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esa ECOSPHERE

Bird collision with power lines: estimating carcass persistence and detection associated with ground search surveys

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Abstract. The quantification of bird mortality due to collision with power lines is complicated by the heterogeneity of survey methods used and the bias related to searching for carcasses on the ground (e.g., carcass persistence and imperfect detection by observers). To estimate the bias associated with ground search surveys, we conducted three 30-d trials to test carcass persistence by placing and monitoring carcasses of red-legged partridges (*Alectoris rufa*) and common pheasants (*Phasianus colchicus*) below power lines at 14 sites. We also conducted two detection experiments, testing the ability of 19 observers to detect bird carcasses. We used survival analysis and generalized linear mixed-effects models to investigate the effects of site, habitat, carcass size, and survey period on both carcass persistence and detection. We also investigated the effect of carcass age on carcass persistence and the effect of the observer on carcass detection. Our findings show significant variations in carcass persistence between sites and survey periods, as well as significant interaction between these variables. The daily carcass persistence probability was highly variable between sites, with an up to eightfold variation. Carcass detection increased with increasing carcass size and was significantly affected by the microhabitat surrounding the carcass; it also varied between observers. These findings suggest that both carcass persistence and detection vary strongly and unpredictably at a small scale. As a result, conservation managers should be encouraged to conduct carcass persistence and detection experiments on sites where they aim to produce unbiased estimates of bird mortality below power lines, and these trials should be carried out in conditions similar to the mortality survey. A large-scale, unbiased, and accurate estimate of bird collision mortality due to power lines may require substantial field effort, with a survey frequency of more than once a week.

Key words: bird mortality; carcass persistence; detection probability; electrical grid; linear infrastructure; scavenger.

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Introduction

In today's modern societies, most human activities, industrial or domestic, involve the use of electricity. Electricity production choices have required the development of electrical distribution and transmission grids. Where these grids have a high density of above-ground power lines, this leads to the death of individuals due to collision with wires (Bevanger 1998, Jenkins et al. 2010), species disturbance, and behavioral changes (Deng and Frederick 2001, Shimada 2001, Prinsen et al. 2011). Collision with power lines can impact any flying species and affect the viability of a population (Bevanger 1995). Yet an accurate quantification of the impact of power

line collision remains complex due to the large heterogeneity of methods used to conduct mortality surveys and the existence of several sources of bias, which affect the estimation of deaths from this cause (Bech et al. 2012).

Measuring bird mortality from power line collision is mainly carried out by carcass counts on the ground below the lines. However, a high proportion of the birds killed may not be found during these surveys, leading to an underestimation of mortality. For example, in a study on bird mortality due to roads, Loss et al. (2014) estimated that for carcass persistence and detection combined, correction factors ranged from 3 to 11. Four aspects can contribute to underestimating this mortality: (1) the removal by scavengers of carcasses under power lines, that is, carcass persistence (Kostecke et al. 2001), (2) the difficulty for observers to detect carcasses, that is, carcass detection (Rivera-Milan et al. 2004), (3) the accessibility of sites under power lines for effective prospection, that is, habitat bias (Huso and Dalthorp 2014), and (4) the flight of wounded birds that die outside the search area, that is, crippling bias (Bech et al. 2012). Crippling bias is notoriously difficult to estimate experimentally as it requires unbiased monitoring either by direct observation of bird collision with power lines or by telemetry, which is costly in both time and money, as well as ethically sensitive, so this topic has to date been neglected. Habitat bias is quantified by determining the area of the site that cannot be searched by observers and does not require modeling to be estimated. Thus, only carcass persistence and detection can be estimated experimentally to be taken into account in mortality count estimates.

The quantification methodology for bird mortality due to power lines and its inherent biases is shared with other types of bird mortality surveys, such as those related to pesticide use in agricultural fields, oil spills, and infrastructure such as wind farms, roads, fences, buildings, and towers (Erritzoe et al. 2003, Newton and Little 2009, Kerlinger et al. 2012, Bernardino et al. 2013). Many studies have focused on the estimation of bird carcass persistence and detection based on experimental positioning and monitoring of carcasses associated with different types of infrastructure, but few have used standardized field methods combined with robust analytical procedures (Gehring et al. 2009, Stevens et al. 2011, Guinard et al. 2012, Peron et al. 2013). Moreover, extrapolation between types of infrastructure may not be relevant as there could be an infrastructure-related effect on carcass persistence. Different types of infrastructure may vary in the level of wildlife mortality they cause (Calvert et al. 2013), which could lead to variation in the abundance of food resources and thus the attractiveness for scavengers. There may also be a difference in the risks to scavengers feeding near the infrastructure (Fahrig and Rytwinski 2009). Types of infrastructure can also differ in terms of the size of the area to be searched, the vegetation cover, variability in maintenance practices, and the protocol used for detection surveys (by car, on foot, etc.; Guinard et al. 2012)—all of which may affect detection. This makes it inadvisable to use studies estimating carcass persistence and detection associated with other types of infrastructure to correct mortality estimates due to power lines. This has nonetheless been done: For example, Rioux et al. (2013) expanded their inclusion criteria to include estimates of carcass persistence and detection from studies conducted by the wind-power industry in order to correct mortality estimates below power lines. In any case, any studies of the topic are rare—only seven peer-reviewed studies have examined carcass persistence related to power lines, three of which also investigated carcass detection (Savereno et al. 1996, Lehman et al. 2010, Ponce et al. 2010, Shaw et al. 2010, 2015, Schutgens et al. 2014, Costantini et al. 2016). Of these, only Ponce et al. (2010) estimated the parameters using a range of carcass sizes (0.05–1 kg).

In this study, we aimed to simultaneously assess the impact of several factors that may affect bird carcass persistence and detection resulting from collision with power lines, and to analyze how these impacts might affect mortality estimates when not taken into account. To do this, we carried out an intensive field effort, monitoring a total of 235 carcasses on a daily basis for 30 successive days in three separate trials, combined with robust statistical analyses. The parameters we investigated included the effect of carcass size (four size categories), site (N = 14), habitat (N = 3), and survey period (N = 3) on carcass persistence. We also tested carcass detection probability, simultaneously investigating the effects of the observer

(N = 19), carcass size (N = 4), site (N = 4), habitat (N = 2), and survey period (N = 2).

The different phenomena responsible for carcass disappearance, such as scavenging or anthropogenic activities, may affect carcass persistence differently depending on the location of the carcass and the time of year. Vegetation cover (Schutgens et al. 2014) and the distribution, abundance, and composition of scavenger communities (Pain 1991) can affect carcass detection by scavengers. Spatial and temporal variation in these factors can also lead to variability in the pattern of carcass persistence during survey periods and between sites. In addition, scavenger activities and the abundance of alternative food resources can vary throughout the year (Smallwood 2007, Flint et al. 2010), reflecting phenological events such as breeding and rearing (Morrison 2002). Anthropogenic activities may also be a source of variability in carcass persistence between sites: for example, farming practices such as plowing or walkers accompanied by dogs (Paula et al. 2011), as observed during our carcass persistence surveys. Farming practices vary over the seasons, which could also lead to temporal variation in carcass persistence. Meteorological conditions can also vary between survey periods, and these conditions can affect both carcass decomposition and carcass detection by scavengers (Santos et al. 2011).

We expected a moderate effect of spatial heterogeneity on carcass persistence (Ponce et al. 2010, Stevens et al. 2011), related to variability in scavenger presence and abundance and their opportunistic behavior. However, we also expected this heterogeneity to be mitigated by the habituation of scavengers to explore power lines on a regular basis as a food source, which would theoretically result in a similar carcass persistence probability for nearby sites (Meunier et al. 2000). We expected carcass persistence to be higher in dense habitats such as scrubland, as ground cover may interfere with carcass detection by scavengers (Hager et al. 2012). We also expected variation in carcass persistence depending on its size and age (in our case, the elapsed time since experimental positioning of the carcass), as a carcass may become desiccated as it ages and become less palatable to scavengers, and carcass size may affect the probability of a scavenger finding or removing it.

We expected both an increase in detection probability with increasing carcass size (Peters et al. 2014) and spatial variation in detection between sites and microhabitats (i.e., the habitat surrounding the carcass's exact location, including the type of substrate and vegetation height; Grodsky et al. 2013, Schutgens et al. 2014), as ground cover and substrate type and color may affect detection. We also expected detection to vary between observers (Ponce et al. 2010).

Materials and Methods

Study area

The study area was located 21 km west of Montpellier, France (43°35′ N, 3°42′ E). This area is characterized by a Mediterranean climate and consists of a patchwork of agricultural land and scrubland with short vegetation (0.1–0.5 m in height). The terrain is rolling hills between 40 and 190 m in altitude. The area was chosen as it has the highest density of power lines near Montpellier. Within this area, we used satellite imaging from the GIS software QGis 2.6 (Quantum GIS Development Team 2015) to arbitrarily select 17 study sites that spread underneath five power lines in habitats typical of the region: vineyards, olive groves, and scrubland (Fig. 1). These habitats varied in ground cover and land use related to agricultural practices. Each site was 250 m long and 40 m wide and included a stretch of power line. In terms of voltage, power line A was 400 kV and power lines B, C, D, and E were 225 kV. Sites 1 to 14 were used for carcass persistence trials, site 9 was used for both carcass persistence and detection trials, and sites 15–17 were used exclusively for detection trials. The carcass persistence and detection trials were not conducted at the same time to avoid interfering in scavenging activity and possibly biasing the persistence results.

Bird carcasses

We used 347 red-legged partridge (*Alectoris rufa*) and common pheasant (*Phasianus colchicus*) carcasses for the persistence and detection trials over a two-year period. The carcasses came from a free-range farm, and all the birds had died from natural or farming-related causes. We used different species at different developmental stages in order to test a range of sizes: 3- to

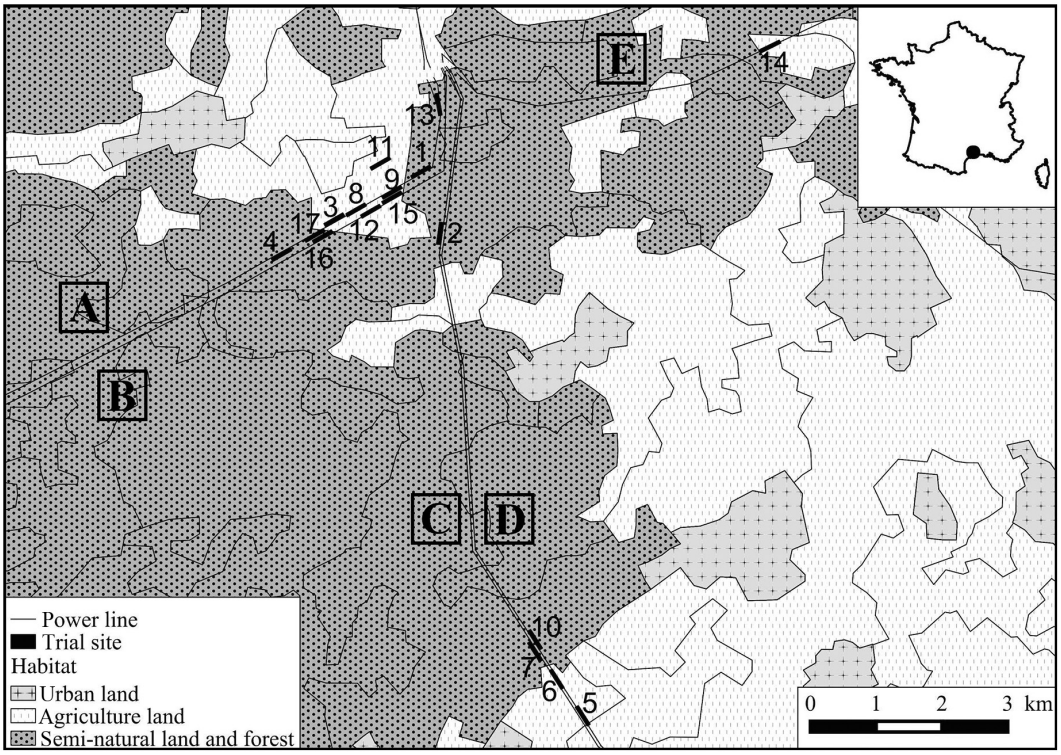

Fig. 1. The location of the trial sites and associated power lines used to assess the persistence and detection of bird carcasses in the region around Montpellier, France. Black rectangles indicate the sites (numbered from 1 to 17); black continuous lines show power lines, which cross vineyards and olive groves (dotted white polygons) and scrubland (dotted dark gray polygons).

7-d-old partridge chicks (9.5 ± 1.83 g; very small), 4- to 8-week-old partridge chicks (73 ± 14.93 g; small), adult partridges (387 ± 46.93 g; medium), and adult pheasants (753 ± 245.46 g; large). We kept the carcasses in a −20°C cold storage room from the moment they died until the trial. The bird carcasses were handled using gloves to avoid traces of human scent that might bias persistence results (Whelan et al. 1994).

Carcass persistence trials

For the carcass persistence trials, we surveyed 14 sites, of which six were located in scrubland, three in olive groves, and five in vineyards. The trials were conducted from 5 July to 3 August 2013 (July 2013), from 3 April to 3 May 2014 (April 2014), and from 24 June to 24 July 2014 (July 2014). The meteorological conditions differed between the trials: April 2014 was about 10°C colder on average and in extremes than both July trials. July 2013 was drier than July 2014, with three times less cumulative monthly rainfall and 21% more sun exposure (Meteo France). The trials were not conducted at all sites simultaneously due to human resource limitations; only sites 1, 3, 4, and 6 were surveyed at each trial (see Appendix S1: Table S1). On each site, we placed three large, three medium, and three very small carcasses in July 2013 (nine carcasses per site), and four small and four medium carcasses for both April and July 2014 (eight carcasses per site). The change in carcass number and size category between 2013 and 2014 was due to variability in carcass supply since no birds were killed for the trials. We limited the number of carcasses per site in order not to artificially attract scavengers (Smallwood 2007). In the studied area, the scavenger community is diverse (foxes, wild boars, crows, black kites, etc.). The number of carcasses was thus chosen to be relatively low compared to potential scavenger density, but high enough to allow powerful

statistical analysis. Carcass positions within sites were randomly selected using the GIS software QGis 2.6 (Quantum GIS Development Team, 2015) and then transferred onto a Global Positioning System navigation device (GPSMAP 62s Garmin, ±5 m precision). The site was marked at a distance of <30 cm from the carcass using natural materials (wood or rocks). This ensured the effective assessment of whether a carcass disappeared or failed to be detected by the experimenter, especially for very small carcasses. The carcasses were checked every day during the 30-d period or until no remains of the carcass were left on the site. After the disappearance of a carcass was reported, the site was checked again the next day to confirm this.

Carcass detection trials

For the carcass detection trials, we used four sites, two of which were located in scrubland and two in vineyards (see Appendix S1: Table S2). These trials were conducted on 2 August 2013 (2013) and 7 May 2014 (2014). All four carcass-size categories were used, except for the 2013 trial, for which small carcasses were not available. Four bird carcasses of each size category were placed on each site: that is, 12 per site for the 2013 trial and 16 for the 2014 trial. We tested the carcass detection of five observers in 2013 and 14 (different) observers in 2014. These included both men and women, ranging in age from 20 to 38. We selected inexperienced searchers (yet all were skilled naturalists who are used to searching for cryptic animals) as we were interested in testing the practicability of conducting carcass searches on a national scale. Such large-scale studies usually involve many observers, often citizens, most of whom are inexperienced. The position of the carcasses within a site was randomly selected as described previously for the persistence trials. The carcasses were placed on a site about an hour before the observer's arrival and the site's boundaries were marked. A unique number was placed under each carcass. Each observer surveyed each site for 30 min. The size of the search area and the prospection method were consistent with carcass search efforts under power lines described in the literature (Barrios and Rodriguez 2004, Bevanger and Broseth 2004, Barrientos et al. 2012, Costantini et al. 2016). The survey effort was fixed in terms of duration and surface area for all observers to ensure a standardized search that allows direct statistical comparison. When a carcass was found, observers stopped the clock, retrieved the carcass number, put back the carcass as they found it, and continued the survey until the search time was up. The order of the observer's passage was randomly chosen, and 15 min were left between each survey so that observers would not influence each other. After a trial, the presence of the carcasses was checked to make sure that all were available for detection during the entire duration of the survey. When a carcass was missing, it was taken out of the dataset; four carcasses were thus excluded from analysis in 2014. Fewer sites were used for the carcass detection trials compared to the carcass persistence trials as the former require significant human resources and are very time-consuming.

Data analysis

Carcass persistence analysis.—We used known-fate models in Program MARK (White and Burnham 1999) to assess the effect of trial period, habitat type, site, carcass age, and carcass size on carcass persistence probability. Known-fate models compute binary logistic regressions allowing the estimation of carcass persistence probability and the evaluation of whether and how different explanatory variables affect persistence based on an individual's persistence time (Kaplan and Meier 1958). We used data from our 30 daily visits per trial to create models with 30 sampling-occasion encounter histories.

Because there were two nested spatial scales (a site at finer scale nested in habitat at coarser scale), we first evaluated which spatial scale best explained variation in persistence probability. To do this, we built single-effect models that evaluated the effects of either site or habitat on persistence. As variability in persistence was better explained by the effect of site than habitat, we then used sites and not habitat in the multivariate models (see Appendix S1: Table S3).

Next, we built 45 multivariate models that incorporated all combinations of effects: trial period, carcass size, site, and carcass age. The effect of the carcass's age was incorporated in order to assess whether there was significant daily variation in persistence. For each model, we modeled persistence (1) as a constant over carcass age (no

age effect), (2) as a variable over carcass age with a continuous-time linear function (agelinear), and (3) as a variable over carcass age with a Gompertz continuous-time function (agegompertz). Two-way interactions between variables were modeled, except with carcass age in order not to overparameterize the models. Therefore, we considered only the additive effects of carcass age on other variables in the multivariate models.

The Akaike information criterion corrected for small sample size (AIC_c) was used to evaluate the relative quality of candidate models.

Carcass detection analysis.—We fitted generalized linear mixed-effects models with a binomial distribution and a logit link using the lme4 package (Bates et al. 2014) to evaluate the effect of several factors on carcass detection probability. We built multivariate models that incorporated carcass size, site, and year as fixed effects. Two-way interactions between these factors were tested. As several different observers could detect the same carcass, and each observer searched for several carcasses, we included observer identity (observer ID) and carcass identity (carcass ID) as random intercept effects in the models.

First, we selected significant random effects using ANOVA by comparing nested models with the model containing both random effects and with models containing either one or the other random effect. Then, we used the dredge function in the MuMIn package (Kamil 2015) of the R program (R Core Team 2017) to model all possible combinations of fixed effects using a fixed random structure selected at step 1 (resulting in 72 models: see Appendix S1: Table S4).

The AIC_c was used to evaluate the relative quality of candidate models.

Finally, for the selected model that best explained variability in the data, we calculated the amount of variance (R^2) explained by fixed and by random effects (Nakagawa and Schielzeth 2013) and used the predict function in the lme4 package (Bates et al. 2014) to estimate detection probability.

Combined effects of carcass persistence and detection.—In order to explore the combined effects of carcass persistence and detection probabilities and understand the level of their impact on the underestimation of bird mortality, we calculated the probability that a bird carcass did not disappear from a site and was then detected by a human observer. The aim here was not to produce correction factor values, which can be found, for example, in Bispo et al. (2013), Garrido and Fernandez-Cruz (2003), Schutgens et al. (2014), but rather to give some insight on the amount of bias introduced when both these phenomena are not accounted for.

To do this, for each size category (large, medium, small, and very small), we calculated the probability that a carcass remained on a site for 7 d and was then detected by an observer for our range of daily persistence probabilities and for the mean detection probability of each size category:

$P = p_i^7 \times d_j$ (p_i = the carcass persistence probability of the site, with i being the trial period and d_j the average detection probability of size category j).

Results

Carcass persistence

In total, 45 carcass persistence models were built and compared (see Appendix S1: Table S3). The model including an interaction effect of site and trial period was the most parsimonious, best explaining the variability in persistence probability and resulting in the lowest AIC_c of all the models tested (AIC_c = 1020.7; Table 1).

Daily carcass persistence probability varied up to eightfold between sites (Fig. 2), ranging between 0.2 (Confidence interval [CI] = 0.03–0.7) for site 12 and 0.93 (CI = 0.86–0.97) for site 10 in April 2014. Persistence varied between sites in all three trial periods (Fig. 3). Even sites that were in close proximity to each other showed high variability in carcass persistence: For example, sites 12 and 3, which were <250 m apart, respectively, had a daily persistence probability of 0.2 (CI = 0.03–0.7) and 0.82 (CI = 0.68–0.91) in April 2014.

The models also revealed carcass persistence variation in relation to trial period. Persistence was generally higher in July 2013 than in April and July 2014 (Fig. 3). There was no consistent pattern for persistence variability on a particular site across trial periods, with sites 3 and 4 displaying a similar persistence probability across trial periods, whereas sites 1, 5, and 6 showed high variability in persistence across trial periods (Fig. 3).

We found no support for the effects of carcass age and size on persistence probability. The model that added an additive carcass age effect following a continuous-time function to the

Table 1. Known-fate models used to describe persistence probability of bird carcasses placed in the region of Montpellier, France.

Model	AIC_c	ΔAIC_c	No. par	Deviance
site+trial_period+site:trial_period	1021.56	0	30	545.78
agegompertz+[site+trial_period+site:trial_period]	1023.18	2	31	545.30
agelinear+[site+trial_period+site:trial_period]	1023.45	2	31	545.57
site+size+trial_period+site:trial_period	1028.88	7	34	544.66
agegompertz+[site+size+trial_period+site:trial_period]	1030.54	9	35	544.19
agelinear+[site+size+trial_period+site:trial_period]	1030.69	9	35	544.35
site+size+trial_period+site:size	1040.25	19	44	534.67
agegompertz+[site+size+trial_period+site:size]	1040.86	19	45	533.12
agelinear+[site+size+trial_period+site:size]	1041.61	20	45	533.87
site+size+site:size	1051.29	30	42	550.00
agelinear+[site+trial_period]	1052.30	31	17	603.58
agegompertz+[site+trial_period]	1052.69	31	17	603.96
agegompertz+[site+size+site:size]	1053.36	32	43	549.93
agelinear+[site+size+site:size]	1053.43	32	43	550.00
agegompertz+[site+size+trial_period]	1057.20	36	20	602.29
agelinear+[site+size+trial_period]	1057.21	36	20	602.29
site+trial_period	1057.85	36	16	611.18

Notes: +, additive effects between variables, and a colon indicates interaction. Persistence is allowed to vary with the time that a carcass has been placed on a site following a continuous-time linear function (agelinear) and a continuous-time Gompertz function (agegompertz; see *Materials and methods*). Site is a variable factor with 14 values accounting for spatial variation; size is a variable factor with four levels (large, medium, small, and very small). The trials were conducted in July 2013, April 2014, and July 2014 (trial_period). The table also includes the Akaike information criterion corrected for small sample size (AIC_c), the AICc difference (ΔAIC_c), the number of parameters (No. par), and the deviance of each model. Only 17 models are presented: see Appendix S1; Table S3 for more results.

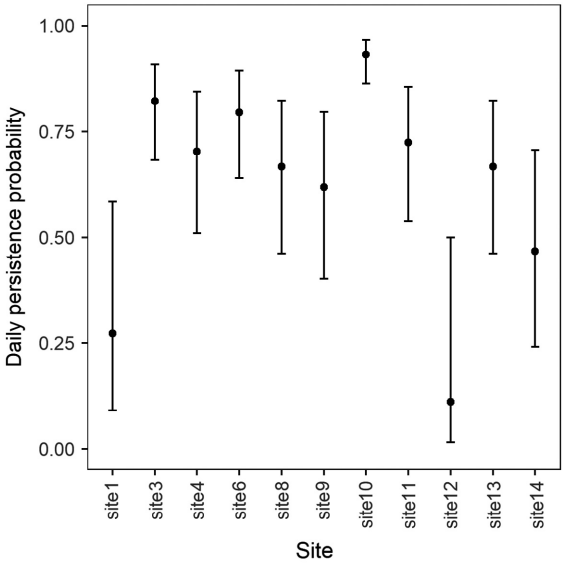

Fig. 2. Example of variation in daily carcass persistence probability across 11 sites in April 2014 (a total of 235 carcasses). The probabilities (shown with 95% confidence intervals) were estimated from the selected model, which included an interaction effect of site and trial period.

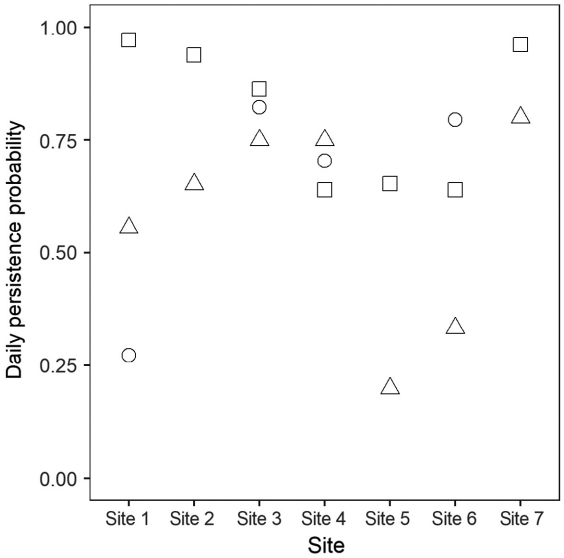

Fig. 3. Example of variation in daily carcass persistence probability across sites and between trial periods (square: July 2013, circle: April 2014, triangle: 2014). The probabilities were estimated from the selected model, which included an interaction effect of site and trial period.

model including an interaction effect of site and trial period did not show a meaningful AIC_c difference ($\Delta AIC_c \leq 2$), but was not the most parsimonious (Table 1). The best model including an effect of carcass size had an AIC 6 points higher than the best model (Table 1), so carcass size did not seem to be significant (AIC = 1026.76).

Carcass detection

The ANOVA showed a significant random effect for both observer and bird carcass (carcass ID: $\chi^2 = 35.77$, $P < 0.001$, and observer ID: $\chi^2 = 4.15$, $P = 0.04$).

Of the fixed effects, size and the additive effects of site and year all resulted in $\Delta AIC_c \leq 2$ (Table 2; see Appendix S1: Table S4). The total variance explained by the model with a size effect was 68%, with 47% explained by fixed effects and 21% explained by random effects.

The mean detection probability was 0.47 (standard error [SE] = 0.01) for large carcasses, 0.18 (SE = 0.01) for medium carcasses, 0.07 (SE = 0.007) for small carcasses, and 0.005 (SE = 0.0006) for very small carcasses (Fig. 4). Standard deviations in detection probabilities for large, medium, small, and very small carcasses were 0.23, 0.17, 0.09, and 0.01, respectively (Fig. 4).

Table 2. Generalized linear mixed-effects models of bird carcass detection by human observers in relation to year, habitat, site and carcass size, and two-way interactions between these factors.

Model	df	AIC_c	ΔAIC_c	Deviance
year+site+size	10	736.97	0.00	716.75
site+size	9	737.08	0.11	718.90
size	6	737.94	0.97	725.86
year+size	7	738.14	1.17	724.03

Notes: Random effects for observer ID and carcass ID are fitted for all models (see *Results*). The table also shows the number of degrees of freedom (df), the Akaike information criterion corrected for small sample size (AIC_c), and AIC_c difference (ΔAIC_c). Only models with $\Delta AIC_c \leq 2$ are presented: see Appendix S1: Table S4 for more models.

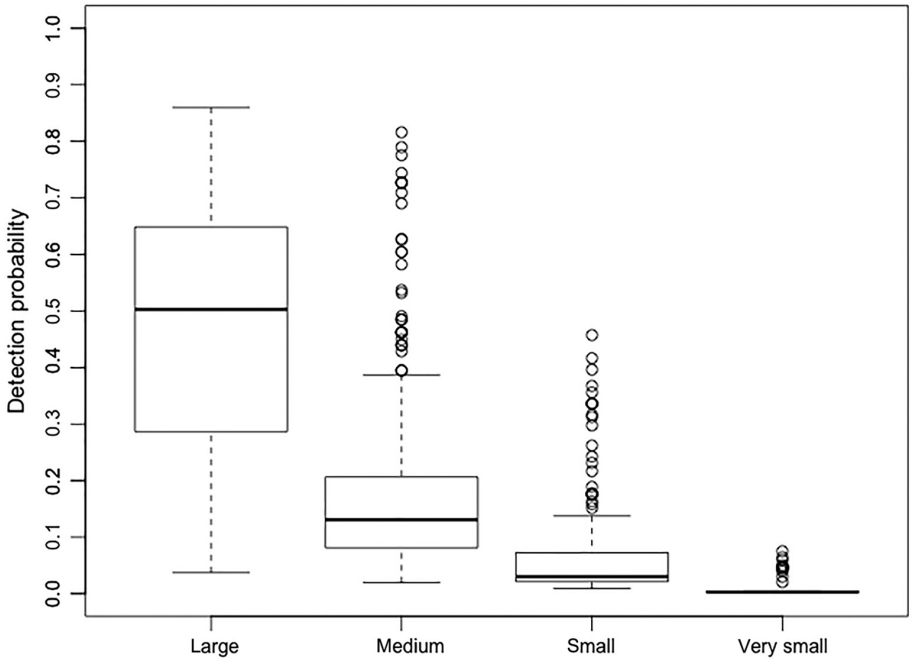

Fig. 4. The variation in detection probability according to carcass size based on the predicted values of a generalized linear mixed-effects model, with size as a fixed effect and observer ID and carcass ID as random effects. For each size category, the thick line represents the median detection probability, the lower and upper hinges show the 25th (Q_1) and 75th (Q_3) percentiles, respectively, the lower whisker shows the largest value between the minimum detection probability and Q_1–1.5*($Q_3 - Q_1$), and the upper whisker represents the smallest value between the maximum detection probability and Q_3 + 1.5*($Q_3 - Q_1$).

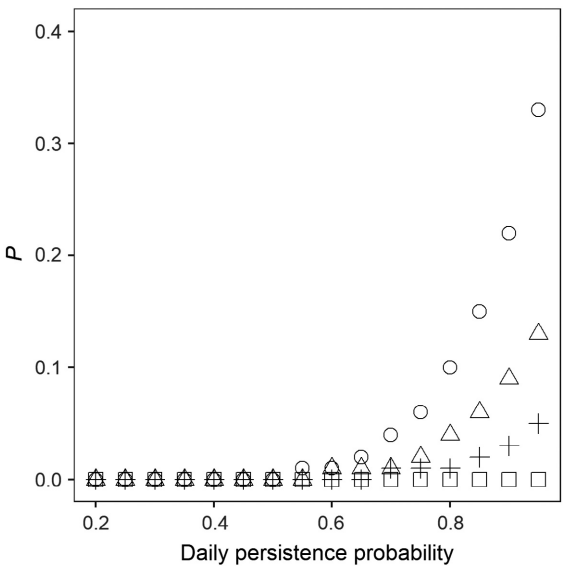

Fig. 5. The probability that a carcass is not removed from a site for seven days and is then detected by an observer (*P*) in relation to daily persistence probability for each carcass-size category (circle: large, triangle: medium, cross: small, square: very small).

Accounting for both carcass persistence and detection

For all carcass sizes, the chance of an observer finding a carcass after 7 d was close to zero when the daily probability of a carcass remaining on site was <0.5 (Fig. 5). The chance of an observer finding a carcass after 7 d was <0.1%, 5%, 13%, and 33% for very small, small, medium, and large carcasses, respectively. In other words, for an accurate estimation of all carcasses present on a site, the number of carcasses found by observers would have to be multiplied by ≈10 for very small carcasses (similar to partridge chicks in size and color) and by ≈3 for large carcasses (similar to pheasants in size and color) if daily persistence was 0.95 and the carcass searches were performed every 7 d.

Discussion and Conclusion

Carcass persistence

Our findings indicate significant variation in carcass persistence in relation to the site and the trial period. Furthermore, we found significant interaction between these factors, which induced differences in persistence variation patterns between sites and trial periods. This is the first study to demonstrate such variability in carcass persistence under power lines. However, similar variable patterns of carcass persistence were observed in a study on communication towers by Flint et al. (2010).

We expected to observe highly deterministic scavenger behavior, with scavengers habituated to finding food under power lines and regularly prospecting underneath the linear infrastructure of power lines (Meunier et al. 2000). This would have resulted in a similar persistence probability for sites near each other. However, our results indicate that carcass persistence can vary significantly between sites despite their proximity, which suggests that scavengers display more opportunistic behavior under power lines than was expected. Our results clearly show a very high variation in carcass persistence even between sites that are close together. Thus, spatial autocorrelation is very low and lack of independence is not a problem here. The literature for other potentially related cases shows mixed results: Flint et al. (2010) demonstrated that scavengers were not habituated to searching for carcasses near towers, whereas Lambertucci et al. (2009) found evidence of scavenger species choosing to feed close to roads to take advantage of the food resources provided by roadkill. It may be that scavenger behavior is less predictable under power lines because mortality due to collision with these may be less frequent than mortality on roads. Additionally, carcasses could be harder for scavengers to detect under power lines than along roads.

Such high variability of carcass persistence probability between sites has never been demonstrated before and cannot only be explained by variation in the distribution, abundance, and composition of scavenger communities or variation in weather conditions. Indeed, in the same season, sites that were close enough to be exposed to the same scavenger community and weather conditions showed high variability in carcass persistence. This may be due to local variation in microhabitats or scavenger behavior. Therefore, the presence and abundance of scavenger communities or the weather conditions cannot be used to predict variability in carcass persistence between sites. This makes it difficult to compare mortality estimates between sites—even for those that are close together. Indeed, a

difference in the number of birds found dead between two nearby power lines could reflect a difference in persistence probability rather than a difference in collision mortality.

The trial period significantly affected persistence probability. Persistence was higher overall in July 2013, which may be due to extreme weather conditions, as this period was drier than April and July 2014 with a cumulative monthly rainfall that was three times lower and sun exposure that was 21% higher. These weather conditions may have accelerated the desiccation of carcasses in July 2013, affecting the olfactory cues they produce and which are used by scavengers (Santos et al. 2011). This may have made the carcasses less attractive to scavengers. Variation in carcass persistence according to trial period may also be related to variation in the seasonal distribution, abundance, and composition of the scavenger community (Smallwood 2007, Flint et al. 2010). Indeed, the April trial period took place during the breeding season for many of the area's scavengers, when pressure for food is higher. This may explain this period's lower carcass persistence probability.

While carcass size affects the visibility, smell, and portability of carcasses (Ponce et al. 2010), despite using a wide range of carcass sizes, we did not find a significant effect of size on carcass persistence probability. However, we may have lacked the statistical power to reveal the effect of carcass size on persistence. Indeed, our representation of carcass sizes throughout all trial periods was imperfect: Large and very small carcasses were used only in 2013, and small carcasses were available only in 2014.

Carcass detection

Carcass detection decreased significantly with decreasing carcass size. As expected, in conditions where vegetation cover or ground color may interfere with carcass visibility to human observers, larger carcasses were more conspicuous than smaller ones (Peters et al. 2014).

We also demonstrated heterogeneity in detection between observers. We would argue that since the search time is not usually standardized between observers (Ponce et al. 2010), carcass detection differences uncovered by previous studies may reflect differences in search time. As we performed our detection trials without selection for observers' experience in bird mortality surveys, their experience could have been lower in our trials compared to other studies; these usually test detection using more experienced observers (Homan et al. 2001, Rivera-Milan et al. 2004, Stevens et al. 2011). Indeed, we had a lower detection rate than in the literature, with 47% detection for large, 18% for medium, and 7% for small size categories, whereas Ponce et al. (2010) observed a 55.8%, 32.1%, and 33.3% detection rate, respectively, for similar size classes.

We did not find support for an effect of site or habitat on carcass detection; however, detection varied between carcasses, indicating an effect on detection of the particularity of the carcass and of the microhabitat surrounding it. Indeed, each carcass was placed in a microhabitat that differed with regard to vegetation cover and ground color; carcasses can also be placed in different positions (spread out, on the back or belly), all of which can affect carcass detection (Stevens et al. 2011). There might also be physical variability in size and color among carcasses of the same species and the same size class, which may affect carcass detection. So each carcass does not have the same chance of being detected by an observer due to individual heterogeneity.

The dispersion of detection probability was much higher when accounting for variability between carcasses than between observers. As detection was much more variable depending on the carcass than depending on the observer, training the observers may not significantly reduce the variability in detection probability. This variation in detection depending on the physical aspect, position, and microhabitat of the carcass is difficult to correct for; a correction factor based on average estimates would not allow an unbiased estimate of mortality.

Recommendations for conservation managers and practitioners

The results of this study could be used to define or improve protocols that aim to take into account carcass persistence and detection to correct surveys estimating mortality from power lines. Modeling the data from our trials demonstrated that carcass persistence was extremely heterogeneous between sites in close proximity and between seasons. These results call into question the use of carcass persistence correction

factors extrapolated from published data for other locations or times of year. Carcass detection varied significantly with carcass size and between observers and also varied widely depending on the carcass, probably due to variability in the microhabitat around the carcass. These factors mean that training observers would not be sufficient to standardize detection. Combining carcass persistence and detection probabilities suggests that a high sampling frequency would be needed to estimate bird mortality under power lines (more than once every seven days). For example, the probability for birds of a size and color similar to pheasants to be found by an observer 7 d after dying under a power line is <33%, even with a high daily persistence probability of 0.95. Achieving an unbiased estimation of bird mortality due to collision with power lines through ground searches might thus require substantial field effort.

We would advocate for a multi-approach strategy that combines local ground search surveys with carcass detection and persistence trials, the results of which could be uploaded to a national databank centralizing local bird mortality counts and associated correction factors, which could be used to provide a national estimate of bird mortality. When the aim of a study was to estimate average bird mortality on a large scale (e.g., a country), then practitioners could use average estimates of carcass persistence and detection associated with a standard deviation to correct for an average bird mortality count. Such a database, even in the case of diverse sampling protocols, could then be used to estimate mean correcting factors at a national scale together with different variables, such as spatial, temporal, species, or observer variance. This can be achieved, for instance, by using generalized linear mixed-effects models. These estimates could then be used to extrapolate mortality at a national scale with confidence intervals propagating all sources of variance. It may be possible to use a Bayesian analysis for such an approach. This type of study (although not using a Bayesian analysis) has been conducted in the United States, where between 8 and 57 million birds a year are estimated to be killed by collision with power lines (Loss et al. 2014). Because of the heterogeneity we have documented, any large-scale estimate will have substantial uncertainty. Managers should consider whether estimates with such large error would meet their objectives before pursuing such studies.

As stakes differ greatly depending on the species, and as biodiversity management decision-making and policy-making is mostly done locally, when the goal is to accurately estimate bird mortality at a fine scale (e.g., a region) or to compare mortality between sites, we suggest that managers conduct carcass persistence and detection experiments using carcasses similar to the species investigated, in sites and at the time of year for which they wish to produce unbiased estimates of bird mortality. We also advise that the duration of monitoring in carcass persistence experiments be consistent with the frequency of mortality surveys. The heterogeneity of the biases associated with this survey method hinders a case-by-case adaptation of the model to specific local conditions and weakens the robustness of estimates. Thus, we also suggest that efforts should focus on improving automated data-recording tools (e.g., the Bird Strike Indicator, radar, thermal infrared imaging) as a substitute to ground search surveys.

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Supporting Information

Additional Supporting Information may be found online at: http://onlinelibrary.wiley.com/doi/10.1002/ecs2.1966/full