OXFORD JOURNALS
Behavioral Ecology

INTERSPECIFIC ANALYSIS OF VEHICLE AVOIDANCE BEHAVIOR IN BIRDS

Journal:	*Behavioral Ecology*
Manuscript ID:	BEHECO-2013-0523.R1
Manuscript Type:	Original article
Keywords:	anthropogenic change, birds, vehicle avoidance behaviour, road ecology

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Running head: Vehicle avoidance in birds

Abstract

Among the most widespread forms of anthropogenic modification of the natural landscape is road construction, with vehicle mortality a major issue affecting amphibians, reptiles, mammals and birds. Why some species are more susceptible to vehicle collision than others however is poorly understood. We examine how roadside vegetation patterns, road size, vehicle speed and brain size influence vehicle avoidance behavior using more than 3700 individuals of eleven species of European birds. We find that on larger roads and at higher vehicle speeds birds were more likely to fly away from the road than to cross it. Moreover, species with a larger relative brain size flew away from the road more often than species with a small brain size, something that may in part explain inter-species differences in vehicle collision mortality rates. Our results provide important insights into factors that influence vehicle avoidance behavior in birds and show that brain size can be an important trait for adjusting to novelties in their environment.

Keywords: anthropogenic change, behavior, road ecology, vehicle avoidance behavior.

Introduction

Road construction is among the most widespread and severe forms of human made modification to the natural landscape (Forman and Alexander 1998; Fahrig and Rytwinski 2009) and have well-documented negative effects on wildlife, including loss of habitat, population fragmentation, pollution, poisoning and direct mortality caused by collision with vehicles (reviewed in (Forman and Alexander 1998; Erritzoe, Mazgajski, and Rejt 2003; Fahrig and Rytwinski 2009; Kociolek et al. 2011). In particular collision with vehicles ('road kills') represents a considerable mortality risk in many species of amphibians, reptiles, mammals and birds (Mumme et al. 2000; Fahrig and Rytwinski 2009; Kociolek et al. 2011).

Theoretical models have clearly demonstrated that the least vulnerable populations are those which show high vehicle avoidance behavior (Jaeger et al. 2005), however empirical attempts to find the mechanisms behind why species vary in their vehicle avoidance behavior are scarce. Variation in vehicle avoidance could be a result of differences in external factors such as, for example, the speed of the approaching vehicle or the type of road (Erritzoe, Mazgajski, and Rejt 2003), but could also be due to interspecies differences in morphology (Brown and Bomberger Brown 2013), previous exposure to vehicles (Mumme et al. 2000) or ability to judge vehicle speed and distance.

Several recent studies have demonstrated that species with a larger relative brain size (i.e. brain size controlled for body size) are more successful when introduced into novel environments (Sol et al. 2005; Sol et al. 2008; Sol et al. 2012), probably because a larger brain can buffer individuals against environmental changes by facilitating novel behavioral responses (Sol 2009). Variation in relative brain size among species may therefore be one potential factor affecting the ability of species to cope with anthropogenic changes such as vehicle traffic, which for many species represents a novelty in their environments.

To examine what contributes to variation in vehicle avoidance behavior among species, we collected data on more than 3700 individuals from eleven different species of European birds. We asked whether the characteristics of the road and the considerable variation in relative brain size among bird species (Iwaniuk and Nelson 2003; Sol et al. 2012) may contribute to among species variation in vehicle avoidance behavior and therefore species vulnerability to vehicle collision (Jaeger et al. 2005).

Materials and Methods

Data collection

Data on vehicle avoidance behavior of individual birds were collected in Norway along different types of roads in both rural and urban areas during the years 2003-2010. While driving a vehicle, we recorded the flight direction of birds sitting on or near the road when approached by the vehicle according to whether they flew away from the road or if they crossed the road. Only birds that were observed before moving and that were located on or within approximately 1 meter from the road verge (i.e. approx. 1 meter into the road from the verge and approx. 1 meter outside the road from the verge) and that moved by flying were recorded. Birds located closer to each other than approximately 100 meters were not recorded as the behavior of the first individual may have influenced the behavior of the second individual. Similarly, for flocks (two or more individuals in the same area) we only recorded the behavior of the bird closest to the car, which was normally the individual that moved first. Birds that flew vertically up from the road and crossed the road lanes at a height of more than approximately 3 meters were recorded as flying away from the road as these were assumed to be outside the collision zone. Not all birds could be identified to species and these individuals were excluded from the analyses.

Vehicle speed was categorized as being ≤ 50 km/h (n =1848), between 50 – 80 km/h (n = 1417), or above 80 km/h (n = 526). The type of road was classified as major paved road with heavy traffic (n = 742, road type 1), minor paved road with intermediate traffic (n = 1608, road type 2), or gravel road with little traffic (n=1441, road type 3). The vegetation in the immediate vicinity of the road was classified according to: i) similar height or no vegetation on both sides of the road (vegetation type 1), ii) higher on the side where the bird was sitting compared with the other side (vegetation type 2) or iii) lower on the side where the bird was sitting compared to the other side (vegetation type 3). We categorized each species according to whether its natural habitat was open landscape, semi-open or forest to control for between-species differences in ecology and potential differences in exposure to vehicles.

Observations were collected in all months of the year, but the majority during spring and summer (April, May, June, July and August together constitute 80 % of all observations). To control for this we included season as a two level factor in the statistical analyses (summer= April, May, June, July and August, winter = other months).

Data on body mass and brain mass were obtained from (Maklakov et al. 2011) except for *Larus canus* and *Turdus iliacus* which were obtained from (Garamszegi, Møller, and Erritzoe 2002) and (Møller, Erritzoe, and Garamszegi 2005) respectively (sex-averaged values were used for *T. iliacus*). These are reported in Table 1 together with number of observations.

Reconstructing phylogeny.

To control for shared ancestry of species we used a phylogenetic tree that was constructed using sequence data from 12 mitochondrial genes (Thomas 2008). The phylogenetic variance-covariance matrix was then used as a random effect in a Bayesian phylogenetic logistic mixed model using the R package MCMCglmm (Hadfield 2010), see statistical analyses.

Statistical analyses.

Test of departure from random vehicle avoidance behavior (i.e. 50% crossing the road) for each species was done using exact binomial tests (Table 1). We tested for between-species variation in the extent to which individuals fly away or crossed the road by fitting species as a fixed effect in MCMCglmm. Because it is not possible to obtain an ANOVA table from a MCMC object, we used a weighted Z-test (Zaykin 2011) to test for among-species differences.

To test for a phylogenetic signal we compared a model with a phylogenetic variance covariance matrix as random effect with a similar model including species as random effect.

We examined how variation between species in their vehicle avoidance behavior was related to road type, roadside vegetation pattern, vehicle speed, body mass, brain size, season and the ecology of the species using Bayesian mixed models as implemented in the R package MCMCglmm (Hadfield 2010; Hadfield and Nakagawa 2010) running 110,000 iterations with a burn in period of 10,000 and a thinning interval of 100 and using uninformative priors. We checked that autocorrelation between samples were less than 0.1.

The logarithm of brain mass and body mass were used as covariates in the model (Freckleton 2002), which also controls for a positive relationship between body mass and flight initiation distance in birds (Carrete and Tella 2011). Using 'relative brain size' (residuals from a log-log regression of brain size on body mass) gave similar results (see supplementary materials).

Results

When a vehicle approaches a bird sitting on the road, the bird can avoid it by either taking the shortest distance away from the vehicle and fly directly away from the road, or it can avoid the vehicle by flying across the road. Individuals that fly directly away from the road will spend less time in the vehicle collision zone and have lower mortality risk compared to individuals that fly across the road before leaving it. One would therefore expect that most individuals fly directly away from the road rather than cross it. Consistent with this we found that in all species, apart from *Larus canus* and *Turdus iliacus,* a significantly larger proportion of individuals avoided vehicles by flying directly away from the road rather than crossing it (Table 1). However, there was significant variation between species in their vehicle avoidance behavior (weighted *Z*-test: P < 0.0001). For example, whereas *Corvus monedula* avoided vehicles by flying away from the road in more than 80 % of observations (Table 1), *Larus canus* did not show any consistency in flight direction (52 % flying away from the road, Table 1). To better understand this interspecies variation in vehicle avoidance behavior we tested whether differences among species were related to characteristics of the road or due to variation in brain size (corrected for body mass). Because a Bayesian phylogenetic model to control for the shared ancestry of species had a higher Deviance Information Criteria (DIC) compared to a model using species as random effect (ΔDIC =0.79), we used a logistic regression mixed model with species (instead of phylogeny) as random effect in the following analyses. However, using phylogenetic models gave same result and estimates from the phylogenetic model are reported in table S1.

The best model included brain mass, body mass, road type, vegetation type, vehicle speed and the species ecology, whereas there was no indication of differences in vehicle avoidance behavior between summer and winter season (Table 2a).

The relationship between the probability that an individual will fly directly away from the road and the relative size of the brain was positive (Table 2b), indicating that species with a large brain relative to their body size generally avoided vehicles by flying directly away from the road more often compared to species that had a small brain (Fig. 1). It should be noted that brain size and body mass are highly correlated in our data both on observed ($r_p = 0.919$, $P < 0.001$) and on a log-log scale ($r_p = 0.966$, $P < 0.001$), something which could cause co-linearity problems. To examine this we also analyzed our data using relative brain size (residuals from a log-log regression of brain size on body mass) and again found a positive relationship between probability to fly away from the road and relative brain size (Table S2), indicating that the results are not caused by problems with co-linearity. Moreover, there was a significant negative relationship between body mass (controlled for brain size) and escape direction indicating that species with a larger relative body mass crossed the road more frequently compared to species with a small relative body mass.

Roadside vegetation pattern also had a significant influence on flight direction (Table 2b). Although the probability of flying away from the road did not differ between areas which had no or equal vegetation height on both sides of the road or where the vegetation was higher on the side of the road from which the bird left, there was a significant increase in probability of crossing the road if the vegetation was higher on the opposite side to which the bird took off from (Table 2b). This suggests that at least for some species seeking vegetation cover is an important escape strategy when avoiding vehicles.

The type of road, classified as highway with high traffic volume, paved road with intermediate traffic volume and minor gravel road with little traffic, also influenced vehicle avoidance behavior: The probability of flying away from the road was significantly larger on highways compared to the other two road types (Table 2b), indicating that birds perceive the risk associated with crossing the road differently at varying levels of traffic volume or road size.

As the speed of the vehicle increased so did the probability of a bird flying away from the road (Table 2b). When testing each road type separately we found that this was only true on minor roads ($b = 0.595$, lower-95%= 0.396, upper-95% = 0.834, pMCMC = < 0.001) and gravel roads ($b = 0.358$, l-95%= 0.056, u-95% = 0 649, pMCMC= 0.02) and not on highways ($b = 0.077$, l-95% = -0.32, u-95% = 0.38, $P = 0.64$), possibly because there is less variation in vehicle speed on highways compared to the other two road types.

Discussion

Vehicle collisions constitute a significant mortality source for many animal species with tens of millions of birds killed annually in both Europe (Erritzoe, Mazgajski, and Rejt 2003) and the United States (Erickson, Johnson, and Young 2005). However, we still know little about why some species are more susceptible to vehicle mortality than others. We show here that both characteristics of the road and relative brain size is associated with vehicle avoidance behavior.

Why would species with a larger brain be better at avoiding vehicles? Previous studies have found that individuals with a large relative brain size may have increased cognitive ability (Sol et al. 2005; Kotrschal et al. 2013), although this is a controversial issue (Chittka and Niven 2009; Sol 2009). A larger relative brain size may result in the ability to judge vehicle speed and/or direction more accurately through increased spatiotemporal information processing skills. In addition, a larger brain may also facilitate vehicle avoidance through learning. Learning has been shown in Florida Scrub Jays (*Aphelocoma coerulescens*) where immigrant birds with no previous experience living next to roads have higher mortality than birds with such experience (Mumme et al. 2000). It should be noted that the association between brain size and vehicle avoidance behavior is based on a limited number of species, largely within the same order (Passeriformes) and thus examining vehicle avoidance behaviour also in other groups of birds is needed to evaluate the generality of this finding across the avian phylogeny.

Vegetation along roadsides generally attract different animal and plant species and have been extensively documented (Forman and Alexander 1998; Orłowski 2008). However, roadside vegetation can also lead to increased mortality rates, for example in birds who use it as an attractive place for breeding, resting and foraging (Erritzoe, Mazgajski, and Rejt 2003; Orłowski 2008). Our results demonstrate that roadside vegetation patterns can also influence vehicle avoidance behavior as there was a higher probability for a bird to cross the road if the vegetation was higher on the opposite side to which the bird was leaving from (Table 2b). In contrast, if vegetation was higher on the side of the road where the bird was sitting the bird was more likely to fly away from the road and this was also the case if there was no vegetation or when the vegetation was of equal height on both sides of the road.

Not only roadside vegetation patterns altered vehicle avoidance behavior, also the size of the road and hence traffic density were important determinants of flight direction (Table 2b). It is well known that vehicle collision mortality rates in many species of animals are higher on large roads with high traffic density (Forman and Alexander 1998; Erritzoe, Mazgajski, and Rejt 2003; Orłowski 2008; Kociolek et al. 2011). That traffic density and road size should influence vehicle avoidance behavior is therefore not surprising, birds were less likely to cross the road at major highways with more traffic compared to smaller roads with less traffic (Table 2b). The differences in vehicle avoidance behavior between road types could, for example, be a result of habituation to vehicles on highways due to more frequent exposure to vehicles.

Another characteristic of the road that we did not examine here but that could also play an important role for the vehicle avoidance behavior of birds is the age of the road because this determines the amount of exposure birds have had with vehicle traffic. As the study on Florida Scrub Jays demonstrates previous exposure to vehicles can impact mortality patterns and it would be interesting to study the role of experience on vehicle avoidance behaviour in more detail.

A larger proportion of individuals flew directly away from the road when the vehicle speed was high compared to when it was low (Table 2b). This suggests that birds adjust their vehicle avoidance behavior according to the speed limit of the car or the speed limit in the area (we did not record speed limit in the area but of course these two measures will be near identical). A recent study found that birds adjust their flight initiation distance in relation to the speed limit of the road but not vehicle speed, with longer flight initiation distance in areas where the speed limits were higher (Legagneux and Ducatez 2013). Our study extends this work to show that also the direction in which birds chose to leave the road to avoid being hit by a car is changing with vehicle speed (and/or speed limits). Together our study and that of Legagneux & Ducatez (2013) suggest that behavioral adjustments to anthropogenic changes can be flexible.

In summary, our results demonstrate that the size of the road, roadside vegetation pattern and vehicle speed as well as brain size are important in determining vehicle avoidance behavior. The positive association between brain size and vehicle avoidance behavior is particularly interesting and support other studies that have found brain size to be an important predictor for behavioral innovativeness and flexibility (Lefebvre, Reader, and Sol 2004; Sol et al. 2012). The ability of different species to adjust to anthropogenic changes in the environment may therefore in part be determined by differences in the relative size of the brain.

Acknowledgments

We are grateful to Per Inge Værnesbranden for help in collecting data, to Terje Kolaas for access to photographs and to Mirjam Amcoff for assistance with the phylogeny. Comments from Tore Slagsvold, Staffan Ulfstrand, Anna Qvarnström, Alexander Kotrschal, David Wheatcroft and two anonymous reviewers greatly improved the manuscript. Financial support was received from the Norwegian Research Council (grant number 176633/V40 to MH and grant number 214553 to AH).

Data accesbility

The data are deposited in Dryad (#accession nr provided upon acceptance).

References

Brown CR, Bomberger Brown M. 2013. Where has all the road kill gone? Current Biology 23:R233–R234.

Carrete M, Tella JL. 2011. Inter-Individual Variability in Fear of Humans and Relative Brain Size of the Species Are Related to Contemporary Urban Invasion in Birds. PLoS ONE 6:e18859.

Chittka L, Niven J. 2009. Are bigger brains better? Curr. Biol. 19:R995–R1008.

Erickson WP, Johnson GD, Young DP Jr. 2005. A summary and comparison of bird mortality from anthropogenic causes with an emphasis on collisions. USDA Forest Service General Technical Report PSW-GTR-191:1029–1042.

Erritzoe J, Mazgajski TD, Rejt L. 2003. Bird casualties on European roads — a review. Acta Ornithologica 38:78–93.

Fahrig L, Rytwinski T. 2009. Effects of roads on animal abundance: an empirical review and synthesis. Ecology and Society 14.

Forman RTT, Alexander LE. 1998. Roads and their major ecological effects. Annual Review of Ecology and Systematics 29:207–231.

Freckleton RP. 2002. On the misuse of residuals in ecology: regression of residuals vs. multiple regression. J Anim Ecol 71:542–545.

Garamszegi LZ, Møller AP, Erritzoe J. 2002. Coevolving avian eye size and brain size in relation to prey capture and nocturnality. Proc. Biol. Sci. 269:961–967.

Hadfield JD, Nakagawa S. 2010. General quantitative genetic methods for comparative biology: phylogenies, taxonomies and multi-trait models for continuous and categorical characters. Journal of Evolutionary Biology 23:494–508.

Hadfield JD. 2010. MCMC Methods for Multi-Response Generalized Linear Mixed Models: The MCMCglmm R Package. Journal of Statistical software 33:1–22.

Iwaniuk AN, Nelson JE. 2003. Developmental differences are correlated with relative brain size in birds: a comparative analysis. Can. J. Zool. 81:1913–1928.

Jaeger J, Bowman J, Brennan J, Fahrig L, Bert D. 2005. Predicting when animal populations are at risk from roads: an interactive model of road avoidance behavior. Ecological Modelling 185:329–348.

Kociolek AV, Clevenger AP, St Clair CC, Proppe DS. 2011. Effects of Road Networks on Bird Populations. Conservation Biology:241–249.

Kotrschal A, Rogell B, Bundsen A, Svensson B, Zajitschek S, Brännström I, Immler S, Maklakov AA, Kolm N. 2013. Artificial Selection on Relative Brain Size in the Guppy Reveals Costs and Benefits of Evolving a Larger Brain. Curr. Biol. 23:168–171.

Lefebvre L, Reader SM, Sol D. 2004. Brains, innovations and evolution in birds and primates. Brain Behav. Evol. 63:233–246.

Legagneux P, Ducatez S. 2013. European birds adjust their flight initiation distance to road speed limits. Biology Letters 9.

Maklakov AA, Immler S, Gonzalez-Voyer A, Ronn J, Kolm N. 2011. Brains and the city: big-brained passerine birds succeed in urban environments. Biology Letters 7:730–732.

Mumme RL, Schoech SJ, Woolfenden GE, Fitzpatrick JW. 2000. Life and death in the fast lane: demographic consequences of road mortality in the Florida scrub-jay. Conservation Biology 14:501–512.

Møller AP, Erritzoe J, Garamszegi LZ. 2005. Covariation between brain size and immunity in birds: implications for brain size evolution. Journal of Evolutionary Biology 18:223–237.

Orłowski G. 2008. Roadside hedgerows and trees as factors increasing road mortality of birds: Implications for management of roadside vegetation in rural landscapes. Landscape and Urban Planning 86:153–161.

Sol D, Bacher S, Reader SM, Lefebvre L. 2008. Brain Size Predicts the Success of Mammal Species Introduced into Novel Environments. Am. Nat. 172:S63–S71.

Sol D, Duncan RP, Blackburn TM, Cassey P, Lefebvre L. 2005. Big brains, enhanced cognition, and response of birds to novel environments. Proc. Natl. Acad. Sci. U.S.A. 102:5460–5465.

Sol D, Maspons J, Vall-Llosera M, Bartomeus I, García-Peña GE, Piñol J, Freckleton RP. 2012. Unraveling the life history of successful invaders. Science 337:580–583.

Sol D. 2009. Revisiting the cognitive buffer hypothesis for the evolution of large brains. Biology Letters 5:130–133.

Thomas GH. 2008. Phylogenetic distributions of British birds of conservation concern. Proceedings of the Royal Society B: Biological Sciences 275:2077–2083.

Zaykin DV. 2011. Optimally weighted Z-test is a powerful method for combining probabilities in meta-analysis. Journal of Evolutionary Biology 24:1836–1841.

Table 1. Species data for body mass, brain mass, number of records, number of observations of crossing versus flying away from the road and *P*-values from an exact binomial test if proportion crossing was significantly different from random (i.e. a proportion of 0.5).

Genus	**Species**	**Family**	**Body mass (g)**	**Brain mass (g)**	**Observations**	**Crossed road**	**Away from**	**Binomial test**
Corvus	*corone*	Corvidae	479.78	8.472	660	165	495	**<0.0001**
Corvus	*monedula*	Corvidae	214.39	4.840	262	49	213	**<0.0001**
Pica	*pica*	Corvidae	204.51	5.526	658	166	492	**<0.0001**
Larus	*canus*	Laridae	360.05	3.80	129	61	68	0.5975
Emberiza	*citrinella*	Emberizidae	28.65	0.822	264	112	152	**0.0162**
Fringilla	*coelebs*	Fringillidae	21.40	0.810	114	43	71	**0.0111**
Motacilla	*alba*	Motacillidae	21.11	0.598	655	263	392	**<0.0001**
Sturnus	*vulgaris*	Sturnidae	82.59	1.925	187	53	134	**<0.0001**
Passer	*domesticus*	Passeridae	27.70	0.970	131	39	92	**<0.0001**
Turdus	*iliacus*	Turdidae	65.20	1.215	110	58	52	0.6338
Turdus	*pilaris*	Turdidae	99.80	1.900	623	243	380	**<0.0001**

Table 2.

a) Model comparison of the Bayesian mixed models using species as a random effect. BS is the log10 of brain size, BM the log10 of body mass, RV is roadside vegetation pattern, RT is road type, VS is vehicle speed, E is the ecology of the species and S is the season the bird was observed (see Methods for further details). Best model is indicated in bold.

Fixed terms	**DIC**
BS + BM + RV + RT + VS + E + S	4566.34
BS + BM + RV + RT+ VS + E	**4564.76**
BS + BM + RV + RT + VS	4565.52
BS + BM + RV + RT	4593.39
BS + BM + RV	4661.32
BS + BM	4672.16
BS	4673.01

b) Summary of fixed effects from the Bayesian logistic mixed model that best explain the probability to fly away from the road (from Table 2a). Estimate is the posterior mean, LCI and UCI are the lower and upper 95% credible intervals. Terms are explained in Table 2a.

Coefficient	**Estimate (β)**	**LCI**	**UCI**	**pMCMC**
Intercept	3.677	1.112	6.107	0.014
BS	2.921	0.888	4.649	0.010
BM	-2.125	- 3.515	- 0.634	0.012
RV_2	0.022	-0.221	0.238	0.890
RV_3	-0.552	-0.901	-0.193	<0.001
RT_2	-0.229	-0.497	0.065	0.114
RT_3	-0.599	-0.909	-0.294	<0.001
VS	0.415	0.268	0.564	<0.001
E_2	0.159	-0.339	0.634	0.438
E_3	-0.099	-0.694	0.444	0.714

Figure legends

Fig. 1. There was a significant positive relationship between relative brain size and the proportion of birds that avoided vehicles by flying away from the road. Displayed is the predicted slope from a GLM of the proportion of individuals flying away from the road for each species on residual brain size ($b= 3.5$, $se = 0.77$, $t = 4.85$, $P < 0.001$) and is for illustration purposes only. See Table 2 for coefficient estimates from the Bayesian logistic mixed model.

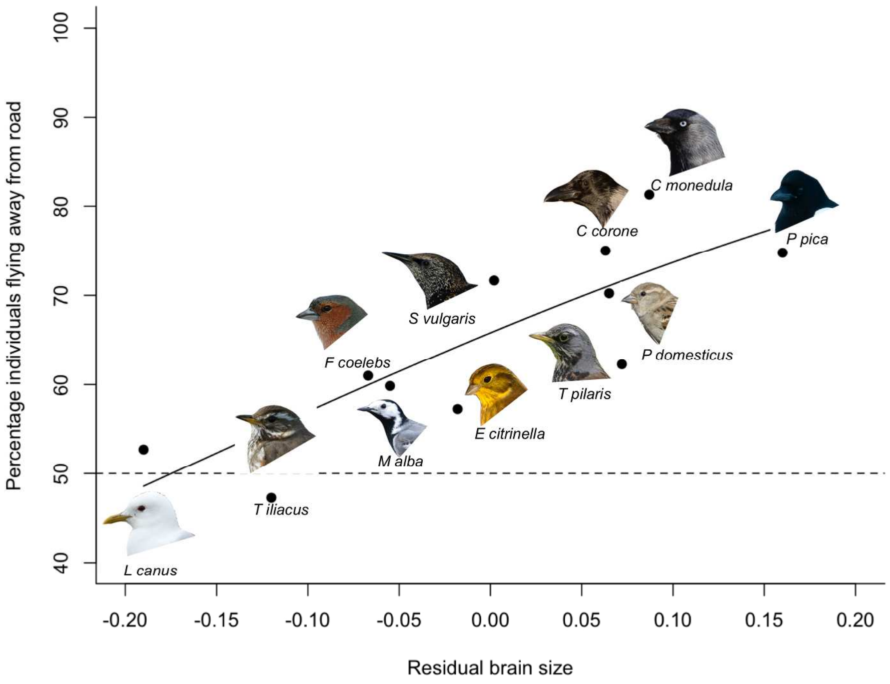

Figure 1
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