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# Making inference from wildlife collision data: inferring predator absence from prey strikes

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Wildlife collision data are ubiquitous, though challenging for making ecological inference due to typically irreducible uncertainty relating to the sampling process. We illustrate a new approach that is useful for generating inference from predator data arising from wildlife collisions. By simply conditioning on a second prey species sampled via the same collision process, and by using a biologically realistic numerical response functions, we can produce a coherent numerical response relationship between predator and prey. This relationship can then be used to make inference on the population size of the predator species, including the probability of extinction. The statistical conditioning enables us to account for unmeasured variation in factors influencing the runway strike incidence for individual airports and to enable valid comparisons. A practical application of the approach for testing hypotheses about the distribution and abundance of a predator species is illustrated using the hypothesized red fox incursion into Tasmania, Australia. We estimate that conditional on the numerical response between fox and lagomorph runway strikes on mainland Australia, the predictive probability of observing no runway strikes of foxes in Tasmania after observing 15 lagomorph strikes is 0.001. We conclude there is enough evidence to safely reject the null hypothesis that there is a widespread red fox population in Tasmania at a population density consistent with prey availability. The method is novel and has potential wider application.

# 1 Making inference from wildlife collision 2 data: inferring predator absence from prey 3 strikes

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## 11 ABSTRACT

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13 irreducible uncertainty relating to the sampling process. We illustrate a new approach that is useful  
14 for generating inference from predator data arising from wildlife collisions. By simply conditioning on  
15 a second prey species sampled via the same collision process, and by using a biologically realistic  
16 numerical response functions, we can produce a coherent numerical response relationship between  
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21 distribution and abundance of a predator species is illustrated using the hypothesized red fox incursion  
22 into Tasmania, Australia. We estimate that conditional on the numerical response between fox and  
23 lagomorph runway strikes on mainland Australia, the predictive probability of observing no runway strikes  
24 of foxes in Tasmania after observing 15 lagomorph strikes is 0.001. We conclude there is enough  
25 evidence to safely reject the null hypothesis that there is a widespread red fox population in Tasmania  
26 at a population density consistent with prey availability. The method is novel and has potential wider  
27 application.

## 28 INTRODUCTION

29 Data arising from vehicle-wildlife collisions (termed “roadkill” for road vehicles, “wildlife strike” for  
30 aircraft, and hereafter “wildlife collision”) are viewed as a potentially informative source of inference on  
31 trends in wildlife abundance. Doubts, however, remain on the appropriate methods for analysing such data,  
32 and whether useful information can be retrieved. Indeed, a key challenge when making inference from  
33 wildlife collision data is that it is essentially presence-only data. As such, we typically cannot resolve  
34 the incidence rate over the temporal and areal extent of the study from the raw data alone as we do not  
35 have information about the vehicle movement (traffic) factors (e.g. speed, volume) and the abundance and  
36 behaviour patterns of the wildlife that leads to their interactions/collisions with vehicles. These factors  
37 clearly matter. For example, Finder et al. (1999) give an example of landscape factors influencing the  
38 collision rate of vehicles with wildlife, D’Amico et al. (2015) show that higher abundance leads to a  
39 higher collision rate, and Hobday and Minstrell (2008) show that vehicle speed influences the probability  
40 of a vehicle-wildlife collision.

41 Despite its limitations, wildlife collision data are sometimes the only source of information that a  
42 species is present in an area of interest (e.g. Boles et al., 1994; Lubis, 2005). Such data may be used as an  
43 alternative method of resighting to make inference on marked predator populations (e.g. McClintock et al.,  
44 2015). Conversely, if sampling effort can be quantified, it should be possible to use a lack of wildlife  
45 collision data for a particular species to make inference on the probability of species presence/absence,

46 and this is the key motivation of the new analysis approach that follows.

47 We note that where a numerical response function between a predator and its prey is known to  
48 exist, one can evaluate the expectation of the abundance of the predator species conditional on the  
49 prey species abundance. Furthermore, if numbers of predator and prey are sampled via the same  
50 observation/sampling process (e.g. vehicle collisions), then an absence of the predator can be used to infer  
51 extinction probabilities. The number of terrestrial carnivore species involved in incidents with aircraft is  
52 non-trivial.

53 In this paper we illustrate how simple conditioning on a second prey species, using biologically  
54 realistic numerical response functions, can produce a coherent numerical response relationship from  
55 wildlife collision data that can be used for practical inference on the population size of the predator  
56 species, including the probability of extinction. We apply the new approach to test hypotheses regarding  
57 the distribution and abundance of the red fox (*Vulpes vulpes*, Linnaeus 1758) population in Tasmania,  
58 Australia by analysing data on the aircraft collision incidence with foxes and their major prey species on  
59 airport runways.

## 60 MATERIALS AND METHODS

### 61 Case study background

62 It has been hypothesized on the basis of extraction of fox DNA from predator scats that the red fox  
63 is widespread (though rare) in Tasmania (Sarre et al., 2013). In contrast, an analysis that inferred the  
64 spatio-temporal distribution of foxes that could have generated the fox carcass discoveries suggests that  
65 the hypothesized widespread population is highly unlikely (Caley et al., 2015). The provenance of the  
66 fox carcass data on which this inference was based has been contested (Marks et al., 2014). Therefore,  
67 additional, independent inference is needed.

68 This paper considers a new, independent line of evidence to further the current debate, but before  
69 describing it we briefly explore the “widespread though rare” hypothesis as posed. We suggest that  
70 this hypothesis does not have a strong empirical basis but is a construct that enabled explanation of the  
71 differential sighting paradox: a widespread population as suggested by DNA evidence from scats, but  
72 too rare for all other observational methods to reliably detect (excluding unverified visual sightings).  
73 In contrast to the widespread though low density hypothesis, empirical evidence of invading red fox  
74 populations in the presence of abundant prey populations (as is the case in Tasmania) predicts highly  
75 irruptive invasion dynamics with peak density typically achieved within 5-10 years of foxes first becoming  
76 apparent, and often sooner. This pattern is repeated across mainland Australia, for examples see Figure 4  
77 in Jarman and Johnson (1977), Figure 3 in Short (1998), and data presented by Abbott (2011). For the  
78 fox bounty data analysed by Short (1998), the mean time from first bounty payment to the peak number,  
79 excluding pasture protection boards that only paid fox bounties in a single year, was 6.4 years ( $n=49$ ) (J.  
80 Short, unpublished data). As would be expected during the irruptive phase when *per capita* resources  
81 are high, litter sizes were reported to be large compared with those back in England (Abbott, 2011).  
82 Finally, we note that the “widespread though rare” hypothesis is difficult to disprove directly through  
83 negative survey results, as the hypothesized population appears to be detectable only by the method that  
84 generated the hypothesis — a statistical modelling approach that makes inference on joint distribution of  
85 the observation process(es) and data is required (Caley et al., 2015).

86 It transpires that collisions between aircraft and foxes during take-off and landing are not uncommon  
87 in mainland Australia. This is not unsurprising, given that Crain et al. (2015) reported that the red fox  
88 made up 12% of reported carnivore incidents involving civilian aircraft in the USA, second only to coyotes  
89 (*Canis latrans*) on 40%, and the widespread nature of red foxes in Australia. If the fox population is indeed  
90 widespread in Tasmania, one would expect that the underlying collision rate should be equivalent, after  
91 correcting for influential covariates, to that observed on the Australian mainland where foxes are indeed  
92 widespread (Van Dyck and Strahan, 2008). The underlying ecological hypothesis is that a widespread  
93 predator population should occur at densities commensurate with the available prey population, as defined  
94 by the underlying numerical response relationship.

### 95 Wildlife collision data

96 Significant resources are dedicated to the regulation and analysis of aviation safety. Reporting of  
97 wildlife strike statistics, including runway collisions, is mandatory under legislation (Transport Safety  
98 Investigations Regulations 2003). We sourced data on runway collisions at airports across Australia’s

99 states and territories from the Australian Transport Safety Bureau (ATSB) for the period 2002–2014  
100 (Australian Transport Safety Bureau, 2012, and ATSB unpublished).

101 The airstrike database for the period 2002–2014 was queried for species identified as fox, the  
102 individual records checked, and tallied for the Australian states and territories (Table 1). The Tasmanian  
103 fox population was inferred to have become widespread by, at latest, mid-way through this period in 2009  
104 (Sarre et al., 2013). Under the null hypothesis of the population being introduced and establishing in  
105 the late 1990s, this would be expected given the previously mentioned high rates of population increase  
106 following successful establishment. Indeed, we argue that due to the presence of abundant prey, an  
107 invading fox population in Tasmania should increase at the maximum (intrinsic) rate.

108 There are about 50 airfields in Tasmania, of which *c.* 27 are spread through eastern Tasmania within  
109 the convex hull incorporating the fox DNA evidence underpinning the widespread hypothesis (Figure  
110 1). Of these airfields, wildlife strike data are recorded for Bridport, Devonport, Hobart, Launceston and  
111 Wynyard — all lie within moderate to high predicted fox occupancy under the widespread hypothesis  
112 (Sarre et al., 2013), and many in close proximity to evidence locations (Figure 1).

State	Fox	Lagomorph
Queensland	7	45
New South Wales	10	34
Australian Capital Territory	3	3
Victoria	8	25
South Australia	10	21
Western Australia	4	9
Northern Territory	0	0
Tasmania	0	15

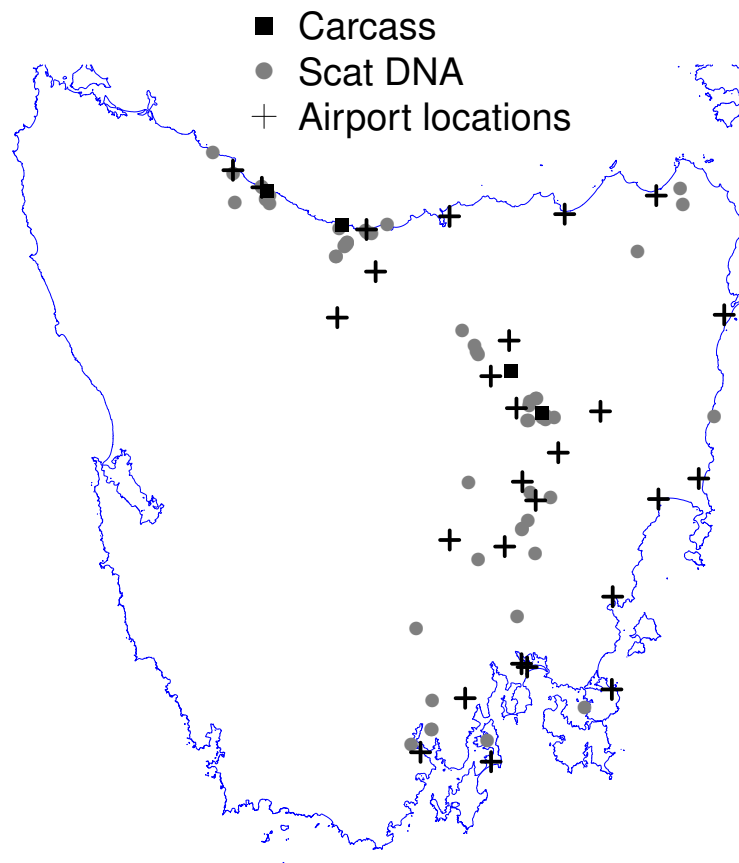
**Table 1.** Number of runway strikes for red foxes and lagomorphs (European hares & rabbits) recorded in Australian states and territories over the period 2002–2014. Source: Australian Transport Safety Bureau (2012) and Australian Traffic Safety Bureau (Unpublished data).

### 113 Analysis

114 Logically, vehicle movements and transport corridor environment needs to be taken into account when  
115 inferring the expected number of wildlife collisions, though these data are typically not available. Indeed,  
116 for our case study, compiling aircraft movement data and attributes of Australian airfields is an onerous  
117 task. There are *c.* 1,650 airfields covered by air services Australia, and even if traffic movement data were  
118 collected for all airfields there is still uncertainty about the resident population of species of interest and  
119 their access to the airport runways (perimeter fencing integrity etc.). Thus collection of more detailed  
120 information may not resolve the uncertainty around interpretation of the raw fox runway strike counts,  
121 and for wildlife collision data more generally.

122 To address these issues we present an alternative method of analysis. European hares (*Lepus eu-*  
123 *ropaeus* Pallas 1778) and European rabbits (*Oryctolagus cuniculus* Linnaeus 1758), collectively termed  
124 lagomorphs, are consistently a significant component of fox diet (Saunders et al., 1995), and there is  
125 expected to be a numerical response relationship between the two (Pech et al., 1992). The distribution of  
126 foxes on mainland Australia is strongly influenced by the distribution and abundance of lagomorphs  
127 where they occur concurrently over the vast majority of their ranges. The numerical response of foxes to  
128 rabbits is strongly non-linear and largely concave (Pech et al., 1992).

129 We propose using the runway strike rate of lagomorphs by aircraft as a proxy for both the hazard  
130 rate posed by aircraft movements as well as reflecting the productivity of the airfield environment and  
131 available access of the runway for small mammals (in this case foxes and lagomorphs). We aggregate the  
132 strike data for each state in Australia and analyse the number of fox runway strikes conditional on the  
133 number of lagomorph runway strikes. A degree of aggregation is necessary to overcome computational  
134 problems that would arise from the sparseness of these data. Other spatial resolutions would be possible,  
135 though the state-based approach had the advantage of the data already being classified by state. We note  
136 that the statistical conditioning enables us to account for unmeasured variation in factors influencing the



**Figure 1.** Map of Tasmania (excluding islands in Bass Strait) showing the locations of fox scat-DNA and carcass evidence underpinning the widespread hypothesis of Sarre et al. (2013) and the locations of active airports from which runway strike data were used. Note that airports not considered are not marked.

137 runway strike incidence for individual airports, enabling valid comparisons — an important point that  
 138 was not immediately apparent to other colleagues when first introduced to this approach.

139 We use a Holling type III numerical response (following Pech et al., 1992) to accommodate the  
 140 possibility that foxes may be particularly reluctant to venture onto airstrips at low rabbit densities  
 141 (analogous to prey-switching behaviour).

142 In statistical terms, the observed number of runway strikes ( $y$ ) model is distributed as Poisson with  
 143 underlying rate parameter ( $\mu$ ):

$$y_i \sim \text{Poisson}(\mu_i) \quad (1)$$

144 The Holling type III numerical response relating the mean fox strike rate ( $\mu_i$ ) to lagomorph runway strikes  
 145 ( $x_i$ ) is:

$$\mu_i = \frac{\beta_0 x_i^2}{\beta_1^2 + x_i^2}. \quad (2)$$

146 The subscript  $i$  denotes the  $i^{\text{th}}$  state or territory, and  $\beta_0$  and  $\beta_1$  are regression coefficients.  $\beta_0$  is the  
147 asymptotic (maximum) prey abundance. Having  $\beta_1$  squared facilitates its interpretation as the prey  
148 density at which the predator density is half of the maximum (see Results). Note, the numerical response  
149 relationship considered here relates predator abundance to prey abundance (Caughley and Sinclair, 1994,  
150 p. 172), as compared to predator population growth rate in relation to prey abundance (Sibly and Hone,  
151 2002).

152 The model was fitted using standard Markov Chain Monte Carlo (MCMC) techniques with normal and  
153 positive zero-truncated normal priors for  $\beta_0$  and  $\beta_1$  with mean 0 and standard deviation 1000, respectively.  
154 Three parallel MCMC chains were run with different starting values for  $\beta_0$  and  $\beta_1$ . Convergence of the  
155 sampler was assessed visually using trace plots and Gelman and Rubin's convergence diagnostic (Gelman  
156 and Rubin, 1992).

157 The model was fitted to the mainland data, with the Tasmanian fox runway data point treated as  
158 missing. This approach enabled sampling a posterior predictive distribution for the Tasmanian fox runway  
159 strike incidence rate (Poisson intensity parameter for the survey period). This posterior distribution for  
160 the intensity parameter was then used in two ways. First, to generate the posterior distribution for the  
161 number of runway strikes of foxes in Tasmanian for the 2002–2014 period, conditional on the observed  
162 number of lagomorph runway strikes, including 95% and 99% prediction intervals. Second, and more to  
163 the point, we can estimate the probability of observing no fox runway strikes in Tasmania, conditional on  
164 the observed number of lagomorph strikes in Tasmania in conjunction with the numerical response fitted  
165 to mainland runway strike data. We also calculated credibility intervals across the range of lagomorph  
166 runway strikes observed across all states and territories. The model was fitted using OpenBUGS within  
167 the R software environment (R Core Team, 2014) with the “R2OpenBugs” R package (Sturtz et al., 2010).

## 168 RESULTS

169 There was a strong relationship between the number of fox strikes and lagomorph strikes (Figure 2).  
170 The 95% credibility interval for  $\beta_0$  was greater than zero (95% C.I. 6.1–15.1), indicating a significant,  
171 positive effect of lagomorph runway strike rate on fox runway strike rate. The *a priori* expectation of  
172 non-linearity of the numerical response is confirmed by the small estimate for  $\beta_1$  (median= 6.2, 95% C.I.  
173 1.5–17.5), which is the number of incident lagomorph runway strikes at which half the maximum number  
174 (asymptote) of fox runway strikes would occur.

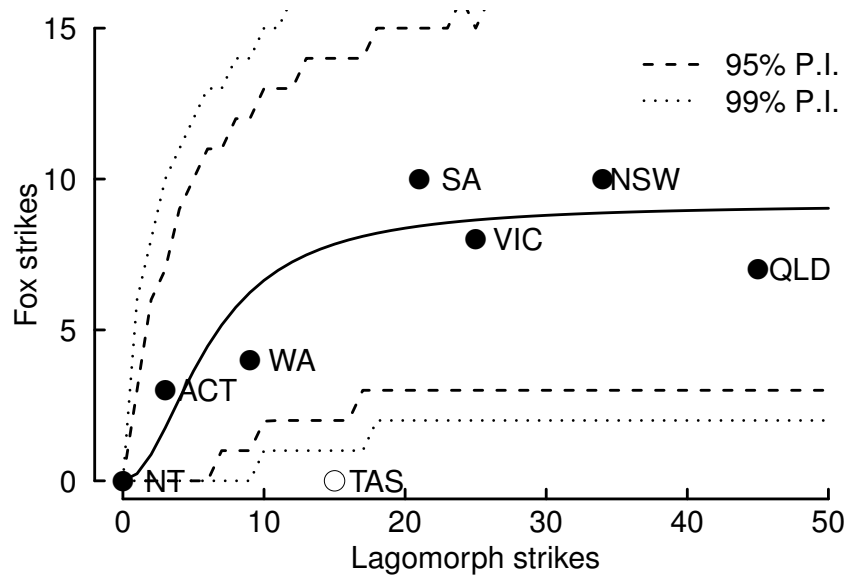
175 Under the hypothesis of a widespread fox population in Tasmania, on the basis of observing 15  
176 lagomorph runway strikes over the 2002–2014 period, Tasmania is predicted to have a mean runway  
177 strike incidence of 7.6 period<sup>-1</sup> (95% credibility interval for the mean 5.3–10.2 period<sup>-1</sup>) (Figure 2).  
178 In terms of observations, the lower 95% and 99% posterior prediction interval bounds are 2 and 1 fox  
179 runway strikes for Tasmania over the 2002–2014 period, respectively (Figure 2).

180 The probability of observing zero fox runway strikes in Tasmania, conditional on the fitted numerical  
181 response and the number of lagomorph strikes in Tasmania, was 0.001. That is, the probability of a  
182 widespread fox population existing in Tasmania whose abundance is consistent with the observed prey  
183 population is very low. That is, we reject the null hypothesis that there is an extant fox population in  
184 Tasmania that is ecologically consistent with the available prey population.

## 185 DISCUSSION

186 Our study is the first that we are aware of to use airport runway wildlife strike data to make inference on the  
187 abundance of an invasive species. It does so through combining ecological theory (in this case a numerical  
188 response function) with an appropriate statistical model. This novel approach neatly circumvents, through  
189 the process of statistical conditioning, the difficulties of measuring the airport-specific risk of runway  
190 strike. Furthermore the Bayesian approach facilitates assigning probabilities to observed outcomes given  
191 the observed data and chosen model. There are undoubtedly additional applications of this approach to  
192 wildlife strike data. For example, Crain et al. (2015) document 1,016 incidents with civilian aircraft in  
193 the United States involving at least 16 species of carnivore. Clearly the method is equally applicable to  
194 roadkill data.

195 We have considered a new, independent line of evidence to further the current debate as to the  
196 distribution and abundance of foxes in Tasmanian. The inference from our analysis of independent data  
197 strengthens the case against their having ever been a widespread fox population in Tasmania that was



**Figure 2.** Numerical response relationship between the number of fox runway strikes versus lagomorph (hare or rabbit) runway strikes over the period 2002–2014 for Australian states and Territories. Labels are: “NT”–Northern Territory; “QLD”–Queensland, “NSW”–New South Wales, “SA”–South Australia; “WA”–West Australia; “VIC”–Victoria; “TAS”–Tasmania. Source: Australian Transport Safety Bureau (2012). Solid line is Holling type III numerical response model fitted to data with Tasmanian data point (open circle) omitted. Dotted and dashed lines are 95% and 99% prediction intervals (P.I.) for observations conditioned on the mainland data only.

198 ecologically consistent with available prey populations, or consistent with the detection probabilities  
 199 of known observation methods. Accepting the alternative hypothesis (that there is not an ecologically  
 200 consistent, detectable fox population in Tasmania) is not equivalent to inferring there is no fox population  
 201 in Tasmania. Note, however, that both Caley and Barry (2014) and Caley et al. (2015) infer that extinction  
 202 is the most likely outcome.

203 Looking to the future, if no further foxes are detected in Tasmania, then exactly how widespread and  
 204 abundant foxes have been in Tasmania will undoubtedly be subject to ongoing debate. There is possibly  
 205 considerable irreducible uncertainty in the provenance of the data used to date (as, for example, argued by  
 206 Marks et al., 2014). We note another novel, independent observational process arising from the predation  
 207 of foxes by wedge-tailed eagles (*Aquila audax*, Latham 1802) that should provide additional, independent  
 208 inference. Like their northern hemisphere counterpart the golden eagle (*Aquila chrysaetos*, Linnaeus  
 209 1758), wedge-tailed eagles are known to effectively prey on red foxes, and red fox remains are consistently  
 210 found in wedge-tailed eagle diets (at non-trivial percentages) in a wide range of habitats wherever foxes  
 211 are present (e.g. Olsen et al., 2010; Sharp et al., 2002; Parker et al., 2007; Brooker and Ridpath, 1980).  
 212 Their range encompasses all of the parts of Tasmania of interest. The nest locations of the wedge-tailed  
 213 eagle pairs could be carefully searched for fox remains. Making inference from such data, particularly  
 214 if no fox remains are found, will need to be conditional on an appropriate eagle-fox detection model.  
 215 Factors such as the territory size of eagle pairs will set the spatial resolution of the resulting inference.

216 Traditional methods of inferring extinction have focussed on making inference from the sighting  
 217 record (e.g. Solow, 1993, 2016), where prior positive observations are used to estimate the sighting  
 218 rate/probability given species presence, and the probability of extinction is estimated accordingly given  
 219 the time or then number of surveys since the last sighting (see Caley and Barry (2014) for a recent Bayesian  
 220 implementation). The method illustrated here can make inference on the probability of extinction without  
 221 the need for prior sightings from the area of interest, provided there are data on a functionally linked  
 222 species available. Our approach is a logical extension of the empirical findings studies such as Barrientos



223 and Bolonio (2009), who showed that the presence of rabbits adjacent to roads increases the rate of  
224 road-kill of the European polecat (*Mustela putorius*, Linnaeus 1758). Calibrating the numerical response  
225 function is the extension that enables inference on the abundance of the predator of interest.

226 Of course, prior sightings are not required for estimating detection probabilities if the detection  
227 power of the search effort is known independently. Quantifying detection probabilities becomes difficult,  
228 however, when search effort varies in space and time, along with the wildlife species of interest. This  
229 necessitates computationally intensive methods that respect the complexity of the underlying population  
230 and surveillance processes (Caley et al., 2015). The key feature of the approach we have illustrated here  
231 is that by statistically conditioning on a second, biologically linked species, it essentially integrates over  
232 the unknown factors underpinning the observation effort and hence detection probability. Reid (1995)  
233 notes how natural the process of conditioning is as a tool in everyday statistics, and our example here  
234 demonstrates how it can be used to extract useful inference from data, for which at first glance may appear  
235 uninformative.

236 Finally, although we have illustrated our approach using wildlife collision data, it is applicable to any  
237 observational process which samples both the predator species of interest and a prey species (or multiple  
238 prey species), for which a numerical response relationship between the two is known to exist and can be  
239 calibrated.

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