Traffic Influence on Roadside Bird Abundance and Behaviour

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Traffic influence on roadside bird abundance and behaviour

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Abstract. Of the many negative effects roads have on wildlife, vehicle-caused mortality is important, killing several hundred million birds on an annual basis worldwide. Mortality is often the result of sitting on the road and failing to avoid an approaching vehicle, or being hit by a car while flying across the road at too low height. Therefore, one would expect that in areas with very high traffic density, birds would stay away from the road and roadside, and that birds flying over the road would do so at an elevation that minimizes the risk of collision. To test these hypotheses, I observed bird numbers along the roads at approximately 1000 car trips of at least 5 km in Iceland, Norway and the United States, and about 1800 flight heights of birds crossing a road before and after it was opened for car traffic. The bird abundance on roads was significantly lower at higher traffic densities. After start of traffic in a new road situation, birds crossed that road at significantly higher elevations than before. As an example, nearly 40% of Hooded Crows *Corvus cornix* and 70% of Western Jackdaws *Corvus monedula* were observed in the high-risk collision zone 0–5 m height before the road was opened; this was reduced to about 20% and 5% respectively for the two species after the road was opened. Heavy bird species flew higher than small birds. The behavioural adaptations shown here together with other publications provide the foundation of a hypothesis that the relationship between traffic density and the number of bird roadkills is non-linear, with a maximum number of roadkills occurring at a certain traffic density. This implies that fewer roads with high traffic density could reduce the number of roadkilled birds compared to many less trafficked roads.

Key words: collision avoidance, collision rate, flight height, flight distance, landscape, traffic, roadkills, road casualties, road construction, urban planning

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INTRODUCTION

Roads constitute a substantial part of our environment, certainly in Europe and North America. For instance, the Netherlands has 1.5 km and the U.S. 1.2 km of roads per km^2 land area (Forman & Alexander 1998). Many studies demonstrate the negative effects roads have on wildlife are due to habitat loss, population fragmentation, pollution, poisoning, noise, and collisions with cars (Erritzøe et al. 2003, Reijnen & Foppen 2006, Fahrig & Rytwinski 2009, Francis et al. 2009, Goodwin & Shriver 2011, Summers et al. 2011). This also extends beyond the road lanes and verges, and bird densities are in some cases reduced as far away as 1–3.5 km from the road (Reijnen et al. 1995, 1996, Reijnen & Foppen 1995, Reijnen et al. 1996, Forman et al. 2002, Benitez-Lopez et al. 2010).

Roads have influenced the environment in many different ways. Especially road mortality and traffic noise seem to have an important effect on birds (Reijnen & Foppen 2006, Kociolek et al. 2011). Collisions with cars kill several hundred million birds every year with country specific estimates of 13.8 million in Canada (Bishop & Brogan 2013), 80–340 million in the United States (Forman & Alexander 1998, Loss et al. 2014), 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 (Erritzøe et al. 2003).

The risk of collisions with vehicles differs among groups of birds. Birds like raptors, gulls, and corvids are often attracted to roads where they scavenge on food leftovers or roadkills (Forman 2000, Mumme et al. 2000, Dean & Milton 2003, Husby & Husby 2014). Other species, like White Wagtails *Motacilla alba* (Erritzøe et al. 2003, Husby & Husby 2014), forage on insects on or next to roads, and e.g. Red-backed Shrike *Lanius collurio* frequently use shrubs, trees and power lines as perches for hunting on road surfaces, and roadside habitat is attractive for their breeding (Ceresa et al. 2012, Morelli 2013). It is also found that reduced predation pressures, streetlights prolonging diurnal activity, and a warm road surface reducing metabolic energy costs make roads attractive to some birds (Morelli et al. 2014). When a car approaches a bird on the road, the most common behaviour is to escape, either flying directly away from the road or crossing it (Husby & Husby 2014).

Since the first petrol-powered car was built in 1886, the number of cars has increased and is still increasing. In Norway, for example, the number of new private cars and vans registered increased by 31.6% and 68.4% respectively from 2002 to 2012, and by the end of 2013 there were close to 3 million private cars and vans registered in Norway, a country with a population of 5 million people (SSB 2014). In eleven large Chinese cities, the number of cars per 1000 households increased from 50 to 185 cars between 2000 and 2010, a growth rate nearly nine times that of the urban population growth (Zhao 2014). It is not clear, however, whether increased car traffic leads to increases in the number of roadkills. According to a review paper by Gunson et al. (2011), rates of roadkills generally do increase with traffic volume. However, in a study in Canada mammal and bird roadkill numbers were consistently higher on a low volume parkway than on high speed and high traffic volume roads nearby (Clevenger et al. 2003). These findings are consistent with research done in Australia where modelling showed that increased traffic volumes on existing roads usually have a lower impact on the number of Koala *Phascolarctos cinereus* roadkills than the building of new roads (Rhodes et al. 2014).

Earlier studies looking for effects of traffic on bird populations primarily focused on a comparison of (breeding) abundances in relation to traffic densities and comparisons between areas next to the road and control sites without traffic influence. In order to study how bird-traffic collisions relate to road and traffic characteristics, I studied behaviour of individual birds staying along or on roads since they are the most likely victims (Husby 2016). I have two important aims. First, I want to know the relationship between traffic densities and the abundances of birds on the road. My hypothesis is that increased car traffic decreases bird abundance on and close to the road. The second goal is to study whether car traffic influences the elevation at which birds fly across a road. I therefore studied bird flight height before and after a road was opened to traffic. The hypothesis is that birds cross a road at higher elevations when there is traffic on a road.

MATERIAL AND METHODS

Estimating abundance of birds on the roads

In order to register the number of birds sitting on and close to different roads, I counted all birds on 2,261 car trips at daytime over a total of 27,986 km, from May 2003 to the end of March 2005 (Table 1). The survey areas were in Norway (mostly Trøndelag), the northeastern part of the United States (Maryland, Delaware, New Jersey, and New York), and the southern half of Iceland (Sudurnes, Reykjavik, and Sudhurland). These three survey regions were selected because they differ in their abundance of birds, road networks, and traffic densities. Bird abundance was lowest in Iceland and highest in the United States, and traffic density was generally higher in the United States than in Norway and in Iceland where there was little traffic. I drove on different types of roads in all three regions to increase the sampling area.

I used a private car, followed the speed limits, and recorded birds sitting within 1 m from the road verge that were frightened enough to fly away by the approaching car. That means birds found in a 2 m band, a range including 1 m from the road verge onto the road to 1 m from the road onto the verge. In the United States this also included the asphalted shoulder on major roads. As birds in a flock often behave similarly, I registered flocks of two birds or more as one entry. I recorded the exact distance driven on each different type of road for each trip.

Table 1. Areas and periods with car driving with registration of number of birds on the roads.

Country	Period	Number of trips	Mean length per trip	Total length
Iceland	July 2003	18	63	1 128
Norway	May 2003–March 2005	2163	11	24 644
USA	July 2003	80	28	2 214

I recorded all car trips, on different types of roads, during the investigation period. This implies that there are most probably no differences between the different types of roads when data was collected according to the time of day (not registered) nor the time of the year (month). The mean month for the trips on the main roads did not significantly differ from other roads (Mann-Whitney U-test: $z = -0.26$, $p = 0.78$). I include all months when I compare the number of birds on different types of roads.

In Norway in 2010 and 2011, I registered the speed of the car according to categories 1) ≤ 50 km/h, 2) 50–80 km/h, and 3) > 80 km/h. I also estimated the distance birds were from my car when they flew away from the road using categories 1) ≤ 10 m, 2) 10–30 m, and 3) > 30 m. I observed most birds at long distances before they left the road, and only 85 of all the 386 birds with flight distance data flew away from the road at distances more than 30 m from my approaching car. As most birds wait to fly away until the car is quite close, the probability that they escape my detection is low even when I drive faster than 80 km/h.

I classified the roads into three different categories: 1) main roads and other busy asphalt roads close to cities, 2) minor asphalt roads, and 3) gravel roads. Until November 2003, I combined the last two road types into one category, so during this period the data comes from two road categories only. This makes it possible to compare main roads only with other types of roads in Iceland and United States, and to compare all three types of roads in most of the Norwegian dataset.

The amount of traffic on the main road (Europaveg 6/E6) in Norway, close to the area where most of the observations were made, was about 10,500 cars per day in 2005. Although January had the lowest number, less than 10,000 cars per day, traffic numbers increased to nearly 13,500 in July, decreasing again to around 11,500 in December (Statens Vegvesen 2014). The amount of traffic on the other roads was far less than on the main roads. This traffic density is still quite low compared to more heavily trafficked roads (Reijnen & Foppen 2006). In the United States, more than 300,000 vehicles can pass per day on some of the roads.

In the United States, major roads have a shoulder that is lacking on secondary roads. In Norway and Iceland the road verges do not differ much between the three categories of roads. Vegetation like grasses and herbs grow close to the road lanes and the vegetation is often kept low by mowing.

The distance driven affected the probability of detecting birds; the longer the trip, the bigger the chance of finding a bird on the road. Number of birds per trip will obviously increase with the length of the trip, but not necessarily the number of birds per km. For example, if one trip is only 500 m, the probability that number of birds detected and number of birds per km is zero for this trip is quite high. This kind of information is not of any value for this investigation. As there were many short trips with low probability of detecting a bird, there was a positive relationship between the number of kilometers driven and the number of birds detected per 100 km ($r_s = 0.137$, $n = 2{,}163$, $p < 0.001$). This relationship became less clear when I eliminated the shortest trips, becoming non-significant when the trips were > 4 km ($r_s = -0.039$, $n = 1{,}084$, $p = 0.19$), and very far from significant for trips > 5 km ($r_s = -0.005$, $n = 921$, $p = 0.87$). I therefore include only trips > 5 km for each road category in all analyses.

In the Norwegian part of the study, the vegetation close to (within about 20 m) the road was classified according to heights of 1) ≤ 0.5 m, 2) 0.5–3 m, or 3) > 3 m where every bird was registered. This value was given for both sides of the road each time a bird met the requirements needed to be included in the analysis. To test possible variation in the vegetation height, I added the category values on the two sides and divided by two, thus giving a mean vegetation height category 1–3 as described above. This was done during the period August 2003–March 2005. It is necessary to analyze the possible effect of roadside vegetation on the number of birds on the road if the vegetation differs along the three road types in this work.

Flight height of birds crossing the road

I investigated the flight height of birds crossing a road section in the middle part of Norway. Observations were done in 1994 and 1995 after the road was constructed but not opened for public traffic, and in 1996 after public traffic was allowed. The same 210 m section of the road was monitored all three years. The road section was elevated a few meters above the surrounding terrain and there was no vegetation close to the road, hence the vast majority of birds were detected before they reached the road. This road section was chosen because I needed an extensive period after the road was constructed and before it was opened for traffic to gather all the data needed.

To observe the birds, I was either sitting in a car at one end of the road section (Zone UTM 32V: 595205, 70372979) or standing in a field about 160 m from the road and nearly perpendicular to it. These two locations were used to a similar extent both before and after road opening. I used cars quite neutral in colours, ranging from light blue-grey or champagne colour. Therefore, I do not believe that variation in the car colour influence my results in any way.

I registered the birds' lowest height above the road when they flew across it. Poles placed along the road at approximately 40 m intervals had markers indicating different elevations up to 5 m, so it was possible to observe the birds' height to the nearest meter at low elevations. All crossing birds were categorized according to elevations of 0–1 m, 2–3 m, 4–5 m, 6–10 m, and > 10 m. As the largest trucks and buses in the area are between 4 and 5 m high, all birds crossing the road below 5 m are in the high-risk zone for collision. For flight heights between 6–10 m, the turbulence created by cars can influence birds' maneuvering abilities, but the collision risk is lower than at heights below 5 m. Birds flying more than 10 m above the road are not in immediate danger to become killed by cars. Flocks with two or more birds together were registered as a single entry using the mean height of the flock, and noting the flock size.

In total 1809 observations of flight heights of birds crossing the road were made, 1208 from the car and 601 from the neighboring terrain. Only species with at least 10 observations both before and after the road opening with a minimum of 50 individuals altogether were included in the analyses. The most common species and groups of species are listed in Table 2.

In addition to the observation place, I also registered flock size, time of day (categorized as 1 — ≤ 10:00, 2 — 10:00–16:00, or 3 — > 16:00) and if the road was opened or not. Mean body mass of the species was also included in the analyses, and Table 3 includes a description of these independent variables and codes used for categorized variables. I $\log_{10}$-transformed continuous variables to make them more normally distributed. Mean body masses for each species are calculated from published data (Haftorn 1971, Cramp & Simmons 1977, 1983, Cramp 1985, 1988, Cramp & Perrins 1994). I used data only from adult birds, and never included birds found starved or roadkilled that might differ from normal body size (Erritzøe et al. 2003, Bujoczek et al. 2011).

Table 2. Species and groups of species included in most of the analyses of birds flight height, with number of observations before and after the road was opened for traffic.

Species/Group of species	N before road opening	N after road opening
All birds	480	1329
Ducks	12	70
Waders	53	117
Gulls	150	426
Corvids	138	276
Passerines	109	403
Northern Lapwing *Vanellus vanellus*	24	65
European Oystercatcher *Haematopus ostralegus*	15	37
Common Gull *Larus canus*	67	305
Black-headed Gull *Chroicocephalus ridibundus*	24	72
Hooded Crow *Corvus cornix*	92	213
Western Jackdaw *Corvus monedula*	44	59
Common Starling *Sturnus vulgaris*	33	86

Statistics

I used IBM SPSS statistics (version 23) for the analysis of the birds on the road, applying only non-parametric tests (Spearman rank correlation, Mann-Whitney U-test, Fisher exact test, and Pearson Chi-Square). The level of significance is 5% and only two-tailed tests are used.

I have considered all observations of birds on the road to be independent, and it was probable

Table 3. Variables analyzed in the multinomial logistic regression test with flight height as dependent variable.

Variable	Type	Description of transformation or codes
Flock size	Continuous	Log_{10} of flock size
Body mass	Continuous	Log_{10} of body mass in gram
Time of day	Categorized	1 = before 10 am, 2 = between 10 am and 4 pm, 3 = after 4 pm
Counting place	Categorized	1 = from inside a car, 2 = from the surroundings
Road opening	Categorized	1 = before road opening, 2 = after road opening

that different birds were encountered when driving a car on new roads. In areas where I was driving more often, the time interval was long between my visits to the same section of road and therefore my car did not influence the number of birds along the road.

When I studied the flight height above the road, the same area was used for all observations. Only the first observation was included for birds that landed on one side of the road and crossed the road again. However, my focus was to detect new birds that crossed the road. It was not possible to detect all birds crossing more than one time during my registration period each day and impossible if it happened on different days. I assume that the individual records of flying birds are independent.

As the flight height is categorized, and the number of observations within each category is impossible to transform to normal distribution, I used multinomial logistic regression. This test compares each consecutive flight height with a reference height. I merged the flight height to three categories according to the risk of collision (see Material and methods). The reference height was 0–5 m, which has a high risk of collision with cars, and this height was compared with 6–10 m and > 10 m respectively.

Some analyses signaled unexpected singularities in the Hessian matrix. This indicates that either some independent (predictor) variables should be excluded or some categories should be merged. I therefore removed time of day first, and if the problem continued, I removed flock size instead. I chose these two variables because analysis of all birds indicated that they were least important to explain the variation in flight height. If this did not help, I had to remove both variables.

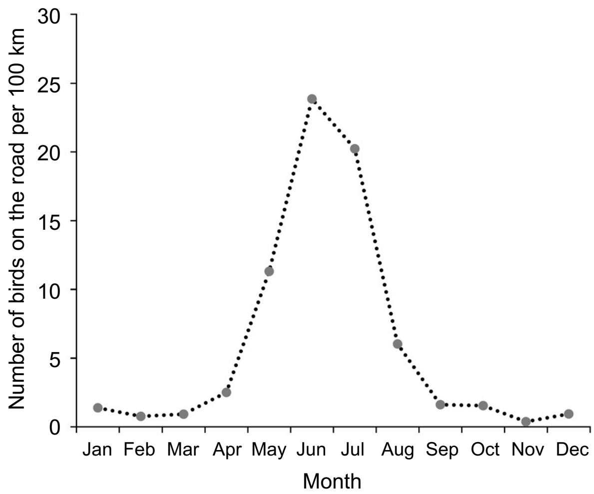

Fig. 1. Monthly number of birds observed on the road per 100 km driving in Norway. Flocks of birds are counted as one bird. The values include only driving trips > 5 km.

RESULTS

Roadside bird abundance and traffic intensity

The number of birds sitting on the road in Norway varied considerably during the year (Fig. 1). There was a 60-fold increase from the lowest number of birds per 100 km driving in November to the highest number in June.

There were fewer birds on the main roads per 100 km driving compared with the smaller roads (Table 4). This was significant for all three countries, even in Iceland with only 18 trips of more than 5 km. When I compared all three types of roads (Fig. 2) in the Norwegian data, the number of birds per 100 km driving was significantly higher on minor asphalt roads compared to the main roads (Mann-Whitney U-test: $Z = -8.698$, $n = 690$ trips, $p < 0.001$). Furthermore, gravel roads contained a significantly higher number of birds per 100 km than minor asphalt roads (Mann-Whitney U-test: $Z = -3.129$, $n = 281$ trips, $p = 0.002$).

The vegetation close to gravel roads in Norway was similar to minor asphalt roads; height category mean was 1.6 (SD = 0.7, n = 665) and 1.5 (SD = 0.6, n = 497) respectively (Mann-Whitney U-test: $Z = -1.175$, $n = 1162$, $p = 0.240$). However, the mean categorized vegetation height (see Material and methods) along main roads was 1.3 (SD = 0.5, n = 154), significantly lower than both

Table 4. Mean number of birds observed on main roads and secondary roads per 100 km while driving in a car. Both minor asphalt roads and gravel roads are considered secondary roads. Only trips more than 5 km are included in this study. The differences in number of birds/km on the two types of roads are analyzed with the Mann-Whitney U-test.

Country	Main roads	Secondary roads	No of trips	Z	p
Iceland	0.2	8.3	18	-2.73	0.006
Norway	1.0	17.3	921	-13.79	< 0.001
USA	0.2	58.2	47	-5.15	< 0.001

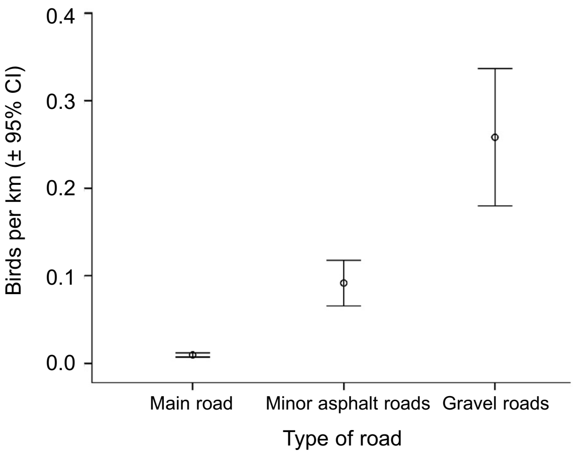

Fig. 2. Number of birds observed on the road per km driving on three types of roads in Norway. Flocks of birds are counted as one bird. Only trips > 5 km are included.

minor asphalt roads (Z = -4.785, p < 0.001) and gravel roads (Z = -5.414, p < 0.001).

Birds flushed away from the road at a mean categorized distance 1.71 from the car of when the speed of the car was less than 50 km/h (n = 151). The values range from 1 (≤ 10 m) to 3 (> 30 m). Flight distance increased to 1.92 (n = 144) when the speed increased to 50–80 km/h (Mann-Whitney U-test: Z = -218505, n = 295, p = 0.004). There was a non-significant increase in flight distance to 2.08 (n = 91) when the speed increased from 50–80 to > 80 km/h (Mann-Whitney U-test: Z = -1.755, n = 235, p = 0.079).

Flight height of birds crossing the road

The 1809 birds registered when they crossed the road, belonged to 47 different species, and in addition some undetermined small-sized passerines. The size range was from Eurasian Siskin *Carduelis spinus* weighing about 12.8 grams to Black-throated Loon *Gavia arctica* weighing near 3 kg.

Table 5 shows all significant multinomial logistic test results, both for all birds, groups of species and individual species. Included are only species with a minimum of observations (see Material and methods), and because of the many tests I included only statistical significant results. The high-risk flight height (a, 0–5 m) is compared with the medium risk (b, 6–10 m), and low risk zone

Table 5. Multinomial logistic regression of flight height as dependent variable. Flight height is in the collision zone (a: 0–5 m), used as reference and compared with the intermediate turbulence zone (b: 6–10 m) and out of collision risk (c: > 10 m). The variables included in the test are listed in Table 3. For categorical variables, the statistical program set the highest category to zero. For body mass and flock size $\log_{10}$-transformed values are used. Only significant results are included.

Test	Significant results	B	SE	Wald	df	p	Exp(B)
All birds: a vs. b	Body mass	0.56	0.16	11.81	1	0.001	1.76
	Counting place	-0.65	0.24	7.35	1	0.007	0.52
All birds: a vs. c	Body mass	1.24	0.14	80.09	1	< 0.001	3.46
	Time of day 2 vs. 3	-0.68	0.26	6.96	1	0.008	0.51
	Road open	-0.95	0.25	4.48	1	< 0.001	0.39
Ducks: a vs. c	Body mass	1.37	0.59	5.41	1	0.020	3.93
Waders: a vs. c	Road open	-2.14	0.76	7.93	1	0.005	0.12
	Time of day 1 vs. 3	-3.73	1.12	11.04	1	0.001	0.02
	Counting place	2.50	0.75	11.21	1	0.001	12.14
Gulls: a vs. c	Time of day 2 vs.3	-1.42	0.59	6.33	1	0.012	0.23
	Counting place	-0.69	0.35	3.89	1	0.049	0.50
Crows: a vs. b	Road open	-1.64	0.41	16.25	1	< 0.001	0.19
Crows: a vs. c	Road open	-1.62	0.26	40.16	1	< 0.001	0.20
Passerines: a vs. c	Road open	-1.29	0.56	5.33	1	0.021	0.28
Eurasian Oystercatcher: a vs. b	Counting place	-2.06	0.93	4.91	1	0.027	0.13
Common Gull: a vs. c	Time of day 2 vs 3	-1.97	0.62	10.11	1	0.001	0.14
Black-headed Gull: a vs. c	Road open	2.62	0.79	11.01	1	0.001	13.68
	Counting place	-1.66	0.66	6.34	1	0.012	0.19
Hooded Crow: a vs. b	Road open	-2.26	0.65	11.93	1	0.001	0.10
	Counting place	-1.13	0.46	6.05	1	0.014	0.32
Hooded Crow: a vs. c	Road open	-0.79	0.30	6.96	1	0.008	0.46
	Counting place	-1.18	0.35	11.51	1	0.001	0.31
Western Jackdaw: a vs. c	Road open	-3.77	0.71	28.32	1	< 0.001	0.02
Common Starling: a vs. c	Flock size	1.40	0.67	4.39	1	0.036	4.05

(c, > 10 m). When controlling for the variation by other independent variables, road opening was the main independent variable according to the number of significant changes in flight height, both when comparing flight height a and b, and a and c. The results were quite consistent, as seven of eight significant results showed increased flight height after the road was opened for traffic.

Counting place explained significantly flight height variation in seven tests, and six of them gave increased flight height when I was standing away from the road compared with when I was sitting in my car along the road. The only exception was waders.

Variation caused by time of day was consistent, with three significant result comparing the time periods 2 (10:00–16:00) and 3 (> 16:00), and one significant comparing the time periods 1 and 3. The flight height was mostly higher after 4 pm than earlier in the day, when controlling for other variables.

Body mass corresponded significantly with flight height in three of the tests, and they all showed that heavier birds flew higher. This relationship was significant for all birds combined, and for ducks. Larger Common Starling *Sturnus vulgaris* flocks flew higher than small flocks, the only test with significant effect of flock size.

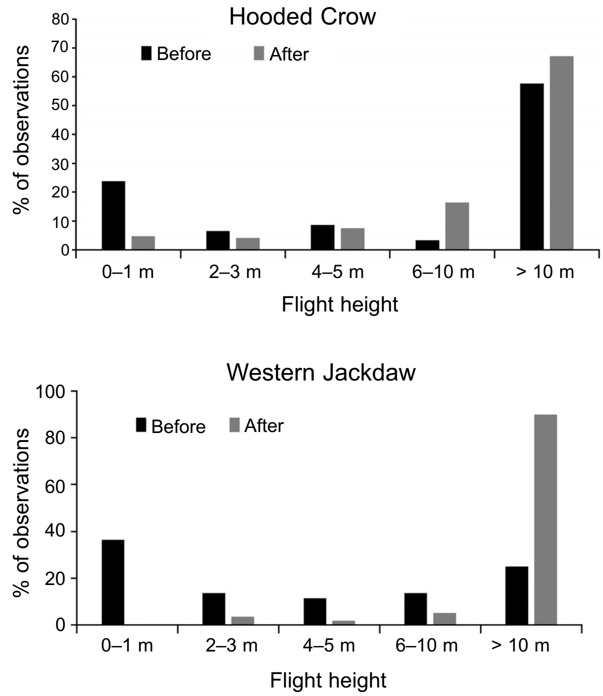

Fig. 3. Number of Hooded Crows and Western Jackdaws in different height classes when crossing a road in Norway before and after the road was opened for public traffic. All road-crossing times of the day are included.

An important aspect of increased flight height is whether the birds increase the height enough to move out of the collision zone. After the road opening, the number of individuals in the high collision risk zone (0–5 m) decreased and the numbers clearly outside the risk zone (> 10 m) increased (Table 6). It did significantly so for all birds, and for Common Gull *Larus canus*, Hooded Crow *Corvus cornix*, and Western Jackdaw *Corvus monedula*, and for Common Starling before 4 pm. For Northern Lapwing *Vanellus vanellus*, Eurasian Oystercatcher *Haematopus ostralegus*, and Black-headed Gull *Chroicocephalus ridibundus* there was no significant change. Change in the proportion of birds at different height classes is outlined in detail for Hooded Crow and Western Jackdaw in Fig. 3. Nearly 40% of Hooded Crows and 70% of Western Jackdaws were observed in the high-risk collision zone 0–5 m height before the road was opened; this was reduced to about 20% and 5% respectively for the two species after the road was opened (Table 6).

Table 6. Pearson Chi-square or Fisher exact probability tests comparing the number of individuals in the high-risk zone (0–5 m) and outside the risk zone (above 10 m) before and after the road was opened for public traffic. DF = 1 in all analyses. Percent of observations in the high risk zone are given before and after the road was opened.

Species	% in 0–5 m zone		All observations			Observations before 4 pm		
	Before	After	χ^2	n	p	χ^2	n	p
All birds	47.7	24.8	71.35	1515	< 0.001	63.02	1350	< 0.001
Northern Lapwing	30.0	28.3	0.02	73	0.89	2.83	55	0.15
Eurasian Oystercatcher	50.0	41.4	0.23	39	0.72	0.23	39	0.72
Common Gull	51.0	21.9	18.25	302	< 0.001	11.81	272	< 0.001
Black-headed Gull	45.5	47.1	0.01	79	0.92	0.01	79	0.92
Hooded Crow	40.4	19.7	13.13	267	< 0.001	15.78	204	< 0.001
Western Jackdaw	71.1	5.4	44.96	94	< 0.001	25.01	65	< 0.001
Common Starling	88.5	79.3	1.84	92	0.18	6.64	87	0.009

DISCUSSION

In the middle part of Norway there was distinct seasonal variation in the number of birds sitting on the road with a peak in June. The traffic density varied only between about 10,000 to 13,500 cars per day throughout the year (Statens Vegvesen 2014). Seasonal variation in bird numbers and their behaviour can probably explain the variation in bird numbers on the road. In winter, for example, especially during December–March, snow could be a factor in reducing the available amount of food in the surroundings for many bird species. Cereals lost during transport as well as food thrown out of cars might invite some species to spend time on the road during this time of the year, especially corvids, finches and sparrows. In March–April the snow normally melts, and the bare ground exposes food in many locations. In April, and especially in May, many migrating birds arrive to the investigation areas. Some of them search for food on the road thus increasing the number of birds on the roads despite the fact that many resident birds have moved on to their breeding grounds. In June many corvid have fledglings that might search for food on the roads (Husby 1986, Husby & Slagsvold 1992). The seasonal variation in the number of roadkilled birds in the northern part of Europe (Erritzøe et al. 2003, Husby 2016) is similar to the seasonal patterns in the number of birds sitting on the road found in this study.

The number of birds observed on the roads clearly declined with road size, and this was similar in all three countries. My experience with the roads in this investigation is that it was a strong positive correlation between traffic volume and road size. There is a significant positive correlation between the number of birds of a particular species sitting on the road and the number of roadkills (Møller et al. 2011). Also Husby (2016) found that birds sitting on the road increased their susceptibility of becoming a roadkill, while the abundance of the different bird species in the surrounding did not. If birds were flying, there was no similar relationship between the number of birds of each species that flew below 2 m and the number of roadkills (Møller et al. 2011). So, this indicates that on large and busy roads the number of casualties is also lower.

What might be the reason for the lower number of birds along major roads? Main roads have on average a shorter vegetation close by, and this might be more unattractive. However, there were many more birds along gravel roads than along minor asphalt roads, despite the fact that there was no difference in the vegetation close to these two types of roads. Many bird species need pebbles for their grit (Best & Gionfriddo 1991, Gionfriddo & Best 1996). The surface with grit on a gravel road is much larger than on asphalted roads. However, grits are easily accessible also on asphalt roads because they have pebbles on the road verges. Likewise, more car traffic probably results in more garbage and possible food along major roads, so more scavengers could be attracted. It is therefore reasonable to believe that birds are chased away from roads to a higher extent when traffic density increases.

Birds crossing the road at a low elevation are at higher risk of collision with cars. When controlling for the effect of other variables, road opening was the variable that most often gave significant change in flight height. My observations therefore indicate that car traffic causes birds to fly higher, thereby reducing the probability of being killed by a car. It is likely that birds show active avoidance behaviour; they alter height when approaching a road. Birds probably seem to adjust their flight height some distance away from the road. This might be in the same way as my observation point influenced flight height. As I was standing on an open grassland, without camouflage, birds seemed to increase their flight height probably because of my presence.

We need further investigations to understand the increased flight height in the afternoon, by heavier birds and larger flocks.

These results reveal a non-linear relationship between traffic density and road mortality. Logically, a very low traffic density results in a small number of roadkills. At first a linear relationship can be expected but this is altered at higher traffic densities because birds start to avoid roads or (when flying) approach at higher altitudes. This will lower the number of casualties. It also means that studies differ in conclusions dependent on the traffic densities within the study (i.e. Clevenger et al. 2003 vs Gunson et al. 2011). Studies on both birds and mammals (Clevenger et al. 2003, van Langevelde et al. 2009, Rhodes et al. 2014) support this hypothesis. Similar reports on mammals support the idea that road mortality might be highest at intermediate traffic levels. For example, in Wild Boar *Sus scrofa* more roadkills happen at intermediate traffic levels compared to low and high traffic levels (Thurfjell et al. 2015). Similarly, mortality of Badger *Meles meles* was higher on minor roads than on major roads (van Langevelde et al. 2009). Behavioural adaptation found in several mammals, like change in home range, movements and diurnal activity patterns, as well as escape response to vehicle traffic, can result in reduced number of roadkills (Trombulak & Frissell 2000, Seiler & Helldin 2006, Baker et al. 2007). A conceptual model showing a curved (parabolic) relationship between traffic density and number of roadkill is earlier presented based on empirical data on moose-vehicle collisions (Seiler & Helldin 2006), but as far as I know this is the first time for birds.

My hypothesis about a non-linear relationship between car density and number of roadkilled birds might also explain why the number of roadkilled Cliff Swallows *Petrochelidon pyrrhonota* declined over an investigation period of 30 years, despite the fact that car traffic volume over time in that area either increased or did not change significantly. In addition, the Cliff Swallow population has increased in the same period (Brown & Brown 2013). Young Cliff Swallows were not overrepresented among the roadkills, so the relative number of young birds does not explain this reduced mortality trend (Brown & Brown 2013). The authors also proposed that social learning might make the birds smarter over time, a hypothesis that has been supported in Florida Scrub Jays *Aphelocoma coerulescens*. Immigrant birds with no previous experience living along roads experienced a gradual decrease in traffic mortality their first three years as they learned ways to cope with these new variables (Mumme et al. 2000).

Behavioural responses to traffic differ among species. Birds with relatively smaller brains put themselves in more dangerous situations on the roads (Husby & Husby 2014). It is possible that Black-capped Chickadees *Poecile atricapillus* have adapted to traffic in some areas, as they are equally numerous along roads as they are far away from the roads, and they show no physical variation indicating stress along the roads (Proppe et al. 2013).

It is anticipated that traffic probably has only a small effect on the survival of common wildlife populations (Seiler & Helldin 2006). However, for some species there is no doubt that roadkills cause a significant decrease of the population size (i.e. Reijnen & Foppen 2006). For many species traffic noise appears to be the most important causal factor for differences in breeding densities (Reijnen & Foppen 2006). One investigation compared areas with similar noise levels, and found stronger declines in bird populations in areas with higher roadkill mortality rates (Jack et al. 2015), thus supporting the statement of Reijnen & Foppen (2006).

There have been attempts to model roadkill probability (Jaarsma et al. 2006). Behavioural adaptations to car traffic have usually not been taken into consideration. Therefore, the models are not suited for calculating the absolute number of roadkills in any given situation, but can be useful if they are used to compare alternative roads in an area (Jaarsma et al. 2006). An important issue for road planners is whether to build many small roads or fewer highly trafficked roads. My results support that fewer roads with higher traffic density will reduce the number of roadkilled birds. However, other things should also be taken into consideration including which species live in the area, their road crossing abilities, their behavioural adaptations, effects of fragmentation, and other possible effects of few wider roads compared with more secondary roads.

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STRESZCZENIE

[Natężenie ruchu samochodowego wpływa na liczebność i zachowanie ptaków przy drogach]

Jednym z negatywnych efektów, jaki drogi wywierają na dziką przyrodę jest śmiertelność wynikająca z kolizji z samochodami. Co roku ginie z tego powodu kilkaset milionów ptaków na całym świecie. Następuje to często w wyniku zderzenia ze zbliżającym się pojazdem ptaków, które przebywają na drodze lub jej poboczach, a także zderzenia z pojazdem podczas przelotu nad drogą na zbyt niskiej wysokości. Można byłoby oczekiwać, że w miejscach o bardzo dużym natężeniu ruchu samochodowego ptaki będą unikały dróg i poboczy, oraz, że ptaki przelatujące nad drogą powinny to robić na wysokości, która będzie minimalizować ryzyko kolizji z pojazdami. Aby przetestować te hipotezy, autor obserwował ptaki obecne wzdłuż dróg podczas około 1000 przejazdów samochodowych na odległość co najmniej 5 km mających miejsce na Islandii, w Norwegii i Stanach Zjednoczonych (Tab. 1). Prócz tego przeprowadził około 1800 obserwacji wysokości przelotu ptaków przekraczających drogę przed i po otwarciu na niej ruchu samochodowego, rozpatrując w analizach zarówno poszczególne gatunki, jak i grupując je w wyższe jednostki systematyczne, oraz m. in. wielkość obserwowanych stad i porę dnia (Tab. 2, 3).

Liczebność ptaków obserwowanych na drogach była zmienna sezonowo (Fig. 1) i znacznie mniejsza przy wyższym natężeniu ruchu, przy głównych drogach (Tab. 4, Fig. 2). Po otwarciu ruchu samochodowego na nowej drodze ptaki przecinały tę drogę na znacznie wyższej wysokości, niż zanim zaczęła być użytkowana (Tab. 5). Szczególnie dobrze jest to widoczne dla dwóch grup wysokości przelotu: strefy wysokiego ryzyka kolizji tj. 0–5 m nad powierzchnią drogi, oraz strefy poza możliwością kolizji >10 m (Tab. 6). Dla przykładu, przed otwarciem tej drogi 40% obserwacji wron siwych i 70% obserwacji kawek dokonano w strefie wysokiego ryzyka kolizji (0–5 m wysokości). Natomiast po otwarciu ruchu samochodowego te liczby zostały zredukowane odpowiednio do około 20% i 5% (Fig. 3). Gatunki ptaków o większej masie ciała przelatywały nad drogą wyżej niż małe ptaki (Tab. 5).

Przedstawione w pracy przystosowania behawioralne oraz wyniki innych badań stanowią podstawę hipotezy, zgodnie z którą zależność między natężeniem ruchu samochodowego a liczbą zabijanych na drogach ptaków jest nieliniowa, z niższą liczbą ptaków ginących na drogach o niskim i bardzo wysokim natężeniu ruchu. Uzyskane wyniki sugerują, że budowa niewielkiej liczby dróg o bardzo wysokim natężeniu ruchu samochodowego powinna wiązać się z niższą śmiertelnością ptaków niż budowa gęstej sieci wąskich dróg o mniejszym natężeniu ruchu.