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Factors affecting road mortality in birds

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Several hundred million birds are killed on an annual basis worldwide due to collisions with vehicles. While this is well documented, less data exists on specific factors affecting the number of roadkills. I examined roadkill patterns while driving a car during a 44-month period (617 days, twice daily) along a 25 km stretch of road in the middle of Norway. In total, 121 roadkills were detected during that period. I used information on body mass, speed limit, vegetation in the vicinity, flight distance, abundance of birds in the surrounding environment and number of birds sitting on the road in order to elucidate their effects on the number of roadkills and susceptibility to become a roadkill for 30 different bird species/groups of species. Roadkill numbers were highest in summer, and at certain parts of the road the mortality rate was much higher than in others. Heavier birds flew away from the approaching car at a longer distance than smaller birds, but they still had a relatively high mortality rate. Birds known to search for food on roads were more likely than other birds to become roadkill. Birds observed on the road explained a significant amount of the variation in roadkills between the species, in contrast to the abundance of birds in the surroundings. Fewer birds than expected were found where the speed limit was highest, and roadkilled birds were visible for a longer period when their body mass was higher.

1. Introduction

Roads constitute a substantial part of our environment. In the Netherlands and the United States the density of roads is 1.5 km and 1.2 km per km^2 respectively (Forman & Alexander 1998). However, the negative effects of roads on wildlife extend far beyond the road lanes. Bird densities are reduced as far as 1–3.5 km away from the roads (Reijnen & Foppen 1995, Reijnen *et al.* 1995, Reijnen *et al.* 1996, Forman *et al.* 2002, Benitez-Lopez *et al.* 2010). Public roads directly affect 15–20% of the land area in the United States (Forman & Alexander 1998, Forman 2000). Some of the well-known negative effects of roads on wildlife include population fragmentation, habitat loss, pollution, poisoning, noise, and collisions with vehicles (Erritzoe *et al.* 2003, Peris & Pescador 2004, Fahrig & Rytwinski 2009, Francis *et al.* 2009, Goodwin & Shriver 2011, Kociolek *et al.* 2011, Summers *et al.* 2011, McLaughlin & Kunc 2013).

Some species of birds such as scavenging raptors (Forman 2000, Dean & Milton 2003), corvids (Mumme *et al.* 2000, Dean & Milton 2003, Husby & Husby 2014), and some insect eaters like White Wagtails (*Motacilla alba*; Erritzoe *et al.* 2003, Husby & Husby 2014) are attracted to roads where they can find food. Some species, such as Red-backed Shrike (*Lanius collurio*), frequently use shrubs, trees and power lines as perches for hunting on bare soil, cultivated margins and road surfaces, and find this habitat attractive for breeding (Ceresa *et al.* 2012, Morelli 2013). Other factors, e.g., reduced predation pressures, a warm surface assists in conserving metabolic energy and street lights prolonging diurnal activity, make roads attractive to some birds (Morelli *et al.* 2014). Birds that are attracted to roads are often frightened off the ground by approaching cars, and behavioral mistakes can be fatal (Husby & Husby 2014).

Collisions with cars kill a large number of birds every year. In Canada the annual number of roadkills is estimated to be 13.8 million (Bishop & Brogan 2013) and in the United States about 80 million (Forman & Alexander 1998) or up to 89–340 million (Loss *et al.* 2014). In some European countries the estimated number of birds killed each year has been 27 million in England, 653,000 in the Netherlands, 9.4 million in Germany, 1.1 million in Denmark, 8.5 million in Sweden, and more than 7 million in Bulgaria (Erritzoe *et al.* 2003). Roadkills may also have both positive and negative effects on the quality of the avian populations. Birds infested by blood parasites seem to suffer a higher mortality rate due to collision with vehicles, compared to uninfected individuals (Valkiunas 1998, Møller *et al.* 2011). Another study showed that roadkilled birds had better nutritional health than birds of the same species killed by raptors (Bujoczek *et al.* 2011). Interestingly, most studies find that roadkilled birds seem to have been in good condition before they were killed (Erritzoe *et al.* 2003).

The roadkill rate is sometimes found to increase with traffic volume (Gunson *et al.* 2011), while at other times it does not (Clevenger *et al.* 2003). The speed limit is found to positively correlate with the roadkill rate (Chambers *et al.* 2010). In addition, some areas have more frequent collisions with wildlife than other areas (Ramp *et al.* 2005, Gomes *et al.* 2009). It is crucial to detect such hotspots in order to make an effort to reduce the problem. Mitigation measures to reduce roadkill have been only partly successful (Trombulak & Frissell 2000) and continued action is needed in order to change the ecological impacts of roads (Karlson *et al.* 2014).

These studies underline the importance of understanding how road characteristics and road surroundings influence roadkill numbers. The aim of this paper is therefore to examine how the number of roadkilled birds changes during the year and on different parts of the road, as well as to examine how environmental and ecological factors affect the number of roadkills and the susceptibility to become a roadkill in different species. In addition, this text also considers whether the frequency of roadkilled birds is positively correlated to their body mass, as has been argued in previous studies (Guinard *et al.* 2012). It is the hope that these insights will be valuable for road planners and policy makers when mitigating the negative effects of transportation on surrounding wildlife (Coffin 2007, Balkenhol & Waits 2009).

2. Material and methods

2.1. Roadkills

I searched the road and roadsides for roadkilled birds while driving a car along the same 25 km stretch of road in the middle part of Norway (63°42' N, 11°09' E), in a variable landscape consisting of farmland, forests, and some minor stretches with cliffs and one small city (9,200 inhabitants). Observations were typically made in the morning and in the afternoon, twice per day for a total of 617 days. The investigation period lasted 44 months over five years (August–December, 1996; January–August, 1997; June–December, 2003, and January–December in 2005 and 2006). If I observed a roadkill, I drove more slowly or eventually stopped if the traffic situation allowed. Since this was not always possible, some of the observations are recorded as bird families and not individual species.

The main road (E6) comprising 20.0 km of the distance is 7–8 m wide. Minor asphalted roads comprising 4.7 km are 5–6 m wide. The route also included a 300 m gravel road that is 5 m wide. All roads have two lanes without any physical separation between them, and no shoulders. In 2005 the amount of traffic about 10 km further north on the same main road (E6 Stamphusmyra) was 10,321 cars day^{-1}. The lowest number was 9,795 in January, increasing to 13,364 in July, and decreasing to 11,456 in December (Statens Vegvesen 2014). The speed limits were noted (50, 60, 70, 80 or 90 km / h) for each stretch of road, as well as where the roadkills were found.

2.2. Road vicinity

I described the vegetation in the nearest 50 m of the road continuous for the whole distance, as well as specifically where roadkilled birds were found. All the roads that were a part of the observation route had some form of vegetation, except 1.6 km in the city which had pavement and houses close to the road. I classified the vegetation as open, and it means low vegetation consisted of grasses, herbs or farmland crops. This open landscape either had no trees or bushes, or in few places scattered trees or bushes. The vegetation was usually less than 1m high, so birds planning to cross the road should have a good view of the approaching cars. The other type of vegetation along the route was forest, defined as trees or bushes at least 3 m high, but usually containing trees or bushes 10 m high or higher. Most of the forests were spruce, but also some mixed spruce and deciduous forests, and a few short distances with deciduous trees. In addition, there were some low cliffs or houses quite close to the road. I therefore classified the roadside to be: (1) open on both sides; (2) open on one side with forest on the other; (3) forest on both sides; or (4) cliffs or houses close to the road on at least one side.

The route had one estuarine area 320 m from the road, and the road crossed a small river (creek) that flowed into the estuary. Waterbirds were periodically abundant in the estuary, some of them in the river and on the riverbeds as close as 70 m from the road. In two other places wetlands occurred within 50 m from the road: For a distance of 135 m the road followed a brackish fjord which lay as close as 35 m from the road. This fjord was about 1×2 km large, and connected to the main fjord by a narrow strait. The road followed the fjord again for 415 m, getting as close as 32 m from the fjord. On the other side of the road from all three wetland areas, there was either a forest or open landscape which did not entice many waterbirds to cross the road.

To look for any roadkill hotspots, I divided the stretch of road into 5 km lengths and recorded where the roadkills were found. This division is artificial, and the purpose is to have several zones with identical length. However, I did not register the zone where the roadkills were found the whole investigation period, so for 27 of the roadkills I have no zone information. As variables in each zone, I categorized the amount of wetlands relatively close to the road ranging from no wetland (1) to the zone with most wetlands (3). In addition, I categorized the amount of human settlements ranging from none (1) to relatively many (4) where 1.6 km of the 5.0 km long zone is a city.

2.3. Bird census

If five individual birds of one species and fifteen of another are killed by cars, this does not necessarily mean that their mortality rates are different as rates depend on how common bird species are in the area. To quantify the abundance of birds in the surroundings of the road in the breeding season, I conducted standardized point counts (Koskimies & Väisänen 1991, Bibby *et al.* 1992, Gregory *et al.* 2004) as a part of the Norwegian Breeding Bird Survey (BBS) (Husby & Stueflotten 2009). The point count consisted of 5 minutes at each point, registering every pair of birds heard or seen. Within one route, the distance between each point was a minimum of 350 m in open landscape and 250 m in forests. Each route consisted of 20 points, and possible double registrations were reduced to a minimum by the use of distance and direction to very high-singing birds.

In total, seven routes were examined in 2001. Four of them had the closest point to the actual road less than 1km away, one 3.2 km away, and the two furthest away were 6.0 and 6.5 km respectively.

As all routes had mostly the same type of habitat as that in the immediate vicinity of the actual road, I anticipated that the survey gave realistic information about the abundance of the different bird species in the surroundings of the road. I selected BBS data from 2001, which complimented the investigation period for the roadkills. In total, 1,954 pairs of birds were recorded in the 140 BBS points.

I also added the number of the different species registered in the brackish fjord on 19th of June 2015, when the entire area was investigated (Husby & Reinsborg 2015). This investigation provided data closest to the time period with most roadkills.

The birds observed in the areas surrounding the road are therefore the result of 140 census points in terrestrial areas, and in one investigation of the wetland area. These data cannot be attributed to a certain stretch of the road.

2.4. Birds on the road

Data on the number of birds sitting on the road or the verge within 1m from the road edge were collected in the same region as the actual road in this investigation. That investigation lasted from 2003 to 2011. Despite the fact that the region covered a much wider area than the actual road in this analysis, all data are from the middle part of Norway in urban and rural areas. Only birds that were observed before they flew away were included. The bird closest to the car was noted if two birds were located closer to each other than 100 m as the behavior of the first may have influenced the behavior of the second. Similarly, for flocks (two or more individuals in the same area) I only recorded the bird closest to the car.

Nearly all birds were frightened enough to escape the approaching vehicle, and the few still sitting or walking away when the car passed are not included. In total, 5,102 birds identified by species were observed during all months of the year, and included in the statistical analyses.

I also registered the categorized distance (1: < 10 m, 2: 10–30 m, and 3: > 30 m) from a car when 381 individual birds identified by species ($n = 38$) flew away in 2010 and 2011. From these observations, I calculated the mean flight distance of 14 different species/groups of species coinciding with roadkill data included in this paper. These data cannot be attributed to a certain stretch of the road.

2.5. Persistence

By paying continuous attention to roadkilled birds, it was possible to discover how long each bird was visible on the road after I observed it for the first time (persistence). The period between morning and evening on the same day made up 0.3 of the total day, and from evening one day to the morning of the next day was considered to be 0.7 of a day. The number of days before the bird disappeared was noted for all 46 birds from 1996 and 1997, but not in later years. Body masses were gathered from the literature as close to the investigation area and in the breeding season if available (Haftorn 1971, Cramp 1983, Cramp 1988, Husby 1991, Cramp & Brooks 1992, Cramp *et al.* 1994). I used a mean value if there were several investigations, and mean of the sexes if the body mass of males and females were given separately. If two or more species were combined, I used the mean masses of the species. The body mass of undetermined gulls was calculated as the mean of the masses of determined gulls weighed according to the number of roadkills of each species. Small undetermined passerines are given the mean body mass of the two very common *Phylloscopus* (*P. collybita* and *P. trochilus*) species in the area. Table 1 includes all species and groups of species with their body masses and number of roadkills found.

2.6. Statistics

Table 2 provides an overview of the different variables used in the analyses, a short explanation, and how they were transformed to become as normally distributed as possible (Orlowski 2005, Møller *et al.* 2011). Before $\log_{10}$-transformed, I added 1 to the number of registered birds to avoid problems with abundance of zero. In order to achieve normality, I square-root arcsine-transformed all relative values.

Most statistical approaches assume that each data point provides equally precise information about the deterministic part of the total variation (Sokal & Rohlf 1995). Standard deviations (SD), for example, are proportional to the mean. Therefore, I log-transformed measured values to make the data homoscedastic (McDonald 2014). For the same reason, I weighed each observation of species or group of species to the same sample size as the numbers found killed on the road. That means the total number of birds in the surroundings and observed sitting on the road were both reduced in the same proportion so the sum of birds in each was identical to the number of roadkills.

To evaluate the susceptibility to become a roadkill according to abundance in the surroundings, I compared the relationship between the number of roadkilled birds of a certain species divided by the total number of roadkills, with the number of the same species observed in the surrounding divided by the total number of birds observed in the surroundings (Møller *et al.* 2011, Otterbeck *et al.* 2015). Log_{10}–transformation of this relationship leads to the formula in Table 2. Species that are found relatively more often as

Table 1. All roadkilled birds identified by species or groups of species including their body mass (g). Although all birds in the surrounding area including wetlands and those sitting on the road were identified by species, they are here classified in the same groups as the roadkills. The percentages of birds are given for each main group.

Name	Body mass (g)	N of roadkills	N in surr.	N in the wetland	N on road
Gulls		**28%**	**5%**	**26%**	**3%**
Common Gull (*Larus canus*)	386.5	7	79	9	131
European Herring Gull (*Larus argentatus*)	1060.5	1	1	1	22
Great Black-backed Gull (*Larus marinus*)	1606.5	1	4	0	1
Gull sp.	596.9	25	12	4	23
Thrushes		**12%**	**30%**	**–**	**24%**
Fieldfare (*Turdus pilaris*)	105.0	6	267	–	708
Other undetermined thrush-sized	105.0	9	322	–	519
Small passerines		**22%**	**48%**	**–**	**35%**
Meadow/Tree Pipit (*Anthus pratensis/trivialis*)	20.5	1	22	–	42
Phylloscopus* (*Phylloscopus trochilus/collybita*)	8.3	18	291	–	9
Other warblers		0	57	–	1
Willow/Marsh Tit (*Poecile montanus/palustris*)	11.5	1	7	–	2
House Sparrow (*Passer domesticus*)	30.4	3	7	–	144
Eurasian Siskin (*Carduelis spinus*)	12.4	2	84	–	129
Yellowhammer (*Emberiza citronella*)	31.4	2	66	–	315
Other small passerines		0	413	–	1,168
Corvids		**33%**	**5%**	**–**	**35%**
Eurasian Magpie (*Pica pica*)	213.5	20	20	–	741
Hooded Crow (*Corvus cornix*)	521.6	16	76	–	719
Western Jackdaw (*Corvus monedula*)	229.4	4	1	–	284
Other corvids		0	9	–	20
Others		**5%**	**11%**	**74%**	**2%**
Eurasian Oystercatcher (*Haematopus ostralegus*)	507.3	5	13	19	7
Other waders		0	43	6	47
Tawny Owl (*Strix aluco*)	471.5	1	0	–	0
Other groups (Nine different sub-groups)		0	160	14	70
Total		**121**	**1,954**	**53**	**5,102**

* Unable to identify conclusively on the road, but they looked like warblers, especially *Phylloscopus* warbler.

roadkills than their relative abundance in the surroundings, will have a susceptibility value > 1.

I compared the observed patterns of mortality with the expected patterns in each of the five zones of 5 km each, by assuming that the number of roadkills should be equal in each zone as they are of identical length. I used Pearson χ^2-tests when I compared the observed mortality pattern with this expected pattern.

I used multiple linear regression analysis, stepwise backwards, to elucidate the factors that significantly co-varied with dependent variables (Orlowski 2005, Møller *et al.* 2011). The dependent variables are the number of roadkills within each species or group of species, the susceptibility to become a roadkill relative to the abundance in the surroundings, and susceptibility to become a roadkill relative to numbers sitting on the road. As the number of roadkills is included in the susceptibility formula, the number of roadkills is not included as an independent variable when one of the susceptibility variables was the dependent variable. The independent variables are given for each model in Table 3.

I used Pearson product moment correlation to test the relationship between body mass and persistence (transformed values).

As information was missing for some species for some variables, sample sizes differ slightly between analyses.

IBM Statistics (SPSS, ver. 23) were used in all statistical analyses (IBM 2013).

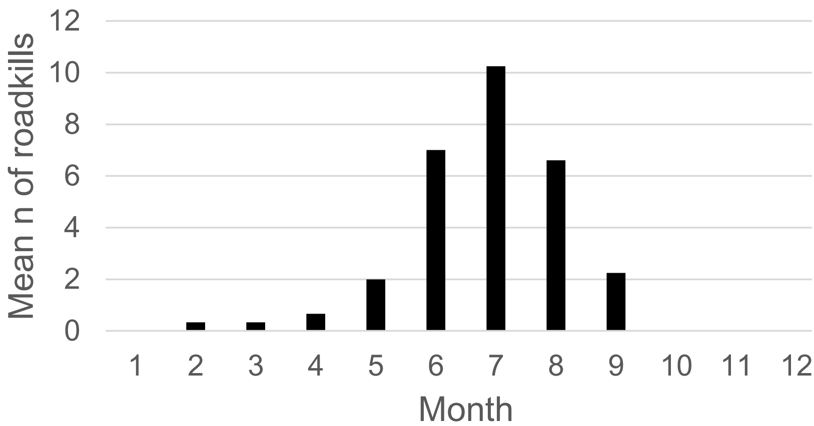

Fig. 1. The mean monthly number of roadkills registered.

3. Results

3.1. General mortality pattern

In total, 121 roadkilled birds where found during the study period (Table 1). The corvids were found most often, followed by gulls. Less commonly found were small passerines and thrushes. During the year, the number of roadkills was very low in the winter season, increasing during the spring and summer to a maximum number in July, and thereafter gradually declining in the late autumn (Fig. 1).

There was a non-random distribution of the number of roadkills along the 25 km route, with one zone (zone 4) having 55.3% of all the roadkills (n = 94). This deviates significantly from an expected uniform distribution of roadkills between the five zones ($\chi^2_4 = 25.186$, $p < 0.001$). I found a nearly identical number of birds (10 or 11) in each of the other four zones. For each of the five main groups of birds (Table 1), no zone had a higher number of roadkills than zone 4. This zone had wetlands and scattered human settlements, but I could not find any significant correlation between the number of roadkills and transformed environmental variables (not presented).

Despite the existence of a roadkill hotspot along the route, this mortality pattern differs between species and groups of species. Relatively more small passerines were found dead in zone 1–3 than in zone 4–5, while the opposite was true for

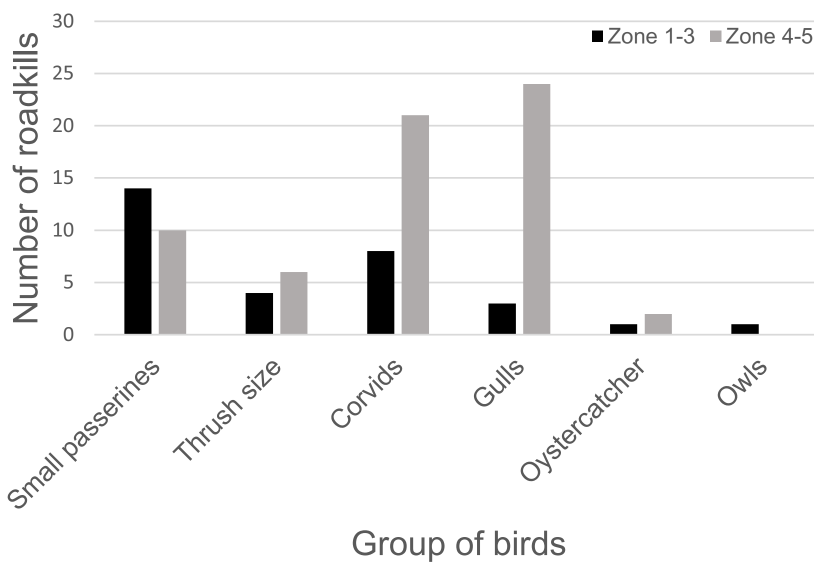

Fig. 2. The observed number of roadkills of different groups of birds in zone 1–3 compared with zone 4–5.

Table 2. Variables used in the analyses describing the birds, the road, and road surroundings.

Variable	Explanation	Transformation of variable
RK	N of roadkills of each species or group of species i. RK_i or total RK_t.	Log(RK + 1)
N in Surr.	N of birds in the surroundings of the road of species i ($NSurr_i$) or total ($NSurr_t$).	Log[weighed (N in Surr + 1)]
N on Road	N of birds observed on the road of a species (N on $Road_i$) or total (N on $Road_t$).	Log[weighed (N on Road + 1)]
BM	Body mass (g).	Log(BM)
Rel. Speed	Relative speed: Mean speed limit were birds were found dead divided by the max speed limit (90) on the whole distance.	Square root arcsine
Rel. Vic.	Relative vicinity: Mean categorized vegetation in road vicinity were the bird species was found dead divided by the max value (4) of the vicinity on the whole distance.	Square root arcsine
Rel. Zone	Relative zone: Mean zone number where the birds were found dead divided by 5 (n of zones)	Square root arcsine
Susc. RK–Surr	Susceptibility of a bird species or group of species to become a roadkill relative to the weighed number of birds of that species in the surroundings.	$Log(RK_i)$ – $Log[(NSurr_i / NSurr_t) × RK_t]$
Susc. RK–on Road	Susceptibility of a bird species or group of species to become a roadkill relative to the weighed number of birds of that species observed on the road.	$Log(RK_i)$ – Log[(N on $Road_i$ / N on $Road_t$) × RK_t]
Rel. FD	Mean categorized flight distance (FD) when the species flew away from the approaching car divided by the max FD value (3).	Square root arcsine

corvids and gulls (Fig. 2). This pattern was similar for all three zones 1, 2 and 3 (not shown), and they are therefore combined. For the same reason zones 4 and 5 were combined also. This mortality pattern between the two groups of zones and all four groups of birds with more than 10 observations was significant ($\chi^2_3 = 13.565$, $p = 0.004$).

3.2. Interspecific variation in mortality

This differential mortality in the zones indicated that environmental and ecological variables probably influence the mortality. The variables in the analyses might also correlate with each other. I conducted a more in-depth investigation of the variables that might affect roadkill mortality in the different species or group of species, analyzing three dependent variables connected to interspecific roadkill rates or roadkill susceptibilities (Table 2). The effect of the other variables on each of these three dependent variables (Models A–C) are presented in Table 3. In the preliminary analyses, body mass influenced mortality or susceptibility significantly in all three models. However, there was a significant positive correlation between body mass and mean flight distance from a car in the 14 actual species with this data ($r_P = 0.720$, $n = 14$, $p = 0.002$). More importantly, the persistence varied significantly according to body mass (see later). Therefore, I excluded body mass in the further analyses. Instead, flight distance was an explanation for a significant or near significant amount of variation in all three models (Table 3).

Bird species that flew away at longer distances from the car suffered higher mortality and were more susceptible to becoming roadkills. Surprisingly, the roadkill rate and susceptibility to becom-

Table 3. Best-fit models of the relationship between various dependent variables, and independent variables in multiple linear regression analysis, stepwise backwards. In model A, the dependent variable is the number of roadkills of each species/group of species (RK), and independent variables are N on road, N in surrounding, vicinity (Rel. Vic), zone (Rel. Zone), speed (Rel. Speed) and flight distance. In model B the dependent variable is susceptibility according to abundance in the vicinity (Susc. RK–Surr), and in model C susceptibility according to numbers on the roads (Susc. RK–on Road), both with the same independent variables as in model A, except number of birds in the surroundings and number of birds on the road respectively. All variables are transformed according to description in Table 2. *P* and r_p are from Pearson product–moment correlation coefficients in the linear regression analyses. Limit for removal of variables in the regression analysis is $p = 0.010$.

Model	*B*	SE	*t*	*p*	r_p
Model A. Dependent variable: N of roadkill of species/group of species					
Rel. Speed	–2.07	1.10	–1.89	0.092	–0.09
Flight distance	3.38	1.24	2.73	0.023	0.43
N on Road	0.33	0.16	2.09	0.066	0.21
Constant	–0.14	1.10	–0.12	0.905	–
$F_{3,9} = 2.90$, $P = 0.094$, $R^2 = 0.49$					
Model B. Dependent variable: Susceptibility according to number in surroundings					
Rel. Zone	3.11	0.92	3.38	0.007	0.65
Flight distance	3.46	1.86	1.86	0.093	0.28
Constant	–5.16	1.81	–2.85	0.017	–
$F_{2,10} = 6.66$, $P = 0.015$, $R^2 = 0.57$					
Model C. Dependent variable: Susceptibility according to number on road					
Rel. Speed	–4.29	1.61	–2.66	0.024	–0.38
Flight distance	5.58	1.87	2.98	0.014	0.47
Constant	–0.13	1.83	–0.07	0.946	–
$F_{2,10} = 5.99$, $P = 0.020$, $R^2 = 0.55$					

ing roadkill according to the number of birds observed on the road, decreased as the speed limit increased.

The variation in mortality in the different zones does not significantly affect the interspecific roadkill variation (Table 3). However, zone explained a significant amount of the variation in susceptibility for becoming roadkill according to abundance of birds in the surroundings. This positive relationship is in accordance with higher mortality in zone 4 and 5 compared to zone 1–3 (Fig. 2).

The proportion of individuals sitting on the road is included in model A, which shows that relatively more birds on the road increases the mortality rate for that species. The number of birds in the surrounding area does not have as high a correlation with the number of roadkills ($r_p = 0.322$, $n = 30$, $p = 0.082$) as with the numbers observed on the road ($r_p = 0.551$, $n = 30$, $p = 0.002$). Moreover, as susceptibility according to numbers in the surroundings correlates significantly with the numbers observed on the road ($r_p = 0.572$, $n = 30$, $p = 0.001$), only the one with the strongest explanation is included.

Some bird species are attracted to roads more than others (see Introduction). Among the species found dead in this investigation, gulls, corvids, House Sparrow and Yellowhammer are the species that often find food on the road in this area, while the other species or groups do so more seldom. The birds/groups of birds often eating on roads ($n = 9$) had a significantly higher susceptibility of ending up as roadkills compared to their abundance in the surroundings (SuscRK-Surr, Table 2) than the other species ($n = 8$) (Mann–Whitney *U*-test: $Z = –2.02$, $n = 17$, $p = 0.043$). The corresponding relationship between "eating on road" and susceptibility according to number of birds observed on the road was far from significant (Mann–Whitney *U*-test: $Z = –0.481$, $n = 17$, $p = 0.63$).

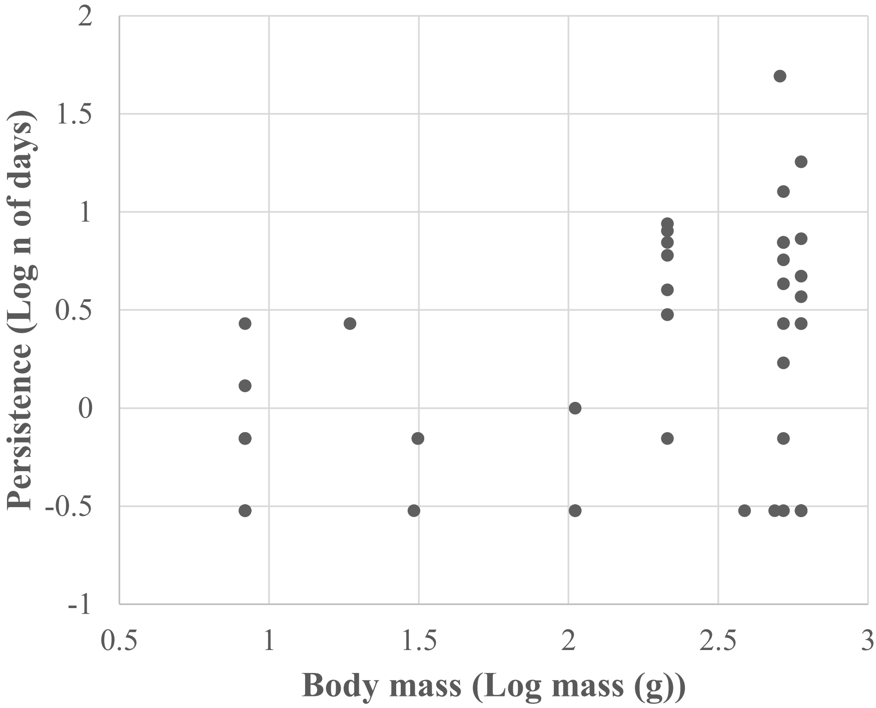

Fig. 3. The number of days before roadkilled birds with different body masses became undetectable. The regression line is $y = 1.2x – 1.6$ ($r_P = 0.399$, $n = 46$, $p = 0.006$).

The vegetation, cliffs or buildings in the vicinity of the road did not significantly explain mortality nor susceptibility in any of the models. All three models explained about 50% ($R^2 = 0.49–0.57$) of the variation in the number of roadkills and susceptibility to roadkills (Table 3).

The time from the first observation of a roadkilled bird until it was no longer visible was noted for 46 birds. The persistence was on average 4.21 days (SD = 7.74), and increased significantly with increased body mass (Fig. 3). Small birds of Fieldfare size or smaller ($n = 16$) disappeared on the average after 0.89 days (SD = 0.78), and larger birds ($n = 30$) disappeared after 5.98 days (SD = 9.12).

4. Discussion

4.1. General mortality patterns

I found the highest number of roadkills in July, but also many in June and August (Fig. 1). That is probably caused by inexperienced fledglings (Orlowski 2005), and because the number of birds are higher shortly after breeding than in other periods, especially in winter when most of the birds have left the investigated area.

I also found that one zone of the road had a much higher proportion of roadkills than other zones in this study. The existence of such roadkill hotspots is consistent with other reports examining roadkill rates (Ramp *et al.* 2005, Gomes *et al.* 2009). As shown here (Fig. 2), different groups of birds are found dead in significant different numbers in different sections of the road. There were a particularly high number of roadkilled corvids and gulls in zones 4 and 5 relative to zones 1–3. This is reasonable, as both zones were closer to wetland areas than the other three zones, and therefore more gulls were close by. In addition, zones 4 and 5 had a small city and more scattered human settlements not far from the road than zones 1–3, a habitat suitable for Magpies and Jackdaws.

4.2. The effects of bird abundance and behavior on roadkill rate

Species with relatively big brains compared with total body mass, such as corvids, escape cars by flying directly away from the road to a larger extent than others (Husby & Husby 2014). Therefore, this study found a surprisingly high number of corvids killed by cars (Table 1). Of the 40 roadkilled corvids, 35 died in June, July and August. This is after fledging (Husby & Slagsvold 1992) and most likely these individuals are young birds less experienced with traffic than adults. A high number of roadkilled corvids are also found in other European countries (Erritzoe *et al.* 2003). Interestingly, I found that birds attracted to roads to search for food, like gulls, corvids, House Sparrow and Yellowhammer, had significantly higher susceptibility to become roadkill relative to their abundance in the surroundings compared to the other species that find most of their food away from roads. There was no significant relationship in a similar analysis with birds observed on the road. This underlines the difference between a composition of bird species in the surrounding area and birds on the road. Only some birds in the surroundings are attracted to roads. So even though a road can support them with easy accessible food, the cost is a higher mortality rate.

There was a significant correlation between the abundance of birds in the surroundings and birds observed on the road. However, the effect on mortality rates from birds sitting on the road was stronger than the effect from abundance in the surroundings. Similarly, another investigation showed that the proportion of individuals on the road explained a significant amount of variation in roadkills (Møller *et al.* 2011).

I found that although heavier birds flew away from an approaching car at longer distances than smaller birds, flight distance still explained a significant amount of the variation in roadkills and susceptibility to become roadkilled (Table 3). The heavy birds should have left the road at longer distances from the car than they did. One possible explanation is that they take increased risks because there is food on the road that can be taken by other birds if they fly away too early (own observations). Heavier birds probably need more time to escape than small birds, so therefore increased flight distance does not necessarily increase the time before the car reaches their location on the road. Flight distance was a significant predictor of roadkill and the susceptibility to become a roadkill when I excluded body mass from the analyses. The most important reason for this exclusion is the significant relationship between body mass and persistence. Heavier birds are visible for a longer time, and the probability of detecting them is therefore higher, and they are also easier to detect because of their size. I therefore used flight distance as an independent variable instead of body mass. In another investigation, body mass and not flight distance significantly explained the susceptibility to become roadkill in models where both were included (Møller *et al.* 2011).

4.3. Speed and vegetation

Contrary to what I expected, the roadkill rate and susceptibility to become roadkill according to the number of birds sitting on the road decreased as the speed limit increased (Table 3). Most other studies conclude that the roadkill probability increases with speed limit (Erritzoe *et al.* 2003).

Vehicle collision can happen in two ways: birds may collide when sitting on or along the road and are frightened off by the approaching car, or they may collide when they fly across the road at a low elevation. The speed of the vehicle might influence both of these behaviors. As the speed of the vehicle increases, the probability that a bird will fly away from the road rather than crossing the road increases (Husby & Husby 2014), thus reducing the probability of being killed by a car. Quite often the sound of an approaching vehicle will reach a bird long before it observes it. In addition, the noise from a car increases with the speed (Cai *et al.* 2015). Curved sections of a road have been found to result in more roadkilled birds compared with straight roads (Bergmann 1974, Hernandez 1988), most likely caused by a combination of both reduced vehicle speed (and noise) and because vehicles are visible at a shorter distance. The car appears more dangerous to the bird when it is moving directly towards it, something that happens very quickly in a curve. It is possible that many bird species do not have the cognitive capacity to quickly interpret all the information about distance, direction and speed from a car, and are therefore put at risk in traffic. This problem would likely increase with the speed of the car (DeVault *et al.* 2015), especially if the speed exceeds the speeds the birds are familiar with in nature (DeVault *et al.* 2014).

Another possible explanation of the results of this study, could be that vehicles hit the birds harder when the speed is higher, throwing the birds further off the road and out of sight. Roadside vegetation just one meter from the asphalt can also hide roadkilled birds, and it might be more difficult to detect a roadkilled bird if one is driving faster. If this is the case, roadkill mortality might increase with increased speed of the cars, but these birds escaped detection to a higher extent than roadkills where the speed limit was lower.

In the multiple linear regression (Table 3), there was no significant effect of vegetation and cliffs or houses along the road on the variation in roadkills or susceptibility. A variable landscape with a variety of bird species differing in ecology might be the reason. One possible mitigating action is to plant trees near the road, thereby forcing non-forest birds to cross the road at higher elevations. This seems to be useful for gulls and most waders and other birds living in open landscape. However, trees and bushes will also attract breeding, foraging, and resting birds (Orlowski 2005, Morelli *et al.* 2014). We should not plant trees if we want to protect a forest dwelling bird species as that can function as an ecological trap with increased mortality rates (Erritzoe *et al.* 2003, Orlowski 2008). In hotspots for roadkills, it is important to know which bird species are most vulnerable, consider their ecology, and thereafter plan mitigating action.

It is important to note that some of the findings, or lack of significant differences, can be caused by the small sample size in the number of roadkills.

4.4. Persistence

I found that most small birds of the size of the Fieldfare or smaller disappeared within less than 24 hours (Fig. 3). Two personal observations underline the observation that some birds disappear very quickly. Within five seconds after a car collided with a tit (*Poecile* sp.), the bird was taken and eaten by a Common Gull. The second observation was a Blackbird (*Turdus merula*) injured by a car and attacked by Magpies while still alive. These observations show that scavengers can remove some birds very quickly. However, some of the birds flattened in the asphalt gradually disappeared because of the traffic, and seemed to become partly inaccessible for the scavengers. Another study shows a high rate of carcass removal by scavengers as 60%–97% of the carcass disappeared within 36 hours of their placement along roads (Antworth *et al.* 2005). In this study, I found that large birds persisted significantly longer than small birds, a conclusion supported by other researchers (Korhonen & Nurminen 1987, Erritzoe *et al.* 2003, Guinard *et al.* 2012).

These findings indicate that especially small birds are more numerous as roadkills than indicated in my list of roadkills (Table 1).

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Faktorer som påverkar trafikdödlighet hos fåglar

Flera hundra miljoner fåglar dödas årligen som en följd av kollisioner med fordon. Trots att detta är väldokumenterat så saknar vi kunskap om vilka variabler som påverkar fåglarnas trafikdödlighet. I denna studie undersökte jag mönster i fåglars trafikdödlighet på en 25 km lång vägsträcka i centrala Norge. Över en 44 månader lång period (617 dagar, två gånger om dagen) samlade jag data genom att köra bil längs sträckan. Jag identifierade totalt 121 dödade fåglar under denna tidsperiod, noterade information om kroppsmassa, vägens hastighetsbegränsning, närområdets vegetation, flyktdistans, omgivningens fågelmängd samt antal fåglar som befann sig på körbanan. Dessa variabler använde jag för att förklara antalet dödade individer och risken för trafikdödlighet hos 30 fågelarter.

Antalet trafikdödade fåglar var högst under sommaren och på vissa vägsträckor var dödligheten betydligt högre än vid andra. Tyngre fåglar flög undan den närmande bilen på större avstånd än mindre fåglar, men de hade ändå en relativt sett högre dödlighet. Fåglar som man vet att brukar söka mat på vägar löpte högre risk för kollision än andra fåglar. Fåglar observerade på vägen förklarade en signifikant andel av mellanartsvariationen i trafikdödlighet, i motsats till antalet fåglar observerade i omgivningen. Färre trafikdödade fåglar än förväntat påträffades på vägsträckor med de högsta tillåtna hastigheterna. Större fåglar som fallit offer för trafik var synliga över en längre tid.

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