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# Motorways and bird traffic casualties: Carcasses surveys and scavenging bias

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ABSTRACT

Most survey methods developed to estimate abundance of killed animals on motorways may be biased due to the unequal detectability of carcasses, their persistence time on the lanes, and scavengers activities. Unbiased surveys are needed to evaluate the relationships between bird casualties (mortality), motorways characteristics, and the neighbouring avifauna. The present study conducted on four motorways in France, aimed to evaluate factors affecting persistence and encounter probabilities and variations in scavenging activity to obtain unbiased estimates of bird traffic casualties. Each motorway was surveyed once per season during multiple years and we used capture–recapture methods to estimate detection and carcass persistence rates. Results showed that surveys by car were as efficient as surveys by foot in detecting carcasses on the pavement, but less efficient for carcasses on verges. Passeriformes represented the most numerous casualties, and the Barn Owl (*Tyto alba*) was the most frequently killed species. Encounter probabilities were constant and high (0.957 ± 0.007). Average daily persistence probability was 0.976 ± 0.003. Persistence probabilities were higher for large and old carcasses, during summer, and differed between seasons, but were relatively similar between years. Scavenging activities, estimated using experimental carcasses disposed on the safe lanes of motorways, varied between years, seasons, and differed between diurnal and nocturnal periods. A peak in scavenging activity occurred during diurnal periods in spring. Results suggest that surveys must take into account carcass characteristics and seasonal variability to obtain unbiased estimates of road killed birds on motorways, as well as variation in scavenging rates.

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## 1. Introduction

The environmental impact of the road-traffic complex is wide and diverse. Isolation of populations caused by roads was shown to have negative effects (Forman and Alexander, 1998; Lodé, 2000; Rytwinski and Fahrig, 2007). Pollutants (gases, oil, heavy metals, chemicals, salt, and wastes) may negatively affect environmental quality and plant and animal populations of the neighbouring areas (Van der Zande et al., 1980; Seiler, 2001; Erritzøe, 2002; Erritzøe et al., 2003; Reijnen and Foppen, 1991, 1994; Reijnen et al., 1995; Ramsden, 2003). The noise generated by vehicles may also affect several animal species, sometimes over surprisingly long distances (Van der Zande et al., 1980; Reijnen and Foppen, 1991). Roads have also a direct effect on animals by traffic killings, road mortality being a significant source of animal mortality and a major problem for several species of conservation concern (Bennett, 1991; Forman and Alexander, 1998). Previous studies estimated that 2.5 millions birds were killed each year by traffic in Britain (Hodson and Snow, 1965), and that 80 millions birds were killed each year on the US roads (Erickson et al., 2005). Moreover, roads and motorways have direct demographic consequences on bird populations such as the Florida Scrub-Jay (*Aphelocoma coerulescens*) (Mumme et al., 2000), and European Barn Owl (*Tyto alba*) populations (Fajardo, 2001).

Estimating concisely the impact of road mortality on animal populations nearby linear infrastructures of transportation is an important conservation issue. To deal with this question, it is necessary to calculate robust and unbiased estimates of the number of road killed animals on surveyed road sections and to detect the key factors implied in traffic-induced mortality – a necessary step to identify the hot spots of mortality, to estimate the impact of road kills on populations, and to propose suitable mitigation measures. Many survey methodologies of road killed animals are used, either by foot or by bicycle (Erritzøe, 2002; Erritzøe et al., 2003), with a dog (Hell et al., 2005) or from a motorised vehicle (Lodé, 2000; Joveniaux, 2005). Surveys can be made at various frequencies either by ecologists (Hodson and Snow, 1965) or by patrolling agents employed by motorway companies (Joveniaux, 2005). The

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diversity of the methodologies used and the associated potential biases complicates the comparison of the results obtained.

The most common biases in carcass surveys are the detectability and persistence of carcasses. The detectability of carcasses is the probability that a carcass is encountered by an observer. It may be affected by several factors such as the efficiency or experience of the fieldworker, the size, age or colour of the carcass, among others (Slater, 2002). The persistence of the carcasses is the probability that the carcass is still available for detection on the road between surveys. It may also vary between species (Stewart, 1971; Korhonen and Nurminen, 1987; Antworth et al., 2005), and can depend on scavengers' abundance (Ponce et al., 2010). Detectability and persistence may also vary between survey methodologies. For example, surveys by foot are likely to increase detectabilities (Slater, 2002; Erritzøe et al., 2003), but those conducted by car are more adapted for long distances, which are necessary to study the influence of environmental factors (verges, surrounding landscape, etc.) on carcasses distribution. These sources of bias are a general problem for all types of carcass survey methods, and thus, accounting for them would allow to obtain comparable estimates of absolute numbers of road kills even using different survey methods (e.g. foot, car) on different human made structures (e.g. roads, motorways, powerlines).

A number of studies on wind farms have measured the rate at which carcasses were removed by scavengers in various terrestrial habitats (Page et al., 1990; Morrison, 2002; Young et al., 2003; Johnson et al., 2004; Smallwood, 2007). Other studies have also estimated removal of carcasses by scavengers to quantify mortality due to pesticides or disease outbreaks (Kostecke et al., 2001; Prosser et al., 2008), oil spills (Flint et al., 1999; Ford, 2006; Byrd et al., 2009; Ford and Zafonte, 2009; Munilla et al., 2011), power lines (Flint et al., 2010; Ponce et al., 2010), fences (Stevens et al., 2011) or traffic (Lodé, 2000; Slater, 2002; Antworth et al., 2005; Orlowski, 2005, 2008). However, in the case of traffic surveys, whatever the methodology used during carcass surveys, few studies have taken into account detectability and persistence in mortality estimates, and some animal road mortality estimations are thus potentially underestimated.

The objective of this study is to quantify the major biases that can affect the estimates of avian traffic mortality on motorways to obtain more accurate estimates of bird fatalities throughout all seasons. To do so, we applied capture-mark-recapture methods. We estimated the persistence and encounter probabilities of carcasses using a capture-mark-recapture approach from road killed animals (thereafter wild carcasses) and, for comparison, from experimental carcasses whose exact number and location were known and which were compared to the smallest wild bird order: the Passeriformes. Motorways are known to impact bird populations, mainly because of their high traffic intensity, width of infrastructure and speed of vehicles (Erritzøe et al., 2003). Surveys of bird carcasses were conducted by car and by foot for comparison on several motorways sections in south-western France to answer the following questions: (i) what is the difference in carcass detection between surveys conducted by car and by foot? For surveys conducted by car, do carcass persistence and encounter probabilities vary according to: (ii) bird taxa and the age of the carcass, (iii) the specific body mass and (iv) motorways, seasons and years? Persistence and encounter probability estimates were then used as adjustment factors on the number of bird carcasses counted during this study.

## 2. Materials and methods

### 2.1. Hypotheses tested

First, we hypothesised that the encounter and persistence probabilities were affected by time since death. We expected that older carcasses had a higher probability to persist than fresher ones, since most were crushed on the pavement and then are consumed to a lesser degree by scavengers. Carcasses were thus split into two groups, fresh (less than 3-days old) and old (older than 3 days), and we tested for a group effect on encounter and persistence probabilities.

Second, we hypothesised that the taxonomical status and behaviour could affect encounter and persistence probabilities. Most carcasses found (see Appendix A) belonged to the orders Passeriformes (noted by OP hereafter) and Strigiformes (noted by OS hereafter). Other species were distributed in two about equal in numbers categories and based on their different behaviour, size and numbers detected: diurnal raptors and Corvidae (noted by OR hereafter) representing scavengers, and "*others*" group [Anatidae, Gallinae, Columbidae, and Kingfisher (*Alcedo atthis*); noted by OA hereafter]. A last group (noted by OI hereafter) included birds which could not be determined. We expected that small size taxa, i.e. Passeriformes, showed smaller persistence probability than bigger ones, mostly because they were easier to carry off the pavement for scavengers. We only considered two orders: OP vs. OS, which were the most frequently encountered (see Section 3). The other orders were pooled in one group.

Third, to confirm the previous hypothesis that smaller taxa had less probability to persist than bigger ones, we also analysed persistence and encounter probabilities of carcasses as a function of species-specific body mass and its quadratic effect. Species-specific body mass was taken from the French Muséum National d'Histoire Naturelle (MNHN) database.

Fourth, we hypothesised that three environmental factors may affect encounter and persistence probabilities: year, season, and motorway (mtw). Differences in persistence probabilities between years, seasons and motorways may be due to variations in several factors such as scavenging activity, traffic intensity, bird abundance, climate or a combination of these.

Finally, we used a known number of 2-days old dead chickens (*Gallus domesticus*) (thereafter experimental carcasses) as small as passerines as an experiment to further test the above hypotheses concerning the effect of size, year, season and motorway on persistence probability, and to obtain a better estimation of scavenging activity. Using these experimental carcasses we further hypothesised that persistence probabilities may vary between each count session (fully time-dependent models). We were more particularly interested to estimate persistence probabilities during night time between two sessions (nocturnal inter-sessions) and during daytime between two sessions (diurnal inter-sessions), hypothesising that bird scavengers, all diurnal, were more efficient in detecting carcasses than mammalian scavengers which are mainly nocturnal.

For each of these hypotheses tested, we proceeded gradually starting from a general model, first modelling the encounter probability keeping the persistence probability as complex as in the general model, then modelling persistence probability once the best model was identified for encounter probability.

### 2.2. Capture–recapture analysis

To estimate the carcass persistence and encounter probabilities throughout seasons, years, and motorways, the encounter histories of 512 wild carcasses with 1621 encounters, and of 936 experimental carcasses with 3782 encounters, were analysed. Parameters were estimated by maximum likelihood procedure using capture–recapture analyses, and considering the Cormack–Jolly–Seber model (CJS model) as the umbrella model. The CJS model was initially developed to estimate survival and recapture probabilities from individual mark-recapture data in open populations (Lebreton et al., 1992). This enables to separately estimate survival ($\Phi$) and encounter (or recapture) ($p$) probabilities. In our study, the studied population is the sum of the dead birds found during surveys on the motorway sections; the survival probability parameter used in CJS models must therefore be interpreted as the persistence probability of carcasses. Wild and experimental carcasses may disappear from the road due to destruction by the traffic rolling on, or in the vegetation of verges or be taken away by scavengers (Slater, 2002; Erritzøe, 2002; Erritzøe et al., 2003; Antworth et al., 2005). Each carcass that disappeared during our surveys was searched for on the verge and on the pavement. Since most of the carcasses displaced or flatten out by the traffic were found after careful checking, we assumed that most disappeared carcasses were removed by scavengers. This assumption was based on personal observations of Carrion Crows (*Corvus corone corone*) and Black Kites (*Milvus migrans*) catching carcasses on the pavement, and on the presence of a relatively important number of carnivore carcasses. Note that motorway patrols were informed of our experiment and were asked not to remove carcasses. We estimated factors affecting persistence ($\Phi$) and encounter ($p$) probabilities using data including wild carcasses only. The goodness of fit of the umbrella model (fully time dependent model where persistence and encounter probabilities varied between each encounter occasion) was assessed through contingency tables using U-CARE 2.2 program (Choquet et al., 2005). We then searched for less parameterised models and tested the effect of covariates on persistence and encounter probabilities.

All models were built with Program MARK 5.1 (White and Burnham, 1999) and ranked using the corrected Akaike's Information Criteria (AICc; Hurvich and Tsai, 1989) following Burnham and Anderson (2002). When several models were equally supported in terms of AICc ($\Delta$AICc < 2) we calculated model-averaged estimates of parameters of interest. The importance of variables was evaluated by multi-model inference in the candidate set of models and we compared our models with AICc weights ($w$), selecting the model with the heaviest AICc weight (Burnham and Anderson, 2002). Fully time-dependent models – where persistence and encounter probabilities varied between each encounter session – were not tested afterwards because data were insufficient, and many parameters were either not estimated, or at boundary (i.e. equal to 0 or 1), except when analysing the scavengers' activity using experimental carcasses where data were sufficient.

Since all capture–recapture analyses were performed using the same dataset (except analyses with experimental carcasses), all models' AICc can be directly compared to evaluate the more likely hypothesis.

Our estimates of encounter and persistence probabilities can be used to estimate the number of individuals killed by the traffic for each motorway. At the end of a carcass survey, the total number of individuals killed $y$ days before the survey ($N'$) can be estimated as $N' = N/(p\Phi^y)$, where $N$ is the number of carcasses counted, $p$ the encounter probability, and $\Phi$ the "6 h" (see hereafter) persistence probability.

### 2.3. Study area and carcass survey

#### 2.3.1. Study area

Continuous sections on four motorways were studied by the same observers each season from 2006 to 2008 in south-western France (Table 1, Fig. 1). All motorway sections, totalizing 166 km, were part of the same climatic region where avifauna, landscape and weather conditions were similar. The landscape surrounding the motorways mainly consisted of cultivated areas (cereals, vineyards, and to a lesser extent meadows), woodlands and patches of wetlands and hedged farmland.

#### 2.3.2. Survey methodology

Each motorway section was surveyed once each season (autumn: November–December; winter: February–March; spring: June; summer: August–September) during a 2.5-day period, the surveys totalizing 10 days per year. Each survey included five successive counts (2 counts per day on day 1 and 2, and one count on the morning of day 3) to estimate bird carcass encounter and persistence probabilities. Count sessions were respectively separated by intervals of 6, 18, 6, and 18 h. Therefore the first count session of day $d$ occurred 18 h after the last count session of day $d$-1, no count occurring at night for safety reasons. These differential time intervals between count sessions were directly taken into account in our models. Counts were made by car, driving at 40–50 km h$^{-1}$ on the safe lane, with a driver and an observer recording the carcasses, always with the same observers.

During the last afternoon of each 2.5-day period, a comparative count by foot was realised by the same observers walking on verges nearby the pavement on sub-sections of about 10 km long selected randomly inside the sections surveyed by car. To compare the two survey methodologies, the position on the motorway (left/right lane) and on the lane (medium strip, traffic lanes, safe lane or verge) of each carcass found was registered. We then compared the number of carcasses found on all sub-sections from surveys made by car and by foot.

During each 2.5-day survey, all new wild carcasses found were identified and individually marked by painting a white mark on the pavement besides the carcass. The carcass was located using the motorway Kilometric/Hectometric Point (KP) system (±10 m). At each count session during the surveys we thus recorded the new carcasses (i.e., the animals killed since the previous count), distinguishing them from the carcasses that remained since the previous count, as well as the carcasses not recorded during the previous count. For each wild carcass found we recorded the following information: taxonomical group (species, genus, order or class, depending on the freshness of the carcass), location (KP position), and age (fresh or old). We defined birds as fresh when they still had there eyes and plumage brightness.

During the first count of a 2.5-day survey, a known number of experimental carcasses were regularly dropped each kilometre on the safe lane (i.e., each even km on one way and each uneven km on the other way) to better estimate scavenging activity.

Statistical analyses (except capture-mark-recapture analyses) were performed using R statistical software (version 2.12.1., R Development Core Team, 2004). We compared the numbers of carcasses found between motorways using Kruskal-Wallis tests. $\chi^2$ Tests were used to compare the efficiency of the survey methodologies (by foot vs. by car) for each part of the motorways (medium strip, traffic lanes, safe lane and verges).

## 3. Results

The most frequently encountered groups were Passeriformes (OP: 321 individuals) and Strigiformes (OS: 86), the groups OA (58), OR (33), and OI (14) being less numerous. The most frequently encountered species (see Appendix A) was the Barn Owl (*T. alba*) with a total of 63 dead individuals found. For Passeriformes, the most frequently encountered species was the European Robin (*Erithacus rubecula*) ($n$ = 52 carcasses), the Blackbird (*Turdus merula*) ($n$ = 46 carcasses) and the House Sparrow (*Passer domesticus*) ($n$ = 34 carcasses). There was no significant difference between the four motorways in the number of bird carcasses per km and per annual study period (an annual study period corresponding to four surveys per year and thus to 10 days per year; Kruskal-Wallis test, $H = 5.42$, $df = 3$, $p = 0.14$).

For all species and motorways combined, most carcasses (61% and 75% for surveys by car and by foot respectively) were found on the safe lane (Table 2). For surveys by foot far more carcasses were found on verges ($\chi^2 = 52.261$, $p < 0.001$) and fewer on traffic

**Table 1**
Section length, traffic, years and seasons surveyed on each motorway studied.

| Motorways | A10 | A64 | A837 | A89 |
|---|---|---|---|---|
| Section length (km) | 55 | 40 | 32 | 42 |
| Annual daily traffic mean (veh. day$^{-1}$) | 35000 | 35000 | 8000 | 8000 |
| KP position section | 525–470 | 234–274 | 36–4 | 157–115 |
| Year surveyed | 2007–2008 | 2007 | 2007–2008 | 2008 |
| Season surveyed[a] | 3A, 2W, 2Sp, 1S | 1A, 1W, 1Sp, 1S | 2A, 1W, 1Sp, 1S | 1A, 1 W, 1Sp, 1S |

[a] A = autumn; W = winter; Sp = spring; S = summer.

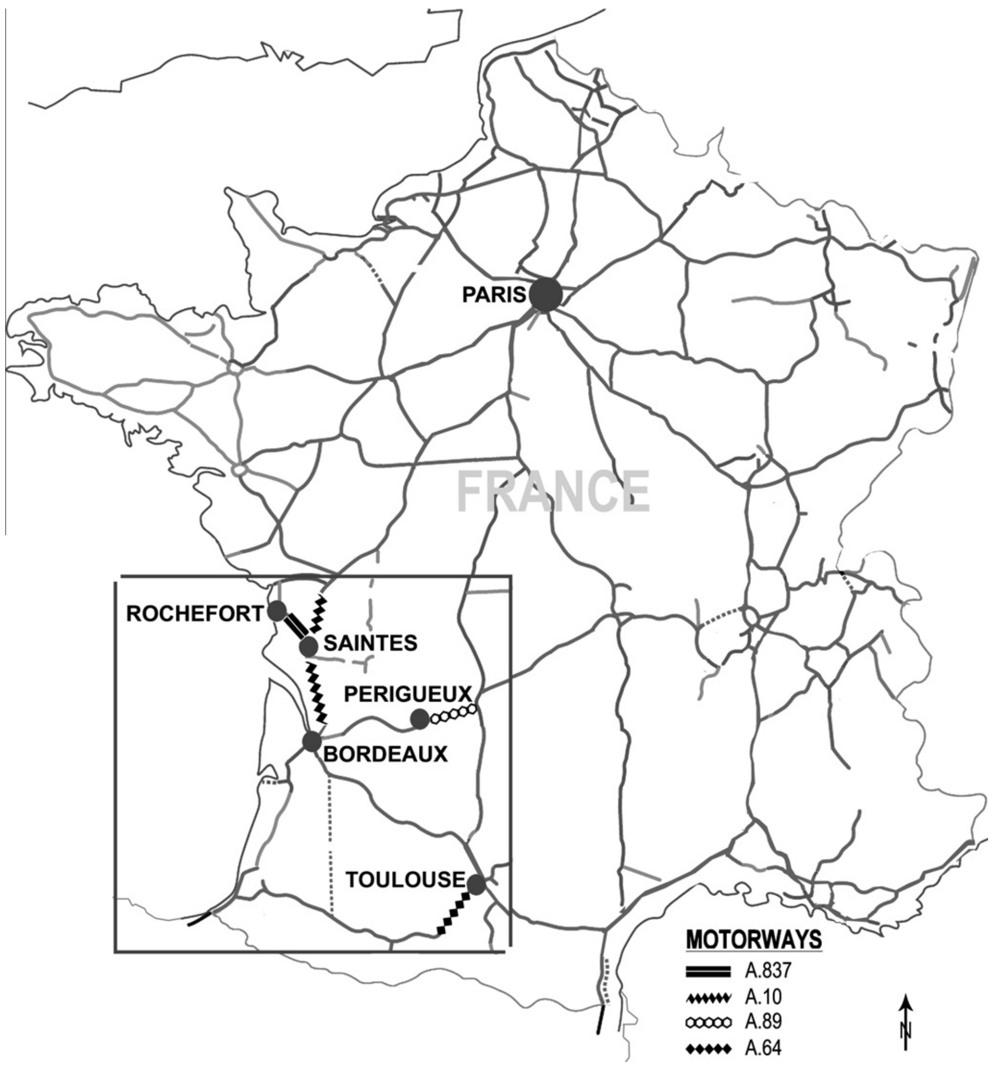


**Fig. 1.** Study area and the A10, A837, A64 and A89 motorways sections studied in south-western France.

lanes ($\chi^2$ = 3.882, $p$ = 0.049) than for surveys by car. No difference between surveys (foot vs. car) was detected in the number of carcasses found on the medium strip ($\chi^2$ = 0.289, $p$ = 0.591) or the safe lane ($\chi^2$ = 1.583, $p$ = 0.208).

### 3.1. Encounter and persistence probabilities of wild carcasses

The CJS model correctly fitted the dataset ($\chi^2$ = 34.358, $df$ = 51, $\hat{c}$ = 0.674, $p$ = 0.964).

#### 3.1.1. Intrinsic factors

There was no evidence for an effect of taxonomic order and age of the carcass on encounter probability (Table 3).

Persistence probabilities differed according to the age of the carcass, and between taxonomic groups (Tables 3 and 4), confirming the first and the second hypotheses. Strigiformes and other orders had higher persistence probabilities (fresh carcasses: 0.983 ± 0.007; old carcasses: 0.999 ± 0.003) than Passeriformes (fresh carcasses: 0.955 ± 0.007; old carcasses: 0.980 ± 0.006). Persistence probabilities were higher for old carcasses than for fresh carcasses. For example, after 10 days staying on the pavement, it can be estimated that the persistence probability of a fresh and old Passeriformes carcass was 0.543 and 0.668 respectively, whereas the persistence probability of a fresh and old carcass of another order was 0.861 and 0.980 respectively, considering that fresh carcasses became old after 4 days and that carcass persistence probability

**Table 2**
Number of bird carcasses counted according to their position on the motorway pavement from 2006 to 2008 on foot and by car, on each of the four motorways (A10, A64, A837 and A89).

| Survey | Position | A10 | A64 | A837 | A89 | Total | Proportion (%) |
|---|---|---|---|---|---|---|---|
| On foot | Medium strip | 7 | 1 | 2 | 1 | 11 | 3.4 |
| | Lanes | 7 | 3 | 1 | 1 | 12 | 3.7 |
| | Safe lane | 80 | 78 | 29 | 14 | 201 | 61.3 |
| | Verge | 46 | 33 | 11 | 14 | 104 | 31.6 |
| By car | Medium strip | 9 | 5 | 2 | 1 | 17 | 7.7 |
| | Lanes | 2 | 24 | 2 | 4 | 32 | 14.5 |
| | Safe lane | 79 | 44 | 29 | 13 | 165 | 75.0 |
| | Verge | 1 | 0 | 3 | 2 | 6 | 2.8 |

**Table 3**
Modelling the effect of the age of the carcasses (A) and taxonomic group (see Section 2) on encounter ($p$) and persistence ($\Phi$) probabilities. g = All sub-populations; OP = group of Passeriformes order only; OS = group of Strigiformes order only; "·" = all parameters constant; ΔAICc = difference in AICc; w = AICc weight; np = number of parameters; Dev = deviance.

| Probability | Model | AICc | ΔAICc | w | np | Dev |
|---|---|---|---|---|---|---|
| Encounter | $\Phi$(A, g) $p$(A, g) | 822.54 | 11.9200 | 0.0019 | 12 | 129.20 |
| | $\Phi$(A, g) $p$(A, other orders in one group, OP) | 818.94 | 8.3237 | 0.0156 | 10 | 121.68 |
| | $\Phi$(A, g) $p$(A, other orders in one group, OS) | 817.59 | 6.9750 | 0.0225 | 9 | 122.37 |
| | $\Phi$(A, g) $p$(A, all orders in one group) | 815.96 | 5.3461 | 0.0508 | 8 | 122.77 |
| | $\Phi$(A, g) $p(\cdot)$ | 813.95 | 3.3363 | 0.1388 | 7 | 122.79 |
| Persistence | $\Phi(\cdot)$ $p(\cdot)$ | 830.68 | 20.0606 | 0.0001 | 2 | 149.60 |
| | $\Phi$(other orders in one group, OS) $p(\cdot)$ | 828.12 | 17.5091 | 0.0001 | 3 | 145.03 |
| | $\Phi$(A, all orders in one group) $p(\cdot)$ | 820.08 | 9.4605 | 0.0065 | 3 | 136.98 |
| | $\Phi$(A, other orders in one group, OS) $p(\cdot)$ | 819.43 | 8.8176 | 0.0090 | 5 | 132.31 |
| | $\Phi$(other orders in one group, OP) $p(\cdot)$ | 818.51 | 7.8979 | 0.0142 | 3 | 135.42 |
| | $\Phi$(A, other orders in one group, OP) $p(\cdot)$ | 810.62 | 0 | 0.7358 | 5 | 122.49 |

**Table 4**
Estimates (± s.e.) of persistence ($\Phi$) and encounter ($p$) probabilities of wild birds carcasses from the selected model (see Table 3: $\Phi$(A, other orders in one group, OP) $p(\cdot)$).

| Probability | Parameters | Estimates (± s.e.) | 95% Confidence interval | |
|---|---|---|---|---|
| | | | Lower | Upper |
| $\Phi$ | Fresh carcasses other orders | 0.983 ± 0.007 | 0.963 | 0.992 |
| | Old carcasses other orders | 0.999 ± 0.003 | 0.919 | 0.999 |
| | Fresh Passeriformes carcasses | 0.955 ± 0.007 | 0.939 | 0.968 |
| | Old Passeriformes carcasses | 0.980 ± 0.006 | 0.965 | 0.989 |
| $p$ | – | 0.957 ± 0.007 | 0.940 | 0.967 |

did not vary in time. Note that we obtained similar results when including experimental carcasses (considered as fresh carcasses) in the data set, with model selection suggesting similar persistence rates between Passeriformes and experimental carcasses, except that the latter were more encountered than other orders (0.973 ± 0.006 and 0.957 ± 0.007 respectively; results not shown).

These results were confirmed by the strong evidence for a quadratic effect of body mass on persistence probability: models where persistence probability was a function of body mass$^2$ were ~22 times more likely than models without such an effect (Table 5), confirming the third hypothesis. Persistence probability was slightly (about 3%) lower for lighter and heavier carcasses. The effect of body mass on encounter probability was less clear.

However, this model had a poorer fit than a model where persistence probability was a function of taxonomic groups and age of carcasses [AICc = 819.75 (Table 5) and AICc = 810.62 (Table 3), respectively].

**Table 5**
Modelling the effect of standardised species-specific body mass (mass) on encounter ($p$) and persistence ($\Phi$) probabilities of wild carcasses. "·" = all parameters constant; ΔAICc = difference in AICc; w = AICc weight; np = number of parameters; Dev = deviance.

| Model | AICc | ΔAICc | w | np | Dev |
|---|---|---|---|---|---|
| $\Phi(\text{mass}^2)$ $p(\cdot)$ | 819.75 | 0 | 0.6221 | 4 | 811.72 |
| $\Phi(\text{mass}^2)$ $p$(mass) | 821.00 | 1.24 | 0.3344 | 5 | 810.95 |
| $\Phi$(mass) $p(\cdot)$ | 826.12 | 6.36 | 0.0259 | 3 | 820.10 |
| $\Phi$(mass) $p$(mass) | 827.71 | 7.95 | 0.0117 | 4 | 819.68 |
| $\Phi(\cdot)$ $p(\cdot)$ | 830.68 | 10.92 | 0.0264 | 2 | 826.67 |
| $\Phi(\cdot)$ $p$ (mass) | 830.96 | 11.20 | 0.0023 | 3 | 824.94 |
| $\Phi(\cdot)$ $p$ $(\text{mass}^2)$ | 832.49 | 12.73 | 0.0011 | 4 | 824.45 |

*3.1.2. Environmental factors*

There was no evidence for an effect of years, seasons and motorways on encounter probability (Table 6).

There was strong evidence for an effect of season on persistence probabilities since models where persistence probability was a function of season were ~4724 more likely than models without such an effect (Table 6), confirming the fourth hypothesis. However, there was very little evidence for an effect of year and motorway on persistence probabilities (evidence ratios of 0.31 and 1.3 respectively). Wild carcass persistence probability was high in summer, intermediate in winter and in autumn, and low in spring (Fig. 2 and Appendix B). Persistence probabilities on motorway A89 tended to be lower than on other motorways (Fig. 2 and Appendix B). However, a model where persistence probability was a function of motorway and season had a larger AICc (813.42, Table 6) than a model where persistence probability was a function of age of the carcass and taxonomic group (810.62, Table 4).

**Table 6**
Modelling the effect of year (year), season (season) and motorway (mtw) on encounter ($p$) and persistence ($\Phi$) probabilities of wild bird carcasses. g = All sub-populations; "·" = all parameters constant; ΔAICc = difference in AICc; w = AICc weight; np = number of parameters; Dev = deviance.

| Probability | Model | AICc | ΔAICc | w | np | Dev |
|---|---|---|---|---|---|---|
| Encounter | $\Phi$(g) $p$(g) | 829.68 | 16.2557 | 0.0002 | 42 | 236.95 |
| | $\Phi$(g) $p$(season) | 823.78 | 10.3543 | 0.0031 | 25 | 267.09 |
| | $\Phi$(g) $p$(year) | 824.70 | 11.2765 | 0.0019 | 24 | 270.10 |
| | $\Phi$(g) $p$(mtw) | 825.28 | 11.8571 | 0.0015 | 25 | 268.59 |
| | $\Phi$(g) $p$(year∗season) | 827.23 | 13.8081 | 0.0006 | 30 | 260.05 |
| | $\Phi$(g) $p$(mtw∗year) | 828.53 | 15.1140 | 0.0003 | 29 | 263.47 |
| | $\Phi$(g) $p$(mtw∗season) | 830.54 | 17.1204 | 0.0001 | 37 | 248.53 |
| | $\Phi$(g) $p$(·) | 820.74 | 7.3141 | 0.0140 | 22 | 270.30 |
| Persistence | $\Phi$(·) $p$(·) | 830.68 | 17.2547 | 0 | 2 | 321.10 |
| | $\Phi$(year) $p$(·) | 831.91 | 18.4896 | 0.0001 | 4 | 318.32 |
| | $\Phi$(mtw) $p$(·) | 832.03 | 18.6132 | 0.0001 | 5 | 316.42 |
| | $\Phi$(season) $p$(·) | 815.29 | 1.8649 | 0.2141 | 5 | 299.67 |
| | $\Phi$(mtw∗year) $p$(·) | 836.29 | 22.8706 | 0 | 9 | 312.58 |
| | $\Phi$(year∗season) $p$(·) | 815.23 | 1.8079 | 0.2203 | 10 | 289.48 |
| | $\Phi$(mtw∗season) $p$(·) | 813.42 | 0 | 0.5439 | 17 | 273.33 |

### 3.2. Encounter and persistence probabilities of experimental carcasses

There was a highly significant effect of the interaction year∗season∗session on the persistence rate of experimental carcasses (Fig. 3 and Appendix C).

The session effect indicated that persistence rate varied between count sessions made during 2.5-day surveys. The persistence rate was higher during the nocturnal inter-sessions compared to the diurnal inter-sessions. Persistence rate varied marginally among the years, being the highest in 2007 and the lowest in 2008 (Fig. 3).

The persistence rate of experimental carcasses varied between seasons. It was clearly the lowest during spring as for wild bird carcasses (see above), and highest persistence rate were observed in summer and autumn (Fig. 3).

### 3.3. Number of individuals killed

The number of Passeriformes and Strigiformes carcasses counted from naïve carrion surveys varied mainly from motorways and seasons. Passeriformes carcasses were at least two times more numerous than Strigiformes (see Appendix D, Fig. D1). More Passeriformes and Strigiformes were killed by the motorway traffic on A64 and A10, and Passeriformes were mainly killed during autumn and Strigiformes during autumn and winter.

Persistence and encounter probabilities can be used to estimate the number of individuals killed by the traffic. For example, with 20 barn owls found dead on A64, including 6 old carcasses and 14 fresh carcasses, using age and group specific persistence and encounter probabilities in Table 4, the number of old carcasses 2.5 days (corresponding to 8 periods of 6 h) before survey was $(6/0.957) \times (0.999)^{-8} = 6.3$ [95% CI: 6.2–12.3], the number of fresh carcasses 2.5 days before the survey was $(14/0.957) \times (0.983)^{-8} = 16.8$ [95% CI: 15.6–19.8], and the total number of Barn Owl carcasses was 23.1 [95% CI: 21.8–32.1]. Similarly, with 26 House Sparrow carcasses counted one can estimate that there were 29.2 carcasses [95% CI: 28.2–30.7) 2.5 days before the survey. Since there were four surveys (one per season), and 2.5 days per survey on an A64 study section of 40 km long in 2007, one can estimate that there were 0.0535 [95% CI: 0.0523–0.059] Barn Owl carcasses $km^{-1}$ $day^{-1}$ and 0.073 [95% CI: 0.0705–0.0768] House Sparrow carcasses $km^{-1}$ $day^{-1}$. This can be extrapolated to 19.5 [95% CI: 19.1–21.5] Barn Owl carcasses $km^{-1}$ $year^{-1}$ and 26.6 [95% CI: 25.7–28.0] House Sparrow carcasses per $km^{-1}$ $year^{-1}$, on a motorway with an annual daily traffic mean of 35 000 vehicles $day^{-1}$.

Such adjustments can be done for the most numerous bird species carcasses using encounter and persistence probabilities issued from the best model [i.e. $\Phi$(A, other orders in one group, OP) $p$(·), Table 4] for all motorways and years (Table 7). These estimates indicate that the underestimation for Strigiformes from naïve carcass surveys may be around 10% for a 2.5 days period, which is not negligible. Such underestimation for Passeriformes from naïve carcass surveys may reach 30% for a 2.5 days period.

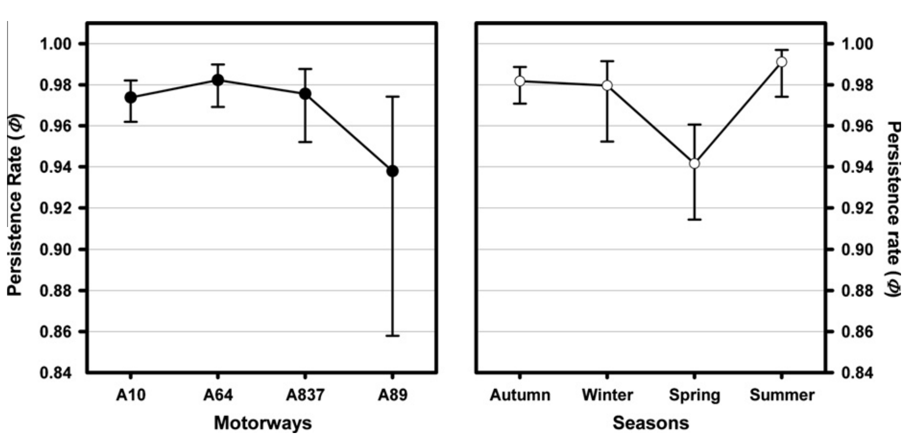


**Fig. 2.** Wild bird carcasses persistence rate ($\Phi$) by motorway and season (error bars indicate ±95% confidence interval) obtained from model $\Phi$(mtw) $p$(·) (left plot) and from model $\Phi$(season) $p$(·) (right plot).

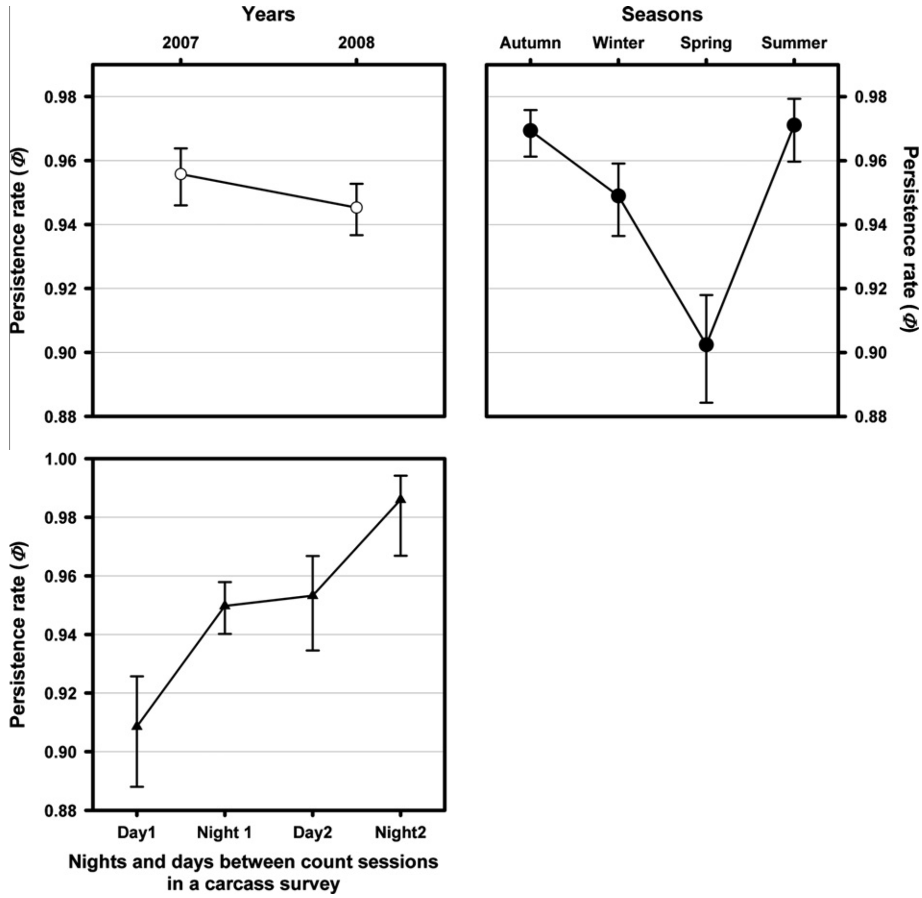


**Fig. 3.** Experimental carcasses persistence rate ($\Phi$) by year, season and inter-session periods (error bars indicate ±95% confidence interval) from model $\Phi$(year) $p$(g) (upper left plot), $\Phi$(season) $p$(g) (upper right plot) and from model $\Phi$(t) $p$(g) (lower plot).

## 4. Discussion

### *4.1. Survey methodology*

In our study, as in previous European studies (Bourquin, 1983; Massemin and Zorn, 1998; Massemin et al., 1998; Fajardo, 2001; Ramsden, 2003), the road killed bird species most frequently found was the Barn Owl. Several species of passerines were also frequently killed including the European Robin, the Blackbird and the House Sparrow.

Surveys by foot seemed more efficient (328 bird carcasses recorded) than by car (220 bird carcasses recorded). Some authors have suggested that surveys of carcasses by foot were more accurate than surveys by car (Slater, 2002; Erritzøe, 2002; Erritzøe et al., 2003). Our results suggest that this was the case for verges, but also that surveys by car were more efficient for lanes. In our study the numbers of bird carcasses detected on foot on safe lanes (where most carcasses were found) and on medium strips were similar to the numbers counted by car. This difference in efficiency for lanes and marginally for the medium strip may be due to the driver who also recorded carcasses and had a closer view of the lanes and the medium strip than the accompanying person. Two persons recording carcasses on medium strip, lanes and safe lanes by car were thus as efficient (214 carcasses found, Table 2) as only

**Table 7**
Annual mean number of old, fresh and total of carcasses ($N$) of the most numerous species found dead, counted on 10 days of surveys during a year on motorways A10, A64, A837 and A89 (totalizing 166 km); $N'$ number of carcasses found on a year ($N' = N/(p * \Phi^8)$) and $N''$ of carcasses per km and per year ($N'' = (N'/1660) * 365$) both adjusted with corresponding carcass persistence $\Phi$ and encounter $p$ probabilities from the selected model (see Table 4: $\Phi$(A, other orders in one group, OP) $p(\cdot)$).

| Species | Number of carcasses | | | Adjusted number of carcasses | |
|---|---|---|---|---|---|
| | Fresh carc | Old carc | All carc ($N$) | $N'$ carc | $N''$ carc km$^{-1}$ year$^{-1}$ |
| *Tyto alba* | 31.4 | 12.8 | 44.2 | 51.117 | 11.24 |
| *Strix aluco* | 4 | 5.1 | 9.1 | 10.166 | 2.24 |
| *Erithacus rubecula* | 30.7 | 8.2 | 38.9 | 56.437 | 12.41 |
| *Turdus merula* | 13.9 | 16.8 | 30.7 | 41.627 | 9.15 |
| *Passer domesticus* | 19 | 11.8 | 30.8 | 43.189 | 9.5 |
| *Sylvia atricapilla* | 15.1 | 1.3 | 16.4 | 24.402 | 5.37 |
| *Turdus philomelos* | 7.5 | 2.3 | 9.8 | 14.152 | 3.11 |
| *Parus major* | 7.9 | 0.5 | 8.4 | 12.545 | 2.76 |
| *Parus caeruleus* | 7.7 | 0 | 7.7 | 11.629 | 2.56 |
| *Troglodytes troglodytes* | 4.8 | 2.1 | 6.9 | 9.829 | 2.16 |

**Table A1**
Species killed and numbers of dead individuals detected for each motorway sections for all seasons and years.

| Species killed | | Motorways | | | | |
|---|---|---|---|---|---|---|
| Latin name | Name | A10 | A64 | A837 | A89 | Total |
| | Passeriformes sp. | 37 | 24 | 8 | 2 | 71 |
| *Tyto alba* | Barn Owl | 36 | 20 | 4 | 3 | 63 |
| *Erithacus rubecula* | European Robin | 25 | 13 | 12 | 2 | 52 |
| *Turdus merula* | Blackbird | 25 | 6 | 14 | 1 | 46 |
| *Passer domesticus* | House Sparrow | 6 | 26 | 1 | 1 | 34 |
| *Phasianus colchicus* | Pheasant | 14 | 6 | 5 | | 25 |
| *Sylvia atricapilla* | Blackcap | 6 | 10 | 2 | 1 | 19 |
| *Parus major* | Great Tit | 10 | 1 | 3 | | 14 |
| *Turdus philomelos* | Song Thrush | 8 | 3 | 1 | 2 | 14 |
| | Bird sp. | 7 | 5 | 2 | | 14 |
| *Strix aluco* | Towny Owl | 7 | 2 | 2 | 2 | 13 |
| *Falco tinnunculus* | Kestrel | 7 | 2 | 2 | | 11 |
| *Parus caeruleus* | Blue Tit | 3 | 2 | 4 | 1 | 10 |
| *Troglodytes troglodytes* | Wren | 5 | 2 | 3 | | 10 |
| *Fringilla coelebs* | Chaffinch | 5 | | 2 | | 7 |
| | Owl sp. | 4 | 2 | | | 6 |
| | Raptor sp. | 3 | 1 | | 2 | 6 |
| *Alcedo atthis* | Kingfisher | 2 | 2 | 1 | | 5 |
| *Buteo buteo* | Buzzard | 3 | 2 | | | 5 |
| *Corvus corone corone* | Carrion Crow | 4 | 1 | | | 5 |
| *Motacilla alba* | White Wagtail | | 3 | 1 | 1 | 5 |
| | Falcon sp. | 3 | 2 | | | 5 |
| *Columba palumbus* | Wood Pigeon | 3 | | | 1 | 4 |
| *Emberiza citrinella* | Yellowhammer | 2 | | 2 | | 4 |
| *Garrulus glandarius* | Jay | 3 | 1 | | | 4 |
| *Prunella modularis* | Dunnock | 3 | 1 | | | 4 |
| *Aegithalos caudatus* | Long-tailed Tit | 1 | | 2 | | 3 |
| *Alectoris rufa* | Red-legged Partridge | 1 | 1 | 1 | | 3 |
| *Asio otus* | Long-eared Owl | | 2 | 1 | | 3 |
| *Carduelis carduelis* | Goldfinch | | 1 | 1 | 1 | 3 |
| *Hippolais polyglotta* | Melodious Warbler | | | 2 | 1 | 3 |
| *Hirundo rustica* | Swallow | | 2 | | 1 | 3 |
| *Pylloscopus collybita* | Chiffchaff | 2 | 1 | | | 3 |
| *Regulus regulus* | Goldcrest | 2 | | 1 | | 3 |
| | Partridge sp. | 3 | | | | 3 |
| | Pigeon sp. | | 1 | 2 | | 3 |
| *Dendrocopos major* | Great Spotted Woodpecker | 2 | | | | 2 |
| *Regulus ignicapillus* | Firecrest | 1 | | 1 | | 2 |
| *Streptopelia decaocto* | Collared Dove | | 1 | 1 | | 2 |
| *Alauda sp.* | Lark | | 1 | | | 1 |
| *Anas platyrhynchos* | Mallard | 1 | | | | 1 |
| *Anthus pratensis* | Meadow Pipit | 1 | | | | 1 |
| *Apus apus* | Swift | | | 1 | | 1 |
| *Athene noctua* | Little Owl | | | | 1 | 1 |
| *Cisticola juncidis* | Fan-tailed Warbler | | | 1 | | 1 |
| *Emberiza cirlus* | Cirl Bunting | | 1 | | | 1 |
| *Ficedula hypoleuca* | Pied Flycatcher | 1 | | | | 1 |
| *Musicapa striata* | Spotted Flycatcher | 1 | | | | 1 |
| *Phoenicurus ochruros* | Black Redstart | | 1 | | | 1 |
| *Pica pica* | Magpie | | 1 | | | 1 |
| *Saxicola torquata* | Whinchat | | | | 1 | 1 |
| *Scolopax rusticola* | Woodcock | 1 | | | | 1 |
| *Streptopelia sp.* | Dove | | 1 | | | 1 |
| *Streptopelia turtur* | Turtle Dove | 1 | | | | 1 |
| *Sturnus vulgaris* | Starling | 1 | | | | 1 |
| *Upupa epops* | Hoopoe | | 1 | | | 1 |
| | Columbidae sp. | | | 1 | | 1 |
| | Warbler sp. | | | 1 | | 1 |
| | Gallinae sp. | | | | 1 | 1 |
| Sum | | 250 | 152 | 85 | 25 | 512 |

one person counting by foot (224 carcasses found, Table 2), except for verges (respectively 6 and 104 bird carcasses found, Table 2). However, surveys by foot on verges are time consuming and limit the length of linear sections of motorways that can be surveyed. Moreover, the height of the vegetation on verges, especially during spring and summer when they are generally not mown in order to protect fauna and flora during the breeding period, may decrease the detectability of carcasses on verges. We therefore suggest that surveys by car must be complemented with surveys by foot on sampled sub-sections to estimate the quantity of carcasses missed on the verges during car surveys.

### 4.2. Carrion persistence and encounter probabilities

#### 4.2.1. Wild carcasses

There was a significant difference in carcass persistence between Strigiformes and Passeriformes, carcass persistence probability for Strigiformes being higher than for Passeriformes. This

**Table B1**
Estimates (± s.e.) of persistence ($\Phi$) and encounter ($p$) probabilities of wild birds carcasses from the selected model $\Phi$(mtw∗season) $p(\cdot)$.

| Probability | Parameters | | Estimates (± s.e.) | 95% Confidence interval | |
|---|---|---|---|---|---|
| | Motorways | Seasons | | Lower | Upper. |
| $\Phi$ | A10 | Autumn | 0.975 ± 0.007 | 0.958 | 0.985 |
| | A10 | Winter | 1.000 ± 0.000 | 0.999 | 1.000 |
| | A10 | Spring | 0.949 ± 0.014 | 0.913 | 0.970 |
| | A10 | Summer | 1.000 ± 0.000 | 0.999 | 1.000 |
| | A64 | Autumn | 0.997 ± 0.003 | 0.977 | 1.000 |
| | A64 | Winter | 0.976 ± 0.018 | 0.900 | 0.994 |
| | A64 | Spring | 0.924 ± 0.028 | 0.849 | 0.964 |
| | A64 | Summer | 0.986 ± 0.008 | 0.956 | 0.996 |
| | A837 | Autumn | 0.966 ± 0.017 | 0.912 | 0.987 |
| | A837 | Winter | 0.974 ± 0.026 | 0.836 | 0.996 |
| | A837 | Spring | 0.940 ± 0.034 | 0.830 | 0.981 |
| | A837 | Summer | 1.000 ± 0.000 | 0.999 | 1.000 |
| | A89 | Winter | 0.806 ± 0.093 | 0.564 | 0.930 |
| | A89 | Spring | 0.929 ± 0.069 | 0.628 | 0.990 |
| | A89 | Summer | 0.975 ± 0.026 | 0.827 | 0.997 |
| | A89 | Autumn | 1.000 ± 0.000 | 0.999 | 1.000 |
| $p$ | | – | 0.957 ± 0.007 | 0.941 | 0.968 |

**Table C1**
Modelling the effect of year (year), season (season) and motorway (mtw) on each encounter session on encounter ($p$) and persistence ($\Phi$) probabilities of experimental bird carcasses. g = All sub-populations; t = time (encounter session); ΔAICc = difference in AICc; w = AICc weight; np = number of parameters; Dev = deviance.

| Probability | Model | ΔAICc | w | np | Dev |
|---|---|---|---|---|---|
| Encounter | {$\Phi$(g∗t) $p$(g)} | 0.0000 | 0.5836 | 105 | 106.32 |
| | {$\Phi$(g∗t) $p$(year∗season)} | 1.1432 | 0.3295 | 93 | 133.06 |
| | {$\Phi$(g∗t) $p$(season)} | 5.2546 | 0.0422 | 88 | 147.78 |
| | {$\Phi$(g∗t) $p$(mtw∗year)} | 5.3346 | 0.0034 | 92 | 139.37 |
| | {$\Phi$(g∗t) $p$(year} | 10.2703 | 0.0003 | 87 | 154.91 |
| | {$\Phi$(g∗t) $p$(season∗t)} | 15.0861 | 0.0002 | 100 | 132.10 |
| | {$\Phi$(g∗t) $p$(mtw∗season)} | 15.6266 | 0.0002 | 100 | 132.64 |
| | {$\Phi$(g∗t) $p$(year∗t)} | 16.2522 | 0.0000 | 96 | 141.79 |
| | {$\Phi$(g∗t) $p$(year∗season∗t)} | 23.2941 | 0.0000 | 120 | 97.34 |
| | {$\Phi$(g∗t) $p$(mtw∗year∗t)} | 24.8082 | 0.0000 | 116 | 107.49 |
| | {$\Phi$(g∗t) $p$(mtw)} | 34.7414 | 0.0000 | 88 | 177.26 |
| | {$\Phi$(g∗t) $p$(t)} | 38.9974 | 0.0000 | 88 | 181.52 |
| | {$\Phi$(g∗t) $p(\cdot)$} | 41.0627 | 0.0000 | 85 | 189.93 |
| | {$\Phi$(g∗t) $p$(mtw∗t)} | 43.5459 | 0.0000 | 100 | 160.56 |
| | {$\Phi$(g∗t) $p$(g∗t)} | 79.1609 | 0.0000 | 168 | 47.72 |
| | {$\Phi$(g∗t) $p$(mtw∗season∗t)} | 79.8661 | 0.0000 | 148 | 92.79 |
| Persistence | $\Phi$(year∗season∗t) $p$(g) | 0.0000 | 0.7589 | 57 | 164.51 |
| | $\Phi$(season ∗t) $p$(g) | 2.2938 | 0.2411 | 37 | 208.04 |
| | $\Phi$(mtw∗season∗t) $p$(g) | 24.2632 | 0.0000 | 85 | 130.13 |
| | $\Phi$(year ∗season) $p$(g) | 42.5964 | 0.0000 | 30 | 262.65 |
| | $\Phi$(mtw∗season) $p$(g) | 44.9576 | 0.0000 | 37 | 250.75 |
| | $\Phi$(g) $p$(g) | 47.9262 | 0.0000 | 42 | 243.41 |
| | $\Phi$(season) $p$(g) | 49.4363 | 0.0000 | 25 | 279.67 |
| | $\Phi$(year∗t) $p$(g) | 64.9533 | 0.0000 | 33 | 278.88 |
| | $\Phi$(mtw∗t) $p$(g) | 68.7620 | 0.0000 | 37 | 274.51 |
| | $\Phi$(t) $p$(g) | 71.3803 | 0.0000 | 25 | 301.61 |
| | $\Phi$(mtw∗year∗t) $p$(g) | 84.8495 | 0.0000 | 53 | 257.65 |
| | $\Phi$(mtw) $p$(g) | 120.4782 | 0.0000 | 25 | 350.71 |
| | $\Phi$(year) $p$(g) | 120.9014 | 0.0000 | 24 | 353.17 |
| | $\Phi(\cdot)$ $p$(g) | 123.3860 | 0.0000 | 22 | 359.71 |
| | $\Phi$(mtw∗year) $p$(g) | 123.6931 | 0.0000 | 29 | 345.78 |

was coherent with the species-specific body mass effect on carcass persistence probability. The quadratic effect of body mass on persistence probability may be due to scavengers removing the heaviest carcasses from the pavement, which cannot be eaten rapidly. Smallest carcasses may have been pushed away by the wind generated by traffic and remained hidden in vegetation on the edge of the pavement. Passerine carcasses are thus underestimated compared to the other orders during surveys because of their lower persistence probability. These findings are coherent with those obtained in previous studies showing that small birds disappeared after 1.2 ± 0.4 days, and larger birds after 2.1 ± 0.7 days (Korhonen and Nurminen, 1987), although our results show longer persistence possibly due to the fact that Korhonen and Nurminen (1987) conducted their study in spring and summer when persistence is lower. Similarly, Ponce et al. (2010) observed under power lines in Spain that 85.7% of very small carcasses disappeared within 2 days, while only 78.8% of medium and 73.6% of large corpses disappeared within the same period. This size-related disappearance rate was described in other studies on motorways (Erritzøe, 2002; Erritzøe et al., 2003), as well as in surveys on carcasses after oil spills (Flint et al., 1999; Ford and Zafonte, 2009). Passeriformes may also be underestimated because of their lower detection probability (Erritzøe, 2002; Erritzøe et al., 2003), although we did not detected such an effect in our study.

The age of the carcass affected equally the persistence probability of all groups. Old carcasses were more persistent than fresh ones. It might be more difficult for scavengers to use old carcasses that are distorted, less recognisable, and more or less encrusted in the road surface. The age effect on carcasses persistence was also observed in another study, varying between seasons (Flint et al., 2010).

Persistence probabilities of wild carcasses (but not their encounter probabilities) differed between seasons, and was lower in spring compared to other seasons. Seasonal variations in persistence probabilities of carcasses were notably noticed in the case of wind turbine studies and disease surveillance (Young et al., 2003; Fiedler, 2004; Prosser et al., 2008; Flint et al., 2010). However, no seasonal variation in carcasses persistence was observed in a study on power lines in Spain (Ponce et al., 2010), suggesting that the scavenging activity may vary with latitude but also among local environmental characteristics. Because of seasonal variations in persistence and/or encounter probabilities, naïve estimates of mortality from surveys conducted any time during the year may underestimate the number of road casualties, and consequently the potential impact on population dynamics. In our study, since carcass persistence probability was smaller in spring, naïve estimates of mortality in spring are probably biased low.

Estimates of persistence probability from wild carcasses suggest that scavenger activity was maximal during spring. Scavenging activity during the day was mainly due to Magpies (*Pica pica*), Carrion Crows (*C. corone corone*), Common Buzzards (*Buteo buteo*) and Black kites (*M. migrans*) (Guinard, pers. obs.), as also noted in other studies (Mason and MacDonald, 1995; Slater, 2002; Erritzøe, 2002; Erritzøe et al., 2003). During the night, scavengers were

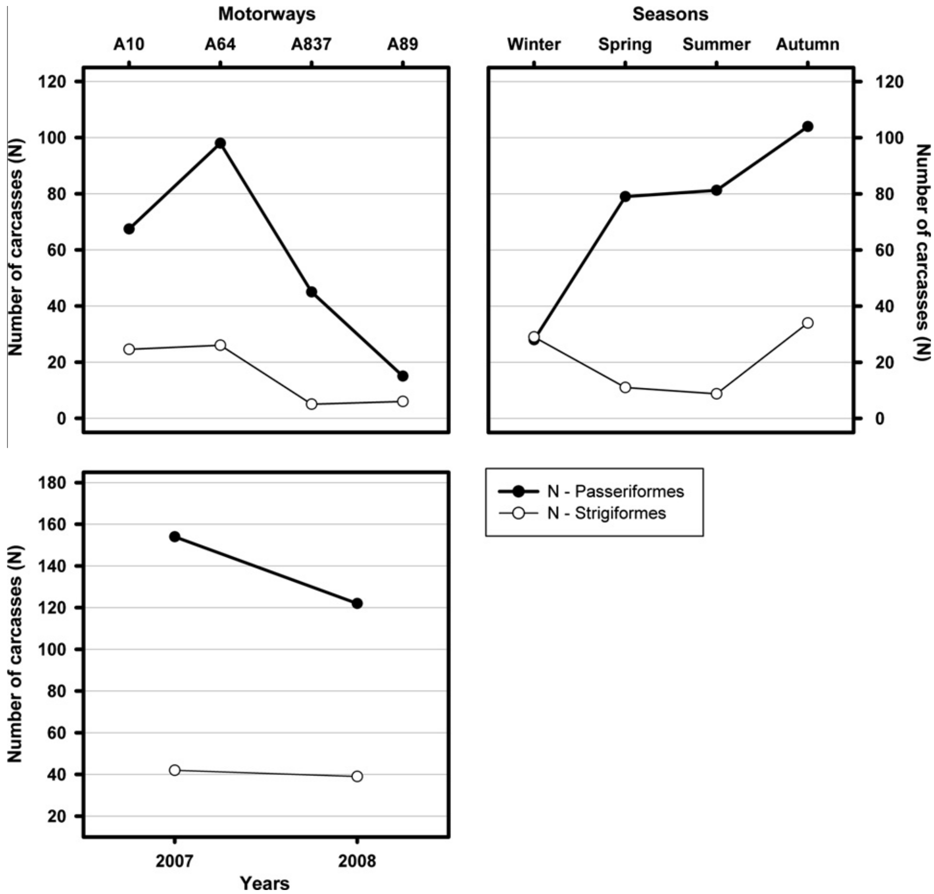


**Fig. D1.** Numbers *N* of Passeriformes and Strigiformes carcasses found on the four motorways, by season and year from all naïve carcass surveys on 2007 and 2008.

probably mammals such as those found dead in the study area during count sessions from 2006 to 2009 (Guinard, unpublished results): Stone Marten (*Martes foina*) ($n = 12$ carcasses), Pine Marten (*M. martes*) ($n = 4$ carcasses), European Polecat (*Mustela putorius*) ($n = 19$ carcasses), Least Weasel (*Mustela nivalis*) ($n = 9$ carcasses), Fox (*Vulpes vulpes*) ($n = 9$ carcasses), Cat (*Felis catus*) ($n = 4$ carcasses), Common Genet (*Genetta genetta*) ($n = 2$ carcasses) or Badger (*Meles meles*) ($n = 2$ carcasses). These species, also mentioned in other studies, are mainly nocturnal (Howes, 1977; Slater, 2002; Erritzøe, 2002; Erritzøe et al., 2003; Wilson and Mittermeier, 2009).

The peak of scavenging activity coincided with the period during which both mammalian and avian scavengers reared their youngs (Prosser et al., 2008). The lowest scavengers' activity period was at the end of summer and in autumn, increasing slightly in winter. During winter, mammalian scavengers are probably less active (Wilson and Mittermeier, 2009) but the food shortage during that season may force bird scavengers to increase their foraging effort. As previously shown (Selva et al., 2003, 2005; Selva and Fortuna, 2007), carrion supply is more predictable in winter, and this represents a crucial food resource for scavengers in that season, even if the quantity of carcasses during winter is low compared to the other seasons (Guinard, unpublished data).

Passeriformes carcasses were more numerous than Strigiformes carcasses as previously observed (Hodson, 1960; Hodson and Snow, 1965; Erritzøe et al., 2003). The peak in Passeriformes carcass numbers (in autumn) was late compared to previous studies which generally show a peak in summer (Erritzøe et al., 2003). The peak in Strigiformes carcass numbers was in autumn and winter as found in previous studies (Massemin and Zorn, 1998), but the seasonal effect was less marked than for Passerines.

Birds were more killed on A10 and A64, probably because the traffic intensity was higher in these motorways compared to A837 and A89 (35 000 veh. day$^{-1}$ vs. 8000 veh. day$^{-1}$), confirming also results from some other studies (Erritzøe et al., 2003). The mortality rates due to traffic found in our study (Table 7) are within the same order of magnitude than those found in other studies: 10.8 House Sparrow carcasses km$^{-1}$ year$^{-1}$ (Hell et al., 2005) and 10.9 House Sparrow carcasses km$^{-1}$ year$^{-1}$ (Orlowski, 2008).

Because the factors expected to affect encounter and persistence probabilities were tested in different analyses, some of the results of a given analysis may be confounded by the factors not considered (e.g. the analysis addressing the effect of year, season and motorway might be confounded by the body size of the birds found). Although there was a limitation on the number of groups we could define to test all these aspects, plots of the number of carcasses found for Passeriformes and Strigiformes as a function of year, season or motorway (see Appendix D, Fig. D1) do not suggest strong confounding effects.

Finally, it should be noted that our estimates of encounter probability were obtained from carcasses immediately positioned and marked after their discovery. These carcasses may have been easier to detect during the following encounter occasions of a same survey. Therefore our encounter probabilities may be overestimated, which implies that the number of carcasses may still be underestimated. Future studies may estimate encounter probability without marking carcasses or use less conspicuous marks to obtain less biased estimates.

*4.2.2. Experimental carcasses*

Two-day-old dead chickens, used in this study to measure scavenging activity, are known to be attractive baits (Slater, 2002), which could generate overestimation of the scavenging activity. However, persistence probabilities of Passeriformes (wild carcasses) and experimental carcasses did not differ, indicating that 2-day-old dead chickens may be adequate to estimate scavenger activity in our study area. Experimental carcasses were more encountered than wild carcasses probably because they were disposed more regularly and therefore easier to detect.

Interannual differences in persistence rate of experimental carcasses and so in scavenging activity were not observed on motorways in previous studies. Carcass availability is known to influence scavengers density and activity (Knight et al., 1995; Roen and Yahner, 2005; Rösner and Selva, 2005; Margalida et al., 2007), notably on roads and motorways (Bautista et al., 2004; Lambertucci et al., 2009). The number of carcasses varying annually (Joveniaux, 2005), as well as densities of scavengers, we may expect interannual variations in persistence rates of carcasses. A year with a poor availability of carcasses because of a bad breeding season for example, would increase competition among scavengers which could result in a lower persistence probability.

Persistence rates during diurnal periods were lower than those of nocturnal periods. As described above, diurnal scavengers were mainly birds (Guinard, pers. obs.; Slater, 2002; Erritzøe, 2002; Erritzøe et al., 2003) and their foraging activity on carcasses was probably higher than the one of nocturnal mammalian scavengers (Antworth et al., 2005). Birds are more efficient in finding carcasses because they fly and can detect them farther than a ground foraging mammal (Rösner and Selva, 2005). Daily variations in persistence rates differed between seasons and years. Annual and seasonal variations may be due for example to the variation in scavenger abundance and/or foraging efforts. Cold winters in certain years could push scavengers to forage more on motorways because of a global lack of food.

One may suggest that by placing experimental carcasses at regular intervals, is it possible that we saturated the local scavenger community such that they were less likely to remove any given carcass, artificially affecting carcass persistence probabilities. However, mean densities of wild carcasses (all vertebrates included) were 0.44 carcass. $km^{-1}$ for A89, 1.29 for A837, 1.45 for A10 and 2.35 for A64 (Guinard, unpublished results). Except for A89, densities in wild carcasses were higher than those in experimental carcasses (1 chicken $km^{-1}$ per survey). We can thus exclude the possibility of saturating the local scavenger community with experimental carcasses.

## 5. Conclusion

Many factors must be taken into account in carcass surveys to obtain unbiased abundance estimates. Taking into account encounter and persistence probabilities of carcasses will permit to obtain more concise mortality estimates in animal populations. The high seasonal variations in scavenging activity suggests that this factor must be taken into account in carcass surveys on motorways, scavengers activity having a strong effect on mortality estimates and especially on those concerning Passeriformes. For example, a 10% and indeed 30% underestimation in traffic mortality rate of an endangered animal population, which could potentially results from a low encounter and/or persistence probability, could have significant implications in population dynamic modelling and potentially on proposed management strategies. To do so, surveys of carcasses on motorways should be done at least once per season, and it is necessary to perform multiple counts ($\geqslant 3$) in a survey to measure persistence and encounter probabilities.

If possible, weekly (or at least monthly) carcass surveys (with trained persons to avoid encounter bias) should also be conducted on several motorways during several years for a better understanding of the annual variations in carcass persistence rate. In the light of our results we also suggest to realise surveys by car on motorway sections longer than 15–20 km each, and to perform surveys by foot on shorter sections. Indeed, to study the effects of verges (vegetation), road profile (buried, raised, level and mixed) and neighbouring landscape on road mortalities with the aim of proposing mitigation measures, we need long distances to be sampled for inference. Given that we found clear differences between surveys by foot and by car and that surveys by foot cannot be managed on distances longer than 20 km, we recommend a double sampling approach where short surveys by foot are used to correct estimates obtained from surveys by car made on long distances. As small carcasses disappear faster than bigger one, a measurement of size and "age" distribution of the carcass population should be included in traffic mortality analyses. Combining such estimations with bird population sampling in neighbouring areas, recording habitat variables such as motorway profile and vegetation structure and traffic measurement, could contribute to explain, predict, and eventually to mitigate the mortality of wild animals due to motorways. Finally, using experimental carcasses such as 2-day-old chickens may be a valuable technique to measure scavenging activity.

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## Appendix A

See Table A1.

## Appendix B

See Table B1.

## Appendix C

See Table C1.

## Appendix D

See Fig. D1.

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