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Killing conspecific adults in mammals

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Mammals kill both conspecific infants and adults. Whereas infanticide has been profusely studied, the killing of non-infants (adulticide) has seldom attracted the attention of researchers. Mammals kill conspecific adults by at least four, non-exclusive reasons: during intrasexual aggression for mating opportunities, to defend valuable resources, to protect their progeny and to prey upon conspecifics. In this study, we test which reason is most likely to explain male and female adulticide in mammals. For this, we recorded the presence of adulticide, the ecological and behavioural traits, and the phylogenetic relationship for more than 1000 species. Adulticide has been recorded in over 350 species from the most important Mammalian clades. Male adulticide was phylogenetically correlated with the presence of size dimorphism and intrasexually selected weapons. Female adulticide was phylogenetically associated with the occurrence of infanticide. These results indicate that the evolutionary pathways underlying the evolution of adulticide differ between sexes in mammals. Whereas males commit adulticide to increase breeding opportunities and to compete with other males for mating, females commit adulticide mainly to defend offspring from infanticidal conspecifics.

1. Introduction

Mammals kill conspecifics under certain circumstances [1–3]. For example, it is widely acknowledged that many species of mammals kill infants and dependent offspring of their own species [1,2,4]. Mammals may also kill conspecifics other than infants and dependent offspring [5,6]. However, unlike infanticide, the killing of conspecific adults in mammals (’adulticide’ hereafter) has seldom attracted the attention of theoretical and empirical biologists, having being studied just in a few species like humans and chimpanzees [3,4]. This lack of attention on mammal adulticide contrasts with what happens in other groups of animals like fishes, spiders, scorpions and mantises where intraspecific killing among adults has been profusely studied both theoretically and empirically [5,7]. By contrast, this phenomenon is considered in mammals a mere incidental consequence of the injuries causes during intraspecific aggression due to intrasexual competition for breeding opportunities and mating preferences among males [4]. According to ESS models, fatal fighting evolution depends on the balance between the values of the contested resource and the expected value of future reproduction [8]. Persistent fighting strategies, offensive behaviour and weapons will evolve if giving up a contest entails a significant reduction in future reproduction. These models predict fights to be less severe in mammals than in other animals, because of their long reproductive life, iteroparous reproduction and multiple mating events [8]. Under these circumstances, competitors will use signals to resolve contests before escalating to dangerous combats [8]. Because it is widely thought that intraspecific killing of adult mammals is just intramale aggression in its maximum expression [4], it is considered an anecdotal phenomenon present only in a small group of mammals where contests should be more likely to escalate into true battles [4,6,9]. There is some evidence, however, questioning the idea that adulticide is a mere incidental consequence of intramale aggression. Mammals may kill non-infants by multiple, non-exclusive reasons even within the same species [6,7,10,11]. In addition, adulticide is sometimes associated with ecological contexts other than reproduction, such as the defence of territory [12] and progeny [10,13], and, in certain circumstances, the consumption of the victim [11]. In addition, intramale competition for mating opportunities could hardly explain adulticide among females [6]. Finally, irrespective of the proximal causes, adulticide in mammals may have important evolutionary consequences. Some authors have suggested that killing conspecific adults during contests can mediate the evolution of weaponry [9,14] or group size in certain mammals [15–17]. Killing conspecific adults may also underlie the evolution of some defensive traits, such as the cervical vertebrae and the uneven distribution of skin thickness in ruminants [18–20] or the mane in male lions [21].

The main goal of this study is to explore how adulticide may have evolved in mammals. We propose the following four potential hypotheses. (i) Adulticide may be the consequence of intraspecific aggression due to intrasexual competition for breeding opportunities and mating preferences among males [4]. Males fighting to have better access to females may occasionally kill other males [4]. Because most aggressive episodes will occur among males [6,22], this hypothesis predicts adulticide to be more frequent between males than between females. Three major features strongly associated with the intensity of selection among males in mammals are male-biased size dimorphism [6,23], polygyny [23–25] and the presence of intrasexually selected weapons [26]. Consequently, if adulticide is a consequence of male–male competition, a positive correlation between male adulticide and these three features is expected. (ii) Adulticide may be the consequence of the defence of valuable resources, such as food or nest sites [12,27]. Under this idea, adulticide should be affected by the intensity of competition for resources. Two traits influencing intraspecific competition for resources in mammals are foraging group size and population density [6,23]. Consequently, this second hypothesis predicts the occurrence of a positive correlation between these two traits and adulticide. (iii) Adults may kill conspecifics when protecting their progeny. It has been observed that females protect their progeny from infanticidal conspecifics in many species of mammals [10,23,28], a defence that can be lethal in some occasions [13,28]. In this case, the valuable resource is the progeny [10]. Defending progeny can be highly costly in some species because adults are often killed while defending their cubs [11]. Therefore, this hypothesis predicts adulticide to be more frequent in infanticidal than in non-infanticidal species. (iv) Adulticide may be related to intraspecific predation [5–7]. The nutritional benefit obtained by the cannibal has been frequently suggested to explain the presence of adulticide in some species. Under this fourth hypothesis, adulticide is assumed to be intentionally perpetrated by predators. Consequently, this hypothesis predicts adulticide to be more prevalent in carnivorous and omnivorous species than in herbivorous ones.

We tested which hypothesis is most likely to explain adulticide in mammals by recording adulticide prevalence, and ecological and behavioural traits in more than 1000 species and correlating them using phylogenetically controlled models.

2. Methods

(a) The database

We conducted computer searches including the terms (alone or in combination) ‘mammal’, ‘mortality factors’, ‘causes of mortality’, ‘death’, ‘conspecific mortality’, ‘conspecific fighting’, ‘intraspecific aggression’, ‘intraspecific strife’ and ‘conspecific aggression’. We considered only lethal conspecific interactions, ignoring non-lethal aggression [3]. We found information on adult mortality from 1384 species (approx. 25% of the total mammal species; see electronic supplementary material, dataset S1).

The mammals included in our dataset were classified as polygynous (including also polygynandry) and non-polygynous (including monogamy and promiscuity) following information on mating system from [29] and other references. Information on body size was obtained from panTheria [30], Amniote [31], Smith *et al.* [32] dataset and Animal Diversity Web (https://animaldiversity.org). In most cases, body size was estimated as body mass (in grams), but in some species, we used alternative proxies to find dimorphism (i.e. body length, length of some body parts). Size dimorphism was calculated as log (male size/female size) [24]. Information on infanticide prevalence was obtained from [1–3]. Population density, estimated as logarithm of the number of individuals per km^2, was obtained for panTheria [30], TetraDENSITY [33] and the IUCN Red List (https://www.iucnredlist.org/). The group size was considered the number of individuals that spend most of the time together, mostly when they are foraging. We obtained this information from panTheria [30], Animal Diversity Web, IUCN Red List and Mammalian Species publications (https://www.mammalsociety.org). The diet of the mammals was obtained from EltonTraits [34], MammalDIET 2 [35] and Phylacine [36] datasets. Once we obtained the dietary information, we classified the species as carnivores (yes, no), considering as carnivores not only those consuming meat but also those consuming insects and other invertebrates, as well as omnivorous species consuming meat at least part of the time. The presence of intrasexually selected weapons was obtained from Animal Diversity Web and from [26]. All this information is provided in the electronic supplementary material, dataset S2.

(b) Robustness of the dataset against potential sampling bias

To control for the potential caveats of considering as non-adulticidal species having a high difficulty of observing this behaviour without a very intensive sampling, all comparative analyses were done using six different proper subsets of species. These subsets were nested using an increasing restrictive criterion. The subsets were:

(I) The entire set of species included in our original dataset. The species included in this set were those from whose we were able to find data on mortality factors. In this set, there were 1041 non-adulticidal species (species where adulticide has not been recorded, irrespective of being infanticidal or not) and 352 adulticidal species.

(II) This subset of species was obtained by keeping all adulticidal species, irrespective of the conditions (natural versus captivity) where adulticide was observed, and removing the non-adulticidal species based on the following criteria:
   1. the only type of mortality reported for the species was non-natural (mostly human-related);
   2. the mortality reported for the species was obtained exclusively from the diet analysis of their predators;
   3. the mortality reported for the species was obtained from studies focused in only one single mortality factor (infanticide, interspecific predation, pathogens, etc.);

4. the mortality of the species was exclusively obtained in non-natural conditions (captivity, zoos, laboratories, etc.);
5. we could not find any study focused on demography, natural history, reproductive or social behaviour.

In this set of species, there were 195 non-adulticidal species and 352 adulticidal species.

(III) This subset of species was obtained by keeping all previous non-adulticidal species but leaving only those adulticidal species where adulticide was observed in natural conditions. In this set of species, there were 195 non-adulticidal species and 280 adulticidal species.

(IV) This subset of species was obtained by keeping all previous non-adulticidal species but leaving only those previous adulticidal species where the victims were adults and excluding those species where the reported victims were only subadults and/or juveniles. In this set of species, there were 195 non-adulticidal species and 273 adulticidal species.

(V) This subset of species was obtained by leaving all previous adulticidal species and including only those non-adulticidal species fulfilling the criteria described in the subset II and where more than 100 events of death were reported in the literature. In this set of species, there were 129 non-adulticidal species and 273 adulticidal species.

(VI) This subset of species was obtained by leaving all previous adulticidal species and including only those non-adulticidal species fulfilling the criteria described in the subset II and where more than 100 events of death and more than two studies. In this set of species, there were 109 non-adulticidal species and 273 adulticidal species.

The identity of the species belonging to each subset appears in the electronic supplementary material, dataset S2.

(c) Mammal phylogeny

The phylogenetic relationship among the mammals included in the database was built using phylogenetic trees in [37] including 5747 extant and extinct mammals. We used this phylogeny because it (i) contains a very large number of mammals, (ii) includes extant and extinct species and (iii) provides many alternative trees following a Bayesian approach allowing the consideration of uncertainty in subsequent analyses.

(d) Statistical analyses

To test the predictions of each hypothesis, we fitted phylogenetic logistic regressions [38] using as dependent variable the adulticide as a binary trait (yes, no) and including all mammalian features (size dimorphism, polygyny, group size, population density, infanticide, carnivory and intrasexually selected weapon) to control for potential indirect effects. These seven variables were weakly correlated ($\rho = 0.12 \pm 0.09$, mean ± 1 s.d. of pairwise Spearman's rank correlations), indicating that multicollinearity did not affect the interpretation of the analyses (variance inflation factor less than 2.8 in all cases). We made separated models for males and females. These analyses were performed using the R package 'phylolm' [39]. To account for phylogenetic uncertainty, we used a set of 30 randomly selected phylogenies in all our analyses. In each phylogeny, we pruned all species not included in the database and, in the few cases where a species was missing in the supertree (this happened only for five species), we selected the closest relative. The robustness of the results of all analyses was explored by performing all them in the six different proper subsets of species described above and comparing their results.

3. Results and discussion

Adulticide has been recorded in at least 352 species belonging to 65 mammalian families and 14 out of the 29 mammalian orders, with adulticide recorded in natural conditions for at least 280 species. Adulticide was more prevalent in some groups of mammals, such as even-toed ungulates, primates, shrews, carnivores, kangaroos and wallabies, whereas it was virtually absent from bats, whales and dolphins or rabbits and hares (figure 1). Because deaths may result directly from the injuries caused during the combats but also indirectly from infections of bite wounds and stress from fighting, the true extent of adulticide is surely underestimated.

When separating between sexes of the perpetrators, we found that adulticide was mainly committed by males (320 species with male adulticide versus 133 species with female adulticide). This contrasts with infanticide, where the prevalence is similar in both sexes (approx. 119 versus 89 species) [1–3,40]. The target of males was in most cases another male. Adulticide between males was reported in at least 232 species, males killing females in 42 species, females killing males in 30 species and females killing females in 35 species. It seems that killing conspecific adults involves mostly males not only in humans and primates [22] but also in other mammals.

(a) Male adulticide

Male adulticide was significantly and positively associated with male-biased size dimorphism in all analyses (table 1), being more prevalent in dimorphic species than in monomorphic ones (61% versus 44%, respectively, using 10% size difference between sexes as a cut-off point to consider a given species as dimorphic) [24]. Sexual size dimorphism is considered a direct consequence of sexual selection in mammals [24,25], and it is widely used as a surrogate of the intensity of the sexual selection operating on each species [25]. Mammals for which male-biased size dimorphism is more frequent, such as carnivores (Otariidae, Felidae, Canidae), primates (Hominidae, Cercopithecidae) and ungulates (Bovidae, Cervidae), are also those where adulticide was more prevalent in our study. Male adulticide was also positively associated with the presence of intrasexually selected weapons (table 1), since adulticide was reported in 37% of species with intrasexually selected weapons but only in 16% of species without those weapons. In fact, size dimorphism goes along with dimorphism in several structures used in male–male combats, such as large canines in primates and carnivores or horns and antlers in ungulates [9,41]. Serious antler and horn wounding has long been considered an important cause of mortality in ruminant mammals [18]. Finally, although male adulticide was reported in 60% of polygynous species and only in 49% of the non-polygynous species (pooling socially monogamous and promiscuous species [29]), no statistical association was found between polygyny and male adulticide (table 1).

Group size and population density were not related to male adulticide, suggesting that this lethal interaction cannot be explained in males by the protection of resources or progeny. Several reasons might explain this absence of relationship. In particular, the effect of resources on adulticide is likely to be expressed at an intraspecific

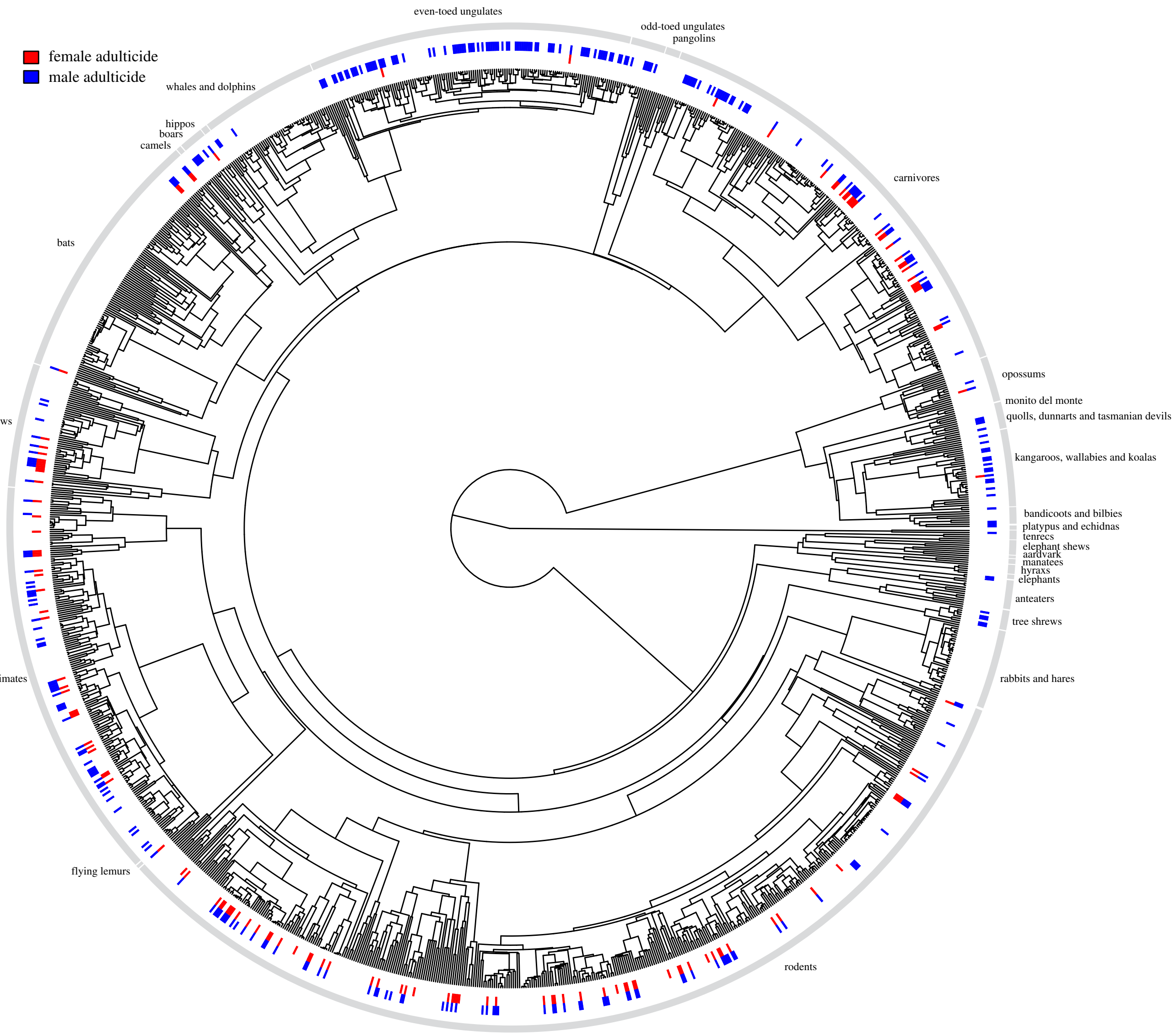

Figure 1. The presence of adulticide committed by males and females in the 1384 mammalian species used in this study. For illustrative purposes, we show one randomly selected tree from the Bayesian sample provided by [37]. (Online version in colour.)

level, with adulticide being more severe in those populations competing more intensely [4]. So, resources would probably influence adulticide at geographical, among-population scale rather than at macroevolutionary, among-species scale.

Carnivory was not related to male adulticide. This finding suggests that, contrasting to what it is observed in spiders, scorpions and some fishes [5,7,9], intraspecific predation does not shape male adulticide evolution in mammals. When associated with predation, adulticide is deliberate rather than incidental [5,6,11]. Deliberate killing can occur in some social species when individuals from different groups come into contact, as observed in social carnivores such as wolves and lycaons [15,16], and primates like chimpanzees [17,22]. Chimpanzees can even display lethal raiding, the incursion of a coalition of males into the territory of another group and the fatal attack against vulnerable neighbours [17]. However, we found a recording of deliberate adulticide only for 47 species (24 rodents, 13 primates, 10 carnivores; electronic supplementary material, dataset S2), suggesting that cannibalism does not mediate the evolution of male adulticide in mammals.

Altogether, our findings support the first hypothesis stating that male adulticide can be caused by intramale competition mediated by reproductive interactions.

(b) Female adulticide

The presence of female adulticide in over one hundred species is hardly explained by intramale competition for mating opportunities. This idea is supported by, otherwise unsurprisingly, the absence of any significant effect of size dimorphism or polygyny on female adulticide (table 1). So, 14% of dimorphic and 22% of monomorphic species were female adulticides. In addition, the negative correlation between the presence of intrasexually selected weapons and female adulticide supports this conclusion (table 1).

The prevalence of female adulticide may be mediated by the defence of valuable resources. Whereas population density seems to be associated in males with intrasexual aggression [42], in females it is mostly associated with competition for food [23,43], an interaction playing indeed a key role in the social organization of many group-living female mammals [27]. Thereby, aggression mediated by competition for food is not rare among females of social

Table 1. The outcome of the phylogenetic logistic regressions testing the effect of seven mammalian features on the probability of occurrence of male and female adulticide. Figures are means ± s.e. of the slopes of the logistic regressions across 30 phylogenetic trees for the six subsets of species considered in this study. In italics those variables that were significant at $p < 0.05$.

variable	I	II	III	IV	V	VI
male adulticide						
size dimorphism	*1.54 ± 0.64*	*1.78 ± 0.80*	*1.58 ± 0.75*	*1.64 ± 0.76*	1.43 ± 0.80	*1.67 ± 0.83*
polygyny	−0.12 ± 0.27	0.10 ± 0.34	0.19 ± 0.35	0.17 ± 0.34	0.08 ± 0.35	−0.01 ± 0.36
group size	0.03 ± 0.09	−0.05 ± 0.12	−0.02 ± 0.12	−0.02 ± 0.12	0.01 ± 0.12	0.02 ± 0.13
population density	*−0.23 ± 0.08*	0.09 ± 0.10	0.04 ± 0.10	0.05 ± 0.10	0.04 ± 0.10	0.08 ± 0.10
infanticide	*0.94 ± 0.18*	0.11 ± 0.24	0.08 ± 0.25	0.14 ± 0.25	0.22 ± 0.26	0.26 ± 0.28
carnivory	−0.56 ± 0.25	−0.12 ± 0.67	−0.11 ± 0.31	−0.12 ± 0.31	0.09 ± 0.32	0.02 ± 0.34
intrasexually selected weapons	*0.97 ± 0.37*	*1.88 ± 0.44*	*1.97 ± 0.45*	*1.84 ± 0.44*	*1.36 ± 0.41*	*1.49 ± 0.46*
female adulticide						
size dimorphism	0.14 ± 0.55	−0.24 ± 0.73	−0.11 ± 0.82	−0.15 ± 0.67	−0.28 ± 0.77	−0.14 ± 0.91
polygyny	−0.67 ± 0.32	−0.66 ± 0.35	−0.43 ± 0.40	−0.50 ± 0.34	−0.34 ± 0.40	−0.34 ± 0.45
group size	0.21 ± 0.10	0.18 ± 0.12	0.10 ± 0.13	0.13 ± 0.11	0.06 ± 0.13	0.03 ± 0.15
population density	0.09 ± 0.08	0.19 ± 0.09	0.17 ± 0.09	0.15 ± 0.09	0.11 ± 0.09	0.13 ± 0.10
infanticide	*1.38 ± 0.21*	*0.90 ± 0.23*	*0.68 ± 0.25*	*0.71 ± 0.22*	*0.88 ± 0.27*	*0.80 ± 0.29*
carnivory	0.54 ± 0.27	*1.04 ± 0.31*	*1.21 ± 0.34*	*1.08 ± 0.32*	*0.85 ± 0.35*	*0.89 ± 0.36*
intrasexually selected weapons	−0.65 ± 0.41	−0.76 ± 0.40	−0.89 ± 0.41	−0.60 ± 0.44	*−1.33 ± 0.44*	*−1.61 ± 0.44*

mammals [44], including our closest relatives, chimpanzees [43] and bonobos [45]. However, this resource hypothesis is not supported by our analysis since no positive relationship was found between either population density or group size and the occurrence of a female adulticide (table 1).

Females may also kill conspecifics when protecting their progeny from infanticide [10,12,13,23]. Female adulticide occurred in 24% of the infanticidal species, pooling together male and female infanticide, but only in 4% of the non-infanticidal species. The consistent association of female adulticide with infanticide (table 1) could be a consequence of the occurrence of reproductive competition among females. However, the prevalence of female adulticide was similar among species committing male (23%) and female infanticide (26%). For this reason, we believe that female adulticide is probably associated with the defence of offspring against infanticidal conspecifics, irrespective of the sex of the infanticidal individual. Nevertheless, with the available information, the reproductive competition among females cannot be ruled out as an alternative explanation for this observed pattern. Our study, being not circumscribed to social species, suggests that females may be overtly and fatally aggressive against infanticidal conspecifics not only in group-living mammals but also in solitary species.

Finally, it is remarkable the observed significant effect of carnivory on female adulticide but not on male adulticide (table 1). A possibility exists for the prevalence of female adulticide to be also a consequence of intraspecific predation. Intraspecific predation has been observed in some species, such as polar bear and mountain lions [6,11], but in most examples, the perpetrators were males. And even in these cases, it was unclear if predation was the real motivation for these killings, because they were often inferred from indirect evidence and in most cases the cause of death of the cannibalized individuals was unknown [46]. So, with the evidence at hand, despite the significant relationship shown in table 1, we cannot conclude that, contrasting with what happens in other animals [5], intraspecific predation shapes adulticide evolution in female mammals.

4. Conclusion

Our study shows that adulticide is more prevalent in mammals than previously thought. In males, adulticide seems to be the mere consequence of the injuries caused by intraspecific aggression mediated by reproductive interactions. When adulticide occurs in this context, it is mostly incidental, death happening from two males fighting so intensely that they may fatally wound each other. By contrast, in females, adulticide appears to be driven by the defence of offspring. This suggests that the evolutionary pathways underlying the evolution of adulticide differ between sexes in mammals.

Data accessibility. Datasets are included as electronic supplementary material in xls format [47].

Authors' contributions. J.M.G.: conceptualization, data curation, formal analysis, investigation, methodology, writing-original draft, writing-review and editing; M.V.: conceptualization, data curation, formal analysis, investigation, methodology, writing-original draft, writing-review and editing; A.G.-M.: conceptualization, data curation, formal analysis, investigation, methodology, writing-original draft, writing-review & editing.

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