The Relationship Between Relative Brain Size and Avoidance of Vehicular Collisions in Birds Is Subtle

Robert M. Zink[1],* and Brittaney L. Buchanan[1,2]

*[1]School of Natural Resources, School of Biological Sciences and Nebraska State Museum, University of Nebraska-Lincoln, USA 56853. *Correspondence: E-mail: rzink2@unl.edu (Zink)*

[2]Biology Department, University of Florida, Gainesville, Florida, USA 32611. E-mail: buchananbl55@gmail.com (Buchanan)

(Received 15 November 2024 / Accepted 12 January 2025 / Published -- 2025)

Communicated by Jen-Pan Huang

ORCiD

Robert M. Zink: https://orcid.org/0000-0001-9243-4567

Møller and Erritzøe (2017) reported that birds killed by collisions with vehicles had on average relatively smaller brains than birds killed by other causes, which were not identified. Despite concerns about the method used to assess brain mass, we reanalyzed the published data of Møller and Erritzøe (2017) after excluding extraneous species and confirmed a subtle tendency for birds killed by vehicular collision to have somewhat small brains. Some groups of birds (owls, hawks, garden birds and migratory species) did not reflect the overall result. Surprisingly there was no effect of age or sex, whereas one would expect inexperienced immature birds and females in breeding condition to be vulnerable. Overall, plots of brain mass in birds killed by vehicular collisions and other causes greatly overlap, and in some species, individuals killed by collisions have relatively larger brains. That is, the tendency for birds hit by vehicles to be relatively smaller brained is not universal, nor in any species is there an absolute difference in brain size between the two categories. It is possible that in the short time birds have interacted with moving vehicles that selection has acted on brain size to avoid collisions, although we suggest that slightly larger brains might represent an innate tendency to avoid rapidly approaching objects. An interesting question from their study is what was the cause of mortality in the birds not hit by vehicles. Likely sources of mortality of birds post-nestling stage include depredation (natural and house cats) and collisions with windows and other human structures. In fact, relatively large-brained birds might be more susceptible to collisions with windows or being caught by cats (*i.e.*, the other sources of mortality), for which having a relatively larger brain would not appear to mitigate these sources of mortality.

Key words: Bird brains, Brain mass, Cognitive ability, Vehicular collisions, Avian mortality

Citation: Robert M. Zink RM, Buchanan BL. 2025. The relationship between relative brain size and avoidance of vehicular collisions in birds is subtle. Zool Stud **64:**03.

BACKGROUND

Many anthropogenic factors negatively affect bird populations, including habitat loss, pesticides, feral cats, and collisions with buildings, towers, and moving vehicles. Because these threats appear to have had major impacts (Rosenberg et al. 2019), there is interest in their mitigation (Tilman et al. 2017). A threat to bird populations includes roadways (Kociolek et al. 2011; Husby and Husby 2014) because road noise degrades habitat suitability and affects breeding bird success (Ware et al. 2015), and fatalities owing to vehicular collisions (Loss et al. 2014; Legagneux and Ducatez 2013; Morelli et al. 2020). The question arises as to whether birds have innate or learned mechanisms that facilitate avoidance of vehicular collisions.

Møller and Erritzøe (2017) concluded that birds killed by collisions with vehicles had relatively smaller brains than birds killed by other causes; sources of mortality for larger brained birds were not identified. For example, Møller and Erritzøe (2017) noted that some corvids can judge vehicular speed on roads and adapt to traffic (Mukherjee et al. 2013), which might allow individuals with relatively larger brains to avoid collisions with vehicles. These conclusions assume a link between overall brain size and behavioral plasticity, a postulate questioned by some (Healy and Rowe 2007; Chittka and Niven 2009; Roth et al. 2010; Powell et al. 2017) but supported by others (van Schaik et al. 2023). In some species, the relative density of neurons in certain brain regions are correlated with differences in behavior (Olkowicz et al. 2016). For example, a larger hippocampus results in greater memory of cache locations in birds and size changes annually to accommodate seasonal needs (Hampton and Shettleworth 1996; Sherry 2011; Yaskin 2011; Freas et al. 2013), although Pravosudov (2022) suggests evidence for seasonal change is tenuous at best. Sol et al. (2022) suggest that the number of pallial neurons, those associated with innovation propensity, is correlated with general brain size (absolute and relative). Kverkova et al. (2022) make a similar conclusion, especially with land birds and higher primates. Because of conflicting opinions in the literature a null hypothesis seems elusive. In this paper, we revisit Møller and Erritzøe's (2017) conclusion that brain size is correlated with avoidance of moving vehicles. We were interested in whether data for all species support the notion that birds with smaller brains exhibit heightened vulnerability to collision, and for species with a trend, is there a discrete separation between brain masses of individuals killed by collision or by other causes, or is the trend more subtle?

MATERIALS AND METHODS

Measuring brains

Several methods have been used to estimate overall brain size in birds and other animals. Wagnon and Brown (2020) estimated brain size by measuring head dimensions, without verification of its relationship to actual brain size. Laursen and Møller (2021) claimed that for a duck species, skull size was significantly correlated with dried brain mass, although raw data were not provided, nor were the methods involving extraction and desiccation of the 15 brains. In a more sophisticated analysis, Olkowicz et al. (2016) stated that the "brains they examined were dissected into the cerebral hemispheres, cerebellum, diencephalon, tectum, and brainstem. In one individual per species, one hemisphere was dissected into the pallium and the subpallium. In these brain components, the total numbers of cells, neurons, and nonneuronal cells were estimated following the procedure of isotropic fractionation". Inferences about the relationship between brain size and traffic mortality depends on accurate and precise measurement of brain size, for which Møller and Erritzøe (2017) chose brain mass. Møller (in litt. 31 May 2017) stated that the methods used in Møller and Erritzøe (2016) for measuring brain mass were described in a published paper, whereas the methods are actually described in a website maintained by taxidermist and co-author J. Erritzøe, http://www.birdresearch.dk/?page_id=310. The method is described as: "The brain is weighed after removing it from underside of head and placing it on an already weighted [sic] absorbing paper and remaining part of the brain is sucked up with small pieces of same paper. If brain of a specimen has began [sic] to dry, it is not weighed. In cases where whole skeleton is kept for the collection, the brain is weighed using the following procedure: First a piece of absorbing paper and some cotton wool are weighed, the brain is then removed by putting wool inside the brain case through foramen with a pair of pincers, and this wool is moved around before being removed. This procedure is repeated until no more brain tissue is visible on the wool. The brain on the paper and the used and unused wool is finally weighed, and the weight of the paper and the wool before starting the extraction procedure is subtracted." On this website Erritzøe shows that in 5 months the overall mass of a frozen barn swallow drops by 1%. Thus, the measurements of brain size are confounded by an unknown measurement error, yet Møller and Erritzøe (2016 2017) report brain mass to the nearest 0.01 g. For example, the average brain mass (across sex and age) of Chaffinch (*Fringilla coelebs*) that were hit by vehicles was 0.730667 g and for those not hit the comparable value was

0.75309g, a 3% difference. Chaffinches are about the same size as Barn Swallows, and it is possible that 1/3 of the difference between the two categories is artifactual owing to desiccation in a freezer (depending on time in freezer). In summary, the two procedures used by Møller and Erritzøe (2016 2017) to measure brain mass have not been vetted or published in a peer-reviewed journal.

Species sampling

We downloaded the online data set used by Møller and Erritzøe's (2017) and discovered 111 duplicated entries (fide J. Erritzøe, in litt.), which we removed. The data set included individuals that were shot, which Møller and Erritzøe (2016) already claimed had smaller brains (contrary to the conclusions of Zink and Stuber 2017), and for consistency we also excluded them. After removing shot individuals and duplicates, there were 1147 individuals that were hit by vehicles and 2265 that died from other, unspecified causes. In our opinion, to be relevant for assessing the relationship within species between relative brain size and vehicular collisions, a species should have sufficient numbers of individuals killed by vehicles and other causes. Instead, multiple species were represented by either no or one individual that was killed by a vehicle. For example, in 33 hawfinch (*Coccothraustes coccothraustes coccothraustes*), none were hit by vehicles, and therefore it cannot be determined whether they are vehicle-collision avoiders or for some reason are not vulnerable. Møller and Erritzøe (2017) included caged or zoo specimens: spectacled barwing (*Actinodura ramsayi yunnanensis*), red-and-green macaw (*Ara chloropterus*), Major Mitchell's cockatoo (*Lophochroa leadbeateri*), dark-breasted rosefinch (*Procarduelis nipalensis*), three-banded rosefinch (*Carpodacus trifasciatus*), Pallas's rosefinch (*Carpodacus roseus*), speckled mousebird (*Colius striatus*), smooth-billed ani (*Crotophaga ani*), meadow bunting (*Emberiza cioides*), Tristram's bunting (*Emberiza tristrami*), red-billed leiothrix (*Leiothrix lutea*), Patagonian negrito (*Lessonia rufa*), black-faced munia (*Lonchura molucca*), Mongolian lark (*Melanocorypha mongolica*), russet sparrow (*Passer cinnamomeus*), mulga parrot (*Psephotellus varius*), brown bullfinch (*Pyrrhula nipalensis*), streaky-headed canary (*Crithagra gularis*), blue-naped mousebirds (*Urocolius macrourus*), guira cuckoo (*Guira guira*), great spotted cuckoo (*Clamator glandarius*)], which we removed. Many ducks, geese, seabirds (e.g., puffins, fulmar, loons), and shorebirds (sandpipers, plovers) were included, species that spend most of their lives away from roadways. Several farmed species were included: emu (*Dromaius novaehollandiae*), Indian peafowl (*Pavo cristatus*), greater rhea (*Rhea americana*). A number of vagrants from elsewhere were included. We consider these individuals to be irrelevant and we removed them.

For nearly all other species, the distribution of individuals departed from what we consider a valid sample - similar numbers of individuals hit by vehicles and not hit by vehicles distributed across sex and age. For example, 2 of 35 adult male Eurasian sparrowhawks (*Accipter nisus*) were hit by vehicles, 7 of 64 adult females, 4 of 66 immature males and 11 of 109 immature females, whereas one would prefer a more even distribution of hit and non-hit for relative brain-size comparisons. That is, even if a species was collision-averse, individuals of both hit and non-hit categories should be included to illustrate whether there is an effect of brain size. For 68 common kingfisher (*Alcedo atthis ispida*), only four individuals were hit by vehicles, all juveniles. For 33 Bohemian waxwings (*Bombycilla garrulus garrulus*), one adult and two juveniles were hit by vehicles. Thus, we deleted all species that did not have two or more individuals in each category resulting in a reduced data set including 2389 total individuals from 53 species and 41 genera. That is, we excluded duplicated observations from the data set, shot birds, species that did not have at least two observations for both killed and not killed by traffic, and species that did not have at least 10 observations total.

Statistical analyses

Basic data exploration across species

Iwaniuk and Nelson (2003) provided estimates of brain volume and body mass (not necessarily from the same individuals measured for brain volume) that can be used to assess congruence across species. We plotted the residuals of log brain mass (vs body mass) from Møller and Erritzøe's (2017) versus the residuals of log brain volume (vs body mass) from Iwaniuk and Nelson (2003) for 124 species measured in common to assess congruence of estimates of brain size across species.

Basic data exploration within species

Unlike the case across species, we have no way of verifying or testing either the precision or accuracy of Møller and Erritzøe’s (2017) measure of brain size (mass) among sexes and ages of individuals for a given species. However, we concluded that exploration of the basic data was appropriate. We plotted the percent difference in brain mass for individuals hit and not hit by vehicles, to explore whether differences in brain size were consistent or a function of the size of the species, or perhaps attributable to measurement error associated with birds of different sizes. Because the data included species with highly variable numbers of individuals, collision frequency, percent difference between hit and non-hit, and ages and sexes, we plotted the relationship between species' mean residual (log)brain size and the proportion of individuals of each species that were killed by vehicular collision, using the reduced data set. We note that the proportion of individuals hit by vehicles is only assumed to be a random sample of mortalities. To illustrate variation within species we plotted the distribution of residual brain volumes in our reduced data set by species for individual birds hit by vehicles and for death caused by other sources, as well as the overall difference across species between individuals killed by vehicular collision and other causes. Lastly to explore consistency across species, we tallied the number of comparisons (*n* = 211) in which birds of a particular age or sex that were traffic fatalities had larger brains than birds that died from other causes.

Multivariate statistical analyses of differences in brain size in birds killed by vehicles and other sources

We used generalized linear mixed models fit by maximum likelihood (LaPlace approximation as described in Zink and Stuber (2017)) to analyze residuals of log brain mass on log body mass using the reduced data sets. Although Morelli et al. (2020) showed that there was not a phylogenetic component to their avian roadkill data, we added taxonomic order, family, genus, and species of each species as random effects to account for taxonomic biases (sex and age were fixed effects); we did not perform phylogenetic independent contrasts because we analyzed few species (53) across much of avian diversity for which there is no agreed upon phylogeny.

To assess whether the result of Møller and Erritzøe (2017) was general or driven by particular types of birds, we analyzed several subsets of the data. We analyzed raptors and owls separately to see if there was an effect for predators that typically forage during the day and night. We reasoned that nocturnal owls might respond differently to vehicles as they will mostly be confronted with headlights at night. We analyzed separately common "garden" birds (house sparrow (*Passer domesticus*), starling (*Sturnus vulgaris*), wood pigeon (*Columba palumbus*), goldfinch (*Carduelis carduelis*), robin (*Erithacus rubecula*), great tit (*Parus major*), chaffinch (*Fringilla coelebs*), long-tailed tit (*Aegithalos caudatus*)) because they might be most likely to have learned to avoid vehicles living in urban situations, and those that had not been already removed from the population. Although roads do not typically bisect gardens, birds moving from garden to garden might often cross a road and be vulnerable to collision. Because Møller and Erritzøe (2017) specifically mentioned that corvids could judge vehicular speed and direction, we analyzed five species of corvids (common raven [*Corvus corax*], hooded crow [*Corvus cornix*], rook [*Corvus frugilegus frugilegus*], Eurasian jay [*Garrulus glandarius glandarius*], Eurasian magpie [*Pica pica pica*]) as a group, assuming that corvids would avoid vehicular collisions. Migratory and sedentary species were analyzed separately to ascertain whether these two groups of birds with different life histories were differentially vulnerable to collisions. Although altricial young have relatively larger brains than precocial young (Griesser et al. 2023), nearly all species we analyzed were altricial.

As a complement to the above analyses based on individuals we estimated the relationship between species' mean residual log brain size and the probability that a bird was killed by colliding with a vehicle based on the reduced data set,. We compared our result to that obtained by Møller and Erritzøe (2017) including all birds (except those that were shot). These two analyses address the relationship between brain size and vehicular collisions in different ways (within vs between species), but we suggest that they should be equivalent if there is a strong signal supporting the overall result of Møller and Erritzøe (2017).

RESULTS

Basic data exploration across species

Møller and Erritzøe's (2017) measure of residual brain mass is highly correlated with an independent measure of brain volume (Iwaniuk and Nelson (2003) across 124 species pairs (R^2 = 0.86) (Fig. 1).

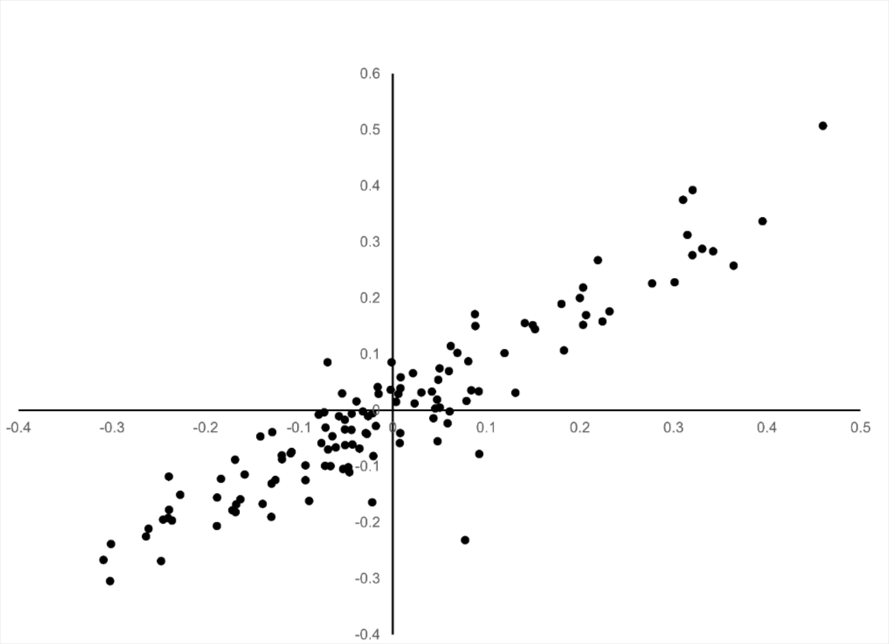

Fig. 1. Relationship between mean residual log brain mass on horizontal axis (from Møller and Erritzøe (2017)) and log of brain volume (from Iwaniuk and Nelson (2003) for 124 species (see appendix).

Basic data exploration within species

We observed considerable variation in the percent difference between the mass of brains in birds hit and not hit by vehicles (Fig. 2), with both categories having species with larger brains. In 211 comparisons for which there were individuals both hit and not hit for each age and sex, 83 (39%) exhibited a reverse trend where birds that were collision fatalities had larger brains. For example, brain mass for adult male *Anthus pratensis pratensis* not hit by vehicles was 42% greater than those that were hit. In contrast, juvenile *Phasianus colchicus* that were hit by vehicles had brain mass that was 47% larger than those that were not hit. Plots of the distribution of residual brain volumes for individual birds hit by vehicles (Fig. S1) and for death caused by other sources (Fig. S1) show a lack of a strong relationship and considerable scatter; *i.e.*, the relationship is subtle. A slight difference was observed in the distributions of residual log brain mass (Fig. 3) between individuals across all species that were hit or not hit by vehicles. The overall relationship between log body mass and log brain size (Fig. 4) is strikingly similar for both birds that died from collisions and other causes, again revealing that any effect of relative brain mass on collision probability is subtle at best.

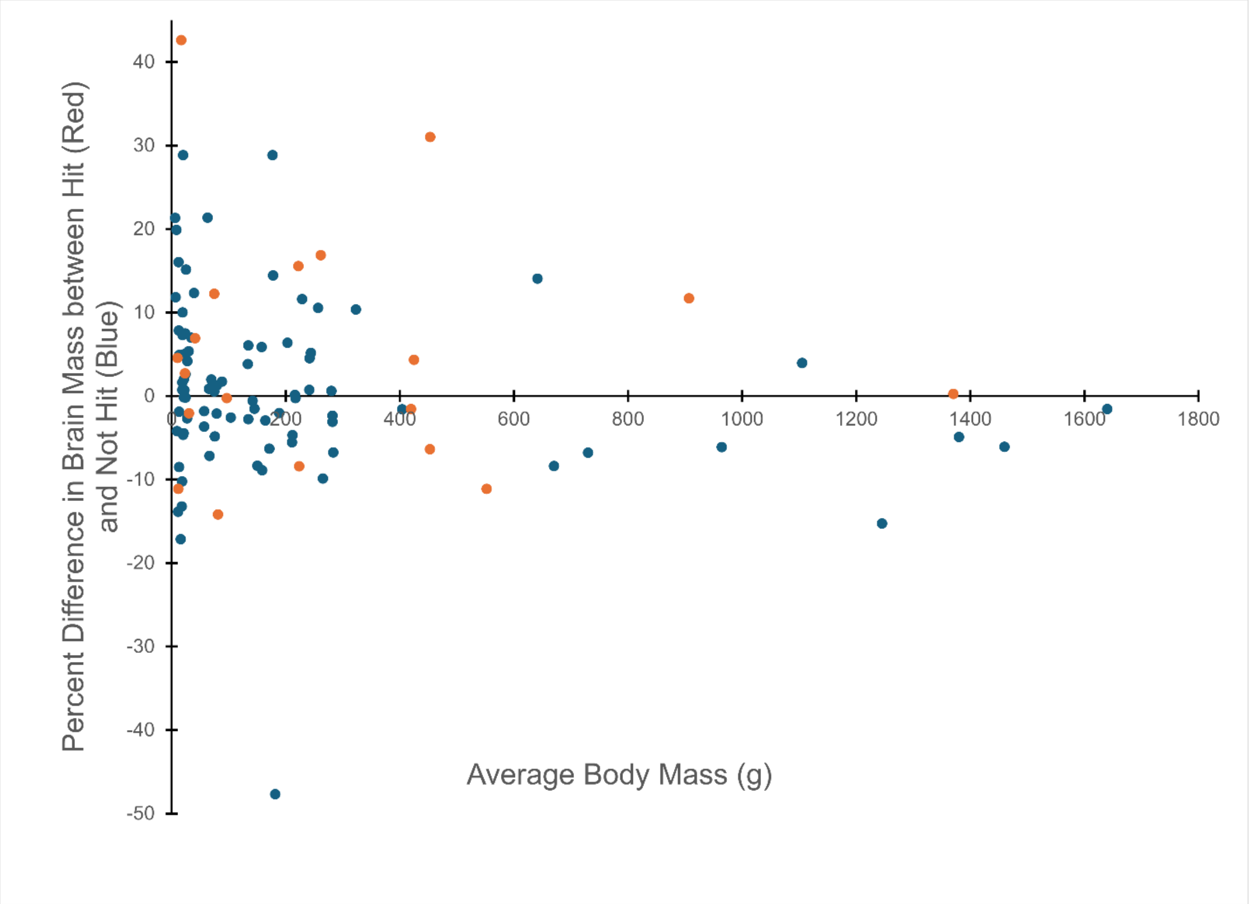

Fig. 2. Plot of species' average percent difference between birds hit (red dots) and not hit (blue dots) by vehicles across ages and sexes. Negative values mean that the brain mass was bigger in the hit-by-vehicle group.

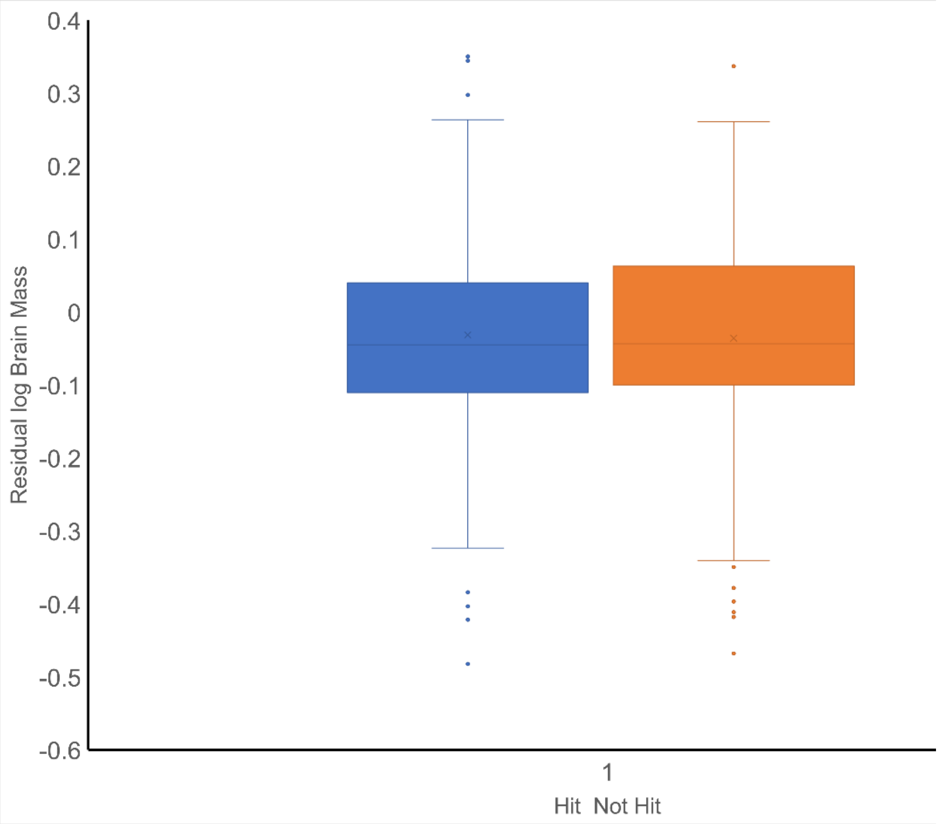

Fig. 3. Distribution of residual log brain mass for all individuals in our reduced data set that were hit (left) or not hit (right) by a vehicle, demonstrating considerable overlap.

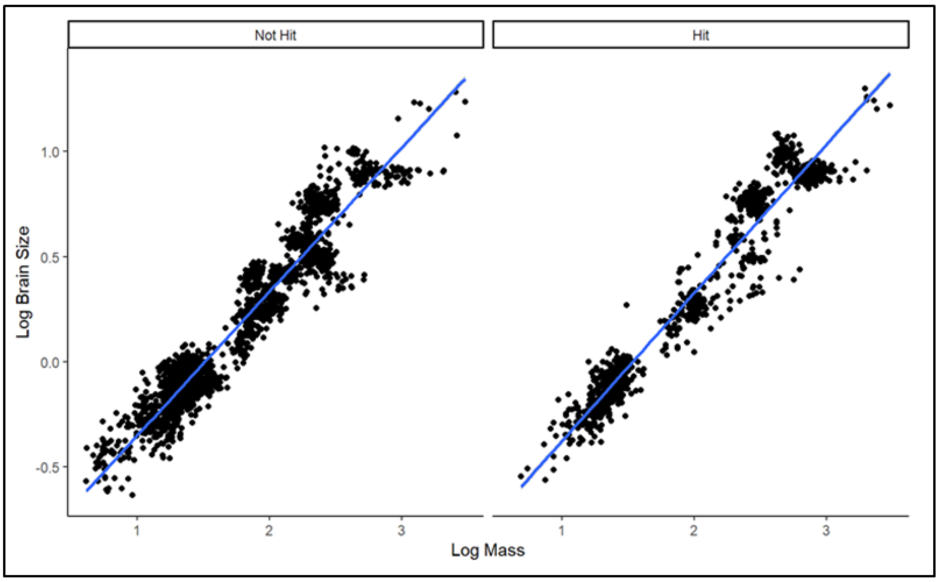

Fig. 4. Scatter plot of log body mass vs log brain size of data set excluding species with small samples, duplicate records, and birds that were shot (see text). Best fit line shown. Two outlier species were excluded (*Alcedo atthis ispida*, *Turdus merula merula*). The plots show visually no difference in the relationship between brain size and mass relative to whether the bird was killed by a vehicle or some other cause.

Multivariate statistical analyses of differences in brain size in birds killed by vehicles and other sources

Our reanalysis of the reduced data set using generalized linear mixed models (Table 1) found an overall significant effect and failed to find a signficant effect for sex or age as reported by Møller and Erritzøe (2017). Not all subsets of the data returned a significant result (Only Corvids, Only Owls, Garden Birds, Migratory Birds Removed and Common Garden Birds). After removing extraneous species and those with insufficient samples (see above) our plot (Fig. 5) of species' mean residual (log)brain size vs the proportion of individuals of each species that were killed by vehicular collision is inconsistent with Møller and Erritzøe's (2017) analysis reveals no support for the hypothesis that the probability of vehicular death is a function of relative brain size.

Table 1. Summary of statistical tests of relationship between residual brain size and whether the bird was killed via vehicular collision or died some other way (other than being shot). Entries such as "corvids removed" indicate that the entire data set (Combined species) was used excluding corvids. Statistically significant results are in bold

Data Set (N)	Residuals, Std Error, *P*-value	Sex effect, Std Error, *P*-value	Age effect, Std Error, *P*-value

Combined Species (2389)	-3.85, 0.296, < **0.001**	-0.129,0.104, 0.215	0.116, 0.111, 0.296
Corvids Removed (2352)	-3.86, 1.107, **0.001**	-0.114, 0.105, 0.279	0.152, 0.112, 0.176
Only Corvids (37)	-6.48, 11.07, 0.558	-0.692, 0.867, 0.425	-1.308, 1.113, 0.240
Owls Removed (2072)	-4.62, 1.19, < **0.001**	-0.208, 0.113, 0.067	0.093, 0.121, 0.442
Only Owls (317)	3.986, 2.92, 0.173	0.301, 0.262, 0.251	0.495, 0.287, 0.084
Raptors Removed (1854)	-3.55, 1.18, **0.003**	-0.112, 0.117, 0.336	0.12, 0.128, 0.351
Only Raptors (535)	-7.42, 3.58, **0.04**	-0.158, 0.229, 0.489	0.185, 0.234, 0.431
Garden Birds Removed (1374)	-2.15, 1.46, 0.140	-0.135, 0.134, 0.316	0.097, 0.141, 0.492
Only Garden Birds (1015)	-5.43, 1.71, **0.001**	-0.109, 0.164, 0.508	0.137, 0.183, 0.455
Sedentary Birds (Migratory Birds Removed; 821)	-2.99, 1.78, 0.093	-0.178, 0.173, 0.304	0.066, 0.189, 0.729
Migratory Birds (Sedentary Birds Removed; 1568)	-4.57, 1.408, **0.001**	-0.100, 0.13, 0.448	0.151, 0.138, 0.274
10 Most Common Garden Birds (402)	-4.90, 2.75, 0.074	-0.008, 0.266, 0.978	-0.189, 0.297, 0.524

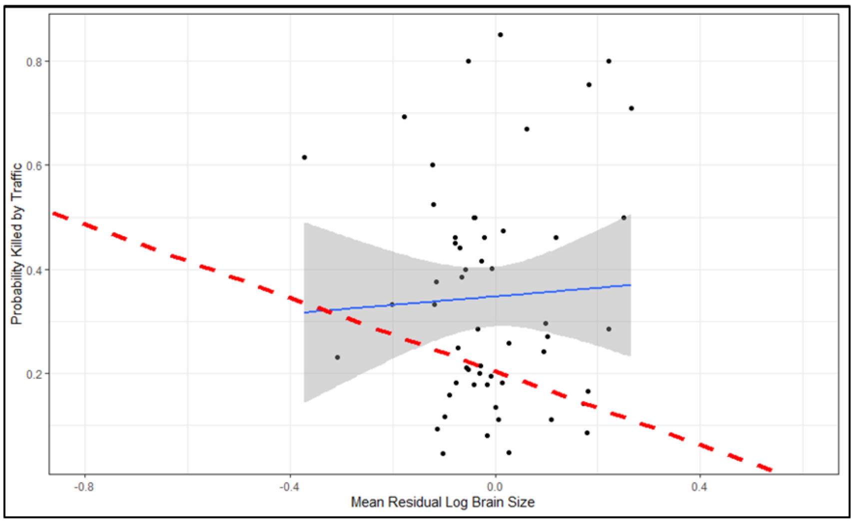

Fig. 5. Relationship between species' mean residual log brain size and the probability that a bird was killed by colliding with a vehicle (black circles, best-fit line). The central plot is based on the reduced data set (removing extraneous and irrelevant species and duplicate records) and reveals no support for the hypothesis that the probability of vehicular death is a function of relative brain size. The dashed line shows the relationship obtained by Møller and Erritzøe (2017) including all birds (except those that were shot),. These two analyses address the relationship between brain size and vehicular collisions in different ways (within vs between species), but we suggest that they should be equivalent if there is a strong signal support in the overall result of Møller and Erritzøe (2017).

DISCUSSION

Birds are an important group in which to assess anthropogenic causes of population declines (Rosenberg et al. 2019) because of their popularity, visibility, and relative ease of monitoring, including by amateurs. One historically identified source of avian mortality is vehicular collision (Loss et al. 2014), which has likely been exacerbated by the increase in the number of roadways (roughly 50% of Europe's land surface is within 1.5 km of a road) and associated noise (Kociolek et al. 2011, Ware et al. 2015). The negative effects of roads will increase as Torres et al. (2016) claimed that by 2050 Earth's roadways stretched end-to-end would reach Mars.

Møller and Erritzøe's (2017) analysis was understandably opportunistic, and they assumed that the birds brought to a taxidermist were a random sample of birds killed by all causes, from which they concluded that those killed by traffic collisions were relatively smaller brained. Although it was not stated, presumably the birds donated to the junior author (and sole specimen preparator) were said to have come from along a roadway (and for practical reasons brains were not preserved). We applaud the extensive sampling but would note that for robust inference one would require a large sample of each species (of similar ages and sexes) crossing the same or similar roads and then analyzing the brains of those that were killed vs not killed. That is, it is impossible to know with the current data set that the larger-brained individuals survived a road crossing, only to perish from some other cause of mortality. For example, out of 261 *Accipiter nisus*, only 21 were coded as traffic fatalities – were those 21 the only individuals that crossed a road, or is this species mostly collision-averse?

Møller and Erritzøe (2017) concluded that "Birds killed by traffic had consistently smaller brains than survivors." At issue is what is meant by "consistently smaller brains". Analysis of the reduced data set returned a significant result consistent with the conclusions of Møller and Erritzøe (2017), whereas some subsets of the data did not, suggesting that only some groups were driving the overall result. Our plots of various aspects of brain mass and whether birds were killed by collisions or not reveal that the effect is subtle and statistical significance possibly a result of large sample sizes (Figs. 2, S1, 4). That is, the tendency for birds hit by vehicles to be relatively smaller brained is not universal, nor in any species is the difference in brain size absolute between the two classes, instead there is considerable overlap within nearly all species. In fact, individuals in some species that were killed by vehicles had larger brains than those that were not. Hence, even if the overall result is biologically as well as statistically significant, it is not a general, or "consistent" result. Our analysis based on means (Fig. 5), for which we suggest there is evidence that Møller and Erritzøe's (2017) measure of brain mass is robust (Fig. 1), failed to support their conclusion of an overall effect of brain mass on the probability of mortality by vehicular collision.

The explicit assumption in the study by Møller and Erritzøe (2017) is that increased overall brain size equates to greater cognitive abilities, specifically the ability to avoid colliding with vehicles. This assumption has mixed support in the literature (Maklakov et al. 2011, Benson-Amram et al. 2016, Sol et al. 2022), and some research suggests that learning specific tasks involves specific regions of the brain, not necessarily overall size (Healy and Rowe 2007, Chittka and Niven 2009, Roth et al. 2010, Powell et al. 2017, but see Sol et al. 2022 and Audet et al. 2024). Powell et al. (2017) wrote "We identify several potential empirical and theoretical difficulties [and] these issues raise doubts about inferring cognitive selection pressures from behavioral correlates of brain size." For example, Freas et al. (2013) showed that chickadees "from harsher environments had significantly larger hippocampal neuron soma sizes”. In addition, there are sex and age differences in neuronal content of some passerine brains such as the brood parasitic brown-headed cowbird (Sherry and Guigueno 2019). Fang et al. (2024) suggested “investigating specific brain regions, as opposed to the whole brain, to unveil the neurotranscriptomic mechanism of behavior.”

Corvids with their high intelligence might be among the first birds to learn to avoid vehicular collisions, which we did not find (although our sample of corvids was small). Iwaniuk and Arnold (2004) wrote “Most of the comparisons [in Corvida] yielded non-significant results, which suggests that cooperative breeding is not related to relative brain size in this parvorder.” Given that cooperative breeding is a complex behavioral phenotype, it lends perspective to the potential for behavioral avoidance of moving vehicles. Owls might be expected to avoid approaching vehicles because of their headlights, although many were found dead along roads, without any tendency for fatalities to be smaller-brained. Possibly, headlights act to blind owls whose eyes have adjusted to low-light levels as they do to white-tailed deer (*Odocoileus virginianus*; Cohen et al. 2014); alternatively, poor peripheral vision in owls could be a factor. Sedentary birds, which have had more time to adjust to a roadway (relative to migrants) when crossing from backyard to backyard or habitat to habitat, might show a trend although that was not the case. Migratory birds might cross a greater number of roadways on their annual journeys, and have developed avoidance behaviors, even though some migrate nocturnally and at relatively great altitudes.

A possible reason for smaller brained birds being more apt to vehicular collisions is that subordinate birds with smaller brains might often secure suboptimal territories near roads, which would heighten their relative vulnerability to vehicular collisions. Other issues concern age and sex. Iwaniuk and Nelson (2002) concluded that “endocranial volume should be used with caution because it cannot account for seasonal and age-related variation and cannot be used to measure differences in brain structure.” One would predict that immature, less experienced birds would be more vulnerable to collisions than adults (e.g., Griesser et al. 2023), whereas this was not found. Adult females, especially during the egg-laying season, with enlarged reproductive systems and lowered maneuverability, should be more vulnerable, but neither we nor Møller and Erritzøe (2017) found a sex difference in collision mortality. A comprehensive test of this would require a large sample of males and females taken during the breeding season.

An equally interesting question concerns the cause of death of the large-brained birds that were not killed by vehicular collisions. That is, what were the causes of death other than vehicular collisions of the relatively larger-brained individuals? Møller and Erritzøe (2017) offer no explanations for their deaths, which of course was not the point of their paper. However, if not shot or killed by vehicles, depredation by feral cats and collisions with windows are two other potential major sources of mortality (Loss et al., 2013; Arnold and Zink 2011). Hence, given that vehicular collisions were ruled out as causes of mortality one might conclude that relatively large-brained birds are more susceptible to collisions with windows or being caught by cats, which would not be advantages of a large brain. Birds have interacted with domestic cats far longer than they have had to interact with fast-moving vehicles, which raises the question as to how relative brain size is related to these other sources of mortality. For example, perhaps relatively large-brained birds are better able to avoid being caught by cats.

CONCLUSION

The notion that anthropogenic effects can result in rapid selection for behavioral attributes has received some support. Snell-Rood and Wick (2013) suggested that mammals in urban environments had larger brains than those living in rural areas, although this does not necessarily imply the evolution of novel brain sizes, but a redistribution of pre-existing brain sizes in different environments. It is possible that in the short time birds have interacted with moving vehicles that selection has acted on brain size to reduce collisions, which was suggested to be unlikely by Møller and Erritzøe (2017). Alternatively slightly larger brains could simply facilitate an innate tendency to avoid rapidly approaching objects in species already selected for this behavior. We found that having a relatively smaller brain in road-killed individuals is not a universal result across species, nor is there an absolute difference in brain size between individuals killed by vehicles vs other sources for any species. Possibly a more refined analysis of specific brain regions would resolve the relationship between brain morphology and collision avoidance. However, we suggest that until the procedure used by Møller and Erritzøe (2017) to measure brain differences between individuals of a given age and sex is vetted, the assertion that birds killed by vehicular collisions have relatively small brains might best be considered subtle, awaiting confirmation with more data.

Acknowledgments: The authors thank Dr. E. F. Stuber for providing code, statistical advice, and the analysis in figure 4.

Authors' contributions: RMZ: Conceptualization, methodology, original draft, analyses. BJB: analyses, review, editing.

Competing interests: The authors declare that there are no competing interests.

Availability of data and materials: All data are online and cited in text.

Consent for publication: Not applicable.

Ethics approval consent to participate: Not applicable.

REFERENCES

Arnold TW, Zink RM. 2011. Collision mortality has no discernible effect on population trends of North American birds. PLoS ONE **69:**e24708. doi:10.1371/journal.pone.0024708.

Audet J-N, Couture M, Lefebvre L, Jarvis ED. 2024. Problem-solving skills are predicted by technical innovations in the wild and brain size in passerines. Nature Ecol Evol **8:**806–816 doi:10.1038/s41559-024-02342-7.

Benson-Amram S, Dantzer B, Stricker G, Swanson EM, Holekamp KE. 2016. Brain size predicts problem-solving ability in mammalian carnivores. Proc Nat Acad Sci **113:**2532–2537. doi:10.1073/pnas.1505913113.

Chittka L, Niven J. 2009. Are bigger brains better? Curr Biol **19:**R995–R1008. doi:10.1016/j.cub.2009.08.023.

Cohen BS, Osborn DA, Gallagher GR, Warren R J, Miller KV. 2014. Behavioral measure of the light-adapted visual sensitivity of white-tailed deer. Wildlife Soc Bull **38:**480–485. doi:10.1002/wsb.438.

Fang Y-T, Ku H-C, Chen C-Y, Chou S-J, Lu C-W, Hung C-M. 2024. Brain gene regulatory networks coordinate nest construction in birds. Mol Biol Evol **41:**msae125. doi:10.1093/molbev/msae125.

Freas CA, Roth TC, LaDage LD, Pravosudov VV. 2013. Hippocampal neuron soma size is associated with population differences in winter climate severity in food-caching chickadees. Funct Ecol **27:**1341–1349. doi:10.1111/1365-2435.12125.

Griesser M, Drobniak SM, Graber SM, van Schaik CP. 2023. Parental provisioning drives brain size in birds. Proc Nat Acad Sci **120:**e2121467120. doi:10.1073/pnas.2121467120.

Hampton RR, Shettleworth SJ. 1996. Hippocampus and memory in a food-storing and in a nonstoring bird species. Behav Neurosci **110:**946–964.

Healy SD, Rowe C. 2007. A critique of comparative studies of brain size. Proc Royal Society B: Bio Sci **274:**453–464. doi:10.1098/rspb.2006.3748.

Husby A, Husby M. 2014. Interspecific analysis of vehicle avoidance behavior in birds. Behav Ecol **25**:504–508. doi:10.1093/beheco/aru011.

Iwaniuk AN, Arnold KE. 2004. Is cooperative breeding associated with bigger brains? A comparative test in the Corvida Passeriformes. Ethology **110:**203–220. doi:10.1111/j.1439-0310.2003.00957.x.

Iwaniuk AN, Nelson JE. 2002. Can endocranial volume be used as an estimate of brain size in birds? Can J Zool **80:**16–23. doi:10.1139/z01-204.

Iwaniuk AN, Nelson JE. 2003. Developmental differences are correlated with relative brain size in birds: a comparative analysis. Can J Zool **81:**1913–1928. doi:10.1139/z03-190.

Kociolek AV, Clevenger AP, St Clair CC, Proppe DS. 2011. Effects of road networks on bird populations. Cons Biol **25**: 241–249. doi:10.1111/j.1523-1739.2010.01635.x.

Kverková K, Marhounová L, Polonyiová A, Kocourek M, Zhang Y, Olkowicz S, Straková B, Pavelková Z, Vodička R, Frynta D, Němec P. 2022. The evolution of brain neuron numbers in amniotes. Proc Nat Acad Sci 11911, p.e2121624119. doi:10.1073/pnas.2121624119.

Laursen K, Møller AP. 2021. Brain mass explains prey size selection better than beak, gizzard and body size in a benthivorous duck species. PLoS ONE **16:**e0248615. doi:10.1371/journal.pone.0248615.

Legagneux P, Ducatez S. 2013. European birds adjust their flight initiation distance to road speed limits. Biol Let **9:**20130417. doi:10.1098/rsbl.2013.0417.

Loss SR, Will T, Marra PP. 2013. The impact of free-ranging domestic cats on wildlife of the United States. Nature Comm **4:**1–8.

Loss SR, Will T, Marra PP. 2014. Estimation of bird-vehicle collision mortality on US roads. J Wildl Man **78:**763–771. doi:10.1002/jwmg.721.

Maklakov AA, S Immler, A Gonzalez-Voyer, J Rönn, N Kolm. 2011. Brains and the city: big-brained passerine birds succeed in urban environments. Biol Let **7:**730–732. doi:10.1098/rsbl.2011.0341.

Møller AP, Erritzøe J. 2016. Brain size and the risk of getting shot. Biol Let **12:**20160647. doi:10.1098/rsbl.2016.0647.

Møller AP, Erritzøe J. 2017. Brain size in birds is related to traffic accidents. Royal Soc Open Sci. **4:**161040. doi:10.1098/rsos.161040.

Morelli F, Rodríguez RA, Benedetti Y, Delgado JD. 2020. Avian roadkills occur regardless of bird evolutionary uniqueness across Europe. Transportation Research Part D: Transport and Environment **87:**102531. doi:10.1016/j.trd.2020.102531.

Mukherjee S, Ray-Mukherjee J, Sarabia R. 2013. Behaviour of American Crows Corvus brachyrhynchos when encountering an oncoming vehicle. The Canadian Field-Naturalist **127:**229. doi:10.22621/cfn.v127i3.1488.

Olkowicz S, Kocourek M, Lučan, RK, Porteš M, Fitch WT, Herculano-Houzel S, an Němec P. 2016. Birds have primate-like numbers of neurons in the forebrain. Proc Nat Acad Sci **113:**7255–7260. doi:10.1073/pnas.1517131113.

Powell LE, Isler K, Barton RA. 2017. Re-evaluating the link between brain size and behavioural ecology in primates. Proc Royal Society B: Bio Sci **284:**20171765. doi:10.1098/rspb.2017.1765.

Pravosudov VV. 2022. Do food-caching chickadees grow their hippocampus every autumn when they need to cache food and then shrink it for the rest of the year? Animal Behaviour, 190(C). doi:10.1016/j.anbehav.2022.06.006.

Rosenberg KV, Dokter AM, Blancher PJ, Sauer JR, Smith AC, Smith PA, Stanton JC, Panjabi A, Helft L, Parr M, Marra PP. 2019. Decline of the North American avifauna. Science **366:**120–124. doi:10.1126/science.aaw1313.

Roth TC, Brodin A, Smulders TV, LaDage LD, Pravosudov VV. 2010. Is bigger always better? A critical appraisal of the use of volumetric analysis in the study of the hippocampus. Phil Trans Roy Soc B: Biol Sci. **365:**915–931. doi:10.1098/rstb.2009.0208.

Sherry DF. 2011. The hippocampus of food-storing birds. Brain Behav Evol **78:**133–135. doi:10.1159/000330314.

Sherry DF, Guigueno MF. 2019. Cognition and the brain of brood parasitic cowbirds. Integ Zool **14:**145–157. doi:10.1111/1749-4877.12312.

Sol D, Olkowicz S, Sayol F, Kocourek M, Zhang Y, Marhounová L, Osadnik C, Corssmit E, Garcia-Porta J, Martin TE, Lefebvre L. 2022. Neuron numbers link innovativeness with both absolute and relative brain size in birds. Nature Ecol Evol **6:**1381–1389. doi:10.1038/s41559-022-01815-x.

Snell-Rood EC, Wick N. 2013. Anthropogenic environments exert variable selection on cranial capacity in mammals. Proc Royal Soc B: Biological Sciences **280:**20131384. doi:10.1098/rspb.2013.1384.

Tilman D, Clark M, Williams DR, Kimmel K, Polasky S, Packer C. 2017. Future threats to biodiversity and pathways to their prevention. Nature **546:**73–81. doi:10.1038/nature22900.

Torres A, Jaeger JAG, Alonso JC. 2016. Assessing large-scale wildlife responses to human infrastructure development. Proc Nat Acad Sci **113:**8472–8477. doi:10.1073/pnas.1522488113.

van Schaik CP, Song Z, Schuppli C, Drobniak SM, Heldstab SA, Griesser M. 2023. Extended parental provisioning and variation in vertebrate brain sizes. PLoS Biology **212**, e3002016. doi:10.1371/journal.pbio.3002016.

Wagnon GS, Brown CR. 2020. Smaller brained cliff swallows are more likely to die during harsh weather. Biol Lett **16:**20200264. doi:10.1098/rsbl.2020.0264.

Ware HE, McClure CJ, Carlisle JD, Barber JR. 2015. A phantom road experiment reveals traffic noise is an invisible source of habitat degradation. Proc Nat Acad Sci **112:**12105–12109. doi:10.1073/pnas.1504710112.

Yaskin VA. 2011. Seasonal changes in hippocampus size and spatial behavior in mammals and birds. Biol Bull Rev **1:**279–288.

Zink RM, Stuber EF. 2017. No relationship between brain size and risk of being shot in hunted birds: a comment on Møller & Erritzøe 2016. Biol Let **13:**20160946. doi:10.1098/rsbl.2016.0946.

Supplementary materials

Fig. S1. A, Distribution of values of residual brain volumes (vertical axis) for individuals that were not traffic mortalities; numbers on horizontal axis are cumulative number of individuals. Each dot is an individual, and colors represent different species. The amount of variance explained is < 1.0%. B, Distribution of values of residual brain volumes (vertical axis) for individuals that were traffic mortalities; numbers on horizontal axis are cumulative number of individuals. Each dot is an individual, and colors represent different species. The amount of variances explained is 4%. Comparison of these two distributions reveals no clear distinction among residual brain volumes within and across species for birds that were traffic fatalities or died for some other reason. (download)