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REVIEW

Runway roadkill: a global review of mammal strikes with aircraft

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ABSTRACT

1. The number of reported collisions (i.e. strikes) between aircraft and wildlife is increasing globally, with consequences for personnel and passenger safety as well as for industry economics. These are important considerations for airport operators that are obliged to mitigate wildlife hazards at airfields. Incidents involving mammals account for approximately 3-10% of all recorded strikes. However, relatively little research has been conducted on mammal strikes with aircraft outside of the USA.
2. We collate mammal strike data from six major national aviation authorities and a global aircraft database and review the available scientific and grey literature. We aim to identify which mammal families are involved in strike events and how widespread the issue is on a global scale. We also aim to demonstrate the importance of consistently recording strike instances in national databases.
3. We identified 40 families that were involved in strike events in 47 countries. Reported mammal strike events have been increasing by up to 68% annually. Chiroptera (4 families) accounted for the greatest proportion of strikes in Australia, leporids and canids in Canada, Germany and the UK, and chiroptera (5 families) and cervids in the USA. More mammals were struck during the landing phase of an aircraft's rotation than any other phase. Circa-diel strike risk was greatest at dusk and circa-annum strike risk was greatest during late summer, with some international variation. The total estimated cost of damage resulting from reported mammal strikes exceeded US$103 million in the USA alone, over 30 years.
4. Mammal strikes represent a substantial risk in airfield environments. Monitoring of existing wild mammal populations is required to understand temporal trends in presence, abundance and activity patterns and to inform management decisions.

Increased and accurate reporting of strike events globally is needed to inform Wildlife Hazard Management Plans and support effective strike mitigation.

RÉSUMÉ EN FRANÇAIS

1. La fréquence des collisions entre avions et animaux sauvages connait une augmentation constante à travers le monde, entrainant des conséquences pour la sécurité du personnel et des passagers ainsi que pour l'économie de l'industrie aéronautique. Il s'agit d'une considération importante pour les exploitants d'aéroports qui sont tenus d'atténuer les risques potentiels liés à la faune sauvage sur les terrains d'aviation. Les incidents impliquant des mammifères représentent environ 3 à 10 % des collisions enregistrées. Cependant, en dehors des États-Unis, relativement peu de recherches ont été menées sur les collisions entre mammifères et avions.

2. Nous rassemblons les données sur les collisions avec des mammifères provenant de six directions nationales majeures de l'aviation civile ainsi que d'une base de données mondiale sur les aéronefs et compulsons l'ensemble de la littérature scientifique et grise disponible. Notre objectif est d'identifier les familles de mammifères impliquées dans les collisions et de déterminer l'ampleur du phénomène à l'échelle mondiale. Parallèlement, nous cherchons à démontrer l'importance de l'enregistrement systématique des cas de collisions dans les bases de données nationales

3. Nous avons identifié 40 familles de mammifères impliquées dans des collisions dans 47 pays, avec une forte augmentation des collisions signalées, pouvant aller jusqu'à 68% par an. Les chiroptères (4 familles) représentaient la plus grande proportion des collisions en Australie, au Canada, en Allemagne et au Royaume-Uni ce sont les léporidés et les canidés qui sont le plus souvent impliqués, et aux États-Unis, les chiroptères (5 familles) et les cervidés. Plus qu'à

toute autre phase, c'est pendant la phase d'atterrissage que le nombre d'impacts le plus importants se produit. Au cours de la journée, le risque d'impact est le plus élevé au crépuscule et il connait un pic annuel à la fin de l'été et en automne, avec cependant quelques variations internationales. Sur une période de 30 ans, le coût estimé des dommages résultant des collisions signalées avec des mammifères dépasse les 103 millions de dollars US rien qu'aux États-Unis.

4. Les collisions impliquant un mammifère représentent un risque environnemental élevé pour les aéroports, tant pour l'intégrité des avions que pour la sécurité des passagers. L'évaluation des populations de mammifères sauvages aux abords des aéroports est nécessaire pour prédire les évolutions temporelles de présence, d'abondance et d'activité de ces populations. Les études permettent d'accompagner les opérateurs d'aéroports dans la prise de décision liées à la prévention des risques naturels. A l'échelle mondiale, il est nécessaire de disposer de rapports plus nombreux et plus détaillés sur les cas de collisions afin d'enrichir les stratégies de gestion des risques animaliers et de réduire efficacement le nombre de collisions.

INTRODUCTION

Airports and the services that they provide are vital to the global economy. In 2018 alone, over four billion passengers were carried by aircraft, and airline industry revenues exceeded US$812 billion (IATA 2019). Whilst airports can contextually constitute environmental disturbances (Blackwell et al. 2013), the airport environment can provide productive habitat for wildlife (Soldatini et al. 2010, Hauptfleisch & Avenant 2015), due to expanses of semi-natural grasslands. In the USA alone, there is in excess of 3300 km^2 of grassland in airfields (DeVault et al. 2012, Washburn & Seamans 2013, Pfeiffer et al. 2018), creating favourable ecological habitats, often in heavily urbanised areas (DeVault et al. 2012). These grasslands can be attractive to a range of animal taxa (e.g. deer - Cervidae, geese - Anatidae, starlings - Sturnidae;

97 Belant et al. 2013, Coccon et al. 2015, Pfeiffer et al. 2018). Some of the animals can be
98 hazardous to aviation if they are involved in wildlife-aircraft collisions or 'strikes' (Blackwell
99 et al. 2013).

100 Incidents with avian species make up the majority of wildlife strikes (e.g. 95% of strike
101 events in the USA involve birds; Dolbeer & Begier 2019) and therefore the bulk of available
102 literature focuses on avian taxa. Strike data are generally lacking for other taxa, including
103 mammals, which are estimated to make up approximately 5% of strikes in the USA (Dolbeer
104 & Begier 2019). Globally, there has been a general increase in the number of reported wildlife
105 strikes with aircraft (Thorpe 2010), with evidence that mammal strikes may also be increasing
106 (e.g. Dolbeer 2015). Airport operators have a legal obligation to reduce wildlife hazard at
107 airfields (Mendonca et al. 2017). It is therefore important for airports to understand the relative
108 risk associated with each species, in order to prioritise and implement effective Wildlife Hazard
109 Management Plans (WHMP).

110 Understanding the importance of wildlife strikes and associated hazards requires the
111 collection and analysis of strike data. Long-term databases recording animal strike incidents
112 and damage (Dolbeer & Wright 2009), kept by national aviation authorities, are valuable tools
113 for this analysis. However, reporting is not always mandatory, and databases often have a large
114 proportion of unidentified species. Additionally, these databases are likely to under-represent
115 the true frequency with which wildlife strikes occur (Biondi et al. 2011). For example, reporting
116 is mandatory within the European Union (EU), but not in the USA. While previous work has
117 been conducted on mammal strikes with aircraft by looking at specific mammal groups in the
118 USA, such as bats (Biondi et al. 2013), deer (Biondi et al. 2011) and carnivores (Crain et al.
119 2015), little work has been conducted looking at the class Mammalia as a whole (but see
120 Schwarz et al. 2014), particularly outside the USA. Therefore, American data are often used as
121 the baseline reference with little global context.

122 We review the available literature and collate mammal strike data from six national
123 aviation authorities (Australia, Canada, France, Germany, UK and USA) and from a database
124 of destroyed aircraft compiled by Avisure (a bird strike risk mitigation company; Avisure 2019).
125 By doing so, we aim to: 1) identify the mammal families reported to have been involved in
126 strike events globally; 2) identify the countries where strike events with mammals have been
127 reported; 3) determine how the number of reported strikes has changed over time; 4) identify
128 periods of increased risk based on reported strike incidents; and 5) emphasise the importance
129 of national databases as a tool to understand the patterns associated with mammal strike events.
130 We expect that reported strike events are increasing over time and that diverse mammalian taxa
131 are involved in these events. This review will help to highlight the extent of mammal strikes
132 with aircraft and inform wildlife management on both national and international scales.

133

METHODS

We surveyed all available literature published before October 2020, using the search engines Web of Knowledge, Science Direct and Google Scholar, to identify published records of aircraft collisions with mammals. The search terms 'mammal strike', 'wildlife-strike', 'animal strike', 'mammal collision', 'wildlife collision', 'animal collision', 'aircraft', 'aviation' and 'airplane' were applied for two searches: 1) with just search terms; and 2) with search terms alongside mammal taxa frequently involved in strike events (Canidae, Cervidae, Chiroptera, Leporidae). Search results, which included both the title and the abstract, were manually sorted to remove irrelevant articles and duplicate publications. Results were also supplemented by references within the literature. Relevant 'grey literature' (i.e. conference proceedings, government reports) were retained.

National aviation authorities were contacted to request mammal strike records (Appendix S1). Data on strikes were obtained from six aviation databases and record centres. Data were obtained from the website of 1) the Australian 'Transport and Safety Bureau' (ATSB; 2008 – 2017; ATSB 2018). Data were provided, upon request, by: 2) 'Transport Canada' (TC; 2008 – 2018; TC 2019); 3) the French 'Service Technique de l'Aviation Civile' (STAC; 2016 – 2018;); STAC 2019) 4) the German 'Deutscher Ausschuss zur Verhütung von Vogelschlägen im Luftverkehr e.V.' (DAVVL e.V.; 2010 – 2018; DAVVL e.V 2019); and 5) the 'UK Civil Aviation Authority' (UKCAA; 1990 – 2018; UKCAA 2019). Finally, data were obtained from the website of 6) the USA's 'Federal Aviation Administration' (FAA; 1990 – 2018; FAA 2019). All data were accessed and provided between February 2019 and March 2020. Wildlife strike reporting was mandatory in all countries analysed, except for the USA. However, reporting became mandatory in different countries at different times (e.g. 2000 in Australia, 2004 in the UK) and countries have different reporting conditions (e.g. in Germany

158 only mammals the size of a rabbit or larger are reported). All databases were screened to
159 remove non-strike incidents (i.e. near misses, disruptions); a strike was deemed to have
160 occurred if there was sufficient evidence (i.e. a carcass was found or damage was inflicted). In
161 all databases, strikes involving helicopters, gyrocopters and military aircraft (but see Zakrajsek
162 & Bissonette 2005, Peurach et al. 2009) were removed, to isolate incidents with civil
163 (commercial and private) airplanes. The databases included reports of strikes with domestic
164 animals, thus we included both wild and domestic non-human mammal taxa (e.g. Hesse et al.
165 2010). As there is no single, central reporting organisation and reporting of strike incidents is
166 voluntary in some areas (e.g. USA), reporting falls to multiple organisations, airports and
167 individuals. Hence, data were largely inconsistent in terms of detail and temporal information.
168 These limitations were overcome by applying a consistent data management framework that
169 was compatible with all databases (i.e. categorising mammals according to taxon and
170 categorising strike data, as outlined below). Available variables from databases are shown in
171 Appendix S2.

172 For the ATSB, TC, DAVVL e.V and FAA databases, strike incidents were summarised
173 for time of day, where phase of flight was also provided, based on the local time reported. We
174 defined both 'day' (08:00 - 18:00h) and 'night' (20:00 - 06:00h) as 10-hour periods, whilst
175 'dawn' (06:00 - 08:00h) and 'dusk' (18:00 - 20:00h) were each two hours (Washburn &
176 Seamans 2013, Crain et al. 2015). Damage was categorised as 'none', 'minor', 'substantial'
177 and 'destroyed' by both the FAA and ATSB, in accordance with International Civil Aviation
178 Organization's (ICAO) aircraft damage taxonomy (ICAO 1989). We classified damage in the
179 same way using data from the DAVVL e.V. and STAC databases, depending on where damage
180 was inflicted. Data on damage from the TC and UKCAA databases were insufficient for
181 inclusion. For all databases, strike incidents were summarised for the phase of flight and

182 categorised as ‘approach’, ‘climb’, ‘en route’, ‘landing roll’, ‘take-off run’ and ‘taxi’ (Biondi
183 et al. 2011, with the addition of 'en route').

184 The FAA database provided a value, in US dollars, for the cost of the damage inflicted
185 to aircraft from strikes with mammals for 397 strike events from a total of 1077 in which
186 damage was inflicted (1990 - 2018). This was the only database which provided any detail on
187 costings. To estimate the economic impact of damaging mammal strikes in the USA using these
188 values, the average (mean) cost of repairs from a strike incident was determined for each
189 damage category (‘minor’, ‘substantial’, ‘destroyed’ and ‘unspecified’). The mean cost was
190 then multiplied by the total number of incidents within each category to obtain an overall
191 estimate of damage costs inflicted by mammal strikes from 1990 - 2018, as per Biondi et al.
192 (2011) and Crain et al. (2015).

193 International guidelines generally report the number of strikes per 10000 aircraft
194 movements (ICAO 2012). However, such reports focus on individual airports, where the
195 proportion of strikes to movements is much higher than across entire countries. For ease of
196 interpretation, we calculated strike rates as the annual number of strikes per one million aircraft
197 movements (MAM), as per Crain et al. (2015). One movement was defined as a take-off run
198 or a landing manoeuvre; both figures were summed to give the total number of movements.
199 For Australia, the number of departures (take-off runs) was obtained for 2008 - 2016 from the
200 Aviation Occurrence Statistics Report (ATSB 2018b) and the number of landings from annual
201 Australian Government reports (BITRE 2008-2017). As only the number of landings could be
202 obtained for 2017, this was doubled to estimate the total number of aircraft movements.
203 Movements for Canada were obtained from Statistics Canada’s annual reports (Statistics
204 Canada 2010, 2014, 2019). Aircraft movements for Germany for 2010 - 2017 were obtained
205 from the Deutsche Flugsicherung (DFS Deutsche Flugsicherung 2010-2017). Aircraft
206 movements for the UK for 1990-2018 were obtained from the Civil Aviation Authority’s

annual summary data (www.caa.co.uk/Data-and-analysis). Finally, for the USA, the FAA Terminal Area Forecast, which provides official data of aviation activity for US airports, was queried as per Biondi et al. (2011; 2013) and Crain et al. (2015) in order to obtain aircraft movement figures.

The Avisure database on destroyed aircraft attributed to wildlife strikes (www.avisure.com; Avisure 2019) was accessed in April 2019 and sorted to isolate incidents with mammals. Data were available for 1966-2015 and were used to identify mammal taxa and countries involved in strike events. Due to the low number of recorded events, some of which were also recorded by aviation authorities included in this review, these data were not included in any analyses.

Data were organised and summarised in the programme R (v. 3.6.1; R Core Team 2018). We used General Linear Modelling with either a Poisson or Quasipoisson error structure, implemented within the 'lme4' package (Bates et al. 2015), to evaluate trends in the number of strike events over time (years), for each country. The strength of association between strikes and year was tested with Spearman's Rho (ρ). As parametric modelling assumptions were not met (for month and phase of flight), we used non-parametric Kruskal-Wallis tests with Dunn's post-hoc test with a Benjamini–Hochberg *P*-value correction (Benjamini & Hochberg 1995) to allow for multiple comparisons. To evaluate trends in strike events across 'month' (categorical with 12 levels) and 'phase of flight' (categorical with six levels), countries were grouped together based on geographic location, into: 1) Australia; 2) North America (Canada and the USA); and 3) Europe (France, Germany and the UK). A further Kruskal-Wallis test was conducted to evaluate trends in strike events across 'phase of flight', with mammal groups divided up between volant (bats) and terrestrial taxa.

RESULTS

The literature survey yielded 44 relevant articles (Appendix S3). A total of 40 mammal families were identified as having been involved in wildlife strikes with airplanes, across 47 countries (Table 1). In addition to these families, the Ursidae (bear) and the Otariidae (eared seals) were reported to have caused disruptions without resulting in strike events (FAA 2019) and the leaf-nosed bats (Hipposideridae) were identified as having been involved in strike events with military aircraft (Peurach et al. 2009). A total of 15 families were identified to have been involved in a strike event with aircraft other than civil airplanes (e.g. Washburn et al. 2017; Appendix S4).

A total of 13 mammal families were involved in strike events in Australia, amounting to 1564 events, or 9.6% of the national total of all strike events (mammalian and non-mammalian species). Only 1024 strikes involved mammals that could be identified to family level; many strikes (n = 540) involving members of the order Chiroptera were recorded as 'bats'. In the USA, 25 mammal families were identified as having been involved in strike events from 6661 events, constituting 3.2% of the national total. A mammal family (Pteropodidae) not naturally found in the USA was reported as the family involved in strike events in two American airports. This may be as a result of misidentification, escaped captives or the bat may have been carried on an airplane from the country of origin and subsequently found in these airports in the USA (see Leader et al. 2006).

The TC, STAC, DAVVL e.V. and UKCAA databases provided bespoke data (i.e. mammal strikes only), thus the percentage of strikes attributed to mammals could not be determined. A total of 398 strikes involving 14 families were reported in Canada, 126 strikes involving six families were reported in France, 140 strikes involving five mammal families

254 were reported in Germany and 115 strikes involving eight families in the UK (Appendices S5
255 and S6).

256 Utilising the data from all six national aviation authorities resulted in a database of 9004
257 confirmed strike events with mammals. In Australia, order Chiroptera accounted for the
258 greatest proportion of reported strikes and were involved in 79% of strike events with mammals
259 overall. In Canada, Germany and the UK, leporids (Leporidae; Canada: 20%, Germany: 79%,
260 UK: 52%) and Canidae (Canada: 21%, Germany: 16%, UK: 17%) were most frequently
261 involved in wildlife strikes, while Chiroptera (38%) and Cervidae (deer; 17%) accounted for
262 the greatest proportion of strikes in the USA. Across all databases, strike events involving
263 multiple mammals accounted for 4.9% of all records.

264 All countries reported an increase over time in the annual recorded strike rate. In
265 Australia, there was an average of 38.7 ± 15.7 (mean ± standard deviation, SD) reported strikes
266 strikes/MAM/year. Strike frequency increased an average of 7% annually (confidence intervals,
267 CI: 2% - 12%; $\rho = 0.66$), with a significant difference between years ($\chi^2_{8, 1564}$, $P<0.05$). Canada
268 reported an average of 8.1 ± 2.9 (mean ± SD) strikes/MAM/year and an average annual increase
269 of 9% (CI: 4% - 13%; $\rho = 0.77$), with significant variation between years ($\chi^2_{9, 398}$, $P<0.01$).
270 France reported an average of 17.4 ± 4.3 (mean ± SD) strikes/MAM/year and an average annual
271 increase of 25% (CI: 4%; 47%; $\rho = 1.0$) with significant annual variation ($\chi^2_{1, 126}$, $P<0.05$). In
272 Germany, there was an average of 3.6 ± 4.9 (mean ± SD) reported strikes/MAM/year; strike
273 events increased by an annual average of 68% (CI: 56% - 80%; $\rho = 0.95$), with significant
274 variation between years ($\chi^2_{7, 140}$, $P<0.001$). In the UK, there was an average of 1.2 ± 2.4 (mean
275 ± SD) reported strikes/MAM/year; reported strike events with mammals increased annually by
276 on average 16% (CI: 7% - 22%; $\rho = 0.52$), with significant variation between years ($\chi^2_{18, 115}$,
277 $P<0.001$). Finally, there were an average of 2.3 ± 2.1 (mean ± SD) reported strikes/MAM/year
278 in the USA; reported strike events with mammals increased annually by an average of 10%

(CI: 9% - 10.5%; $\rho = 0.99$), with significant variation between years ($\chi^2_{27, 6661}$, $P<0.001$; Fig. 1). No country surpassed the ICAO acceptable level given in safety guidelines, of five strikes per 10000 aircraft movements (500/MAM/yr; ICAO 2012).

In Australia ($H_{(11)} = 41.27$, $P<0.01$) and North America ($H_{(11)} = 63.3$, $P<0.01$), there were identifiable peaks in strike frequency between months, but in Europe, strike frequency fluctuated across the year without pattern. For Australia, highest strike numbers were recorded during March to May (37% of strike events), with a significant difference between strike event numbers in March and in all other months, except for April. For North America, the majority of strikes were recorded during July to November (74% of strike events). In Europe, 68% of strike events were recorded between July and November, with the highest strike numbers recorded in October (18%; Fig. 2).

There were significant differences in strike frequency according to phase of flight between volant taxa ($H_{(5)} = 17.1$, $P<0.01$) and terrestrial taxa ($H_{(4)} = 88.0$, $P<0.01$). Across all taxa (volant and terrestrial), there were significant differences in strike frequency according to phase of flight for Australia ($H_{(5)} = 47.67$, $P<0.01$) and North America ($H_{(5),\ 3113} = 98.9$, $P<0.01$). Generally, the landing roll phase, followed by the take-off run, yielded the highest frequency of strike events (Fig. 3). Australia formed an exception to this: both the landing roll and the approach conferred the greatest strike risk (59% of all strikes). In North America, the landing roll was the only phase that resulted in significantly elevated strike risk (21% of all strikes). Australia and North America (USA; $n=615$, CAN; $n=1$) were the only two continents with a high frequency of strikes on approach.

Daily strike patterns varied between countries. Strike incidents were most frequent at night in Australia (42%), Canada (56%), Germany (63%) and the USA (62%). Standardised time periods (number of strikes/ number of hours) provided arbitrary strike rates for each time

period. Dusk was identified as having the highest strike rate per hour for Australia and the USA (n=249 strikes/hour and n=139.5 strikes/hour, respectively) and night conferred the greatest risk in Canada and Germany (n=12.5 strikes/hour and 8 strikes/hour, respectively).

Mammal strikes frequently resulted in damage to aircraft in some areas: damage was reported for 18%, 3%, 1% and 17% of strike events with mammals in Australia, France, Germany and the USA respectively (Fig. 4). Damage could not be classified for UKCAA or TC data. Damage costs were provided for only the USA, where total reported cost of repairs caused by mammal strikes exceeded US$56 million for 397 events across all taxa (1990-2018). Cervidae accounted for 91% of reported repair costs. The total estimated cost of repairs was US$103 million, for all 1077 events where damage was reported. In Australia, the Macropodidae and the Pteropodidae were collectively involved in 64% of damage-inducing strikes. In France and Germany, the Canidae, Cervidae and Leporidae were involved in all damaging strikes (Appendix S5). The FAA and ATSB provided data on human injuries within the database: 25 people were reported to have been injured as a result of mammal strikes, and there was one reported human fatality.

DISCUSSION

Collisions between wildlife and aircraft are a considerable concern for airport authorities, particularly as the number of reported strikes per annum is generally increasing (Dolbeer 2015). However, given the heightened awareness of the importance of reporting strike events in recent years, these increases could merely reflect recording effort rather than an increase in incidences. Mammalian taxa comprise a small proportion of total strikes. Nevertheless, mammals pose a considerable risk, with economic and human health-related consequences. Here, we observed an annual increase in the frequency with which mammals are involved in reported strike events. Strike events were recorded on every continent except Antarctica, confirming that mammal

strike events are a global issue involving a broad range of taxa. While a general increase in air traffic is likely to be partially responsible for this annual increase (but see Soldatini et al. 2011), both the ecological and behavioural traits of mammal populations in proximity to and inhabiting airports need to be understood and integrated into WHMPs if effective management policies are to be developed and implemented.

There is a paucity of information available on mammal taxa involved in strike events, with the exception of Canidae, Cervidae and the Chiroptera. The mammal taxa involved in strike events, the frequency of strikes, and the proportion of strikes that resulted in damage to aircraft vary between countries. This demonstrates the need for more specific recording of information about wildlife strikes by aircraft on a country-by-country basis. Moreover, mammals from different geographical areas represent different threats to aircraft, and this demonstrates the need for more accurate and complete recording of information from each area. The majority of mammal strike research is focused on just two families, the Canidae (e.g. Crain et al. 2015) and the Cervidae (e.g. Biondi et al. 2011), as these two families are involved in 94% of damaging strikes involving mammals in the USA, where the majority of strike research has been undertaken. Elsewhere, damaging strikes were dominated by the Chiroptera in Australia and the Leporidae in Europe. Therefore, mitigiation measures developed in the USA for the specific fauna of North America may not be effective for high-risk species in other parts of the world. As air travel is a global industry, increased research efforts targeted at high-risk mammal families outside the USA would benefit not only the national aviation authorities responsible for the research, but also international authorities and airline operators. A more thorough understanding of the ecology of mammal groups inhabiting and using airfields is required to maximise the efficacy of any mitigation measures (e.g. Scheideman et al. 2017).

In the USA, it is estimated that mammal strikes are five times more likely to cause damage to aircraft than bird strikes (Schwarz et al. 2014), and mammals are estimated to be

352 involved in 8.7% of wildlife strikes causing damage to aircraft in the USA (Dolbeer & Begier
353 2019). We estimated that the total cost of repairs to aircraft after mammal strikes in the USA
354 exceeded US$103 million between 1990 and 2018. While terrestrial mammals are arguably
355 some of the easiest animals to control at airfields through adequate exclusion (e.g. fencing) and
356 habitat management measures, these measures can be costly to implement (>$20/m for fencing;
357 VerCauteren et al. 2006, 2013). Additionally, many strike events occur despite the presence of
358 fencing, thereby representing a substantial additional cost. Damage costings highlight the need
359 for targeted wildlife management in addition to the importance of the upkeep of implemented
360 mitigation measures (VerCauteren et al. 2013). While estimates of damage and costs are
361 conservative (Biondi et al. 2011), they nevertheless highlight the economic severity of the issue.
362 Estimates also allow us to identify the mammal taxa that are most economically damaging if
363 struck (MacKinnon et al. 2004) and to test current WHMPs (Dolbeer & Wright, 2009).
364 Therefore, accurate reporting of all costs associated with each strike event (i.e. parts, labour,
365 time out of service) is needed to quantify the true financial impacts of mammal strikes on local,
366 national and global scales.

367 Wildlife-strike databases allow for the identification of periods of increased risk at
368 national (e.g. Biondi 2011, Biondi et al. 2013) and global (ICAO 2017) scales. We found dusk
369 and night to be the most hazardous times for four countries analysed (see also Parsons et al.
370 2009, Biondi et al. 2011, Schwarz et al. 2014). Indeed, over 70% of mammal species are
371 nocturnal or crepuscular (Bennie et al. 2014), including taxa frequently involved in strike
372 events. For example in Australia, dusk was identified as having the highest strike risk, where
373 85% of strikes were recorded with Chiroptera, most species of which are most active at dusk
374 and dawn (e.g. Welbergen 2006). Additionally, seasonal peaks in strikes coincide with the end
375 of Summer, which is a time of dispersal in many species. Identifying periods of high risk such
376 as these can allow for targeted mitigation measures, such as increased patrols during these

377 times (Crain et al. 2015) or slight modifications to flight schedules to reduce risk. This also
378 demonstrates that data need to be collected at the local scale, to identify periods of risk and
379 adjust mitigation measures accordingly. Data on the number of aircraft movements occurring
380 within each time period were not available, but it is possible that increased air traffic during
381 these times may pose risks additional to those related to faunal activity patterns.

382 Strike frequency is thought to be influenced by local occurrence and abundance of
383 species (e.g. Schwarz et al. 2014), in addition to seasonal life-history traits, such as activity and
384 breeding cycles, that make it difficult to mitigate against strike events. However, once these
385 periods of increased risk are identified, depending on the faunal composition of wildlife in the
386 vicinity of an airport, mitigation measures can be implemented year after year. For example,
387 strikes involving Pteropodidae in Australia occurred most frequently during the breeding
388 season (Vardon et al. 2001). Similarly, Leporidae were the most commonly struck family in
389 three of five countries analysed, inclusive of during high-risk periods. Their high fecundity
390 (Caravaggi 2018), coupled with the potential for airfields to offer good quality, resource-rich
391 habitats that consequently support high density populations (Anthony Caravaggi, unpublished
392 data), can make population management at airfields difficult and expensive (e.g. Dublin Airport,
393 Ireland; Dublin Airport Authority, personal communication). Therefore, management
394 processes aimed at reducing strike frequency and severity should account for species' traits,
395 such as breeding seasons, or aim to exclude mammals entirely. However, mammals are
396 charismatic and popular, and public attitudes are an important consideration in modern wildlife
397 management processes (Liordos et al. 2017, van Eeden et al. 2017, 2019). Moreover, species
398 recorded in strikes may be of conservation concern, be subject to protective legislation, or
399 provide important ecosystem services (e.g. Birkhofer et al. 2018). Hence, the drive to reduce
400 the number of strikes also has a broad, ecological remit that must not be discounted.

401 Higher strike rates were recorded during the landing phase in all six countries, possibly
402 because the reduced speed and agility of aircraft during this phase makes it difficult for pilots
403 to avoid obstacles (Biondi et al. 2011). This, paired with the ability of mammals to habituate
404 to mechanical noises (Weisenberger et al. 1996, Ditmer et al. 2018), reduced engine noise
405 during landing, and a lack of aerial predators, particularly for larger mammals, may mean that
406 incoming (landing) aircraft are not always perceived as a threat (but see Lima et al. 2015).
407 Additionally, the phase of flight in which a strike can occur with a terrestrial mammal is limited
408 to when an aircraft is in contact with the ground (e.g. landing), whereas strike events with
409 volant taxa can occur at all phases of flight.

410 Under-reporting of strikes is recognised on both an international and national level:
411 estimates suggest that only 5-47% of wildlife strikes are reported to aviation authorities
412 (Linnell et al. 1999, Wright & Dolbeer 2005, Dolbeer & Wright 2009, Dolbeer 2015). Indeed,
413 the reporting of strike events remains voluntary in many countries. A total of 2295 mammal
414 strikes were reported to the ICAO during the years 2008-2015. However, during this same time
415 period, 4263 mammal strike events were recorded by five civil aviation authorities included in
416 this review (France only had records from 2016 onwards); this number surpasses the globally
417 reported numbers by 1968 strikes. A similar pattern was observed for the period 2001-2007
418 (ICAO 2009). Therefore, it is unlikely that current estimates are accurate reflections of numbers
419 of mammal strike events. Such discrepancies represent important caveats to, and limit the
420 utility of, broad guidelines developed by civil aviation authorities and the ICAO (e.g. ICAO
421 2012). Despite the FAA's assurance that current data are adequate to track national trends
422 (Dolbeer 2015), improvements are nevertheless required to identify the true extent of the risks
423 posed to and by mammals, and to evaluate the effectiveness of WHMPs and mitigation
424 practises (Dolbeer & Wright 2009). This is particularly true for areas outside of USA, as the
425 numbers reported to the ICAO indicate severe underreporting or a complete lack of reporting

426 for many regions globally. Focusing on the accurate and timely reporting of strike events is
427 important to help improve data in the near future, particularly for regions with established
428 reporting systems (e.g. USA). However, in the long term, we suggest the uptake of mandatory
429 reporting schemes and the centralisation of accurate and timely strike data, to support
430 knowledge synthesis, the derivation of accurate strike statistics and the collaborative
431 development of management procedures on a global scale.

432 Our findings are derived from some of the more economically developed countries
433 (Australia, Europe and North America). Differences in economic development may, in part, be
434 reflective of differences in national flight capacity and frequency, or of levels of compliance to
435 international organisations from other nations. Therefore, it is not possible to infer global strike
436 rates from our data. Nevertheless, the observed increase in strike events over time per million
437 aircraft movements (MAM/year) in all the countries we studied suggests that our findings have
438 broad relevance. Furthermore, terrestrial mammals involved in strikes were not identified to
439 the species level in <1% of instances, and bats were not identified to the species level in 17%
440 of instances in the current study. The specific identification of taxa involved in strike events is
441 not only important to improve WHMPs, but can also play an important role in accident or strike
442 event investigations (Dove et al. 2008a) and in subsequent mitigation. Therefore, we
443 recommend the use of forensic DNA analysis (Peurach et al. 2009, Kelly et al. 2017) to identify
444 otherwise 'unknown' species, thereby giving more nuanced ecological insight and
445 subsequently improving management strategies.

446

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Tables and Figures:

453
454 **Table 1**. Mammal families involved in civil airplane wildlife strikes reported in organisational, grey and scientific literature, and the country or countries of
455 occurrence

Taxon	Country/Countries	References
Antilocapridae	Nigeria, USA	Cleary et al. 1996, 2004, 2005, 2006, Cleary & Dolbeer 2005, ICAO 2009, Dolbeer et al. 2009, 2013, 2014, 2015, Dolbeer & Begier 2019, Dolbeer & Wright 2008, FAA 2019, Schwarz et al. 2014, Usman et al. 2012
Bovidae	Australia, Bolivia, China, Germany, Guyana, India, Kenya, South Sudan, UK,	ATSB 2014, 2018, Avisure 2019, Cleary et al. 2004, 2005, 2006, Cleary & Dolbeer 2005, Dolbeer et al. 2009, 2013, 2014, 2015, Dolbeer & Begier 2019, Dolbeer & Wright 2008, Drey et al. 2014, FAA 2019, ICAO 2017, Schwarz et al. 2014,
Canidae	Australia, Brazil, Canada, Costa Rica, Cyprus, Egypt, France, Germany, Greece, Italy, Namibia, Poland, Portugal, Sweden, UK, USA	ATSB 2014, 2018, Avisure 2019, Barras & Wright 2002, Bergman et al. 2009, CAA Poland 2019, Cleary et al. 1996, 2004, 2005, 2006, Cleary & Dolbeer 2005, Crain et al. 2015, DAVVL e.V 2019, DeVault et al. 2011, Dolbeer 2000, 2013, Dolbeer et al. 2000, 2009, 2013, 2014, 2015, Dolbeer & Begier 2019, Dolbeer & Wright 2008, 2009, Drey et al. 2014, FAA 2019, Hauptfleisch et al. 2013, ICAO 2017, Kitowski 2016, MacKinnon et al. 2004, Metscher et al. 2007, Schwarz et al. 2014, STAC 2019, TC 2019, UKCAA 2019
Castoridae	USA	Dolbeer et al. 2013, 2014, 2015, Dolbeer & Begier 2019, FAA 2019, ICAO 2017, Schwarz et al. 2014
Cercopithecidae	Namibia	Hauptfleisch et al. 2013
Cervidae	Australia, Canada, France, Germany, Poland, Switzerland, UK, USA	ATSB 2018, Avisure 2019, Barras & Wright 2002, Biondi et al. 2011, CAA Poland 2019, Cleary et al. 1996, 2004, 2005, 2006, Cleary & Dolbeer 2005, DAVVL e.V 2019, DeVault et al. 2011, Dolbeer 2000, Dolbeer et al. 2000, 2008, 2009, 2013, 2014, 2015, Dolbeer & Begier 2019, Dolbeer & Franklin 2013, Dolbeer & Wright 2008, 2009, 2014, Drey et al. 2014, FAA 2019, Fagerstone & Clay 1997, Hesse et al. 2012, ICAO 2017, Kelly & Allan 2006, Kitowski 2016, MacKinnon et al. 2004, Metscher et al. 2007, Scheideman et al. 2017, Schwarz et al. 2014, Seamans 2001, STAC 2019, TC 2019, UKCAA 2019, VerCauteren et al. 2013, Wenning et al. 2004, Wright et al. 1998, Wright & Dolbeer 2000, 2005
Chiroptera*	American Samoa, Argentina, Australia, Barbados, China, El Salvador, Dominican Republic, Germany, Ghana, India, Ireland, Israel, Japan, Mauritius, Nigeria, Panama, Philippines, USA, Vietnam	ATSB 2018, Biondi et al. 2013, Cleary et al. 2004, 2005, 2006, Cleary & Dolbeer 2005, DAVVL e.V 2019, DeVault et al. 2011, Dolbeer et al. 2009, 2013, 2014, 2015, Dolbeer & Begier 2019, Dolbeer & Wright 2008, Dove et al. 2008b, FAA 2019, ICAO 2017, Kelly et al. 2017, Kelly & Allan 2006, Kasso & Balakrishnan 2013, Leader et al. 2006, Metscher et al. 2007, Parsons et al. 2008, 2009, Satheesan et al. 1992, Simons et al. 2014, STAC 2019, TC 2019, UKCAA 2019, Usman et al. 2012, Voigt et al. 2018, Peurach 2003, Peurach et al. 2009
Cricetidae	Canada, USA	Cleary et al. 2004, 2005, 2006, Dolbeer et al. 2009, 2013, 2014, 2015, Dolbeer & Begier 2019, Dolbeer & Wright 2008, FAA 2019, ICAO 2017, Schwarz et al. 2014, TC 2019
Dasypodidae	USA	Cleary et al. 2004, 2005, 2006, Dolbeer et al. 2009, 2013, 2014, 2015, Dolbeer & Begier 2019, Dolbeer & Wright 2008, FAA 2019, ICAO 2017, Metscher et al. 2007, Schwarz et al. 2014
Didelphidae	Brazil, Canada, USA	Biondi et al. 2014, Cleary et al. 1996, 2004, 2005, 2006, DeVault et al. 2011, Dolbeer et al. 2009, 2013, 2014, 2015, Dolbeer & Begier 2019, Dolbeer & Wright 2008, FAA 2019, ICAO 2017, Metscher et al. 2007, Noaves et al. 2016, Schwarz et al. 2014, TC 2019
Echimyidae	USA	Dolbeer & Begier 2019, FAA 2019, ICAO 2017
Equidae	Ethiopia, Kenya, USA	Avisure 2019, Cleary et al. 2004, 2005, 2006, Cleary & Dolbeer 2005, Dolbeer et al. 2009, 2013, 2014, 2015, Dolbeer & Begier 2019, Dolbeer & Wright 2008, FAA 2019, Schwarz et al. 2014
Erethizontidae	USA	Cleary et al. 2004, 2005, 2006, Dolbeer et al. 2009, 2013, 2014, 2015, Dolbeer & Begier 2019, Dolbeer & Wright 2008, FAA 2019, ICAO 2017, Schwarz et al. 2014, TC 2019
Erinaceidae	France, Italy, Poland, UK	CAA Poland 2019, STAC 2019, UKCAA 2019
Felidae	Australia, Canada, Poland, USA, UK	ATSB, 2014, CAA Poland 2019, Cleary et al. 2004, 2005, 2006, Dolbeer et al. 2009, 2013, 2014, 2015, Dolbeer & Begier 2019, Dolbeer & Wright 2008, FAA 2019, ICAO 2017, Schwarz et al. 2014, TC 2019, UKCAA 2019

Geomyidae	USA, Canada	Dolbeer et al. 2009, 2013, 2014, 2015, Dolbeer & Begier 2019, Dolbeer & Wright 2008, FAA 2019, Schwarz et al. 2014, TC 2019
Giraffidae	Botswana	Avisure 2019
Herpestidae	USA	Cleary et al. 2006, Dolbeer et al. 2009, 2013, 2014, 2015, Dolbeer & Begier 2019, Dolbeer & Wright 2008, FAA 2019, ICAO 2017, Schwarz et al. 2014
Hyaenidae	Kenya	UKCAA 2019
Leporidae	Australia, Canada, Cyprus, Denmark, France, Germany, Greece, Holland, Ireland, Italy, Mexico, Namibia, Poland, Spain USA, UK	ATSB 2014, 2018, Ball et al. 2020, Biondi et al. 2014, CAA Poland 2019, Cleary et al. 2004, 2005, 2006, Cleary & Dolbeer 2005, DAVVL e.V 2019, DeVault et al. 2011, Dolbeer et al. 2009, 2013, 2014, 2015, Dolbeer & Begier 2019, Dolbeer & Wright 2008, 2009, FAA 2019, Hauptfleisch et al. 2013, Hesse et al. 2012, ICAO 2017, Kelly & Allan 2006, Kitowski 2016, MacKinnon et al. 2004, Metscher et al. 2007, Schwarz et al. 2014, STAC 2019, TC 2019, UKCAA 2019
Macropodidae	Australia	ATSB 2014, 2018
Mephitidae	Canada, USA	Cleary et al. 2004, 2005, 2006, DeVault et al. 2011, Dolbeer et al. 2009, 2013, 2014, 2015, Dolbeer & Begier 2019, Dolbeer & Wright 2008, FAA 2019, Hesse et al. 2012, ICAO 2017, MacKinnon et al. 2004, Metscher et al. 2007, Schwarz et al. 2014, TC 2019
Muridae	Australia, Canada	ATSB 2018, Cleary et al. 2004, 2005, 2006, FAA 2019, ICAO 2017, TC 2019
Mustilidae	France, Germany, Poland, UK, USA	ATSB 2018, CAA Poland 2019, Cleary et al. 2004, 2005, 2006, DAVVL e.V 2019, Dolbeer et al. 2009, 2013, 2014, 2015, Dolbeer & Begier 2019, Dolbeer & Wright 2008, FAA 2019, ICAO 2017, Schwarz et al. 2014, STAC 2019, TC 2019, UKCAA 2019
Myrmecophagidae	Brazil	Noaves et al. 2016
Order Pilosa [X]	Brazil	Noaves et al. 2016
Peramelidae	Australia	ATSB 2014, 2018
Phalangeridae	Australia	ATSB 2014, 2018
Potoroidae	Australia	ATSB 2014
Procyonidae	Canada, USA	Cleary et al. 2004, 2005, 2006, Cleary & Dolbeer 2005, DeVault et al. 2011, Dolbeer et al. 2009, 2013, 2014, 2015, Dolbeer & Begier 2019, Dolbeer & Wright 2008, FAA 2019, ICAO 2017, Schwarz et al. 2014, TC 2019
Sciuridae	Canada, USA	Cleary et al. 1996, 2004, 2005, 2006, Biondi et al. 2014, DeVault et al. 2011, Dolbeer et al. 2009, 2013, 2014, 2015, Dolbeer & Begier 2019, Dolbeer & Wright 2008, 2009, FAA 2019, Metscher et al. 2007, Schwarz et al. 2014, ICAO 2017, TC 2019
Suidae	Poland, USA, Zimbabwe	CAA Poland 2019, Cleary et al. 2004, 2005, 2006, Dolbeer et al. 2009, 2013, 2014, 2015, Dolbeer & Begier 2019, Dolbeer & Wright 2008, FAA 2019, ICAO 2017, Kitowski 2016, Schwarz et al. 2014, Smith 2009
Tachyglossidae	Australia	ATSB 2014, 2018
Tayassuidae	USA	Cleary et al. 2004, 2005, 2006, Dolbeer et al. 2009, 2013, 2014, 2015, Dolbeer & Begier 2019, Dolbeer & Wright 2008,
Unidentified	Barbados, Brazil, Canada, France, Gambia, Mauritius, USA	Barras & Wright 2002, Cleary et al. 2004, 2005, 2006, Dolbeer et al. 2009, 2013, 2014, 2015, Dolbeer & Begier 2019, Dolbeer & Wright 2008, FAA 2019, Mendonca et al. 2018, Schwarz et al. 2014, STAC 2019, TC 2019, UKCAA 2019,
Vombatidae	Australia	ATSB 2014, 2018

*Families: Emballonuridae, Molossidae, Phyllostomidae, Pteropodidae, Rhinolophidae, Unknown, Vespertilionidae [X] Denontes that lowest taxonomic classification provided was Order.

456

Fig. 1. Number of strikes with mammals per one million aircraft movements (take-off run and landing only) for civil airplanes from Australia (2008-2016, AUS), Canada (2008-2018, CAN), France (2016-2018, FRA), Germany (2010-2017, GER) the UK (1990-2018) and the USA (1990-2018).

Fig. 2. Percentage (%) of overall strike events (± 95% Confidence Intervals) occurring in each month (1 = January, 12 = December) for (A) Australia (*n*=1564), (B) Europe (France, Germany, UK; *n*=381) and (C) North America (Canada and USA; *n*= 7059).

Fig. 3. Percentage (%) of overall strike incidents (± 95% Confidence Intervals) with mammals for each phase of flight by country: Australia (2008-2017, AUS; *n*=1199), Canada (2010- 2018, CAN; *n*= 237), France (2016- 2018, FRA; *n*= 28), Germany (2010-2018, GER; *n*=128), the UK (1990-2018; *n*= 105) and the USA (1990-2018; *n*=2877) for terrestrial (top) and volant (bottom) mammals.

Fig. 4. Percentage of strikes (± 95% Confidence Intervals) categorised into each damage class inflicted to airplanes in Australia (2008-2017, AUS; *n*= 1179), France (2016-2018, FRA; *n*= 126), Germany (2010-2018, GER; *n*= 140) and the USA (1990-2018; *n*= 3055)

SUPPORTING INFORMATION

Additional supporting information may be found in the online version of this article at the publisher's website.

Appendix S1. Aviation authorities researched and/ or contacted in order to obtain mammal-strike data. Data were only available from six countries.

Appendix S2. Retained variables across datasets for six countries, provided by aviation authorities.

Appendix S3. Relevant articles that were retained from the literature survey.

Appendix S4. Mammal families involved in wildlife strike events with aircraft other than civil airplanes reported in organisational, grey and scientific literature, and the country or countries of occurrence.

Appendix S5. Strike numbers and percentages of each mammal family involved in strikes in the USA, Australia, Germany and France.

Appendix S6. Strike numbers and percentages for each mammal family involved in strikes in Canada and the UK.

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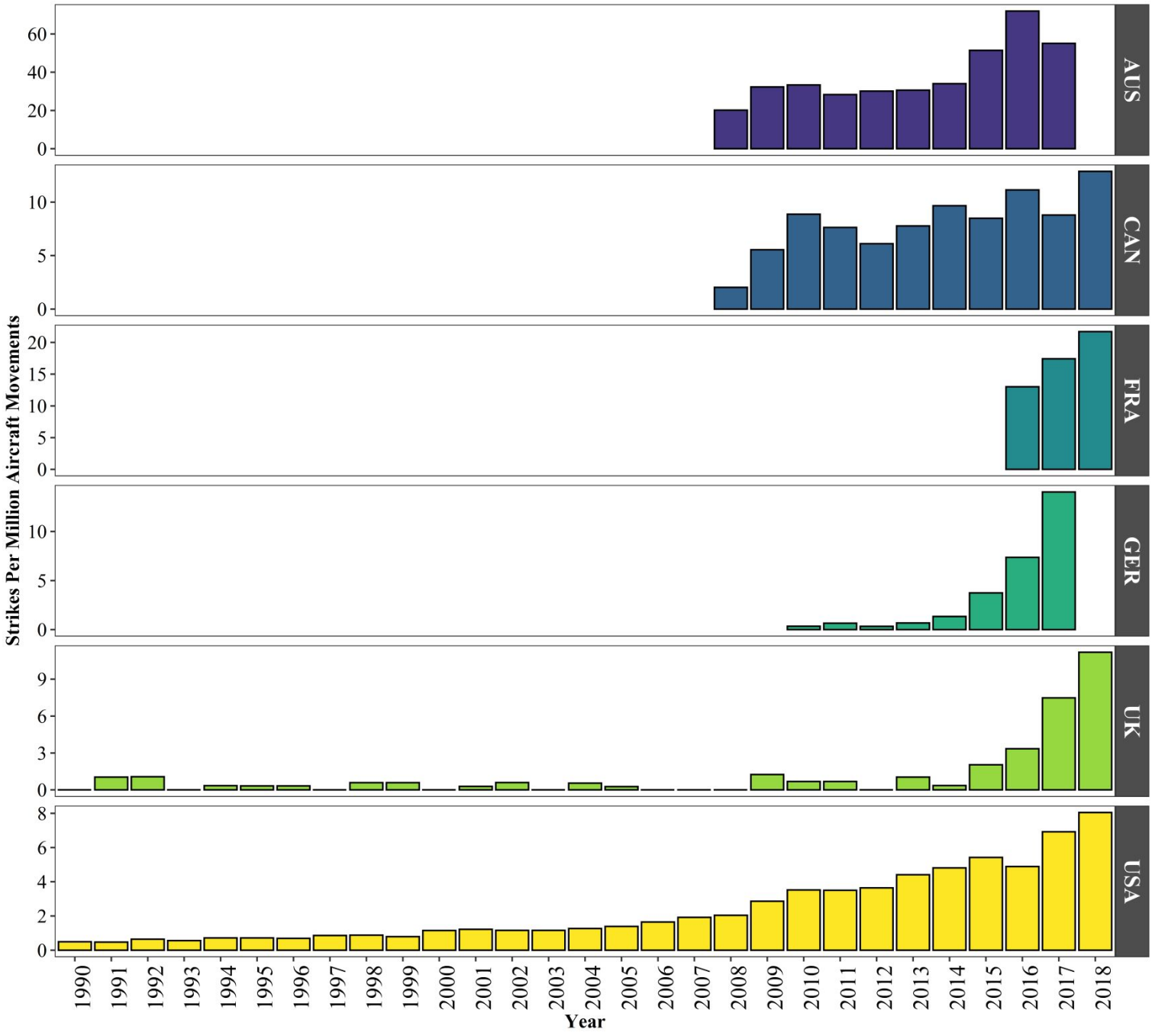


Fig. 1. Number of strikes with mammals per one million air movements (take-off run and landing only) for civil airplanes from Australia (2008-2016, AUS), Canada (2008-2018, CAN), France (2016-2018, FRA), Germany (2010-2017, GER) the UK (1990-2018) and the USA (1990-2018).

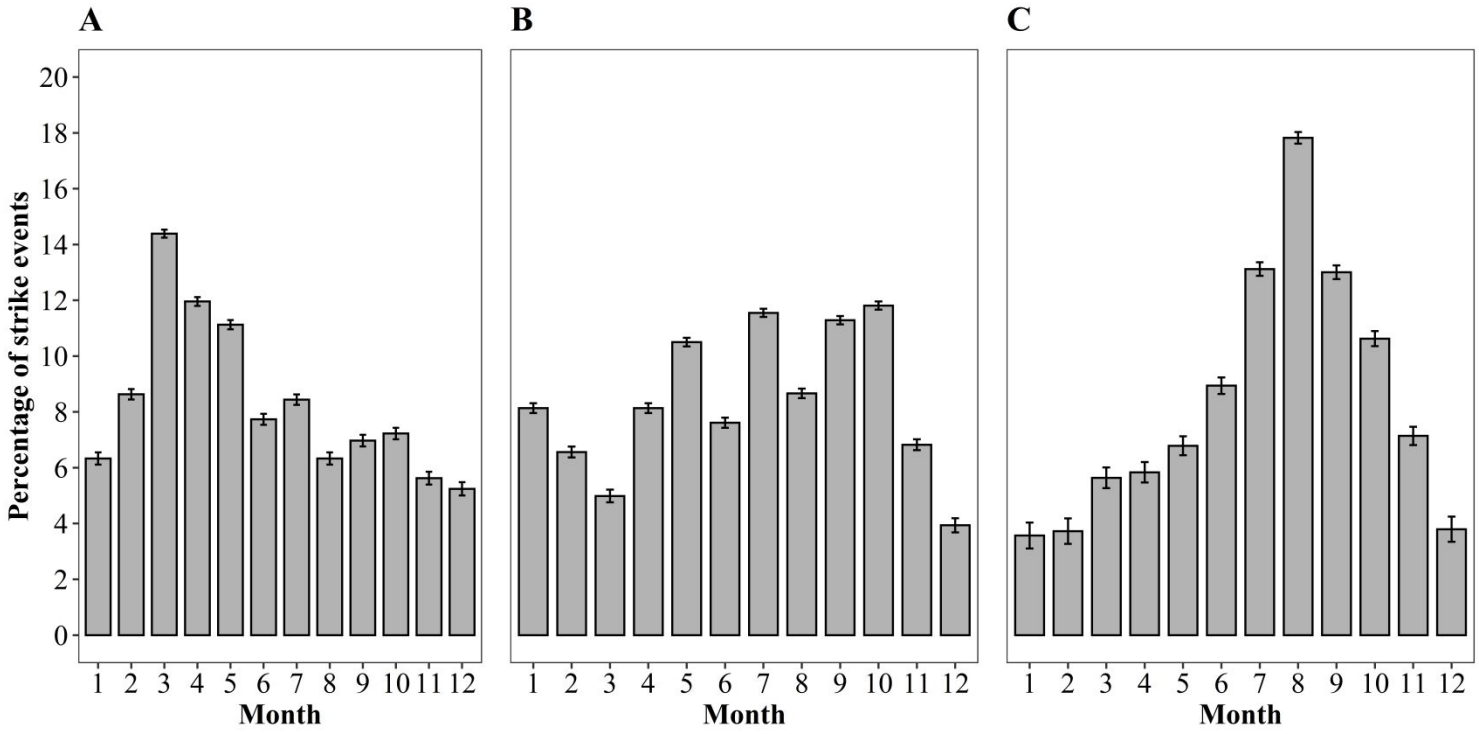


Fig. 2. Percentage (%) of overall strike events (± 95% Confidence Intervals) occurring in each month (1 = January, 12 = December) for (A) Australia (*n*=1564), (B) Europe (France, Germany, UK; *n*=381) and (C) North America (Canada and USA; *n*= 7059).

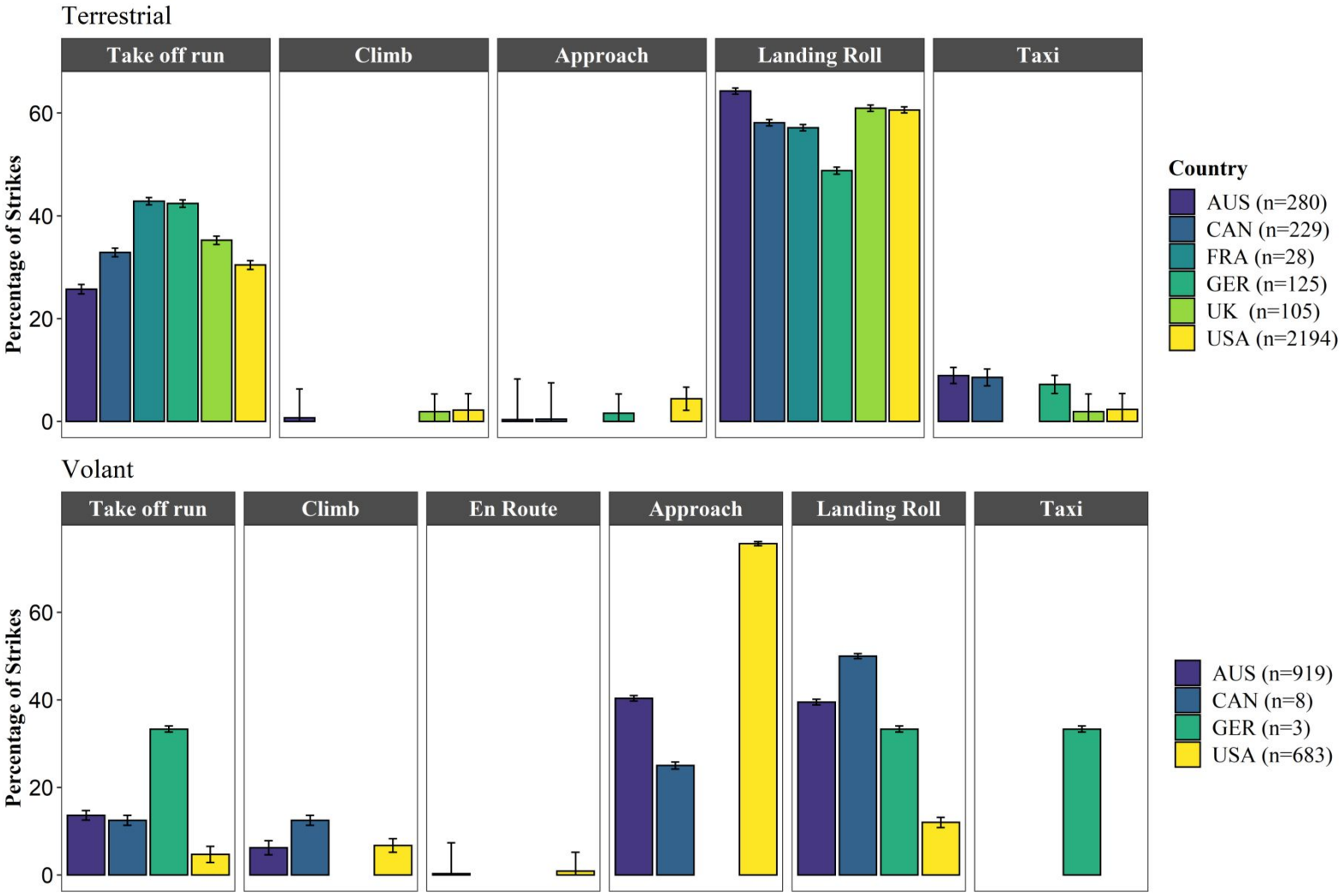


Fig. 3. Percentage (%) of overall strike incidents (± 95% Confidence Intervals) with mammals for each phase of flight by country: Australia (2008-2017, AUS; *n*=1199), Canada (2010- 2018, CAN; *n*= 237), France (2016- 2018, FRA; *n*= 28), Germany (2010-2018, GER; *n*=128), the UK (1990-2018; *n*= 105) and the USA (1990-2018; *n*=2877) for terrestrial (top) and volant (bottom) mammals.

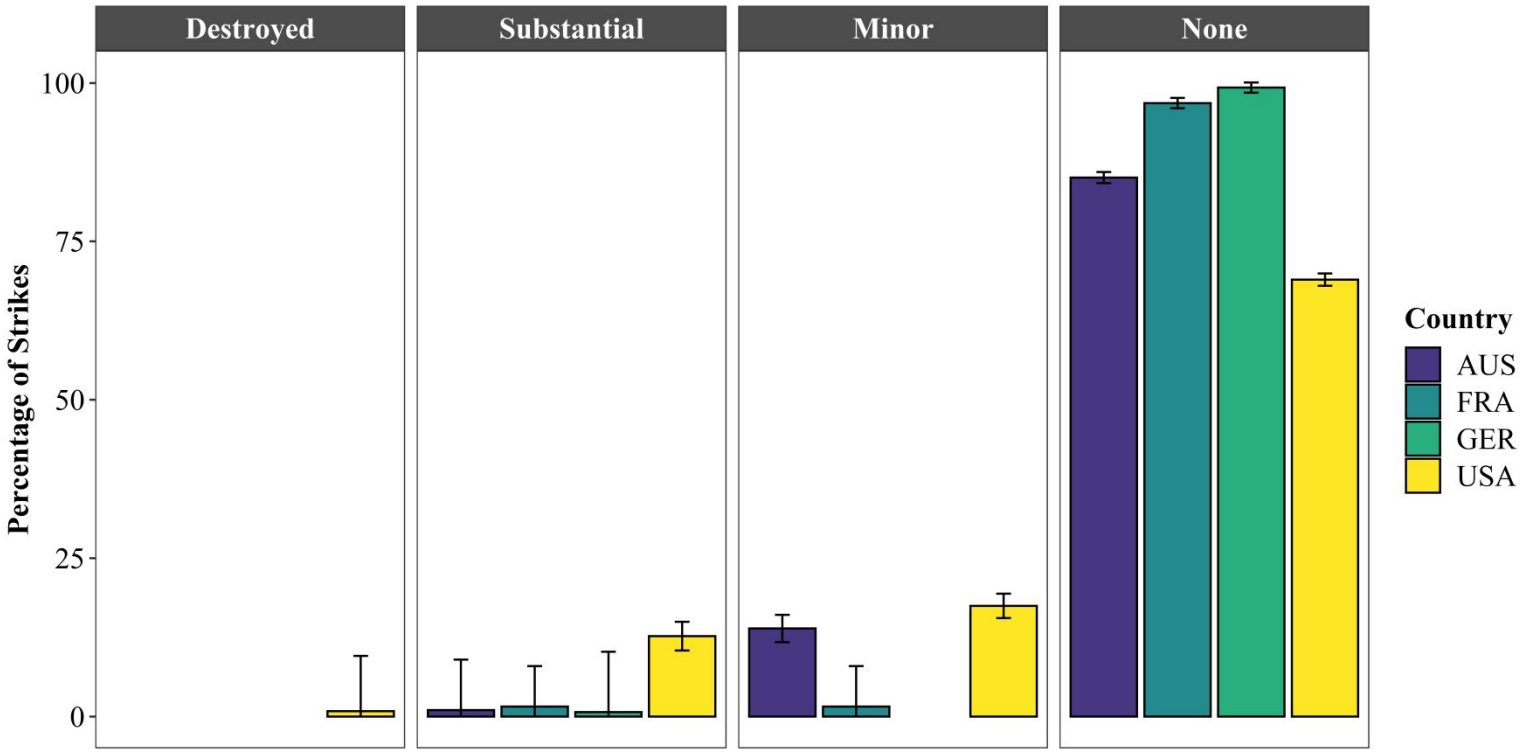
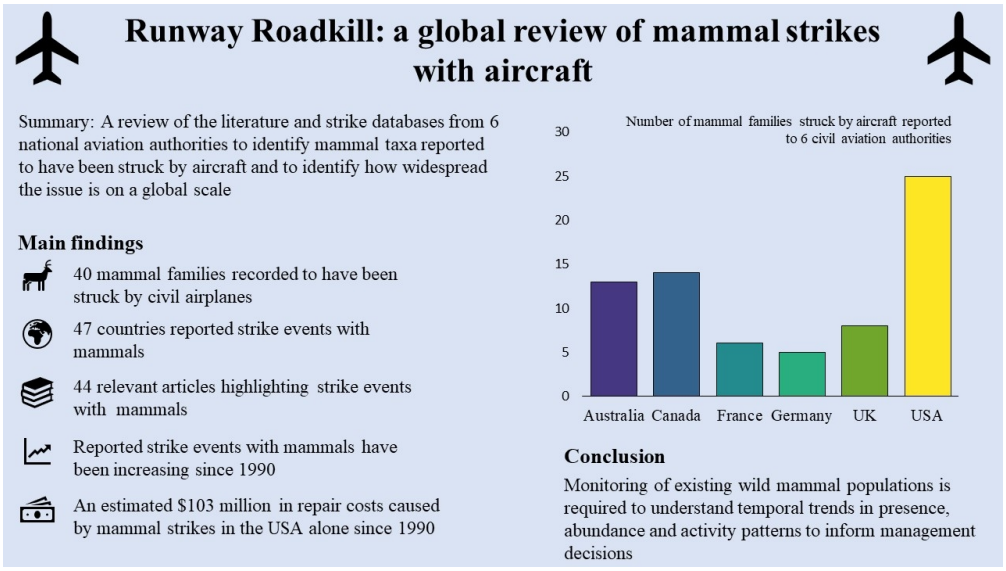


Fig. 4. Percentage of strikes (± 95% Confidence Intervals) categorised into each damage class inflicted to airplanes in Australia (2008-2017, AUS; *n*= 1179), France (2016-2018, FRA; *n*= 126), Germany (2010-2018, GER; *n*= 140) and the USA (1990-2018; *n*= 3055)



Graphical abstract

338x190mm (96 x 96 DPI)