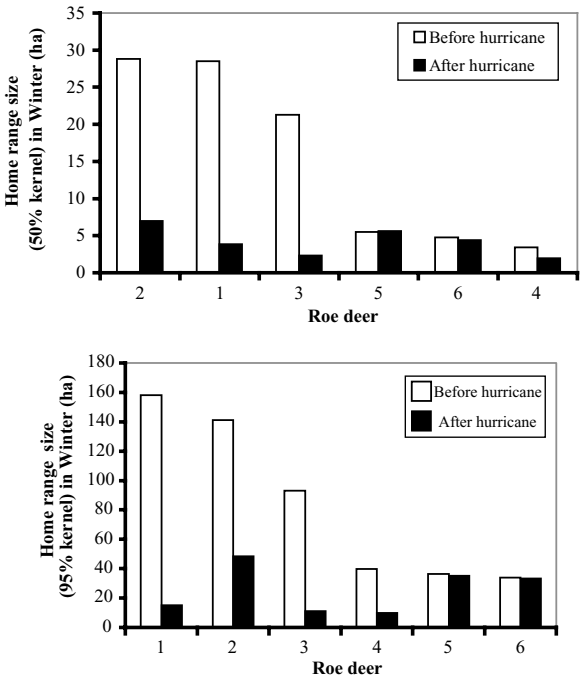

Fig. 2. Variation in home range sizes (kernel 50 and 95%) before and after hurricane Lothar in France.

Fig. 2). The three animals with the largest pre-hurricane ranges showed the greatest variation with >50% declines. The density of windfall trees was higher in the post- than in the pre-hurricane ranges for all the females ($P = 0.02$ for 50% kernel; $P = 0.05$ for 95% kernel, sign test; Fig. 3).

5. Discussion

Hurricane Lothar strongly influenced both the habitat use and the ranging behaviour of the deer. Before the hurricane, their ranges were composed of roughly equal areas of timber stands and coppice: afterwards the deer concentrated almost exclusively in timber stands, where most of the damage had occurred (Table 1, Fig. 1). This change in habitat use after the passage of Lothar could well be due to resource

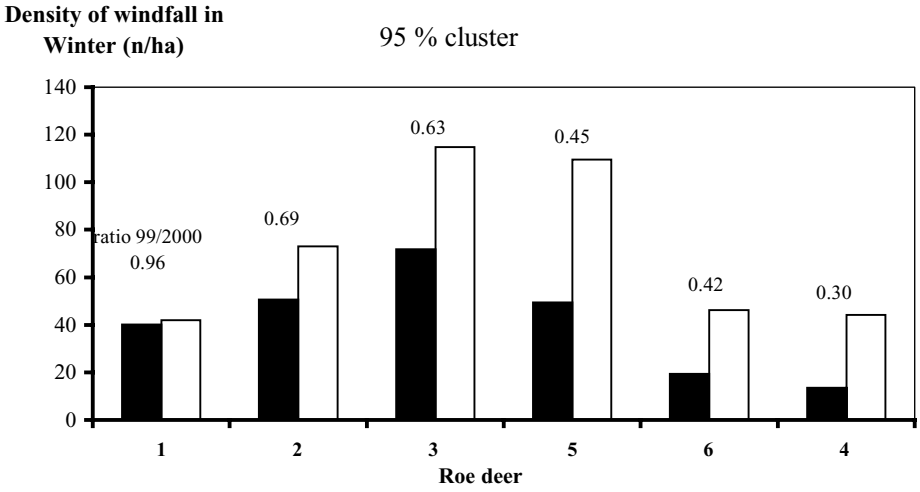

Fig. 3. Comparison of density of windfalls in the home range (cluster 95%) of roe deer before (white bars) and after (black bars) the hurricane.

availability. In Winter, ivy is often the key resource of the deer, and after the storm ivy was abundant on the broken branches close to the ground with fruits and leaves easily accessible to roe deer. These herbivores appear, therefore, to have moved their activity centres towards food sources opportunistically, as do other species (Johnson, 1987; Hansson, 2002).

The second prediction was also supported: the sizes of the home ranges of all six deer declined, by more than half (Fig. 2). The size of home ranges of roe deer is negatively correlated with the abundance of their food resources (Klein and Strandgaard, 1972; Cibien and Sempéré, 1989; Vincent et al., 1995; Guillet et al., 1995; Tufto et al., 1996; San-José and Lovari, 1997), as in many mammalian herbivores (white-tailed deer: Armstrong et al., 1983a,b; Lang and Gates, 1985; wild boar: Massei et al., 1997; Marsupials: Fisher and Owens, 2000; Red deer: Mysterud et al., 2001). The striking changes of the home ranges size of the deer with the largest pre-hurricane ranges suggest that the quality of these ranges was greatly improved by the storm (Fig. 3).

In another study, white-tailed deer (*Odocoileus virginiana*) in the Everglades (Florida, USA), living in heavily vegetated areas with high levels of interspersion of habitat types had smaller home ranges than those in more open, sparsely vegetated habitats (Labisky et al., 1999). Contrary to the results of this study, Labisky et al. (1999) found no differences between the sizes of the home ranges before and after a hurricane in the Everglades. Perhaps there were no food resources (such as ivy) for Everglades deer in the fallen tops of the trees.

6. Management implications

Little is known about the effects of storms on wildlife populations. The evidence available suggests that initial, short-term reductions animal densities are followed by rapid recovery to normal population levels (Conner, 1989; Labisky et al., 1999). This work provides new information on the overall effect of a major climatic perturbation, hurricane Lothar, on roe deer home ranges in Europe. The storm created blowdowns and edges in areas of mature forest. The roe deer adapted immediately, shifting to windfall areas and reducing the size of their home ranges.

The increasing roe-deer populations in Europe (over the last 20 years, Andersen et al., 1998) are causing more damage to young trees (Bergquist and Orlander, 1998). The hurricane provided a short-term supply of alternative browse that might temporarily reduce browsing pressure on tree regeneration. The improvement of the food resources of the deer as a result of the storm, through increased availability of ivy and bramble (*Rubus* spp.). It is also likely that the usually inaccessible crowns of other trees would be better quality for browsers (less chemical repellents against browsers) (Bryant and Kuropat, 1980). Hence, the North American forestry practice of felling trees in winter to provide browse for hares (Bryant and Kuropat, 1980). In the long term, the creation of small openings in mature forests, could provide alternative foods for browsers, being a possible solution to reduce damage to young trees.

Acknowledgements

This study was supported by the *Groupement d'Interêt Public Ecofor* as part of the research program aimed at evaluating the immediate consequences of the hurricane. The constructive comments from anonymous reviewers were greatly appreciated. Many thanks to Eric Baubet for improving earlier drafts of this manuscript.

References

Andersen, R., Gaillard, J.M., Liberg, O., San José, C., 1998. Variation in life history parameters of roe deer: the European roe deer. In: Andersen, R., Duncan, P., Linnell, J.D.C. (Eds.), The Biology of Success. Scandinavian University Press.

Armstrong, E., Euler, D., Racey, G., 1983a. Winter bed-site selection by white-tailed deer in central Ontario. J. Wildl. Manage. 47, 880–884.

Armstrong, E., Euler, D., Racey, G., 1983b. White-tailed deer habitat and cottage development in central Ontario. J. Wildl. Manage. 47, 605–612.

Bergquist, J., Orlander, G., 1998. Browsing damage by roe deer on Norway spruce seedlings planted on clearcuts of different ages. 1. Effect of slash removal, vegetation development, and roe deer density. For. Ecol. Manage. 105, 283–293.

Byford, J.L., 1969. Movement responses of white-tailed deer to changing food supplies. In: Proceedings of the Annual Conference of the Southeastern Association of Game and Fish Commissioners, vol. 23, pp. 63–67.

Bryant, J.P., Kuropat, P.J., 1980. Selection of winter forage by subarctic browsing vertebrates: the role of plant chemistry. Ann. Rev. Ecol. Syst. 11, 261–285.

Cibien, C., Sempéré, A.J., 1989. Food availability as a factor in habitat use by roe deer. Acta Theriol. 34 (7), 111–123.

Conner, J., 1989. Older males have higher insemination success in a beetle. Anim. Behav. 38, 503–509.

Denis, M., 1987. Food composition, winter diets of the roe deer and relative feeding capacity of forest stands in some areas in France. In: Proceedings of the XVIII IUGB congress, Poland.

Duncan, P., Tixier, H., Hoffman, R.R., Lechner-Doll, M., 1998. Feeding strategies and physiology of digestion in roe deer. In: Andersen, R., Duncan, P., Linnell J.D.C. (Eds.), The Biology of Success. Scandinavian University Press.

Fisher, D.A., Owens, I.F.P., 2000. Female home range size and the evolution of social organisation in macropod marsupials. J. Anim. Ecol. 69, 1083–1098.

Gaillard, J.M., Duncan, P., Delorme, D., Van Laere, G., Pettorelli, N., Maillard, D., 2003. Extreme climatic events and ungulate population dynamics: effects of hurricane Lothar on European roe deer. J. Wildl. Manage. 67, 767–773.

Gaillard, J.M., Delorme, D., Boutin, J.M., Van Laere, G., Boisaubert, B., Pradel, R., 1993. Roe deer survival pattern: a comparative analysis of contrasting populations. J. Anim. Ecol. 62, 778–791.

Gaillard, J.M., Boutin, J.M., Delorme, D., Van Laere, G., Duncan, P., Lebreton, J.D., 1997. Early survival in roe deer: causes and consequences of cohort variation in two contrasted populations. Oecologia 112, 502–513.

Gaillard, J.M., Liberg, O., Andersen, R., Hewison, A.J.M., Cederlund, G., 1998. Population dynamics of roe deer: the European roe deer. In: Andersen, R., Duncan, P., Linnell, J.D.C. (Eds.), The Biology of Success, Chapter 13. Scandinavian University Press.

Guillet, C., Bergstrom, R., Cederlund, G., Bergstrom, J., Ballon, P., 1995. Comparison of telemetry and pellet-group counts for determining habitat selectivity by roe deer in winter. Gibier Faune Sauvage 12, 253–269.

Hansson, L., 2002. Mammal movements and foraging at remnant woodlands inside coniferous forest landscapes. For. Ecol. Manage. 160, 109–114.

Harestad, A.S., Bunnell, F.L., 1979. Home range and body weight—a reevaluation. Ecology 60 (2), 389–402.

Hooge, P.N., Eichenlaub, B., 1997. Animal Movement Extension for ArcView Version 1.1. Alaska Biological Science Centre, US Geological Survey, Anchorage, AK, USA.

Johnson, K.L., 1987. Sagebrush over time: a photographic study of rangeland change. In: McArthur, E.D., Welch, B.L. (Eds.), Proceedings of the Symposium on the Biology of *Artemisia* and *Chrysothamnus*. USDA For. Serv. Gen. Tech. Rep. INT-200, Ogden, UT, USA, pp. 223–252.

Kenward, R., 1987. Wildlife radio tracking. Equipment, Field Techniques and Data Analysis. Academic Press, New York.

Klein, D.R., Strandgaard, H., 1972. Factors affecting growth and body size of roe deer. J. Wildl. Manage. 36, 64–79.

Labisky, R.F., Miller, K.E., Hartless, C.S., 1999. Effect of hurricane Andrew on survival and movement of white-tailed deer in the Everglades. J. Wildl. Manage. 63 (3), 872–879.

Lang, B.K., Gates, J.E., 1985. Selection of sites for winter night beds by white-tailed deer in a hemlock-northern hardwood forest. Am. Midl. Natl. 113, 245–254.

Massei, G., Genov, P.V., Staines, B.W., Gorman, M.L., 1997. Factors influencing home range and activity of wildboar (*Sus scrofa*) in a Mediterranean coast area. J. Zool. 242, 411–423.

Mysterud, A., Langvatn, R., Yoccoz, N.G., Stenseth, N.C., 2001. Plant phenology, migration and geographic variation in body weight of a large herbivore: the effect of a variable topography. J. Anim. Ecol. 70, 915–923.

Powell, R.A., 2000. Animal home ranges and territories and home range estimators. In: Boitoni, L., Fuller, T.K. (Eds.), Research Techniques in Animal Ecology, Controversies and Consequences. Columbia University Press, New York.

San-José, C., Lovari, S., 1997. Wood dispersion affects home range size of female roe deer. Behav. Process. 40, 239–241.

Seaman, D.E., Powell, R.A., 1996. An evaluation of the accuracy of kernel density estimators for home range analysis. Ecology 77, 2075–2085.

Silverman, B.W., 1986. Density Estimation for Statistics and Data Analysis. Chapman & Hall, London.

Tixier, H., Duncan, P., 1996. Are European roe deer browsers? A review of variations in the composition of their diets. Revue d'Ecologie (Terre Vie) 51, 3–17.

Tufto, J., Andersen, R., Linnell, J., 1996. Habitat use and ecological correlates of home range size in a small cervid: the roe deer. J. Anim. Ecol. 65, 715–724.

Vincent, J.P., Bideau, E., Hewison, A.J.M., Angibault, J.M., 1995. The influence of increasing density on body weight, kid production, home range and winter grouping in roe deer. J. Zool. 236, 371–382.

White, G.C., Garrott, R.A., 1990. Analysis of Wildlife Radio-tracking Data. Academic Press, San Diego.

Widmer, O., Chastragnat, L., Klein, F., 1998. L'occupation de l'espace par le chevreuil. Bulletin mensuel de l'Office national de la chasse. 236, 4–13.

Worton, B.J., 1989. Kernel methods for estimating the utilization distribution in home-range studies. Ecology 70 (1), 164–168.