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Systematic review

A review of searcher efficiency and carcass persistence in infrastructure-driven mortality assessment studies



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ABSTRACT

Infrastructures in natural areas are expanding rapidly worldwide. Consequently, roads, power-lines, and wind-farms cause millions of fatalities across several animal groups. Assessing the population impact of these infrastructures requires sound estimates of the total number of fatalities. These estimates can be heavily biased due to differences in searcher efficiency and carcass persistence rates, which may ultimately lead to the incorrect quantification of actual mortality, or to the inadequate prioritization of locations for mitigation. We reviewed 294 studies using carcass surveys conducted worldwide and performed analyses on the effects of variables potentially influencing searcher efficiency and carcass persistence rates. Our analytical review, including the largest number of studies to date, the use of multivariate approaches, and the study weighting by sample size, contradicts some previous findings. Whereas body mass is confirmed as the most important variable accounting for both biases, equally important was the use of dogs in searches, as they increased searcher efficiency for small carcasses, and the taxon of carcasses for persistence, as mammals persisted at higher rates than birds and the latter at higher rates than amphibians. Our results provide little support for previous ideas on the influence of the use of domestic or thawed carcasses on persistence rates. Our findings contribute to synthesizing knowledge on the main factors affecting the two main mortality biases across carcass field experiments, and suggest recommendations for improving survey designs in future studies to minimize the biases identified.

1. Introduction

The human footprint is rapidly growing worldwide, with few places on Earth not affected by the vast network of linear infrastructure and its associated impacts (Loss et al., 2015; Ibisch et al., 2016). Several authors have highlighted the mortality of wildlife species, from elephants to invertebrates, caused by roads and railways (van der Ree et al., 2015; Borda-de-Água et al., 2017), or by collision and electrocution with power-lines (Lehman et al., 2007; Loss et al., 2015; Bernardino et al., 2018; D'Amico et al., 2018). The recent development of wind-farms also poses an important source of mortality for birds and bats (Kunz et al., 2007; Marques et al., 2014). Additionally, collisions with other human

structures like communication towers, windows or fences also cause wildlife fatalities (Stevens and Dennis, 2013; Loss et al., 2015). However, great uncertainty exists about the impact of this mortality on the population viability of the affected species, a key question from an ecological perspective (Loss et al., 2015; Barrientos and Borda-de-Água, 2017).

Surveys of dead animals have been widely used to estimate fatality rates caused by infrastructures (e.g. Barrientos et al., 2012; Stevens and Dennis, 2013; D'Amico et al., 2015; Ascensão et al., 2017). The number of carcasses found during surveys is an underestimated measure of the true mortality rate, as it is affected by two major biases: the overlooking of carcasses, the probability of a researcher not finding a carcass present

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in the field; and carcass disappearance, the probability of a carcass disappearing before being counted due to removal by scavengers or other means. These are the two most important biases because they can affect mortality estimates for all infrastructure types, and therefore have been the subject of numerous studies. To a lesser extent, habitat is another bias accounted for but this lacks comparability among studies. Finally, crippling bias might be considerable for certain infrastructure like power-lines, but this has rarely been quantified (but see Savereno et al., 1996; Bevanger and Brøseth, 2004; Murphy et al., 2016). Adequate quantification of biases is needed to better evaluate the impact of roads (Beckmann and Shine, 2015; Skórka, 2016), railways (Barrientos et al., 2017), power-lines (Ponce et al., 2010), and wind-farms (Kunz et al., 2007; Smallwood, 2007, 2013; Arnett et al., 2008) on wildlife. This is not a trivial matter, as the better these estimations are, the better we will be able to identify impacted species, locate mortality hotspots, implement adequate mitigation measures (Barrientos et al., 2011; van der Ree et al., 2015), and parameterize the fraction of mortality associated with human-related causes to forecast its impact on population viability (Hels and Buchwald, 2001; van der Ree et al., 2009; Borda-de-Água et al., 2014). Some authors have argued for more scientifically sound, peer-reviewed research on these biases to develop carcass-monitoring protocols that include fewer, smaller biases (Kunz et al., 2007; Smallwood, 2007, 2013). This reflects the growing interest of both scientists and practitioners in this topic, with an increasing amount of literature available. Nevertheless, despite the existence of some specific protocols, such as those from the American National Wind Coordinating Collaborative (NWCC) (Anderson et al., 1999; Strickland et al., 2011), there is a lack of broadly applicable guidelines to minimize biases in mortality estimates in field trials.

In this study, we performed an analytic review of the main variables affecting the two most important biases in studies which aimed to correct mortality estimators associated with human infrastructures. First, we reviewed studies that quantified overlooked carcass bias by assessing the *searcher efficiency rate* (the percentage of carcasses found by the searchers), by placing trial carcasses and calculating the proportion of them found by uninformed surveyors. Second, we reviewed studies that estimated carcass disappearance bias by estimating *carcass persistence rate* (percentage of carcasses that persisted) by placing trial carcasses and monitoring their persistence in the field for a specified period of time. We focused on these approaches because they are the most commonly employed in the literature, although other methods like mark-recapture have been used as well. Corrections taking these biases into account aim to adjust the number of carcasses found during surveys in order to estimate the actual number of fatalities, which is key to understanding the population-level impacts on wildlife associated with human infrastructure. Despite the fact that these trials are a common component of monitoring programs for some types of infrastructure, like wind-farms or power-lines, they are scarce or absent in others, like road or railway studies (van der Ree et al., 2015; Barrientos et al., 2017). Furthermore, methodological details are highly variable among studies. This is the case, for instance, with the sampling interval between searches, the number of replicates per study area, and the origin (e.g. domestic vs. wild) or condition (e.g. fresh vs. defrosted) of carcasses (Arnett et al., 2008; Smallwood, 2007, 2013). Additionally, the reliability of the correction estimates is often compromised by limitations of time and financial resources, leading to trials with insufficient sample sizes that limit applicability (Arnett et al., 2008; Smallwood, 2013). This can lead to simplistic assumptions in study designs (e.g. a lack of testing of potential taxon-related differences), to discordant results, or even to misleading findings (Arnett et al., 2008; Smallwood, 2007, 2013). To explore the drivers of searcher efficiency and carcass persistence rates we carried out a systematic review, with the additional novelty that we used the trial sample size to weight the importance of every single trial. This approach lends more importance to the patterns found in those experiments with larger sample sizes, thus avoiding spurious conclusions.

Specifically, we aimed to address the following hypotheses, based on previous research: for searcher efficiency trials, we expected that: i) dogs perform better than humans (e.g. Paula et al., 2011; Reyes et al., 2016); ii) searcher efficiency varies among habitats and seasons (Arnett et al., 2008); iii) detectability increases with searcher experience (Ponce et al., 2010); and iv) larger carcasses are detected at higher rates (reviewed for birds at wind-farms in Smallwood, 2007). For carcass persistence trials, we expected that: v) larger carcasses persist at higher rates (Smallwood, 2007); vi) fresh carcasses are removed at higher rates than thawed ones (see Kerns et al., 2005 for bats); vii) mammals are removed more rapidly than birds (Kerns et al., 2005); and viii) carcasses from wild specimens are removed at a different rate than those of domestic specimens (Prosser et al., 2008; Urquhart et al., 2015). These are the most common factors addressed in the literature to date, and are testable with the dataset available. However, it is worth mentioning that other, and perhaps a minority of, hypotheses were not studied here: density of carcasses and scavenger swamping is mainly related to wind-farm studies (reviewed in Smallwood, 2007); carcass colour is not specified in several studies, and we could not test it; very few studies tested whether searchers were aware of the trial; and road traffic flow is only applied to road-related studies (see below). Based on evaluations of our selected hypotheses, we aimed to set recommendations for future trials.

2. Materials and methods

2.1. Data collection

We searched ISI Web of Science in October 2016 for experiments that corrected mortality estimates to obtain a set of papers potentially useful for our review, using a combination of the terms ‘carcass’, ‘trial’, and ‘searching’. We carried out a similar search in Google Scholar™, which also includes reports and other sources. Whereas the inclusion of reports does not bias analytical reviews (Barrientos et al., 2011), they notably increased the number of studies potentially useful for review. However, in order to retain only the most significant studies, and following the recommendations by Haddaway et al. (2015), we focused the Google Scholar search on the first 300 results. We also identified additional studies in the reference lists of the papers and reports found with the above mentioned search engines. In order to facilitate future research, all the studies we reviewed (294) are listed in Table S1. Carcass searches and the assessment of the potential associated biases are usually carried out in studies on the impacts of human infrastructure like wind-farms, power-lines, fences, solar plants or communication towers. Furthermore, as the same methodology has been employed in studies on pesticides, oil spills and epidemic outbreaks, all of these study sources are found in Table S1. In order to focus solely on studies with more reliable research designs, we restricted the studies included in our analyses to those complying with the following conditions: i) a known number of carcasses were experimentally placed in the field; ii) whole carcasses were used (either virtually undamaged or euthanized) or, in the case of incomplete carcasses, their exact weights were provided; and iii) sample sizes were larger than five carcasses. In searcher efficiency experiments, we discarded those studies using decoys, as their realism was highly variable ranging from dissected specimens to simple plastic tubes. In persistence experiments, we only selected studies that reported the persistence rate for the first 24 h.

Although we agree that the inclusion of feather spots could increase the realism of the correction biases (Stevens et al., 2011; Smallwood, 2013; Reyes et al., 2016), we did not take into account these trials because feather spots cannot be related to a known carcass weight. Furthermore, a small number of feathers is not necessarily evidence of mortality (Balcomb, 1986; Ponce et al., 2010). For carcass persistence, we only used studies for which persistence rates were reported after 24 h to reduce heterogeneity, as the use of the average number of days that a carcass persists would have biased the estimates, since there is an

increase in mean days to carcass removal in longer trials as scavengers remove carcasses at faster rates during the first days. This may be because scavengers could have more carcasses available than they can remove at once (Smallwood, 2007), and/or carcasses become less attractive with time as they decay or mummify. Remains that could be associated with former carcass presence (e.g. more than ten feathers in birds; Ponce et al., 2010), partially consumed corpses, or those displaced (but found) were considered as carcass persistence.

Those studies where raw data for response variables (searcher efficiency and carcass persistence rates), or the values for the corresponding explanatory variables (see below), could be not extracted were discarded. If a study presented several experiments (e.g. different trials for different carcass sizes or seasons), these trials were treated as independent experiments. If more than one publication presented results from the same study area and period (i.e. potentially replicated data), we relied on the most complete study or on the one allowing easier data extraction (Barrientos et al., 2011).

2.2. Explanatory variables – searcher efficiency rate

We tested the following explanatory variables:

- i) *Body mass* (range 9–4000 g), which we expect to be positively related to searcher efficiency (e.g. Smallwood, 2007; Ponce et al., 2010). When the authors did not provide carcass weights, we obtained them from the bibliography (Table S2). When several comparable species (with differences in body mass less than four-fold) from the same taxon were used in a single trial, we averaged their weights for that trial. If identification at the species level was not provided, or if the species included varied in weight more than four-fold, the study/trial was discarded. We carried out the analyses by using the logarithm of the body mass.
- ii) *Season* (*spring/summer/autumn/winter*) in which the trials were carried out, as season could affect visibility of carcasses due to changes in the stage of vegetation or snow cover (Smallwood, 2013). When an experiment included two consecutive seasons without separating them, we assigned by default that experiment to the first season.
- iii) *Agent* (*human/dog*) as previous studies suggest that dogs improve human searching efficiency (e.g. Homan et al., 2001; Arnett, 2006; Reyes et al., 2016).
- iv) *Searcher initial experience* (*high/low*) based on the descriptions given in the respective studies. As few studies specifically tested the searcher's experience, we used a binomial variable dividing the searchers between those trained in carcass searching (i.e. high) and those with no or little experience (i.e. low) based on the author's criteria. We expected searcher efficiency to increase with experience (Linz et al., 1991; Ponce et al., 2010).
- v) *Habitat* classified as *wetland*, *grassland* (including cropland), *forest* (including orchards) or *scrubland*. Vegetation structure associated with habitat type may influence searcher efficiency (reviewed in Arnett et al., 2008 for North American bats).

2.3. Explanatory variables – carcass persistence rate

We tested the following explanatory variables:

- i) *Body mass* (range 6–3200 g), which is expected to be positively related to persistence rate (Smallwood, 2007; Flint et al., 2010; Ponce et al., 2010). We carried out the analyses by using the logarithm of the body mass.
- ii) *Group* (*amphibians/birds/mammals*) because persistence rate has been described to vary among taxa (Hels and Buchwald, 2001; Slater, 2002; Santos et al., 2011).
- iii) We tested the use of *domestic* (i.e. individuals reared in captivity) (*yes/no*) vs. wild carcasses because some authors suggest that the

former are poor surrogates, likely because wild individuals have stronger odors (Prosser et al., 2008; Urquhart et al., 2015).

- iv) We analyzed the use of *frozen* (*yes/no*)—and subsequently thawed—carcasses for storage before the experiment started, or if they were fresh (including just refrigerated). Kerns et al. (2005) found that fresh bats seemed to be removed faster than frozen ones, as freezing carcasses might alter odor intensity and tissue attractiveness.
- v) *Season* (*spring/summer/autumn/winter*) in which the trials were carried out. Season affects scavenger abundance and activity, potentially leading to variations in carcass persistence (Prosser et al., 2008; Flint et al., 2010).
- vi) *Habitat* classified as *wetland*, *grassland* (including urban gardens), *forest* (including orchards), or *scrubland* (including coast, riverbanks and dunes), as different habitat types can host different scavenger communities (e.g. Ward et al., 2006; Henrich et al., 2017).

2.4. Statistical analyses

To assess the overall effect of the explanatory variables on the carcass persistence rate and on the searcher efficiency rate, we used linear mixed effects models with rates (asin-square root transformation) as the dependent variables, and study identification as a random factor, as some studies encompassed more than one experiment (Tables S3 and S4). We further included the sample size (carcasses used in every trial) as weights in the model. We carried out two analyses to calculate the variables influencing carcass persistence rates. In the first one, we exclude the variable *domestic* as no study included amphibians of domestic origin (Table S4). In the second one, to test the importance of *domestic*, we excluded the works focused on amphibians (Table S4). For the three analyses, alternative models using all possible combinations of variables were built and ranked according to the Akaike Information Criterion adjusted for small sample sizes (AICc) (Burnham and Anderson, 2002). We used this technique because it yields consistent results regardless of the order in which variables are included in the model, and allowed models with different numbers of parameters to be directly compared (Burnham and Anderson, 2002). We retained the top ranked models ($\Delta\text{AICc} < 10$) and computed the Akaike weights (w_i) to evaluate the relative explanatory power of those competing models. The evidence ratio was calculated to compare the Akaike weights of the best model with competing ones (Burnham and Anderson, 2002). In order to estimate the relative importance of every variable included in any of the best models, we calculated the sum of Akaike weights of the subset models where these variables were included (Burnham and Anderson, 2002). The most parsimonious model was used to predict the carcass persistence and searcher efficiency rates within the range of the explanatory variables. All analyses were performed within the R environment (R Core Team, 2017), using the R packages 'lme4' (Bates et al., 2015) and 'MuMIn' (Barton, 2014).

3. Results

3.1. Searcher efficiency rate

A total of 275 experiments, from 59 studies, totaling 8358 carcasses met our selection criteria (Table S3). Only two models had $\Delta\text{AICc} < 10$ (Table 1), both containing agent and body mass ($\Sigma w_i = 1.00$ in both cases). The larger the carcass size, the higher the searcher efficiency (Fig. 1). Searcher efficiency was higher for dogs compared to humans, particularly for smaller carcass sizes (Fig. 1). Habitat was less influential ($\Sigma w_i = 0.19$). Values for the mean \pm standard errors of the variables explaining searcher efficiency rate are summarized in Table 2.

3.2. Carcass persistence rate

A total of 112 experiments, from 44 studies, totaling 6075 carcasses

Table 1

Set of the best models explaining searcher efficiency rate, and ranked by increasing AICc. The ΔAICc is the difference in AICc values compared to the estimated best model (lowest AICc) that allows the ranking of models from an estimated best (top of the table) to worst. The AICc weight is the estimated probability that a model is the best model in the set. The evidence ratio indicates to what extent one model is better than another.

Model no.	Variables contained in the model	K	ΔAICc (Δi)	AICc weight (w_i)	Evidence ratio
1	Agent + Body mass	2	0	0.81	0
2	Agent + Habitat + Body mass	3	2.84	0.19	314

met our selection criteria (Table S4). Table 3 shows the subset of models with $\Delta\text{AICc} < 10$ best explaining persistence rates. Group and body mass were the only variables included in all of the best models ($\Sigma w_i = 1.00$). Persistence was larger for mammals, followed by birds, with the amphibians having the lowest persistence rates (Fig. 2). The larger the carcasses, the higher their persistence (Fig. 2). The pattern was especially clear for amphibians, as not even the largest (up to 180 g) showed a persistence of 60% in the first 24 h (Fig. 2, Table S4). Mammals showed the highest persistence rates despite having the smallest sizes (Fig. 2). Less influential was habitat ($\Sigma w_i = 0.31$).

Excluding from the analysis the studies with amphibians but including the variable *domestic*, we used 105 experiments from 41 studies, totaling 4896 carcasses (Table S4). Table 4 shows the subset of models with $\Delta\text{AICc} < 10$ that best explain persistence rates. The patterns were identical as before for group and body size, with both variables again included in all of the best models ($\Sigma w_i = 1.00$). Persistence rates were higher for mammals and for larger carcasses (Fig. 3). Whereas *domestic* was included in 2 of the best models ($\Sigma w_i = 0.58$), it showed no clear influence on persistence rates (Fig. 3). Even less influential was habitat ($\Sigma w_i = 0.30$). Values for the mean \pm standard errors of the variables explaining carcass persistence rate are summarized in Table 5.

4. Discussion

Both searcher efficiency and persistence rates were affected by several variables, implying that future trials must be carefully planned to consider these factors. The results from our review have a strong cautionary message against the establishment of protocols based on a few studies, with low sample sizes, or without controlling for potential confounding variables, as some paradigms assumed to date are rejected by the data from our analytical review.

4.1. Searcher efficiency

We found that the competence of searchers (dogs vs. humans) and the size of the carcasses used were the two most important components influencing searcher efficiency. Dogs increased searcher efficiency likely because olfactory-oriented cues are more useful, especially when vegetation coverage is high (e.g. Homan et al., 2001; Arnett, 2006; Paula et al., 2011). However, despite the fact that dogs are more effective than humans, there is still little information to guide the standardization of searches with dogs, as factors like daily fluctuations in temperature and humidity, the repeatability of sampling schema, etc., can limit a dog's proficiency (reviewed in Arnett, 2006; Beebe et al., 2016). Furthermore, dogs are usually trained to make them better carcass finders (Arnett, 2006; Paula et al., 2011; Reyes et al., 2016; but see Homan et al., 2001). This training can be time consuming and expensive exercise, but there are few published studies including details on the methods used for the dog training (see, however, Beebe et al., 2016; Reyes et al., 2016). We found that the larger the body mass, the more likely a carcass was to be detected (Smallwood, 2007; Ponce et al., 2010). However, it is worth noting that these differences are mainly due to human searchers, as detection rates by dogs are consistently high (mean 87%, range 69–100). The influence of body mass was very evident when differences in size among carcasses were large enough to be evaluated within a taxon (e.g. birds), and in accordance, we observed that most studies already included carcasses of several sizes in their designs with birds (reviewed in Smallwood, 2007).

We found that habitat had a small influence on the searcher efficiency rates, and season had no influence. A previous review, although focused only on bat fatalities at wind energy facilities in North America, identified that the potential influence of habitat and vegetation condition, and their respective changes throughout the year, were often neglected issues in searcher efficiency trials (Arnett et al., 2008; but see Johnson et al., 2003; Kerns et al., 2005; Stevens et al., 2011). It is possible that our wider approach, including other taxonomic groups, human infrastructure and reducing, for analytical purposes, the habitat types to four main types, or even the joining of two consecutive seasons if they had not been differentiated by the authors, could have failed to capture the influence of habitat and season on searcher efficiency. However, our multivariate analysis suggests that carcass body size (together with agent) absorbs much of the variance, reducing the influence of other variables. Thus, only after homogenizing the most influential variables, could habitat and season affect searcher efficiency rates.

Searcher efficiency rate did not vary with initial searcher experience. This result is surprising, as studies specifically testing it found that

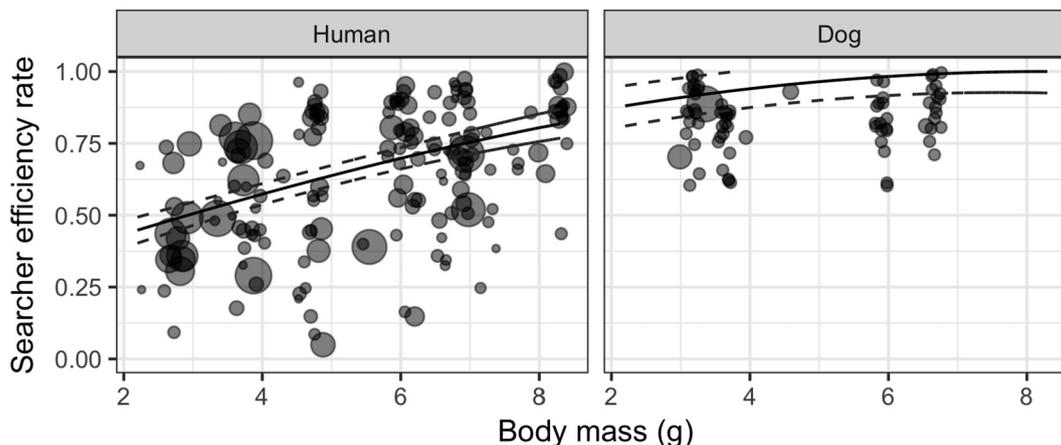


Fig. 1. Observed searcher efficiency rate (dots) related to carcass body mass, and separated by searcher agent. The predicted values for the model and its confidence intervals are represented by continuous and dashed lines, respectively. The dot size is proportional to the number of carcasses employed in the corresponding individual trial. Body mass is shown in logarithmic scale.

Table 2

Values for the mean \pm standard errors of the variables explaining searching efficiency rate, with the number of individual experiments used shown in brackets. Body mass was categorized in ranges that roughly contain the same number of individual trials. The values per infrastructure are also shown.

Variable	Categories					
Agent	Humans	Dogs				
	65.19 \pm 1.81 (186)	86.84 \pm 1.08 (89)				
Body mass	0–99 g	100–299 g	300–499 g	500–999 g	1000–4000 g	
	66.99 \pm 2.49 (96)	60.12 \pm 5.28 (34)	80.06 \pm 2.56 (48)	78.96 \pm 3.02 (47)	76.52 \pm 2.41 (50)	
Infrastructure	Wind-farms	Fences	Power-lines	Roads	Solar plants	Chemicals
	62.14 \pm 2.84 (83)	54.00 \pm 1.00 (2)	77.55 \pm 1.58 (176)	55.75 \pm 3.38 (4)	62.25 \pm 9.89 (4)	78.17 \pm 7.35 (6)

Table 3

Set of the best models explaining carcass persistence rate, and ranked by increasing AICc. The Δ AICc is the difference in AICc values compared to the estimated best model (lowest AICc) that allows the ranking of models from an estimated best (top of the table) to worst. The AICc weight is the estimated probability that a model is the best model in the set. The evidence ratio indicates to what extent one model is better than another. This analysis does not include the variable *domestic*.

Model no.	Variables contained in the model	K	Δ AICc (Δ i)	AICc weight (w_i)	Evidence ratio
1	Group + Body mass	2	0	0.69	0
2	Group + Habitat + Body mass	3	1.59	0.31	122

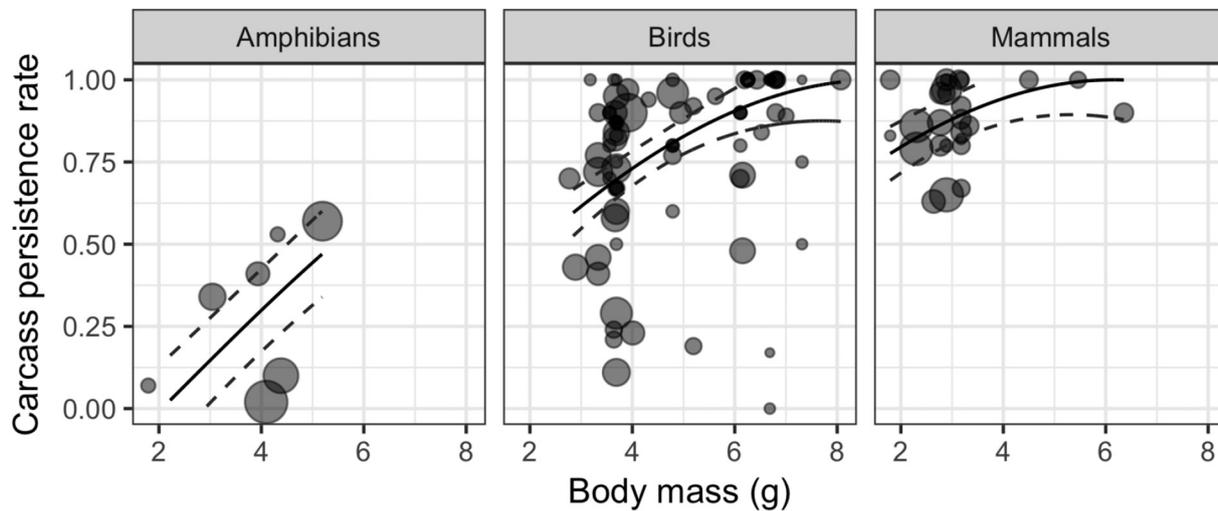


Fig. 2. Observed persistence rate after 24 h (dots) related to carcass body mass, and separated by taxonomic group. The predicted values for the model (after excluding the variable *domestic* from the analysis) and its confidence intervals are represented by continuous and dashed lines, respectively. The dot size is proportional to the number of carcasses employed in the corresponding individual trial. Body mass is shown in logarithmic scale.

either experienced searchers discovered more carcasses (Ponce et al., 2010; but see Stevens et al., 2011), or that practice improves searcher skills (Linz et al., 1991). The explanation for this discordant pattern could be that most studies were not interested in testing the influence of searcher experience, and thus only 4% of the trials were carried out by inexperienced searchers. Indeed, having skilled workers is an important factor in winning the contracts that produced most of the technical reports used in this review (Table S1).

4.2. Carcass persistence

Trials usually treat body mass as the most important variable, and sometimes the only one, affecting persistence rates (reviewed for birds in wind-farms by Smallwood, 2007). Carcass size is certainly important because, while small carcasses are usually removed all at once, large ones are partially eaten on the spot, and their remains are easily recognized in successive surveys (Ponce et al., 2010; Schutgens et al., 2014). However, we found that carcass taxon is also important, as mammals persisted at higher rates than birds, and birds at higher rates than amphibians, after controlling for size. This fact has important

Table 4

Set of the best models explaining carcass persistence rate, and ranked by increasing AICc, after excluding the studies with amphibians. The Δ AICc is the difference in AICc values compared to the estimated best model (lowest AICc) that allows the ranking of models from an estimated best (top of the table) to worst. The AICc weight is the estimated probability that a model is the best model in the set. The evidence ratio indicates to what extent one model is better than another.

Model no.	Variables contained in the model	K	Δ AICc (Δ i)	AICc weight (w_i)	Evidence ratio
1	Domestic + Group + Body mass	3	0	0.40	0
2	Group + Body mass	2	0.66	0.29	39
3	Domestic + Group + Habitat + Body mass	4	1.69	0.17	133
4	Group + Habitat + Body mass	3	2.28	0.13	213

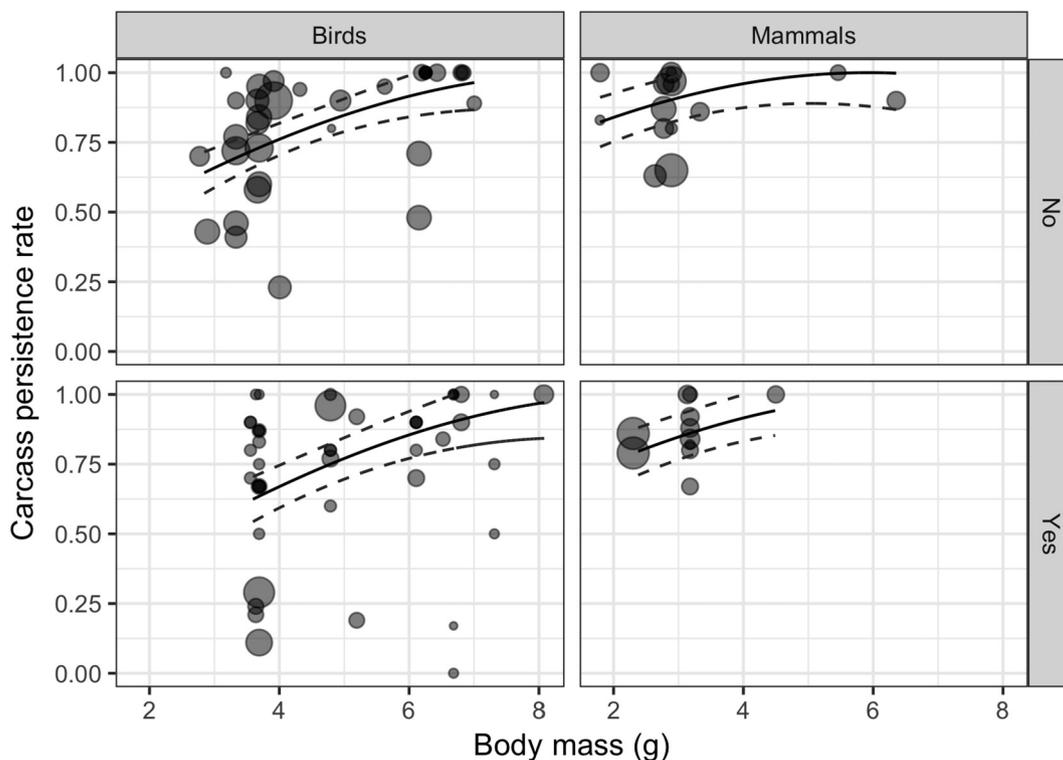


Fig. 3. Observed persistence rate after 24 h (dots) related to carcass body mass, and separated by taxonomic group and the domestic origin (yes/no) of the carcasses. The predicted values for the model (after excluding the studies with amphibians from the analysis) and its confidence intervals are represented by continuous and dashed lines, respectively. The dot size is proportional to the number of carcasses employed in the corresponding individual trial. Body mass is shown in logarithmic scale.

consequences for trial designs, especially for those studies that use birds as surrogates of bats.

Several authors have suggested that the oversimplification of study designs to facilitate logistics, including the widespread use of surrogates, may be misleading (Smallwood, 2007; Prosser et al., 2008; Urquhart et al., 2015). Our findings partially support this call for caution. For instance, while most studies on bat fatalities at wind-farms used birds as surrogates because they are more easily obtained (Arnett et al., 2008), some authors suggest that this may not provide reliable assessments of bat scavenging, as the latter persists at lower rates (Kerns et al., 2005; see also the review from Arnett et al., 2008). Our findings also advise against the use of birds as surrogates of bats but for exactly the opposite reason: mammals persisted at higher rates (see also Erickson et al., 2004). The differences between our data and those from previous studies could be due to the lack of control for body size in former studies, with the lower persistence of bat carcasses being an artifact associated with their smaller size compared to that of most birds (see Table S2). At least two non-mutually exclusive explanations could account for the higher persistence of mammal carcasses compared to birds, and of these compared to amphibians, once controlled for body size: i) taxon-specific differences in skin traits (e.g. amphibians have

softer, unprotected skins) could affect persistence rates (Hels and Buchwald, 2001; Slater, 2002; Santos et al., 2011); and ii) scavengers could select some taxa over others, minimizing intra-group scavenging (Selva et al., 2005; Moleón et al., 2017). This could explain our results as the scavenging intensity is usually higher within the mammal guild than within birds (e.g. Paula et al., 2014; Henrich et al., 2017). However, in our case, we acknowledge that because all studies on amphibians were carried out on roads, this could have influenced persistence rates for this group (see below).

On the contrary, the use of domestic carcasses had no clear influence on carcass persistence and the use of previously frozen ones did not affect persistence rates, which is at odds with previous works (Kerns et al., 2005; Smallwood, 2007; Prosser et al., 2008; Urquhart et al., 2015). Whereas the small sample size of previous works could have limited their findings, the lack of control for confounding variables could have been important as well. For instance, the use of domestic rock doves (360 g) as surrogates of large raptors (over 1500 g) underestimates persistence rates of the latter, because this is a body mass-mediated pattern (see above; see also Smallwood, 2007). This was also likely the case in the study by Prosser et al. (2008) comparing persistence rates of a variety of wild species, mostly small passerines (ca.

Table 5

Values for the mean ± standard errors of the variables explaining carcass persistence rate, with the number of individual trials used shown in brackets. Body mass categories are the same as for searcher efficiency rate. The values per infrastructure are also shown.

Variable	Categories				
Group	Birds	Mammals	Amphibians		
	76.58 ± 2.85 (79)	87.73 ± 2.22 (26)	29.14 ± 8.60 (7)		
Body mass	0–99 g	100–299 g	300–499 g	500–999 g	1000–3200 g
	72.10 ± 3.17 (69)	78.92 ± 6.29 (13)	79.88 ± 5.83 (8)	87.12 ± 7.31 (17)	82.80 ± 9.40 (5)
	Infrastructure	Power-lines	Roads	Chemicals	
	83.29 ± 1.63 (56)	75.86 ± 9.25 (14)	60.07 ± 10.34 (15)	70.67 ± 5.54 (27)	

25 g), with carcasses from domestic chicks to domestic partridges (38–450 g). On the contrary, [Urquhart et al. \(2015\)](#) used two species of similar body mass, one of a predator and the other of a prey species, and suggested that scavenging rates may have differed because predator carcasses are less scavenged, possibly as a mechanism to reduce the risk of disease transmission between predators (see also [Selva et al., 2005](#); [Moleón et al., 2017](#)). To our knowledge, no study compared persistence rates of domestic and wild individuals belonging to the same species, which would be the most suitable approach to test this idea. Finally, our results reject the idea that removal rates of fresh carcasses differed from those of thawed ones ([Kerns et al., 2005](#)). In fact, studies in European temperate forests have shown that low temperatures (and consequently, carcass freezing) increased the rates of visitation to ungulate carcasses during winter ([Selva et al., 2005](#)).

The habitat in which the carcasses were placed had little influence on their persistence, and this rate did not vary with season. Nevertheless, we acknowledge that our analyses may be masking potential patterns related to these variables, as temporal and spatial variations in scavenger foraging activity and abundance could influence carcass persistence rates ([Prosser et al., 2008](#); [Flint et al., 2010](#)). However, their potential importance is much lower compared to that of body mass or carcass taxa (see above). We could have better tested this potential influence if, instead of using surrogates of scavenging activity like habitat and season, studies had provided an estimate of predator abundance. However, in most studies this information is missing.

It is notable that there is a scarcity of studies on carcass persistence (and searcher efficiency) on roads ([van der Ree et al., 2015](#)), and a total lack of studies on railways ([Barrientos et al., 2017](#)). These are certainly needed as the influence of traffic on carcass persistence is far from being understood, and appears to be complex. On the one hand, carcasses placed on the road are repeatedly run over by passing vehicles, which can displace the carcasses away from the road ([Beckmann and Shine, 2015](#)). Consequently, the impact of traffic is lower for those carcasses placed at the road edge ([Beckmann and Shine, 2015](#)). On the other hand, those carcasses that are repeatedly run over are flattened, becoming unattractive for scavengers, and their persistence increase ([Ratton et al., 2014](#)). If the carcasses are not flattened, they are removed more quickly when on the pavement than when on the shoulder, likely because they are more easily detected against a dark surface ([Skórka, 2016](#)). Finally, higher traffic flows cause road avoidance by scavengers, increasing persistence times ([Slater, 2002](#); [Santos et al., 2011](#)). Thus, traffic intensity seems to be a key parameter in carcass persistence, although there is a lack of studies that quantify traffic influence in trials (but see [Beckmann and Shine, 2015](#); [Skórka, 2016](#)).

5. Summary and suggestions for future research

Our results show that several study-specific factors prevent the extrapolation of searcher efficiency and carcass persistence rates, making it necessary to carry out study-specific trials. However, some patterns arise, leading to the following conclusions:

- 1) For both searcher efficiency and carcass persistence trials, body mass of trial carcasses should, as accurately as possible, reflect those of the target species. We included within the same category those species with less than a four-fold difference in body mass, but alternative thresholds could be explored in future studies.
- 2) Dogs were more effective searchers than humans. However, the limitations of dogs, such as the difficulty of setting a standard searching schema or variability in dog psychology (under which conditions they work best), should be taken into account before deciding on their use.
- 3) Our results suggest that habitat and season had little or no influence on searcher efficiency, or at least that their importance was lower compared to that of other variables.
- 4) When testing persistence rates, the use of carcasses from other taxa

is not suitable, as the persistence rate seems to be a taxon-related pattern.

- 5) Carcasses from domestic individuals can be employed as they had persistence rates similar to those of wild ones.
- 6) Thawed carcasses are suitable for trials as their persistence rates were similar to those of fresh ones.
- 7) Our results suggest that habitat and season had little or no influence on carcass persistence, likely because they are poor surrogates of scavenger activity at a global scale. So, the evaluation of scavenger activity would be more accurate to estimate persistence rate.

Finally, although these topics are outside of the scope of the present work, and were not statistically analyzed, three issues evident from our review are worth mentioning for practitioners planning experiments: (i) when testing searcher efficiency rate, the most recommended method is that a second researcher to experimentally place a known number of carcasses, with the number of carcasses available for detection being verified immediately after the trial to ensure that no carcasses were removed by scavengers between the time they were placed and the time the experimental searches began. Once this is checked, the remaining carcasses can be used for carcass persistence trials. (ii) We focused on persistence in the first 24 h. However, for studies interested in obtaining persistence curves for longer time frames, we recommend daily searches for the first 4 days as, on average, we found that 24% of carcasses disappear within the first 24 h. The visits can be spaced after day 4 because persistence rates subsequently stabilize as carcasses become less attractive to scavengers. (iii) The present review focused on field methodology in order to standardize future trials. However, once the most accurate field estimates possible have been obtained, mathematical methods to correct biases are needed. Detailed information on these estimates can be found in [Bevanger \(1999\)](#), [Korner-Nievergelt et al. \(2011\)](#), [Bernardino et al. \(2013\)](#), [Teixeira et al. \(2013\)](#) and [Huso et al. \(2016\)](#).

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Appendix A. Supplementary data

Supplementary data to this article can be found online at <https://doi.org/10.1016/j.biocon.2018.04.014>.

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