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Brain size and the risk of getting shot

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Hunting kills hundreds of millions of animals annually, potentially constituting an important selection pressure on hunted species. We hypothesized that hunted individuals differing from survivors by having better ability to distinguish between dangerous humans and other human beings would be at a selective advantage. We tested whether shot individual birds had smaller brains than survivors, under the assumption that individuals with larger brains had superior escape ability. We used a large database on birds from Denmark to test whether getting shot was predicted by brain mass, while controlling statistically for the potentially confounding effects of age, sex, body mass and body condition. Analyses based on all species, or only species that were hunted, while controlling for differences in sampling effort in random effects models, showed consistently that shot individuals had smaller brains than survivors.

1. Introduction

Hunting kills several hundred million animals annually, with the kill in North America alone exceeding 200 million animals (In Defense of Animals, http://www.idausa.org, accessed 25 July 2016), although other anthropogenic causes of mortality are also significant [1]. Hunting may not cause random mortality, but rather result in bias with respect to sex, age and other factors [2,3]. Selection due to hunting is likely to have significant impact on the life history of hunted species of animals [4,5]. In fisheries, selective fishing of large specimens has resulted in reductions in size with consequences for age at first reproduction, clutch size and other life-history traits (e.g. [6,7]).

Interspecific variation in brain size has been shown to relate to a number of life-history traits including risk of predation [8], feeding innovation rate [9] and song complexity [10], although such effects have received criticism [11]. Recently, intraspecific variation in brain mass has been shown to be related to spring arrival date at the breeding grounds from the African winter quarters, capture and recapture probability and breeding colony size in the barn swallow *Hirundo rustica* [12] and the response to predation risk in the eider *Somateria mollissima* [13,14], suggesting that brain size is under current selection. Here, we propose that one such important directional selection pressure on brain size is hunting.

The objectives of this study were to assess whether brain size of potential bag species was larger in survivors than in shot individuals. Because numerous factors may contribute to the risk of getting shot, we also controlled for the effects of body mass, body condition, sex and age in the statistical analyses. Larger body mass implies a larger target, and also a slower rate of escape from an approaching hunter. Larger body condition reflects a larger wing-load and hence greater risk of being shot before out of reach of a hunter with a shotgun. Older individuals may have more experience with hunters, but potentially also differ in life-history decisions from juveniles. Males may suffer higher risk of being shot because of larger size, but also due to greater

Table 1. Probability of birds being shot in relation to brain mass and body mass (covariates), age (fixed factor) and species (random factor) across all species of birds. Sample size was 3467 with an adjusted R^2 of 0.73. The variance component for species was 0.107, s.e. = 0.012, 95% CI 0.084–0.131, accounting for 84% of the variance.

term	F	d.f.	p-value	estimate	s.e.
intercept		951.9	<0.0001	−0.353	0.058
brain mass	10.17	2977	0.0014	−0.146	0.046
body mass	101.07	2473	<0.0001	0.286	0.028
age (adult)	0.86	3307	0.86	0.003	0.003
sex (female)	6.89	3303	0.0087	−0.007	0.003

risk taking caused by males competing more intensely for access to mates. For these tests, we used an extensive database on brain mass and other phenotypic traits of shot and surviving birds, while controlling for differences in sampling effort among species by using random effects models. We conducted a general analysis based on all species and an analysis restricted to species that were hunted to test for effects of the sample of species included in the analyses.

2. Material and methods

(a) Specimens used for this study

All taxidermists in Denmark are by law required to record the date when a specimen was received, but also the cause of death. For this study, J.E. verified by a subsequent autopsy the cause of death as reported by the person delivering the specimen. Most specimens originated from 1960 to 2015 from an area surrounding Christiansfeld, Denmark. Hunting in Denmark is mainly performed by hunters finding and flushing birds and mammals rather than all animals being driven towards hunters.

All specimens were carefully examined, including weighing of the extracted brain to the nearest 0.01 g and body mass to the nearest 0.1 g. None of specimens included in this study had a damaged head from hunting, because such individuals were excluded, thereby avoiding problems of biased measurements. Body condition was recorded on a seven-point scale as the amount of fat on the sternum from −3 (very fat), −2 (fat), −1 (little fat), 0 (normal), +1 (slightly lean), +2 (lean) and to +3 (very lean). Detailed information on the procedures is reported in [15].

Age was determined as juvenile or adult according to standard criteria [16]. All data on brain size were collected by J.E. without prior knowledge of the cause of death, and hence there was no possibility of bias in measurements. The data are reported in the Dryad data repository [17].

(b) Statistical analyses

We used generalized linear mixed models with cause of death (shot or not) as a dichotomous response variable, while species was entered as a random effect to account for large differences in sampling effort among species, age was used as a fixed factor, and brain mass, body mass and body condition were used as continuous covariates. We started by conducting an analysis for all specimens. This analysis was based on 197 species that varied in sample size from 1 to 238, in total 3781 individuals [17]. This was followed by an analysis restricted to species that had at least one individual that was shot and one that was not shot in order to test if inclusion of protected species that were not shot affected the conclusions. This analysis was based on 74 species which varied in sample size from 1 to 56 individuals. All analyses were made with JMP [18].

3. Results

A total of 299 (7.9%) out of 3781 birds were shot. Among these 3781 birds, brain mass was on average 2.99 g (s.e. = 0.05), range 0.23–19.96 g, and body mass was 260.71 g (8.89), range 4.16–13 000 g.

Whether an individual was shot or not was related to brain mass (individual birds with smaller brains being shot more often), body mass (larger individuals being shot more often) and sex (higher probability in males), while the effect of age did not reach statistical significance (table 1). The random effect of species accounted for 86% of the variance. The probability of getting shot decreased from 29% in birds with an estimated brain mass of 0.23 g to 1% in birds with a brain mass of 19.96 g across the range of brain masses recorded in this study (figure 1). Thus, there was an almost 30-fold difference in risk of getting shot associated with an almost 87-fold difference in brain mass (figure 1). Least-square means for log-transformed brain mass in a model that included species as a random factor, age, sex and shot or not as fixed factors and body mass as a covariate were 0.433 (s.e. = 0.024) for shot individuals and 0.456 (0.025) for other individuals. Back-transformed values were 2.710 g for the mean of shot individuals and 2.858 g for other individuals, or a mean difference of 5.5%.

If we restricted the analysis to species that were hunted, brain mass and body mass still were statistically significant predictors of the risk of getting shot (electronic supplementary material, table S1). Individuals with larger body mass were more likely to get shot, whereas individuals with smaller brain mass were more likely to be shot (electronic supplementary material, table S1). We tested for potentially confounding effects of age and body condition, but still found a significant effect of a larger brain mass decreasing the probability of getting shot, while body mass increased the risk (electronic supplementary material, table S2). In addition, birds in better body condition were more likely to get shot, while there was a non-significant effect of age (electronic supplementary material, table S2).

4. Discussion

The main findings of this study of brain mass and hunting showed a much smaller brain mass in birds that were killed by hunters compared with those that survived hunting. These effects of hunting were statistically independent of age, body condition, body mass, sex and species. The probability of getting shot decreased almost 30-fold when brain mass increased almost 87-fold.
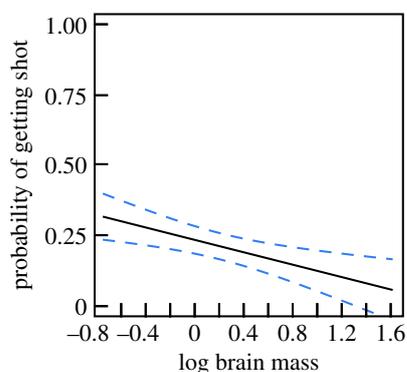
Figure 1. Probability of birds getting shot in relation to relative log-transformed brain mass after controlling statistically for the random effect of species, the fixed effect of age and the effect of the covariate body mass. The solid black line is the regression line and the confidence intervals for the predicted relationship are shown as blue dashed lines. (Online version in colour.)

If hunting accounted for most or a large fraction of mortality in birds, we should expect an increase in brain mass over time, if brain mass had an additive genetic basis. However, as hunting only accounts for a small proportion of total mortality, then we should not expect any temporal change in brain mass for that reason.

Larger birds were shot more often than smaller birds. This effect may arise from larger birds taking a longer time to be air-borne when approached by a hunter, but also from larger individuals constituting a larger target and hence a greater probability of being killed by a hunter.

The findings reported here have a number of implications for studies of brain size. First, hunted and protected populations of the same species should differ in brain mass with the former having larger brains. Second, we also hypothesize that if there are costs associated with an increase of brain size in hunted species, such as increased metabolic costs or increased use of antioxidants during brain development; this could potentially change the bias in brain mass in hunted compared with protected species.

In conclusion, hunting selects for increased brain mass in birds, and this effect is independent of a number of potentially confounding variables, such as age, body condition, sex and body mass.

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