Effect of a Motorway on Mortality and Isolation of Wildlife **Populations**

Although motorways could affect wildlife species, only few studies have been documented on their effects on mortality and isolation. With 2266 road-killed animals representing 97 species, the results of a study on a motorway section emphasised that traffic considerably affected vertebrate populations (14.5 animals day⁻¹ 100 km⁻¹). Road-killed animals were mainly mammals (43.2%), but predators also suffered a critical impact (21.7% vertebrates). Rare or endangered species such as the Midwife toad, the Blue throat, the little Horseshoe bat, or the European otter were found. Animal mortality exponentially increased with traffic volume. Mortality reached almost 100% of migrants when no passage existed, and this barrier effect was only reduced when underneath passages crossed the road restraining the mortality to 31% of migrants in Field mice and 23% in Common toads, while mortality always exceeded 74% in road section with fauna ducts. It is reasonable to conclude that traffic severely influenced both wildlife species demography and population exchanges resulting in effective population isolation.

INTRODUCTION

During the last decades, the construction of many linear infrastructures has radically changed the landscapes and modified animal communities. Roads can largely affect wildlife populations notably by intensifying the toxic contamination among roadside populations (1, 2), by inducing a direct mortality (3, 4), and by increasing habitat fragmentation (5, 6). Nevertheless, only few studies have dealt with the impact of motorways on animal mortality and isolation (3, 7) although their traffic volume is higher than in other roads.

Various toxic rejects of vehicles are soluble in fatty tissues and, e.g. heavy metals accumulate in organisms. These compounds, which are biologically persistent in variable concentrations, could alter animal reproduction and have lethal effect in the long term (8, 9). Traffic is also responsible for road-killed animals and can have a strong impact on small-sized populations (10-12) and, especially periods of intense road traffic provoke an increase in animal mortality (13-15). Furthermore, motorways constitute barriers subdividing natural habitats and result in subsections of small isolated populations (5, 6). The effects of subdivision and isolation on wildlife populations have received a great deal of attention since they may reduce the long-term survival of populations (16-18). By limiting population exchanges, this fragmentation can considerably affect the reproductive ability and the genetic diversity of wildlife populations, and even increases extinction rates (16-18).

On most motorways, compensatory measures have been recommended to reduce the undeniable impact of habitat loss and the partitioning of populations. Among the ecological measures performed, protective fences have prevented the passage of the biggest animals, ungulates notably, and fauna passages have been built over or underneath motorways in order to re-establish earlier connections. However, these measures generally remained empirical and almost nothing was known about their real efficiency.

Road-killed Barn owl Tyto alba Photo: Thierry Lodé.

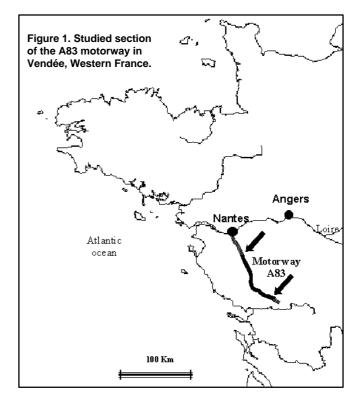


This study was designed to determine the impact of a recent motorway, one year after its opening on the isolation and mortality of vertebrate populations. Here I present a census of the animal mortality due to the automobile traffic on a 68.2-km section of a recently constructed motorway during weekly surveys over a period of 7.5 months.

Since isolation of populations is an essential factor in determining their long-term survival, fieldwork on anuran and mammal dispersal was conducted in close vicinity of the motorway.

MATERIALS AND METHODS

The study was performed in western France between Montaigu and Fontenay-Le-Comte (department of Vendée, Fig. 1), in 1995, on a 68.2-km section of the A83 motorway, which was opened to road traffic in October 1994. Mean weekly temperatures remained moderate (min. 4°C in April, max. 30.9°C in August), and precipitation averaged 18 mm week⁻¹ (range 0-97mm). The impact of the motorway on vertebrate mortality was investigated by a census of road-killed animals between April and November 1995 from a car displacing at a speed <40 km/h. Regular stops were made for close examination, and regular explorations on foot were performed on authorised sections of the road. Each



animal was specifically identified, sexed, often after a limited autopsy to examine the gonads, and its location was noted during a regular weekly survey. The method probably provides an underestimate of the mortality as predators could infact, have removed numerous small-sized dead animals (19-21).

The construction of a motorway imposes precise norms, and the level of the ground has often been modified to limit variations in the profile and to facilitate easy traffic movement. The location of killed animals was distinguished according to three different levels: ground level, sunken; embanked road sections. A wide-mesh fence was disposed along the 68 km to prevent access by animals. However this fence was not continuous but was intersected by numerous gates. In addition, there were some non specific ducts, with numerous connections for crossing the road; such as water pipes, channels and over- or undergroundpassages which were built to allow agricultural vehicles to cross, but, these were usable by terrestrial animals. No preliminary studies had been performed on population exchanges, notably on amphibians, and migratory passages were disregarded on this motorway.

The effect of the motorway on population isolation was studied measuring the movements of two terrestrial species, the Common toad (Bufo bufo) and the Field mouse (Apodemus sylvaticus). Although numerous amphibians (Rana dalmatina, Alytes obstetricans) or microtids (Clethrionomys glareolus and Microtus arvalis) were also identified, the former two species were chosen because they were common in the studied site. During their dispersal towards breeding ponds in the close vicinity of the motorway, toads were directly counted on each side of the motorway at 4 sites: Site 1 near a nonspecific fauna duct (0.8 m diameter); Site2 near a nonspecific over-passage (5m wide bridge); Site 3 near an underground-passage (9m wide); and Site 4 with no passageway through the road. Field mice were trapped live using 100 Firobind live-traps on each side of the motorway, during 4 days, representing 800 trap nights per site. Trapping was carried out on four different sites with no passage, with nonspecific fauna passage (0.8 m diameter), with over-passage (9 m wide bridge) and with underground-passage (6 m wide). Both sides of the motorway were studied during a summer session. The animals were marked by toe clipping and immediately released.

RESULTS

Mortality

During the 33 weekly surveys on 68.2 km of motorway, the total number of road killed vertebrates reached 2266 individuals representing 97 species including some uncommon or rare species such as Barbastella barbastellus, Rhinolophus hipposideros, Lutra lutra, Genetta genetta, Luscinia svecica, Petronia petronia, Alytes obstetricans (Table 1). On 442 sexed individuals, 55.4% were males and 44.6% were females. The number of road-killed species differed from the number of available species in the study area, in regard to classes ($c^2 = 12.3$, df3 p < 0.01) and corresponded to 60% amphibians species present in Vendée, 36.4% the reptiles, 23.9% birds and 57.4% mammals. Terrestrial animals paid the heaviest tribute, i.e. 73.5% of total vertebrate casualties. The most road-killed animals were rodents (27% of the vertebrates), but the impact of the motorway on rodent predators was considerable (Falconiformes + Strigiformes + Carnivora: 21.7% of total vertebrates) since 2 road-killed predators (n = 492) were found for 3 prey species (rodents and lagomorphs, n = 716). Road-killed Hedgehogs Erinaceus europaeus represented only 2.8% of the vertebrates (n = 63), but 68.3% were found before summer during the first 3 months of the study. The Field vole Microtus arvalis predominated in roadkilled vertebrates with 19.7% corresponding to 45.6% of dead mammals while the Common toad Bufo bufo (16.6% of total vertebrates) represented 56.7% of amphibians and the Palmated newt *Triturus helveticus* (8.3% of the vertebrates) totalled 28.4%. of the amphibians. The Barn owl *Tyto alba* was 8.1% of the dead animals and 30.7% of the bird population and the Dark green snake *Coluber viridiflavus* 0.9% of the vertebrates but 80% of the reptiles.

The number of weekly road-killed vertebrates averaged 68.7 individuals week⁻¹ km⁻¹ (sd 59.4) or 4.43 individuals month⁻¹ km⁻¹ (sd 2.47) but showed seasonal variations (Kruskall-Wallis ANOVA KW = 13.26, p < 0.01) with 22.1 ind/week (sd 8.7) in spring while 83 (sd 48.9) and 82.3 (sd 77.5) respectively, were found in summer and autumn (Fig. 2). Peaks observed in October an November were mainly due to the movement of amphibians towards their winter rest sites.

Animal road casualties averaged 14.52 ind day⁻¹ 100km⁻¹ (sd 6.85). The motorway traffic was 19320 vehicles day⁻¹ (sd 4152) or 805 hr⁻¹ (sd 173), and correlated significantly with variations in the number of road-killed vertebrates ($r_{Pearson} = 0.862$, p < 0.0001). An exponential curvilinear function was the most likely to explain the link between road-killed animal numbers and traffic ($Y = 1.523e^{0.012x}$, $R^2 = 0.768$) (Fig. 3). Nevertheless, mammals ($r_{Pearson} = 0.841$; p < 0.001) and amphibians ($r_{Pearson} = 0.631$, p < 0.007) clearly suffered the increase of traffic, whereas the number of dead birds ($r_{Pearson} = 0.402$, p > 0.05) or reptiles ($r_{Pearson} = 0.043$, p > 0.05) were not significantly related to this increase.

The number of road-killed animals greatly differed ($c^2 = 85.53$, df6, p < 0.0001) according to the three different levels distinguished; ground-level (17.8% of total vertebrates), sunken (35.6%) or embanked (46.7%) road sections but mammals were more often found in the sunken road section (44.6% of the total number of mammals, KW = 7.13, p < 0.03), birds (51.7% of the bird total, KW = 14.2, p < 0.001), amphibians (56.4% of total amphibians) and reptiles (48% of the reptile total) were mostly killed in embanked road section (Table 2).

Isolation

Although numerous compensatory adjustments existed on the road, such as fences, passages and tree hedges (mean number 1.57 passages km⁻¹, i.e. 0.72 ducts km⁻¹, 0.56 over passages km⁻¹ and 0.29 underneath passages km⁻¹), the distribution of dead terrestrial vertebrates did not significantly vary in the 100-m-long

Table 1. Road-killed vertebrates found on the motorway during a weekly survey on a 68.2-km road section during 33 weeks in western France.

	N species		N individuals	%
Amphibians	4	Urodela	196	8.6
	5	Anuran	466	20.6
	9		662	29.2
Reptiles	4	Squamata	25	1.1
	4		25	1.1
Birds	1	Ciconiiformes	1	<0.1
	1	Anseriformes	9	0.4
	2	Falconiformes	29	1.3
	3	Galliformes	20	0.9
	1	Cuculiformes	1	<0.1
	2	Gruiformes	5	0.2
	4	Charadriiformes	11	0.5
	3	Columbiformes	5	0.2
	1	Coraciiformes	7	0.3
	1	Piciformes	2	0.1
	4	Strigiformes	304	13.4
	33	Passeriformes	206	9.0
	56		600	26.5
Mammals	3	Insectivora	73	3.2
	8	Rodentia	612	27.0
	2	Lagomorpha	104	4.6
	8	Carnivora	159	7.0
	6	Chiroptera	31	1.4
	27	•	979	43.2
Total	97		2266	

motorway sections with no passages crossing the road or sections with passages (*Kolmogorov-Smirnov* = 0.115, $c^2 = 3.09$, p > 0.2). But mortality differed among classes ($c^2 = 98.3$; df3, p < 0.0001) since breeding adults were chiefly killed among mammals and amog amphibians during their movements towards spawning ponds, while killed birds were mainly dispersal juveniles (Table 3).

During the survey, 74.8% (n = 175) of Common toads *Bufo bufo* moving towards their breeding ponds were found road killed, but the mortality greatly differed among sites ($c^2 = 15.4$, df 3, p < 0.002) and road sections with underground passages were significantly less lethal (23.1%) than others (Fig 4). In the same way, on 1105

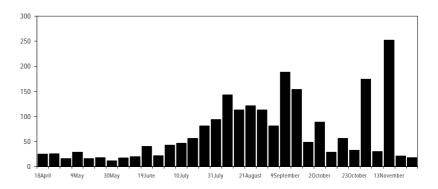
Field mice *Apodemus sylvaticus* intercepted by live trapping, 16.4% (n = 181) were attempting to cross the motorway. They were mainly males (69.6%) and juveniles predominated (76.2%). On average 73.5% of these transient mice were found road-killed, but the mortality of mice significantly varied among four sites (χ^2 =10.9, df 3, p < 0.02) and was higher in sections with no passages, or with over passages while the mortality reached 31.1% in sections with underground passages. Nevertheless, numerous animals (minimum 23.1% *Bufo bufo* and 31.1% *Apodemus sylvaticus*) always tried to cross the motorway directly without using the different passages.

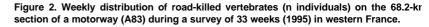
DISCUSSION

These results clearly showed that, one year after the opening, a motorway can considerably affect animal communities, provoking direct mortality and isolating populations.

The motorway studied had a major impact on mammals but a great diversity of species is concerned with 97 road-killed different vertebrate species. The number of road killed animals, i.e. 14.52 animals day⁻¹ 100 km⁻¹ was greater than recorded elsewhere either on roads or motorways (3, 13, 21-23). Nevertheless, no dead ungulate was found, indicating a certain efficiency of fences. This high mortality might be attributed both to the increase in traffic and to the recent opening of the motorway. Due to the habitat modifications, it could be predicted that the number of killed animals was highest soon as the opening of the motorway, but may stabilise later.

The number of road-killed vertebrates increased with increased road traffic according to a curvilinear exponential function, but mammals and amphibians mainly suffered from the increase in the number of vehicles. The impact of traffic volume was especially high, and Gelder (24) has estimated that a flow of 10 vehicles hr⁻¹ resulted in 30% mortality in animals while a flow around 40 vehicles hr-1 might kill at least half of the migrant Common toads (10, 11). Thus, the recorded flow for the motorway studied averaging 805 vehicles hr⁻¹ may be regarded as fatal enough to decimate local populations. The density-depressing effect of roads has been measured in amphibians (25) and birds (12), whereas numerous vertebrates were able to take advantage of road verges, mainly eurytopic species such as rodents or ravens (20, 26-29). Mortality was also correlated with the densities of small mammals (28). However, although rodents were the most frequently road-killed animals, predators paid a heavy tribute to the motorway. Two main causes explained this mortality, either habitats were destroyed or disturbed and they were exploiting roadside prey (30). Because they have a key function in ecosystem equilibrium, the critical impact of motorway on predators might affect whole communities in the long term. The increased road traffic was one factor relating to the small-sized populations or number of endangered species. Several road-killed individuals of rare or endangered species such as the Midwife toad, the Blue-throat, the little horseshoe bat, the Genet and the





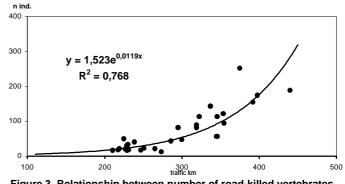


Figure 3. Relationship between number of road-killed vertebrates on the motorway (A83) and traffic intensity (vehicles/km) as expressed by an exponential curvilinear function.

 Table 2. Proportions of road-killed vertebrates found on the motorway according to three levels of the road section.

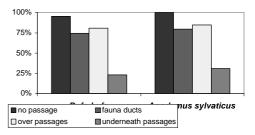
Road section	Mammals	Birds	Reptiles	Amphibians	Total
Sunken	44.6	27.8	40	29.1	35.6
Ground-level	18.6	20.5	12	14.4	17.8
Embanked	36.8	51.7	48	56.4	46.6
n	979	600	25	662	2266

Table 3. Proportions of road-killed adults and juveniles on identified animals (n = 1543) on the motorway.

	Mammals	Birds	Reptiles	Amphibians
Juveniles	41.9	67.9	45.0	33.7
Adults	58.1	32.1	55.0	66.3
N total	615	306	20	602

Figure 4. Mortality rates of migrants of two terrestrial vertebrate species. the Common toad Bufo bufo and the Field mouse Apodemus sylvaticus on four sites in the immediate vicinity of the motorway (A83) according to the type of passages crossing the road.

Mortality rate of migrants



European otter were discovered. Road casualties represented 26.7% of known mortality in European otter Lutra lutra from Pays de Loire (31). On the other hand, that birds were mainly killed on embanked road sections revealed the importance of some compensatory measures such as hedge plantations on roadsides.

Road construction and traffic induced a real barrier effect which was worsened by disturbance and environmental instability (5, 6, 32, 33). It has been argued that roads were behavioural barriers inhibiting mammal movements because the mammals hesitated to venture into open spaces (22, 34). But, in spite of an average of 1.57 passages km⁻¹, these results emphasised that the immediate risk of being killed by the traffic to animal crossing the road, resulted in effective isolation of populations.

Although dispersers only constituted a small fraction of natural populations, dispersal was regarded as an important phenomenon influencing demography and population genetics (35). Here, the Apodemus sylvaticus dispersers corresponding to 16% of intercepted mice, were mainly juveniles. Juvenile dispersal is often related to adult densities (36-38) and roads affected their movements (5, 7). Small mammals were able to move long distance and distance increased in answer accordance with landscape fragmentation (39, 40). However, dispersers were highly vulnerable and exposed to mortality. For birds and reptiles, mortality was also related to juvenile dispersers or unusual movements (41-43) whereas road-killed amphibians were mostly adults moving towards breeding sites (11, 24). Traffic affected

References and Notes

- 1. Jefferies, D.J., and French, M.C. 1972, Lead concentrations in mammals trapped on
- 2
- Serieris, D.J., and Frenci, M.C. 1972. Evaluations in manifest appect on road sides verges and field sites. *Environ. Pollut.* 3, 147-156.
 Muskett, C.J. and Johnes, M.P. 1980. The dispersal of lead cadmium and nickel from motor vehicules and effects on road sides invertebrate macrofauna. *Environ. Pollut.* 23, 231-242
- Case, R.M. 1978. Interstate highway road-killed animals, A data source for biologists. 3. *Wildl. Soc. Bull.* 6, 8-13. Reichholf, J. and Esser, J. 1981. Daten zur Mortalität des Igel (*Erinaceus europaeus*)
- 4 verursacht durch den Strassenverkehr. Z. Säugetierk. 46, 216-222. Mader, H.J. 1984. Animal Habitat isolation by roads and agricultural fields. *Biol.* 5
- Conserv. 29, 81-96
- Andrews, A. 1990. Fragmentation of habitat by roads and utility corridor: a review. *Aust. Zool.* 26, 130-141. 6. 7. Wilkins, K.T. 1982. High ways as barriers to rodent dispersal. S. West Nat. 37, 459-
- 8. Welch, W.R. and Dick, D.L. 1975. Lead concentration in tissues of road mice. Environ.
- Pollut. 8, 15-21. Getz, L.L., Verner, L. and Prather, M. 1977. Lead concentrations in small mammals 9
- living near highways. Environ. Pollut. 13, 151-157. 10. Heine, G. 1987. Einfache Mess- und Rechenmethode zur Ermittlung der Überlebenschance wandernder Amphibien beim überqueren von Strassen. Beitr. Veröff.
- Naturschutz und Landschftspflege Baden Württemberg 41, 473-479. Khun, J. 1987. Strassentod der Erdkröte (Bufo bufo L.): Verlusquoten und Verkehr-11.
- 12.
- Knuii, J. 1967. Strassentod der Erdkrote (*Buffo Buffo L.*): Verfusquoten und Verkenf-saufkommen, Verhalten auf der Strasse. *Beith. Veröff. Naturschutz und Landschaftspflege Baden-Württemberg 41*, 175-186.
 Zande, van der A.N., Terkeurs, W.J. and Weijden, van der W.J. 1980. The impact of roads on the densities of four bird species in an open field habitat-evidence of a long-distance effect. *Biol. Conserv. 18*, 299-321.
- Hodson, N.L. 1966. A survey of road mortality in mammals (and including date for the Grass snake and Common frogs). J. Zool. Lond. 148, 576-579. 13. 14.
- Massey, C.I. 1972. A study of hedgehog road mortality in Seaborough district. *Naturalist* 992, 103-105. 15. Berthoud, G. 1980, Le Hérisson (Erinaceus europaeus L.) et la route, Rev. Ecol. (Terre
- Vie) 34, 361-372 Lacy, R.C. 1987. Loss of genetic diversity from managed populations: Interactions ef-16
- fects of drift, mutation, immigration, selection and population subdivision. Conserv. Biol. 1, 143-158.
- Slatkin, M. 1987. Gene flow and the geographic structure in subdivided populations. 17. *Science 236*, 787-792. Kawata, M. 1997. Loss of genetic variability in a fragmented continuously distributed 18.
- Partial, M. D', Los of generic varianty in a negligible commonly in 19.
- 608 20.
- Austin, G.T. 1971. Roadside distribution of the common raven in the Mohave Desert. *California Birds* 2, 98.
 Waechter, A. 1979. Mortalité animale sur une route à grande ciculation. *Mammalia* 21.
- 43, 577-579 22
- (A), 517-517.
 (A), 517-517.
 (A), S. (1997). The effect of roads on populations of small mammals. J. Appl. Ecol. 11, 51-59.
 Saint Girons, M.C. 1984. Impact du trafic routier sur les Vertébrés dans le bocage breton. Bull. Ecol. 15, 175-183.
 Coldurate LL 1072. 23
- 24 Gelder, van J.J. 1973. A quantitative approach to the mortality resulting from traffic
- Getter, van J.J. 1975. A quantative approach to the mortanty resulting from traine in a population of *Bufo bufo L. Occologia 13*, 93-95.
 Fahrig, L., Pedlar, J.H., Pope, S.E., Philip, D., and Wegner, J.F. 1995. Effect of road traffic on amphibian density. *Biol. Conserv.* 73, 177-182. 25 Vay, J.M. 1977. Road side verges and conservation in Britain: a review. Biol. Conserv. 26
- 12.66-74 Bourquin, J.D. and Meylan, A. 1982. Les peuplemennts de micromammifères le long 27. des autoroutes: inventaire faunistique et exemples d'occupation par *Microtus arvalis* (Pallas). *Rev. Suisse Zool.* 89, 977-991.
- Adams, L.W. and Geis, A.D. 1983. Effects of roads on small mammals. J. Appl. Ecol. 28 20, 403-415.

both animal demography and gene flow when casualties occurred among breeding adults. Traffic disturbance also affected breeding in birds (12, 44, 45). Assessing habitat fragmentation in Moor frog, Vos and Chardon (46) stressed that the negative impacts of roads are often underestimated. The number of dead animals found did not differ significantly between sections with passages and the sections without. Thus, the motorway had an effective barrier effect. Numerous animals persisted in crossing the road directly, neglecting all types of passages. Because passages were mostly associated with streams or woods, the number of animals crossing the road was probably greater than that in the sections with no passages. Thus, the proportion of road-killed animals may be lower in road-sections with passages than it is in sections without. This is suggested by the results for mice and toads which showed that mortality was lowest in those sections that had underground passages. The barrier effect was reduced by the underground passages, while non specific fauna ducts interested only a few dispersers. Perhaps this is the case because they appeared too narrow or because the animals needed more time to learn to use them.

In spite of some compensatory adjustments for wildlife species, it is reasonable to conclude that the opening of a new motorway clearly resulted in an immediate demographic depletion and effective population isolation. The construction of new motorways clearly required studies on migrations and population exchanges to preserve local populations and minimise the impact on ecosystem equilibrium.

- Meunier, F.D., Corbin, J., Verheyden, C. and Jouventin, P. 1999. Effects of landscape 29 type and extensive management on use of motorway road sides by small mammals. Čan. J. Zool. 77. 108-117.
- Pienaar, V. de 1968. The ecological significance of roads in a national park. *Koedoe* 30. 11. 169-174
- Lodé, T. 1993. The decline of otter Lutra lutra populations in the region of the Pays 31. Lote, I. 1997. The decline of our days and populations in the region of the de Loire, western France. *Biol. Conserv.* 65, 9–13. Kozel, R.M. and Fleharty, E.D. 1979. Movements of rodents accross roads. *S. West.*
- 32. Nat 24, 239-248. 33
- Kozakiewicz, M. and Jurasinska, E. 1989. The role of habitat barriers in Woodlot
- Rozakiewicz, M. and Sutanski, E. 1995. Interference of national metrics in woodoft recolonization by small mammals. *Holarctic Ecol.* 12, 106-111. Kozakiewicz, M. 1993. Habitat isolation and ecological barriers- the effect on small mammal populations and communities. *Acta theriol.* 38, 1-30. 34. 35
- Merriam, G. 1988. Landscape dynamics in farm land. *TREE 3*, 16-20. Wolff, J.O. 1993. What is the role of adults in mammalian dispersal ? *Oikos* 68, 173-36. 176.
- Teferi, T. and Millar, J.S. 1994. Effect of supplemental food on the dispersal of young *Peromyscus maniculatus. Ecoscience 1*, 115-118. Plesner-Jensen, S. 1996. Juvenile dispersal in relation to adult densities in wood mice 37.
- 38. Apodemus sylavticus. Acta theriol. 41, 177-186. Liro, A. and Szacki, J. 1987. Movements of field mice Apodemus agragrius (Pallas)
- 39
- Bio, A. and Szacki, J. 1987. Movements of rend inice Apoaemus agragnus (Panas) in suburban mosaic of habitats. *Oecologia* 74, 438-440.
 Wegner, J. and Merriam, G. 1990. Use of spatial elements in a farmland mosaic by a woodland rodent. *Biol. Conserv.* 54, 236-276.
 Wegner, J. and Merriam, G. 1979. Movements by birds and small mammals between the birds of the color of the birds. 40.
- 41. wood and adjoining farmland habitats. J. Appl. Ecol. 16, 349-357 Tucker, J.K. 1995. Notes on Road-killed snakes and their implications on habitat modi-
- 42 fications due to summer flooding on the Mississippi river in west central Illinois. Trans. Ill. St. Acad. Sc. 88, 11-22. Bonnet, X., Naulleau, G. and Shine, R. 1999. The dangers of leaving home: dispersal
- 43.
- Bonnet, X., Natheau, G. and Shine, K. 1999. The dangers of leaving nome: dispersal and mortality in Snakes *Biol. Conserv.* 89, 39-50. Reijnen, M.J.S.M., Thissen, J.B.M. and Bekker, G.J. 1985. Effects of road traffic on woodland breeding birds. *Actes Coll. "Route et Faune sauvage" Strasbourg*, 261-264. Paruk, J.D. 1990. Effects on roadside management practises on bird richness and re-water direction. *Biol. 42*, 49, 49, 49, 49, 410. 44
- production. *Trans. Ill. St. Acad. Sc.* 83, 181-192. Vos, C.C. and Chardon, J.P. 1998. Effects of habitat fragmentation and road density
- 46. on the distribution pattern of the moor frog *Rana arvalis. J. Appl. Ecol. 35*, 44-56. I thank Cormier J.P., Grosselet O., Le Jacques D., Lechat I., Luyen V., Robert Y. and
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Thierry Lodé is professor in the Laboratory of Animal Ecology, Faculté des Sciences, University of Angers-Belle-Beille, Angers, France. He studies evolutionary ecology and population genetics and has published numerous papers on mustelid biology and conservation and a book Génétique des Populations, Ellipses, Paris. His address: Laboratoire d'Ecologie Animale UFR Sciences 2 Bd Lavoisier, 49045 Angers-Belle-Beille, France

E-mail: thierry.lode@univ-angers.fr