The evolution of infanticide by females in mammals

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Keywords: social competition; sexual selection; phylogenetic comparison; sociality; kinship

Abstract

In most mammalian species, females regularly interact with kin, and it may thus be difficult to understand the evolution of some aggressive and harmful competitive behaviour among females, such as infanticide. Here, we investigate the evolutionary determinants of infanticide by females by combining a quantitative analysis of the taxonomic distribution of infanticide with a qualitative synthesis of the circumstances of infanticidal attacks in published reports. Our results show that female infanticide is widespread across mammals and varies in relation to social organization and life-history, being more frequent where females breed in groups and have intense bouts of high reproductive output. Specifically, female infanticide occurs where the proximity of conspecific offspring directly threatens the killer's reproductive success by limiting access to critical resources for her dependent progeny, including food, shelters, care or a social position. In contrast, infanticide is not immediately modulated by the degree of kinship among females, and females occasionally sacrifice closely related juveniles. Our findings suggest that the potential direct fitness rewards of gaining access to reproductive resources have a stronger influence on the expression of female aggression than the indirect fitness costs of competing against kin.

Introduction

Recent work has emphasized that competitive strategies of female mammals are often strikingly symmetrical to those observed in males, including displays and ornaments, fighting and weaponry, dominance hierarchies, and reproductive suppression [Clutton-Brock 2007, 2013; Stockley & Bro-Jørgensen 2011; Clutton-Brock & Huchard 2013]. However, while interactions among conspecific male mammals are often contextual and temporally limited to competition over access to mating partners [Emlen & Oring 1977; Connor & Krützen 2015], interactions among females tend to occur across extended periods and multiple settings [Gowaty 2004; Clutton-Brock 2016]. Females may thus compete over a diversity of resources - including food, resources necessary to breed (burrows, home-range), or offspring care [Clutton-Brock 2007]. In addition, since female mammals are typically philopatric, they may often compete with kin. It has therefore proven difficult to identify the determinants of overt female-female competition, in particular in societies that are structured around female kinship. The challenge has been to understand how the direct benefits of competition may be balanced with the indirect fitness costs of competing against kin, especially in the case of extremely harmful behaviour such as infanticide [Clutton-Brock et al. 2001; Young et al. 2006].

The killing of rivals' offspring represents one violent manifestation of intrasexual competition, and a significant source of juvenile mortality in some populations [Palombit 2012], with adults of both sexes committing infanticide. It has been intensely studied in male mammals, where fifty years of field research have shown that it has evolved as a sexually selected strategy over access to mating partners [Hrdy 1974]. In cases where the presence of a dependent offspring prevents the mother from becoming pregnant again, committing an infanticide allows the killer to create extra reproductive opportunities. This strategy is particularly common in

polygynous societies where one or a few alpha male(s) monopolize mating opportunities over short periods before losing dominance to others [van Schaik & Janson 2000; Lukas & Huchard 2014; Palombit 2015]. Since in most instances infanticide is committed by males who recently joined the group, they are unlikely to kill any related offspring [Hrdy 1979]. In contrast, as for other forms of female competition, little is known about the determinants and consequences of infanticide by females other than the mother, although it may be more prevalent than infanticide by males, both within and across taxa [Hrdy 1976, Blumstein 2000; Digby 2000]. Unlike males, female killers do not benefit from extra mating opportunities [Agrell et al. 1998; Digby 2000], because male mammals generally do not invest into offspring care to the extent that it would prevent them from mating with other females [Kleiman & Malcom 1981]. If anything, killing a dependent juvenile may exacerbate female mating competition by speeding-up the resumption to fertility for the mother of the victim. Several plausible scenarios explaining the occurrence of infanticide by females have been proposed based on a synthesis of natural observations [reviewed by Digby 2000]. Symmetrically to the patterns observed for male infanticide, predation for nutritional gains (H1: 'exploitation' hypothesis) may not provide a general explanation for female infanticide as killers have relatively rarely been observed to consume victims partially or entirely (e.g. [Goodall 1986; Blumstein 2000]). Instead, hypotheses regarding the adaptive benefits of female infanticide have focused on how killings might facilitate access to resources that are critical to successful reproduction (H2: 'resource competition' hypotheses) [Digby 2000]. Female killers might be defending access to an exclusive territory or shelter, or attempting to expand their breeding space when they target victims outside their home-range (H2.1: 'breeding space' hypothesis) (as in black-tailed prairie dogs [Hoogland 1985] or Belding's ground squirrels [Sherman 1981]). In species where females only associate temporally to breed, killers may defend access to their own

milk, by discouraging attempts to suckle from unrelated juveniles (H2.2: 'milk competition hypothesis) (as in Northern elephant seals: [Le Boeuf et al. 1973]). In species who breed cooperatively, killers may defend access to extra offspring care by group mates other than the mother by altering the helper-to-pup ratio in their own group (H2.3: 'allocare' hypothesis) (as in meerkats [Clutton-Brock et al. 2001; Young et al. 2006], banded mongooses [Gilchrist 2006; Cant et al. 2014], or marmoset [Digby 1995]). Finally, in species who live in stable groups, killers may defend their offspring's future social status (in species with stable hierarchies) or group membership (in species with forcible evictions) by eliminating future rivals (H2.4: 'social status' hypothesis) (as in some Old World primates [Hrdy 1976; Digby 2000]). Finally, it is unclear whether females might refrain from committing infanticide when this is likely to lead to indirect fitness costs. If so, they might be less likely to commit infanticide in species where most interacting females are related, or they might be able to target unrelated offspring exclusively. Alternatively, the benefits of competition in any or all these circumstances might be high enough to outweigh any potential indirect fitness costs.

Here, we present an investigation of the distribution and circumstances of infanticide by female mammals, based on data from 289 species from across 14 different Orders collected from the primary literature. The combination of a quantitative synthesis of the taxonomic distribution of infanticide with a qualitative analysis of the circumstances of infanticidal attacks (including traits of the killer and victim) can contribute to reveal the ecological, life-history or social determinants of female reproductive competition across mammalian societies, and their relevance to the occurrence of female associations and interactions within and among matrilines. Our aim is to provide a starting point for the investigation of the likely causes and situations under which female infanticide occurs, bearing in mind that our

analytical framework suffers from several caveats. First, infanticide is uncommon and difficult to observe, so that some species might wrongly be classified as 'non-infanticidal'. Second, the analyses rely on a rough categorization of the circumstances of infanticide and may oversimplify its determinants, which could be influenced by multiple factors in a given species. We first summarize the social organisation and life-histories of species in which infanticide by females has been observed, in order to evaluate the conditions under which infanticide is most common (Table 1). In particular, we investigate whether philopatry and average relatedness among groups of interacting females reduce the occurrence of female infanticide. Next, we perform specific phylogenetic analyses to test core predictions generated by each hypothesis and assess whether females have been observed to commit infanticide in species in which they are most likely to benefit from such killings. In addition, we investigate whether population-level information on the traits of killers and victims are compatible with predictions generated by each hypothesis. All our predictions and tests are summarized in Table 2. We first show that, across all species, the distribution and occurrence of infanticide by females is better explained by resource competition than by exploitation. We next test support for each for the four resource-competition hypotheses. We assess whether (i) instances where females kill offspring in neighbouring ranges ('breeding space hypothesis') are most likely explained by competition over breeding space; whether (ii) instances where females kill offspring born in the same breeding association by competition over milk ('milk competition hypothesis'); whether (iii) instances where females kill offspring in groups where usually only a single female reproduces by competition over offspring care ('allocare hypothesis'); and whether (iv) instances where females kill offspring born in groups with multiple breeders by competition over social status or group membership ('social status hypothesis').

Materials & Methods

Following Digby [2000], we use a broad definition of infanticide as an act by one or more non-parents that makes a direct or significant contribution to the immediate or imminent death of conspecific young. This definition excludes instances where mothers kill their own offspring (which are considered to result from parent-offspring conflict [O'Connor 1978] rather than from intrasexual competition) and includes cases where infants die as the result of the physical aggression (direct infanticide) as well as cases where the enforced neglect of an infant, such as kidnapping, ultimately causes death (indirect infanticide). Although the latter cases are often excluded from studies of infanticide due to their proximate form of 'overzealous' allomaternal care [Hrdy 1976], their ultimate consequence - infant death - contributes to shape their evolution as infanticidal behaviour. We included infanticide records from both wild and captive populations for which the killer was unambiguously identified as an adult female. For each species, we recorded whether observations occurred in a captive setting or under natural conditions. Species for which no case of infanticide has ever been observed were included only if detailed observations on individual females and juveniles were available, either from repeated captive observations or from field studies occurring across at least three reproductive seasons, to minimize the risk of misclassifying them as "non-infanticidal". Given that infanticide is difficult to observe, we focused on studies that were performed in circumstances under which it could be expressed and detected (co-housing of multiple females; detailed observations or specific females from before birth until weaning) or on studies that followed the fate of one or more offspring cohort(s) and recorded the causes of juvenile mortality. Data were collected from searches through the scientific literature, starting with major reviews on the topic of female infanticide [Wasser & Barash 1983; Agrell et al. 1998; Ebensperger 1998; Blumstein 2000; Digby 2000; Ebensperger & Blumstein 2007;

Stockley & Bro-Jorgensen 2011; Clutton-Brock & Huchard 2013] and performing backward and forward citation searches to identify relevant observations. While we might not have included all species in which the status of infanticide by females is documented (i.e., known to be either absent or present), we believe that this search strategy should not lead to systematic biases with regards to the tested hypotheses. We repeated all analyses excluding the 42 species for which we only found observations in captive settings (27 species with and 15 species without female infanticide), which did not change any of the results.

For the comparative analyses, we extracted data for each species on variables linked to the four different hypotheses (see Table 2). From published databases, we obtained information on: social organisation (classified as: solitary breeders [breeding females have exclusive ranges in which they do not tolerate any other breeding individual], pair breeders [home-ranges contain a single breeding female and a single breeding male but may contain additional non-breeding individuals], associated breeders [females share the same space for breeding but associations are unstable and tend not to last beyond the breeding season], or social breeders [several breeding females share the same home-range across multiple breeding seasons]) [Lukas & Clutton-Brock 2017]; female philopatry and dispersal (whether most breeding females have been born in their current locality/group or elsewhere) [Lukas & Clutton-Brock 2011]; carnivory (whether the diet of a species includes meat or not) [Wilman et al. 2014]; infanticide by males (whether males have been observed to kill conspecific young) [Lukas & Huchard 2014]; environmental climatic harshness (a principal component, with high values indicating that rainfall is low and temperatures are cold and unpredictable across the known range of a species) [Botero et al. 2014]; maternal investment (mean body size of offspring at weaning multiplied by the mean number of offspring per year, divided by mean body mass of

adult females) [Sibly et al. 2014]; the use of burrows or nest holes for breeding (information was taken from the papers used to extract information on the absence or presence of infanticide by females); litter size (number of offspring per birth); offspring mass at birth (grams); weaning age (age at which offspring are independent, in days); inter-birth interval (time between consecutive births, in days) [Jones et al. 2009]; energetic value of milk (MJ/ml based on the protein, sugar, and fat composition) [Langer 2008; Barton & Capellini 2011; Hinder & Milligan 2011]; offspring care by fathers and/or non-parental group members (whether offspring receive milk or food from or are being regularly carried by group members who are not the mother) [Lukas & Clutton-Brock 2017]. In addition, we completed information obtained from these databases by collecting extra data from the primary literature on dominance hierarchies and mechanisms of rank acquisition in social groups (whether all adult females can be arranged in a dominance hierarchy and if so, whether an individual's rank is influenced by age and/or nepotism); and forcible evictions (whether females use aggression to exclude other females from their own social group). For each species in which females had been observed to kill conspecific young, we used the primary literature to record as much information as possible regarding the characteristics of the killer (age and reproductive state) and of the victim (age, sex, and relatedness to killer) to test specific predictions. The full dataset is provided in Supplementary Table 1 (comparative data) and Supplementary Table 2 (individual characteristics data), with all references for data specifically collected here in Supplementary File 1.

In addition to performing comparisons assessing contrasts in the presence or absence of infanticide across all species in our sample, we classified species into different types according to each of the four resource competition hypotheses (Table 2). This classification also aimed

at controlling for a potential confounding effect of social organization, as our analysis might otherwise detect factors associated with the evolution of sociality if females are more likely to have been observed to commit infanticide in some social systems. For the breeding space hypothesis, we only included instances of infanticide in which females did not share a home-range with the mother of the victims; for the milk competition hypothesis, we restricted the sample to associated breeders; for the allocare hypothesis, we only included pair; and for the social competition hypothesis, we only looked at social.

For the comparative analyses, the phylogenetic relatedness between species was inferred from the updated mammalian supertree [Rolland et al. 2014]. We fitted separate phylogenetic models using MCMCglmm [Hadfield & Nakagawa 2010] to identify the extent to which each of the predicted variables (Table 2) explains the presence of infanticide by females across species (binary response, assuming a categorical family of trait distribution). Following the recommendations of Hadfield [2010], we set the priors using an uninformative distribution (with variance, V, set to 0.5 and belief parameter, nu, set to 0.002). Each model was run three times for 100,000 iterations with a burn-in of 20,000, visually checked for convergence and for agreement between separate runs.

Results

Social organisation and infanticide by females

Infanticide by females has been observed in 89 (31%) of the 289 mammalian species in our sample (Table 1). Female infanticide (of any type) varies with the social organisation and is more frequent when females breed in groups (Figure 1): it has been observed in 43% of associated breeders, in 36% of pair breeders, and in 30% of social breeders, but only in 18% of solitary breeders. Across all species, females are equally likely to kill offspring when they are philopatric (47 of 135 species, 34%) than when they disperse to breed (17 of 59 species, 29%) (effect of female dispersal on presence of infanticide by females: -10.1, 95% CI -39.3 – 11.3, p=0.34) but there are differences for two types of social organisation: across associated breeders infanticide only occurs in philopatric species; while across pair breeders infanticide is more likely to occur in species in which females disperse (Table 1). Across all group-living species (associated breeders, pair breeders with helpers, social breeders), there is no relationship between levels of average relatedness among female group members and whether infanticide by females of offspring born in the same group does (median levels of average relatedness across 10 species 0.09, range 0.01-0.38) or does not occur (median levels of average relatedness across 24 species 0.21, range -0.03-0.52) (effect of levels of average relatedness on presence of infanticide by females: -21.1, 95% CI -81.4 – 10.1, p=0.18). Across species in which groups are stable (i.e., excluding associated breeders where groups are sometimes difficult to define and can be very large), levels of average relatedness are slightly higher when infanticide occurs (see also [Lukas & Clutton-Brock 2018]). The population-level information show instances of killers being close kin of the victim in 33% of species (22/65), with either grandmothers killing their grandchildren or aunts killing their nieces, with kin being

common victims in cooperative breeders (8 of 12 cooperative breeders) but also in several social breeders (14 of 51 social breeders).

Life-histories and infanticide by females

Energetic investment into reproduction by mothers is higher in species with any form of infanticide by females compared to the remaining species (Table 1). However, these patterns encountered across all species do not reflect a general association between infanticide and all these traits, but rather the fact that each different scenario of infanticide is associated with specific life histories, with species having either larger offspring mass at birth, shorter time to weaning and between births, and/or larger litter sizes. Females in infanticidal species where there is usually a single breeding female per home range (extraterritorial infanticide and infanticide in pair breeders) have larger litters than females in species without infanticide (Table 1). Species in which females kill offspring in a breeding association are characterized by fast-growing offspring, while offspring are relatively small at birth in species in which females kill offspring in stable groups (Table 1).

Figure 1: The distribution of the different forms of infanticide by females in relation to the social organisation across the mammalian species in our sample (for picture credit see Supplementary File 2).

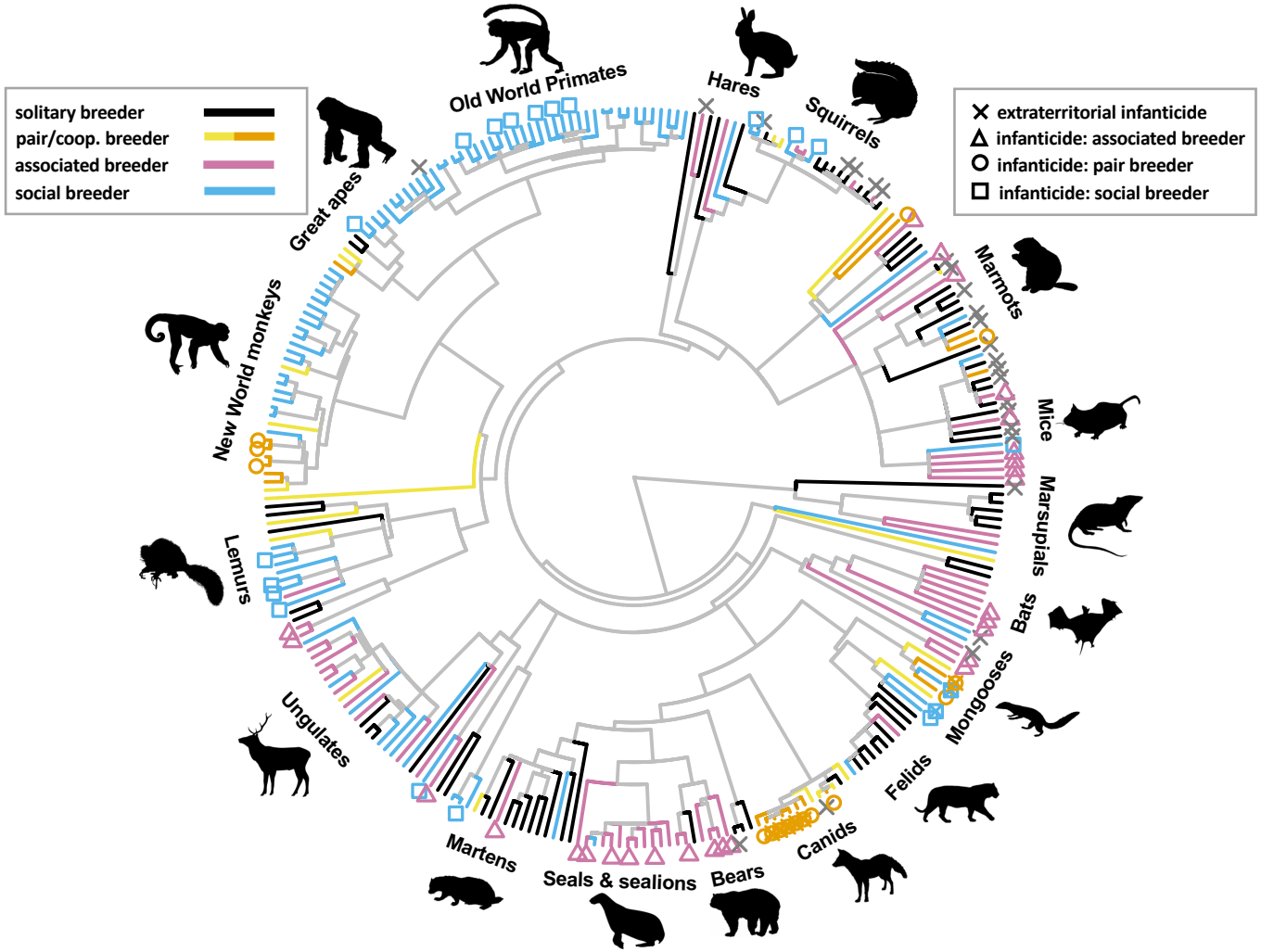


Table 1: The social and life-history conditions associated with the distribution of infanticide by females

Females are more likely to commit infanticide in group-living species, but whether breeding females are philopatric or disperse does not appear to be associated with the distribution of infanticide. In general, species with infanticide by females are characterized by high maternal investment, which is either expressed as females having large litters, short lactational and interbirth periods, and/or relatively large offspring.

Sample of species	**all**		**all**		**associated breeders**		**pair breeders**		**social breeders**	
Type of infanticide	**any**		**extraterritorial**		**within-group**		**within-group**		**within-group**	
Infanticide is	**absent**	**present**	**absent**	**present**	**absent**	**present**	**absent**	**present**	**absent**	**present**
Sample size	200	89	253	33	34	19	29	16	92	20
Females solitary (% species)	38%	16%	39%	76%	NA	NA	NA	NA	NA	NA
Female philopatric (% species)	73%	68%	70%	70%	65%	100%	48%	31%	64%	63%
Maternal investment (per year relative to bodyweight)	39%	118%	47%	150%	48%	86%	110%	169%	29%	45%
Litter size	1.6	2.6	1.7	3.9	1.5	2.1	1.9	4	1.3	1.3
Interbirth interval (days)	365	180	340	104	308	212	308	181	453	522
Age at weaning (days)	127	61	113	35	107	59	105	42	229	273
Offspring weight (relative to bodyweight)	3.6%	3.9%	3.9%	2.8%	3.5%	5.9%	5.1%	2.8%	5.1%	3.0%

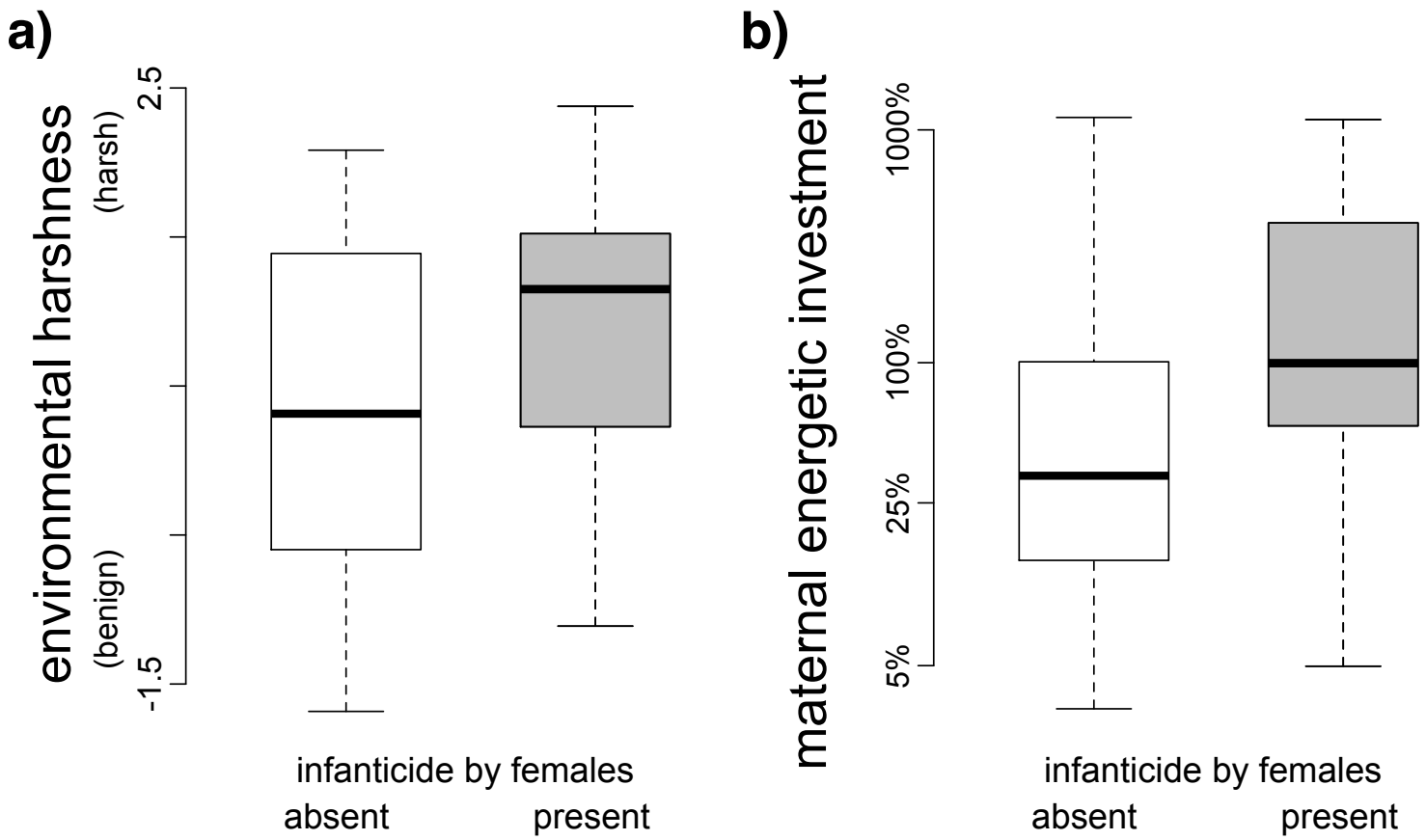
Table 2: Testing the core predictions generated by the different hypotheses proposed to explain the distribution of infanticide by females

For each of the main hypotheses, we tested two core predictions in phylogenetic comparisons and two predictions about the individual traits from the field observations. For the comparisons, we list the sample of species included.

Hypothesis	Type of infanticide / Sample of species	Core prediction(s)	Support?	Predictions of individuals' characteristics	Support?
H1: exploitation	*any form of infanticide*	- primarily in carnivores	No	- killer: any reproductive state	No
	across all species	- infanticide also by males	No	- victim: any age	No
H2: resource competition	*any form of infanticide*	- harsher environments	Yes	- killer: gestating/lactating	Yes
	across all species	- higher maternal investment	Yes	- victim: dependent on care	Yes
H2.1: over breeding space	*extraterritorial infanticide*	- more burrow use	Yes	- killer: gestating/lactating	Yes
	across all species	- exclusive home-ranges	Yes	- victim: unweaned	Yes
H2.2: over milk	*within group infanticide*	- higher energetic milk content	No	- killer: lactating	Yes
	across associated breeders	- faster offspring growth	No	- victim: attempting to nurse	Yes
H2.3: over allomaternal care	*within group infanticide*	- allocarers present	Yes	- killer: gestating/lactating	Yes
	across pair breeders	- more helpers/competitors present	Yes	- victim: dependent on care	Yes
H2.4: over social status	*within group infanticide*	- nepotistic hierarchy present	Yes	- killer: high social rank	Yes
	across social breeders	- evictions occur	Yes	- victim: any age	Yes

Figure 2: Factors associated with female competition and the distribution of infanticide by females

Species in which female infanticide is present are, on average, characterized by (a) living in harsher environments (lower and more unpredictable rainfall and temperatures) and by (b) higher maternal energetic investment (total mass of weaned offspring produced per year relative to maternal mass). Black lines indicate the median across the species in the sample, boxes contain 75% of the values, and whiskers extend to the extremes.



H1: Exploitation

We find no support for predictions suggesting that females kill conspecific offspring primarily for exploitation (Table 2). Across species, infanticide by females is as likely to occur in the absence of infanticide by males (44 of 147 species, 30%) as in its presence (43 of 135 species, 32%) (effect of presence of male infanticide on presence of female infanticide 2.1, 95% CI -13.5 – 16.9, p=0.74). Similarly, carnivorous species are not more likely to show infanticide by females (18 of 56 species, 32%) than species in which meat does not constitute an important part of the diet (59 of 192 species, 31%) (effect of carnivory on presence of female infanticide -0.7, 95% CI -11.2 – 10.0, p=0.89). The age of victims varies from birth to beyond independence across species, but is more homogeneous within each type of infanticide (see below), so that killings do not appear simply opportunistic.

H2: *Resource competition*

Infanticide by females appears more likely to occur where competition over resources is expected to be more intense (Table 2). The climatic environments of species in which females commit infanticide are harsher (as estimated by a principal component reflecting low unpredictable rainfall and cold seasons) than the environments of species in which infanticide has not been observed (effect of environmental harshness on presence of female infanticide 7.0, 95% CI -0.2 – 14.7, p=0.03, 54 species with infanticide and 193 without) (Figure 2a). In species where females commit infanticide, they invest substantially more energy into the production of offspring, being able to produce the equivalent of 1.0 times their own body mass in offspring mass per year (number of offspring times mass of weaned offspring; median across 41 species, range 0.05 – 12.1 times) compared to 0.33 times in species in which infanticide has not been observed (median across 77 species, range 0.03 – 11.1) (effect of

maternal energetic investment on presence of female infanticide 25.8, 95% CI 1.5 – 58.7, p<0.001) (Figure 2b).

H2.1: Competition over breeding space

Thirty-two of the 33 species in which females kill juveniles outside their own home-range keep their offspring in burrows or holes, compared to 93 of the 163 species in which infanticide by females appears absent (effect of burrow use on the presence of infanticide by females 14.4, 95% CI 6.0 – 22.9, p<0.001). The exception is *Semnopithecus entellus*, where "females occasionally steal infants from a neighboring troop" [Hrdy 1976; Mohnot 1980]. In most species in which females kill offspring in neighbouring home-ranges (25 of 33), females generally appear not to tolerate other breeding females close by and most home-ranges only contain a single breeding female (solitary or cooperatively breeding species), while in most other species females form associations or groups (home-ranges contain a single breeding female in 105 out of 268 species) (effect of presence of a single breeding female per home-range on presence of infanticide by females 12.4, 95% CI 0.3 – 30.1, p=0.007). In all cases, the killer was either pregnant or had dependent young of her own (17 species with observations), and all offspring that were killed were not yet weaned (17 species).

H2.2: Competition over milk

Across associated breeders, the energy content of milk produced by mothers in species in which females have been observed to kill offspring within the same breeding space (2.8 MJ/100ml, median across 8 species, range 1.2-4.7) does not differ from that of species in which such killings have not been observed (2.1 MJ/100ml, median across 7 species, range 0.8-5.7) (mean effect of milk energy on presence of infanticide by females 2.0, 95% CI -66.3 –

83.1, p=0.97). In associated breeders with female infanticide, offspring do not seem to have greater growth rates (they gain on average 0.28% of their adult body mass per day until weaning, median across 9 species, range 0.04% - 1.72%) than in species in which females have not been observed to kill juveniles (offspring gain on average 0.17% of their adult body mass per day until weaning, median across 11 species, range 0.05% - 0.73%) (effect of presence of infanticide by females on offspring growth rate 6.1, 95% CI -16.2 – 35.4, p=0.59). Killers are either pregnant or have dependent young (21 out of 21 species) and are old, with most reports suggesting that they had been observed to give birth in previous years (they are not primiparous). All victims were reported to be unweaned (22 out of 22 species). In 7 out of 14 infanticide reports from associated breeders, victims were killed as they attempted to suckle from the killer.

H2.3 Competition over allomaternal care

Infanticide by females in pair breeders occurs only when fathers provide care (all 16 species) while fathers care for offspring in only 16 of the 39 pair breeding species in which this form of infanticide is absent. In 15 of the 16 pair breeders with female infanticide, additional helpers are present (cooperative breeders), while there are only a further 7 cooperatively breeding species in which females have not been observed to kill juveniles from their own group (female infanticide occurs in 68% [15/22] of cooperative breeders versus in 4% [1/23] of pair breeders in which there are no other helpers). Across species in which offspring receive allocare, the number of potential allocarers is higher in species with, compared to species without female infanticide (infanticide present: 3 allocarers per group, median across 15 species, range 2-23; infanticide absent: 2 allocarers per group, median across 13 species, range 1-20; effect of number of allocarers on presence of infanticide 25.3, 95% CI 1.9 – 48.6,

p=0.02). The killer was usually the dominant breeder (as was regularly the case in 9 of 12 species) and was pregnant or with dependent infants in all cases. In most instances the killer and the victim belonged to the same group (11 of 14 species), and were consequently related (10 out of 13 species). Victims were often a few days old and all dependent.

H2.4: Competition over social status

Of the 27 social breeders with female philopatry (and available data), female group members do not form social hierarchies in three species, hierarchical rank is determined by age in five species, and rank is influenced by nepotism in 19 species. Females have been observed to kill offspring born to other group members in eight of these latter 19 species, but in none of the species where nepotism does not influence female rank (effect of presence of nepotistic rank acquisition on presence of infanticide by females 134.1, 95% CI 28.8 – 238.1, p<0.001). Females are more likely to kill offspring born to other females in social breeders in which they also aggressively evict other females from their group (infanticide has been observed in 6 of 10 species with evictions and 7 of 35 without evictions) (effect of occurrence of evictions on presence of infanticide by females 7.8, 95% CI -0.2 – 14.4, p=0.02). In all twelve social breeders in which infanticide events have been observed, killers were old and high-ranking. Killers were never pregnant, but in all cases had dependent young of their own. Victims were not yet weaned, and victims might be related to the killer in 5 out of 12 species. There is only one species where the data suggest that females might preferentially kill offspring of one sex: in *Macaca radiata* (a species with female philopatry), female offspring appear to be the predominant victims.

Discussion

Our findings establish that female infanticide is widespread across mammals and that it is frequently expressed as intensely as competition among males. Females have been observed to kill conspecific juveniles in various species and our comparative analyses provide support to the idea that this behaviour may be adaptive under a wide range of circumstances. Infanticide is more likely to occur in species in which multiple adult females live or breed together than where females breed solitarily, and infanticide appears most frequent in species where females only associate temporarily to breed. Since infanticidal behaviour is relatively rare and may be difficult to detect, this association may reflect the fact that opportunities to commit and to observe infanticides may be greater where females live or breed together. Within each type of social organisation, we do however find that females, like males, appear to commit infanticide when the presence of the victim might otherwise limit their own reproductive success. While infanticide by males has evolved primarily in response to mate competition across mammals [Lukas & Huchard 2014; Palombit 2015], the evolutionary determinants of infanticide by females are apparently more complex, as females may compete over multiple resources.

Several lines of evidence indicate that female infanticide is adaptive, with females killing conspecific offspring in response to competition over resources that are critical for successful reproduction. First, infanticide appears associated with variation in ecology and life-history. Specifically, it is most frequently observed in species facing harsh climatic conditions and making the greatest reproductive efforts; it is unlikely that such associations are due to variations in opportunities to observe or commit infanticides across species. Rather, the

potential costs of sharing critical resources might outweigh the risks associated with committing infanticide in such circumstances.

Second, specific determinants of female infanticide identified at the population level by field studies also seem to predict its distribution across species. Extraterritorial infanticides were found to be most frequent in solitary species where females use burrows to give birth and territories to raise offspring, allowing killers to free-up reproductive space for their own offspring. Anecdotal reports suggest that mothers of victims in these species frequently move away after the loss of their offspring [Sherman 1981]. The strong association with burrow use might occur because burrows represent a clear defendable resource, because offspring kept in burrows tend to be altricial [Kappeler 1991] and unable to flee or defend themselves, or because infanticide is more easily observed if researchers know where offspring are. Our findings further show that female infanticide occurs in pair breeders where helpers – fathers or additional group mates – are present. A lower number of helpers per offspring reduces their weight and their chances to survive at independence, such that females might even kill offspring born to close kin, such as their grandchildren [Clutton-Brock et al. 2001; Hodge et al. 2008]. Finally, patterns are slightly more complex in social breeders. There, infanticide preferentially occurs in species where aggressive competition among females leads to the eviction of some individuals – generally young adults - from the group, especially at times when group size increases (e.g. [Kappeler & Fichtel 2012]). In such cases, killing unrelated juveniles may limit future competition and the related risk of being evicted for the killer's offspring. In addition, in social breeders where females are philopatric, infanticide was only found to occur where female rank acquisition is nepotistic, a hierarchical system where each

additional offspring may contribute to strengthen the social status of a matriline – and where infanticide may consequently weaken competing matrilines on the long term.

Anecdotal reports of female pinnipeds killing orphans as they attempted to suckle from them inspired the hypothesis that females compete over milk in species where they only associate to breed [Digby 2000]. While our comparative analyses did not reveal any difference in the energy content of milk of associated breeders in which infanticide is present versus absent, associated breeders nevertheless comprise the species with the highest energy content of milk and the fastest growth rates, and we further found that offspring are larger at birth and weaned at an earlier age in associated breeders with infanticide compared to those without it. The lack of support for the milk competition hypothesis in our analyses may be explained by a noisy dataset, where the absence of infanticide in some species may be due to the fact that it goes undetected if it is hard to observe, or to the evolution of counter-adaptations that protect offspring against infanticide. Alternatively, milk is not the only resource over which these females compete. For example, in the large breeding colonies of pinnipeds, space is sometimes very restricted [Baldi et al. 1996], especially in the immediate vicinity of the harem leaders. These bulls often protect their females and calves from attacks by younger males, and may represent another source of competition for lactating females.

It is likely that, in any given species, infanticide may be triggered by more than one determinant - including some that may not be considered here. A killer may accordingly get multiple benefits from one infanticide event, but may also commit infanticides in more than one context. For example, half of the species of pair breeders committing intra-group infanticides also commit extraterritorial infanticides. It is therefore possible that different

types of female infanticide – following our classification - have followed a common evolutionary path. Specifically, it is possible that infanticidal behaviour initially emerged in response to one particular pressure (e.g., competition over access to allocare) in a given species, which subsequently started to express it in other competitive contexts (e.g., competition over breeding territories). However, the limited number of species for which observational data on infanticide are available, as well as heterogeneities in the sample – such as an over-representation of group-living species – introduce uncertainty when attempting to reconstruct the evolutionary history of the trait. It is consequently hard to infer the ancestral state, whether each infanticide type has evolved independently, or how many times infanticidal behaviour has emerged across mammals. Similar difficulties limit causal inferences regarding the association between infanticide and social organization. In some lineages the risk of infanticide might prevent breeding females from forming groups, while in others the evolution of infanticide might be favoured by the constraints or opportunities of a specific social system, in line with patterns observed in males [Lukas & Huchard, 2014].

In addition to the nature of the resources that may directly limit female reproductive success in various types of social organisations [Cavigelli et al. 2003, Saltzman et al. 2009, Rosvall 2011], contrasts in the occurrence of infanticide across species reveal other broad patterns on female reproductive competition in mammals. In particular, the lack of association between female infanticide and philopatry across species (Table 1), as well as a synthesis of observations revealing that killers and victims are commonly related in some contexts, such as in pair breeders where reproductive suppression is common [Lukas & Clutton-Brock 2018], suggest that matrilineality and subsequent increases in average kinship among associated females does not necessarily lead to a reduction in competition among females. Some

previous work suggested that mammalian females might be predisposed to behave positively and cooperatively with kin [di Fiore & Rendall 1994], such that species with female philopatry would be characterized by stable social bonds [Silk 2007]. However, the factors leading to limited dispersal and the spatial association of kin frequently also result in high local competition [Frank 1998] which can overcome the potential benefits of cooperation among kin [West et al. 2002]. Studies of competition among males in such circumstances have shown that contrasts in levels of aggression can be explained by variation in the potential direct fitness benefits of winning [West et al. 2001], and it is likely that this also applies to the observed pattern of infanticide by females – where the direct benefits of infanticide in terms of increased access to a critical resource might outweigh its costs, including the indirect fitness costs associated with killing related juveniles.

Our study compiles five decades of behavioural data across species and within populations to elucidate the determinants of infanticide by mammalian females, which are less well understood than those of male infanticide. Our analyses suggest that the distribution of female infanticide across species reflects contrasts in social organisation; infanticide is most frequent in species that breed in groups, which probably have more opportunities for killings and also face greater breeding competition. Female infanticide occurs where the proximity of conspecific offspring directly threatens the killer's reproductive success by limiting access to critical resources for her dependent progeny, including food, shelters, care or a social position. Finally, these data support the idea that female killers occasionally sacrifice related juvenile conspecifics, and may therefore actively harm their indirect fitness in order to maximize their direct fitness.

Acknowledgements

We thank Tim Clutton-Brock, Peter Kappeler, Oliver Höner and Eve Davidian for useful discussions.

Data Accessibility

All data are provided in the supplementary material and are deposited at the Knowledge Network for Biocomplexity doi:10.5063/F1ZG6QFR.

Authors' Contributions

Both authors contributed to the conception and design of the study, collected and interpreted the data, wrote the article, and gave final approval; the analyses were done by DL with input from EH.

Competing Interests

We have no competing interests.

Funding

DL was supported by the European Research Commission (grant 294494-THCB2011 to Prof. T. Clutton-Brock) and the Max Planck Society. EH was supported by the Natural Environment Research Council (grant NE/RG53472) and during the writing-up of this manuscript funded by the ANR (grant ANR-17-CE02-0008).

Supplementary Material

This submission includes all data in Supplementary Tables 1 (comparative data) and 2 (population observations), with references for observations on infanticide by females in Supplementary File 1, and credits for the animal drawings used in Figure 1 in Supplementary File 2.

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Supplementary File 1 for Lukas & Huchard: The evolution of infanticide by females in mammals

Parts A (citations for comparative data), B (citations for population data), and C (reference list).

A) Citations for new data in comparative analyses

The table lists the references with the observations on the presence or absence of infanticide by females for each species, and the references with details on the interactions among females in group-living species. All references are listed in full below the second table.

Species	Reference infanticide by females	Reference eviction/dominance hierarchy
Acinonyx jubatus	Hunter & Skinner, Transactions of the Royal Society of South Africa 56, 79 (2003).	NA
Acomys cahirinus	Ebensperger, Biological Reviews 73, 321 (1998).	NA
Acrobates pygmaeus	Ward, Australian Journal of Zoology 38, 503 (1990).	NA
Aepyceros melampus	Averbeck, Doctoral dissertation, Technische Universität München (2002).	NA
Aethomys namaquensis	Fleming, African Zoology 39, 123 (2004).	NA
Ailurus fulgens	Glatston, Red panda: biology and conservation of the first panda. Andrew, Ed., Noyes Series in Animal Behavior, Ecology, Conservation and management (2010), pp. 488.	NA
Alces alces	Sæther et al., Wildlife Biology 10, 51 (2004).	NA
Alouatta caraya	Ebensperger, Biological Reviews 73, 321 (1998).	NA
Alouatta guariba	Galetti et al., Neotropical Primates 2, 6 (1994).	Galetti et al., Neotropical Primates 2, 6 (1994).
Alouatta palliata	Ebensperger, Biological Reviews 73, 321 (1998).	Zucker & Clarke, International Journal of Primatology 19, 433 (1998).
Alouatta pigra	Treves et al., Ethology 109, 135 (2003); van Belle et al. Primates 51, 279 (2010).	NA
Alouatta seniculus	Ebensperger, Biological Reviews 73, 321 (1998).	Pope, Behavioral Ecology and Sociobiology 48, 253 (2000)
Antechinus stuartii	Holleley et al., Molecular Ecology 15, 3439 (2006).	NA
Antechinus swainsonii	Holleley et al., Molecular Ecology 15, 3439 (2006).	NA
Antilocapra americana	van Noordwijk & van Schaik, in Infanticide by Males and Its Implications, Van Schaik, Janson, Eds. (Cambridge University Press, Cambridge, 2000); Jacques & Jenks, Western North American Naturalist 70, 570 (2010); Dunn et al., Molecular Ecology 20, 4889 (2011); Van Vuren et al., Journal of Mammalogy 94, 155 (2013).	NA
Antrozous pallidus	O'Shea & Vaughan, Journal of Mammalogy 58, 269 (1977).	NA
Aotus azarae	Huck et al., International Journal of Primatology 32, 1133 (2011); Huck & Fernandez-Duque, Behavioral Ecology and Sociobiology 66, 505 (2012).	NA
Apodemus sylvaticus	Blumstein, in Infanticide by Males and Its Implications, C. P. van Schaik, C. H. Janson, Eds. (Cambridge University Press, Cambridge, 2000); Ebensperger & Blumstein, in Rodent societies: an ecological and evolutionary perspective, J. O. Wolff, P. W. Sherman, Eds. (The University of Chicago Press, Chicago, 2007).	NA
Arctocephalus forsteri	Bradshaw et al., Journal of Mammalogy 84, 65 (2003).	NA

Arctocephalus galapagoensis	Trillmich, Behavioral Ecology and Sociobiology 19, 157 (1986).	NA
Arctocephalus gazella	Doidge et al., Journal of Zoology 202, 449 (1984); Harcourt, Journal of Zoology 202, 449 (1992);	NA
Arctocephalus pusillus	Gibbens & Arnould, Canadian Journal of Zoology-Revue Canadienne De Zoologie 87, 902 (2009).	NA
Arctocephalus tropicalis	Beauplet et al., Journal of Animal Ecology 74, 1160 (2005).	NA
Ateles belzebuth	Gibson et al., American Journal of Primatology 70, 485 (2008); Link et al., in Sexual coercion in primates and humans: An evolutionary perspective on male aggression against females, N., W., Eds. (Harvard University Press, Harvard, 2009), pp. 157-183.	NA
Ateles geoffroyi	Gibson et al., American Journal of Primatology 70, 485 (2008); Slater et al., American Journal of Primatology 71, 21 (2009).	NA
Ateles paniscus	McFarland Symington, Behavioral Ecology and Sociobiology 20, 421 (1987); Symington, American Journal of Primatology 15, 45 (1988)	NA
Avahi laniger	Fuentes, International Journal of Primatology 23, 953 (2002).	NA
Bison bison	Lott, Applied Animal Behaviour Science 29, 135 (1991); van Noordwijk & van Schaik, in Infanticide by Males and Its Implications, Van Schaik, Janson, Eds. (Cambridge University Press, Cambridge, 2000); Daleszczyk, Acta Theriologica 49, 555 (2004)	Rutberg, A Ethology 63, 206 (1983) ; Vervaecke et al. 2005, Animal Behaviour 70, 763 (2005).
Brachyteles arachnoides	Strier, Faces in the forest: the endangered muriqui monkeys of Brazil. (Oxford University Press, Oxford, 1992).	NA
Brachyteles hypoxanthus	Strier & Mendes, The Northern Muriqui (Brachyteles hypoxanthus): lessons on behavioral plasticity and population dynamics from a critically endangered species. Kappeler, Watts, Eds., Long-term field studies of primates. (2012), pp. 125-140.	NA
Bunopithecus hoolock	Alfred, J. R. B. & Sati, J. P. 1991 On the first record of infanticide in the hoolock gibbon Hylobates hoolock in the wild. Records of the Zoological Survey of India 89, 319-321; Kumar et al., in Rare animals of India, Singaravelan, Ed. (Bentham Science Publisher, 2013), pp. 242-266.	NA
Callimico goeldii	Porter, Folia primatologica 72, 69 (2001).	NA
Callithrix flaviceps	Digby & Saltzman, in The smallest anthropoids: the Marmoset/Callimico radiation, Ford, Porter, Davis, Eds. (Springer, New York, 2009), pp. 135–153; Hilario & Ferrari, Journal of Ethology 28, 195 (2010).	NA
Callithrix jacchus	Digby, Behavioral Ecology and Sociobiology 37, 51 (1995).	NA
Callorhinus ursinus	Ebensperger, Biological Reviews 73, 321 (1998).	NA
Canis dingo	Corbett, Ethology 78, 177 (1988).	NA
Canis latrans	Camenzind, in Coyotes: Biology, Behavior, and Management, M. Bekoff, Ed. (Academic Press, New York, 1978), pp. 267-294; Ebensperger, Biological Reviews 73, 321 (1998); van Noordwijk & van Schaik, in Infanticide by Males and Its Implications, Van Schaik, Janson, Eds. (Cambridge University Press, Cambridge, 2000).	NA
Canis lupus	McLeod, Canadian Journal of Zoology 68, 402 (1990); van Noordwijk & van Schaik, in Infanticide by Males and Its Implications, Van Schaik, Janson, Eds. (Cambridge University Press, Cambridge, 2000).	NA
Canis mesomelas	van Noordwijk & van Schaik, in Infanticide by Males and Its Implications, Van Schaik, Janson, Eds. (Cambridge University Press, Cambridge, 2000); Jenner, Zoological Society of London's Institute of Zoology, London and University of Kent, Canterbury, UK (2008).	NA

Canis simensis	SilleroZubiri et al., Behavioral Ecology and Sociobiology 38, 331 (1996); van Noordwijk & van Schaik, in Infanticide by Males and Its Implications, Van Schaik, Janson, Eds. (Cambridge University Press, Cambridge, 2000).	NA
Capreolus capreolus	Andersen & Linnell, Canadian Journal of Zoology 76, 1217 (1998).	NA
Cavia aperea	Ebensperger, Biological Reviews 73, 321 (1998); Hennessy et al., Journal of Comparative Psychology 120, 12 (2006).	NA
Cavia intermedia	Ebensperger, Biological Reviews 73, 321 (1998).	NA
Cavia magna	Ebensperger, Biological Reviews 73, 321 (1998); Kraus et al., Journal of Mammalogy 86, 763 (2005).	NA
Cavia porcellus	Ebensperger, Biological Reviews 73, 321 (1998); Sachser, Naturwissenschaften 85, 307 (1998).	NA
Cebus apella	Janson et al., in Long-Term Field Studies of Primates, P. M. Kappeler, W. D. P., Eds. (Springer-Verlag, Berlin Heidelberg, 2012), pp. 185-212.	Janson, Behavioral Ecology and Sociobiology 18, 125 (1985) ; Ferreira et al. American Journal of Primatology 68, 765 (2006); Izawa, Primates 21, 443 (1980)
Cebus capucinus	Manson et al., Folia Primatologica 75, 104 (2004).	Perry, International Journal of Primatology 40, 167 (1996); Bergstrom & Fedigan, Behaviour 147, 899 (2010).
Cebus nigritus	Ramírez-Llorens et al., American Journal of Primatology 70, 473 (2008).	Tiddi et al. Plos One 7, e36641 (2012)
Cebus olivaceus	Ebensperger, Biological Reviews 73, 321 (1998); van Noordwijk & van Schaik, in Infanticide by Males and Its Implications, Van Schaik, Janson, Eds. (Cambridge University Press, Cambridge, 2000).	NA
Cercocebus atys	Range & Noë, American Journal of Primatology 56, 137 (2002).	Range & Noë, American Journal of Primatology 56, 137 (2002); Range, Behavioral Ecology and Sociobiology 59, 511 (2006).
Cercocebus torquatus	van Noordwijk & van Schaik, in Infanticide by Males and Its Implications, Van Schaik, Janson, Eds. (Cambridge University Press, Cambridge, 2000); Range, Behavioral Ecology and Sociobiology 59, 511 (2006).	NA
Cercopithecus albogularis	Henzi & Lawes, Folia primatologica 48, 125 (1987).	NA
Cercopithecus ascanius	Ebensperger, Biological Reviews 73, 321 (1998).	NA
Cercopithecus campbelli	Galat-Luong, A. & Galat, G. 1979 Consequences comportementales des perturbations sociales repetees sur une troupe de Mones de Lowe, Cercopithecus campbelli lowei, de Cote d'Ivoire. Terre et Vie 33, 4-57; Bourlière et al., in Old World Monkeys: Evolution, Systematics and Behavior, J. R. Napier, P. H. Napier, Eds. (Academic Press, New York, 1970).	NA
Cercopithecus mitis	Ebensperger, Biological Reviews 73, 321 (1998).	NA
Cervus elaphus	Guinness et al., Journal of Animal Ecology 47, 817 (1978).	NA
Chalinolobus gouldii	Dixon & Huxley, Mammalia 53, 395 (1989).	NA
Cheirogaleus medius	Fietz et al., Behavioral Ecology and Sociobiology 49, 8 (2000); Fietz & Dausmann, Folia primatologica 74, 246 (2003).	NA
Chiropotes albinasus	Treves, Folia primatologica 69, 81 (1998).	Treves, Folia primatologica 69, 81 (1998).
Chiropotes satanas	Treves, Folia primatologica 69, 81 (1998).	NA
Chlorocebus aethiops	Horrocks, Life-history characteristics of a wild population of vervet monkeys (Cercopithecus aethiops) in Barbados, West Indies. International Journal of Primatology 7, 31 (1986); van Noordwijk & van Schaik, in Infanticide by Males and Its Implications, Van Schaik, Janson, Eds. (Cambridge University Press, Cambridge, 2000); Isbell et al., International Journal of Primatology 30, 103 (2009).	Isbell & Pruetz, International Journal of Primatology 19, 837 (1998).
Chlorocebus sabaeus	Treves, Folia primatologica 69, 81 (1998).	NA
Colobus guereza	Ebensperger, Biological Reviews 73, 321 (1998).	NA

Colobus vellerosus	Teichroeb et al., Behavioral Ecology 23, 1348 (2012).	Wikberg et al. Behaviour 150, 295 (2013).
Connochaetes taurinus	Estes & Estes, Zeitschrift für Tierpsychologie 50, 45 (1979).	NA
Crocidura russula	Cantoni & Vogel, Animal behaviour 38, 205 (1989).	NA
Crocuta crocuta	Kruuk, The Spotted Hyena: A Study of Predation and Social Behaviour. (University of Chicago Press, Chicago, 1972); Hofer & East, in Serengeti II. Dynamics, Management and Conservation of an Ecosystem, A. R. E. Sinclair, P. Arcese, Eds. (University Press, Chicago, 1995), pp. 332-363.	White, Behavioral Ecology 16, 606 (2005)
Cryptomys damarensis	Clarke et al., Proceedings of the Royal Society of London. Series B: Biological Sciences 268, 899 (2001).	NA
Cuon alpinus	Johnsingh, Journal of Zoology 198, 443 (1982); van Noordwijk & van Schaik, in Infanticide by Males and Its Implications, Van Schaik, Janson, Eds. (Cambridge University Press, Cambridge, 2000).	NA
Cynictis penicillata	Vidya et al., Journal of Zoology 278, 57 (2009).	NA
Cynomys gunnisoni	Blumstein, in Infanticide by Males and Its Implications, C. P. van Schaik, C. H. Janson, Eds. (Cambridge University Press, Cambridge, 2000).	NA
Cynomys leucurus	Hoogland, Behaviour 69, 1 (1979).	NA
Cynomys ludovicianus	Blumstein, in Infanticide by Males and Its Implications, C. P. van Schaik, C. H. Janson, Eds. (Cambridge University Press, Cambridge, 2000).	Hoogland, Science 230, 1037 (1985)
Cynomys parvidens	Ebensperger & Blumstein, in Rodent societies: an ecological and evolutionary perspective, Wolff, Sherman, Eds. (The University of Chicago Press, Chicago, 2007).	NA
Cystophora cristata	Perry & Stenson, Behaviour 122, 1 (1992); Lydersen et al., Journal of Comparative Physiology B-Biochemical Systemic and Environmental Physiology 167, 81 (1997); Haug et al., Northwest Atlantic Fisheries Organization Scientific Council Studies 26, 101 (1996).	NA
Dasyurus hallucatus	Kraaijeveld et al., Proceedings of the Royal Society of London. Series B: Biological Sciences 270, S251 (2003).	NA
Dasyurus viverrinus	Kraaijeveld et al., Proceedings of the Royal Society of London. Series B: Biological Sciences 270, S251 (2003).	NA
Diceros bicornis	Weladji & Laflamme-Mayer, African Journal of Ecology 49, 471 (2011).	NA
Dicrostonyx groenlandicus	Blumstein, in Infanticide by Males and Its Implications, C. P. van Schaik, C. H. Janson, Eds. (Cambridge University Press, Cambridge, 2000).	NA
Didelphis virginiana	Hopkins & Forbes, The Murrelet 61, 20 (1980).	NA
Dolichotis patagonum	Taber & Macdonald, Journal of Zoology 227, 439 (1992).	NA
Enhydra lutris	Riedman & Estes, Biological report 90, 1126 (1990); van Noordwijk & van Schaik, in Infanticide by Males and Its Implications, Van Schaik, Janson, Eds. (Cambridge University Press, Cambridge, 2000).	NA
Eptesicus fuscus	Kilgour, Ethology 119, 189 (2013).	NA
Equus burchellii	Pluhacek et al., Journal of Mammalogy 87, 35 (2006).	NA
Equus caballus	van Noordwijk & van Schaik, in Infanticide by Males and Its Implications, Van Schaik, Janson, Eds. (Cambridge University Press, Cambridge, 2000).	NA
Equus zebra	Smith et al., African Journal of Ecology 46, 207 (2008); Lloyd & rasa, Behavioral Ecology and Sociobiology 25, 411 (1989).	NA
Erythrocebus patas	Enstam et al., International Journal of Primatology 23, 85 (2002).	Pruetz & Isbell, Behavioral Ecology and Sociobiology 49, 38 (2000); Isbell & Pruetz, International Journal of Primatology 19, 837 (1998).

Eubalaena australis	Cerqueira Santos et al., Ensaios e Ciencia 14, 83 (2010); Payne, Reports of the International Whaling Commission Special Issue, 161 (1986).	NA
Eulemur fulvus	Jolly et al., International Journal of Primatology 21, 21 (2000).	Jolly et al. International Journal of Primatology 21, 21 (2000).
Eulemur macaco	Pereira & Weiss, Behavioral Ecology and Sociobiology 18, 141 (1991); Andrews, Folia Primatologica 69, 14 (1998); Jolly et al., International Journal of Primatology 21, 21 (2000).	Andrews, Folia Primatologica, 69, 14 (1998).
Eumetopias jubatus	Bruemmer, Natural History 103, 26 (1994).	NA
Felis catus	Ebensperger, Biological Reviews 73, 321 (1998); Pontier & Natoli, Aggressive Behavior 25, 445-449 (1999).	NA
Galea monasteriensis	Hennessy et al., Journal of Comparative Psychology 120, 12 (2006); Adrian et al., Journal of Zoology 265, 97 (2005).	NA
Galea musteloides	Blumstein, in Infanticide by Males and Its Implications, C. P. van Schaik, C. H. Janson, Eds. (Cambridge University Press, Cambridge, 2000); Ebensperger & Blumstein, in Rodent societies: an ecological and evolutionary perspective, J. O. Wolff, P. W. Sherman, Eds. (The University of Chicago Press, Chicago, 2007).	NA
Gazella dorcas	Baharav, Journal of Zoology 200, 445 (1983).	NA
Giraffa camelopardalis	Carter et al., Animal Behaviour 85, 385 (2012); Bercovitch & Berry, Journal of Zoology 290, 281 (2013); van Noordwijk & van Schaik, in Infanticide by Males and Its Implications, Van Schaik, Janson, Eds. (Cambridge University Press, Cambridge, 2000).	NA
Gorilla beringei	Ebensperger, Biological Reviews 73, 321 (1998).	NA
Gorilla gorilla	Stokes et al., Behavioral Ecology and Sociobiology 54, 329 (2003).	NA
Halichoerus grypus	Anderson et al., Journal of Zoology 189, 407 (1979); Le Boeuf & Campagna, in Infanticide and parental care, S. Parmigiani, F. vom Saal, Eds. (Harwood Academic Publishers, 1994), pp. 257-276.	NA
Hapalemur griseus	Nievergelt et al., American Journal of Primatology 57, 157 (2002).	NA
Helogale parvula	Rasa book chapter (1994)	NA
Herpestes sanguineus	Rood, Animal Behaviour 39, 566 (1989); Waser et al., Animal Behaviour 47, 289 (1994).	NA
Heterocephalus glaber	Faulkes, in Cooperative Breeding in Mammals, Solomon, French, Eds. (Cambridge University press, New York, 1997).	NA
Hippopotamus amphibius	Karstad & Hudson, Mammalia 50, 153 (1986); van Noordwijk & van Schaik, in Infanticide by Males and Its Implications, Van Schaik, Janson, Eds. (Cambridge University Press, Cambridge, 2000).	NA
Hippotragus equinus	Beudels et al. Biological Conservation (1992)	NA
Hyaena brunnea	Owens & Owens, Nature 308, 843 (1984); van Noordwijk & van Schaik, in Infanticide by Males and Its Implications, Van Schaik, Janson, Eds. (Cambridge University Press, Cambridge, 2000).	NA
Hyaena hyaena	van Noordwijk & van Schaik, in Infanticide by Males and Its Implications, Van Schaik, Janson, Eds. (Cambridge University Press, Cambridge, 2000); Wagner et al., Molecular Ecology 16, 4356 (2007); Wagner et al., Animal Behaviour 75, 1131 (2008).	NA
Hydrochoeris hydrochaeris	Ebensperger & Blumstein, in Rodent societies: an ecological and evolutionary perspective, J. O. Wolff, P. W. Sherman, Eds. (The University of Chicago Press, Chicago, 2007).	NA
Hylobates lar	Borries et al., Behavioral Ecology and Sociobiology 65, 685 (2011).	NA
Lagothrix lagotricha	Stevenson, Primates 47, 239 (2006); Di Fiore et al., American Journal of Primatology 68, 637 (2006).	NA

Lasiopodomys brandtii	Blumstein, in Infanticide by Males and Its Implications, C. P. van Schaik, C. H. Janson, Eds. (Cambridge University Press, Cambridge, 2000).	NA
Lemmus lemmus	Blumstein, in Infanticide by Males and Its Implications, C. P. van Schaik, C. H. Janson, Eds. (Cambridge University Press, Cambridge, 2000); Ebensperger & Blumstein, in Rodent societies: an ecological and evolutionary perspective, J. O. Wolff, P. W. Sherman, Eds. (The University of Chicago Press, Chicago, 2007).	NA
Lemur catta	Sauther et al., Evolutionary Anthropology 8, 120 (1999); Jolly et al., International Journal of Primatology 21, 21 (2000).	Jolly et al., International Journal of Primatology 21, 21 (2000).
Leontopithecus chrysomelas	De Vleeschouwer et al., Folia Primatologica 72, 1 (2001).	NA
Leontopithecus rosalia	Digby & Saltzman, in The smallest anthropoids: the Marmoset/Callimico radiation, S. M. Ford, L. M. Porter, L. Davis, Eds. (Springer, New York, 2009), pp. 135–153; Henry et al., Hormones and Behaviour 63, 675 (2013).	NA
Leopardus pardalis	van Noordwijk & van Schaik, in Infanticide by Males and Its Implications, Van Schaik, Janson, Eds. (Cambridge University Press, Cambridge, 2000); Hunter & Skinner, Transactions of the Royal Society of South Africa 56, 79 (2003).	NA
Lepilemur edwardsi	Rasoloharijaona et al., International Journal of Primatology 21, 41 (2000).	NA
Leptonychotes weddellii	Le Boeuf & Campagna, in Infanticide and parental care, S. Parmigiani, F. vom Saal, Eds. (Harwood Academic Publishers, 1994), pp. 257-276; Proffitt et al., Oikos 119, 1255 (2010).	NA
Lepus americanus	Krebs et al., BioScience 51, 25 (2001).	NA
Lophocebus albigena	Arlet et al., Folia Biologica 61, 3 (2013).	Chancellor & Isbell, Behavioral Ecology and Sociobiology 63, 1447 (2009).
Lophostoma silvicolum	Knörnschild et al., PLoS One 6, e25001 (2011).	NA
Loris lydekkerianus	Nekaris, Folia primatologica 74, 312 (2003); Radhakrishna & Singh, Current Science 86, 1121 (2004).	NA
Loris tardigradus	Nekaris, Folia primatologica 74, 312 (2003); Nekaris, American Journal of Primatology 68, 1171 (2006).	NA
Loxodonta africana	Moss, Journal of Zoology 255, 145 (2001); Wittmeyer & Getz, Animal Behaviour 73, 671 (2007).	Archie et al. Animal Behaviour 71, 117 (2006).
Lycaon pictus	van Lawick, Solo: the story of an African wild dog. (Houghton Mifflin Company, Boston, MA. , 1974); van Noordwijk & van Schaik, in Infanticide by Males and Its Implications, Van Schaik, Janson, Eds. (Cambridge University Press, Cambridge, 2000).	NA
Lynx canadensis	Hunter & Skinner, Transactions of the Royal Society of South Africa 56, 79 (2003).	NA
Lynx pardinus	Lopez et al., Wildlife Biology in Practice 6, 67 (2010).	NA
Macaca arctoides	Solanski & Zothansiama, Current Science 104, 1081 (2013).	Gouzoules, Primates 16, 405 (1975)
Macaca fascicularis	Ebensperger, Biological Reviews 73, 321 (1998).	De Waal, Zeitschrift für Tierpsychologie 44, 225 (1977); Thierry 2007 Evolutionary Anthropology 16, 224 (2007).
Macaca fuscata	Kutsukake, Primates 41, 321 (2000).	Koyama, Primates 8, 189 (1967); Koyama, Primates 11, 335 (1970) ; Kutsukake, Primates 41, 321 (2000).
Macaca mulatta	Hrdy, Ethology and Sociobiology 1, 13 (1979); Maestripieri & Carroll, Psychological Science 9, 143 (1998); Ebensperger, Biological Reviews 73, 321 (1998).	Maestripieri, Behaviour 131, 97 (1994).
Macaca nemestrina	van Noordwijk & van Schaik, in Infanticide by Males and Its Implications, Van Schaik, Janson, Eds. (Cambridge University Press, Cambridge, 2000).	Maestripieri, Behaviour 131, 97 (1994).

Macaca nigra	A. Engelhardt, Pers. Comm.	Engelhardt, pers com; Duboscq et al., American Journal of Primatology 75, 361 (2013)
Macaca radiata	Ebensperger, Biological Reviews 73, 321 (1998).	Silk et al. Animal Behaviour 29, 1106 (1981).
Macaca silenus	van Noordwijk & van Schaik, in Infanticide by Males and Its Implications, Van Schaik, Janson, Eds. (Cambridge University Press, Cambridge, 2000).	Singh et al. 2006 Journal of Bioscience 31, 369 (2006)
Macaca sinica	Dittus, Animal Behaviour 36, 1628 (1988).	Dittus, Behavioral Ecology and Sociobiology 19, 257 (1986)
Macaca sylvanus	Ebensperger, Biological Reviews 73, 321 (1998); Paul & Kuester, Behavioral Ecology and Sociobiology 39, 139 (1996)	Paul & Kuester, Behavioral Ecology and Sociobiology 39, 139 (1996)
Macaca thibetana	Berman et al., International Journal of Primatology 28, 1123 (2007).	Berman et al. International Journal of Primatology 25, 1283 (2004).
Macaca tonkeana	Muroyama & Thierry, International Journal of Primatology 17, 219 (1996).	Muroyama & Thierry, International Journal of Primatology 17, 219 (1996).
Macropus giganteus	Nave, Doctoral dissertation, The University of Melbourne (2002).	NA
Madoqua kirkii	Hendrichs, Zeitschrift für Tierpsychologie 38, 55 (1975); Brotherton & Manser, Animal Behaviour 54, 1413 (1997); van Noordwijk & van Schaik, in Infanticide by Males and Its Implications, Van Schaik, Janson, Eds. (Cambridge University Press, Cambridge, 2000).	NA
Mandrillus leucophaeus	van Noordwijk & van Schaik, in Infanticide by Males and Its Implications, Van Schaik, Janson, Eds. (Cambridge University Press, Cambridge, 2000).	NA
Mandrillus sphinx	Setchell et al., American Journal of Physical Anthropology 131, 498 (2006).	Setchell et al. International Journal of Primatology 23, 51 (2002).
Marmota caligata	Ebensperger & Blumstein, in Rodent societies: an ecological and evolutionary perspective, Wolff, Sherman, Eds. (The University of Chicago Press, Chicago, 2007).	NA
Marmota caudata	Blumstein, in Infanticide by Males and Its Implications, C. P. van Schaik, C. H. Janson, Eds. (Cambridge University Press, Cambridge, 2000).	NA
Marmota flaviventris	Blumstein, in Infanticide by Males and Its Implications, C. P. van Schaik, C. H. Janson, Eds. (Cambridge University Press, Cambridge, 2000).	Brody & Melcher, Animal Behaviour 33, 673-674 (1985).
Marmota marmota	Ebensperger, Biological Reviews 73, 321 (1998).	NA
Marmota monax	Maher & Duron, Journal of Mammalogy 91, 628 (2010).	NA
Martes americana	Erb et al., Minnesota Department of Natural Resources Summaries of Wildlife Research Findings 2009, 12 (2010)	NA
Martes pennanti	Erb et al., Minnesota Department of Natural Resources Summaries of Wildlife Research Findings 2009, 12 (2010)	NA
Megaderma lyra	Knörnschild et al., PLoS One 6, e25001 (2011).	NA
Meles meles	Ebensperger, Biological Reviews 73, 321 (1998).	NA
Mellivora capensis	Begg et al., Journal of Zoology 265, 23 (2005).	NA
Mephitis mephitis	Sargeant et al., Canadian Field Naturalist 96, 312 (1982); van Noordwijk & van Schaik, in Infanticide by Males and Its Implications, Van Schaik, Janson, Eds. (Cambridge University Press, Cambridge, 2000).	NA
Meriones unguiculatus	Blumstein, in Infanticide by Males and Its Implications, C. P. van Schaik, C. H. Janson, Eds. (Cambridge University Press, Cambridge, 2000); Ebensperger & Blumstein, in Rodent societies: an ecological and evolutionary perspective, J. O. Wolff, P. W. Sherman, Eds. (The University of Chicago Press, Chicago, 2007).	NA
Mesocricetus auratus	Blumstein, in Infanticide by Males and Its Implications, C. P. van Schaik, C. H. Janson, Eds. (Cambridge University Press, Cambridge, 2000); Ebensperger & Blumstein, in Rodent societies: an ecological and evolutionary perspective, J. O.	NA

	Wolff, P. W. Sherman, Eds. (The University of Chicago Press, Chicago, 2007).	
Microcebus murinus	Eberle & Kappeler, Behavioral Ecology and Sociobiology 57, 91 (2004); Eberle & Kappeler, Behavioral Ecology and Sociobiology 60, 582 (2006).	NA
Microtus agrestis	Blumstein, in Infanticide by Males and Its Implications, C. P. van Schaik, C. H. Janson, Eds. (Cambridge University Press, Cambridge, 2000); Ebensperger & Blumstein, in Rodent societies: an ecological and evolutionary perspective, J. O. Wolff, P. W. Sherman, Eds. (The University of Chicago Press, Chicago, 2007).	NA
Microtus arvalis	Heise & Lippke, Aggressive Behavior 23, 293 (1997).	NA
Microtus californicus	Blumstein, in Infanticide by Males and Its Implications, C. P. van Schaik, C. H. Janson, Eds. (Cambridge University Press, Cambridge, 2000); Ebensperger & Blumstein, in Rodent societies: an ecological and evolutionary perspective, J. O. Wolff, P. W. Sherman, Eds. (The University of Chicago Press, Chicago, 2007).	NA
Microtus canicaudus	Blumstein, in Infanticide by Males and Its Implications, C. P. van Schaik, C. H. Janson, Eds. (Cambridge University Press, Cambridge, 2000).	NA
Microtus ochrogaster	Ebensperger & Blumstein, in Rodent societies: an ecological and evolutionary perspective, J. O. Wolff, P. W. Sherman, Eds. (The University of Chicago Press, Chicago, 2007).	NA
Microtus pennsylvanicus	Ebensperger & Blumstein, in Rodent societies: an ecological and evolutionary perspective, J. O. Wolff, P. W. Sherman, Eds. (The University of Chicago Press, Chicago, 2007).	NA
Microtus townsendii	Blumstein, in Infanticide by Males and Its Implications, C. P. van Schaik, C. H. Janson, Eds. (Cambridge University Press, Cambridge, 2000)	NA
Mirounga angustirostris	LeBoeuf et al., Behaviour 43, 121 (1972); LeBoeuf & Briggs, Mammalia 41, 167 (1977).	NA
Mirounga leonina	McCann, Animal Behaviour 30, 268 (1982); LeBoeuf et al., Behaviour 43, 121 (1972).	NA
Mirza coquereli	Stanger et al., American Journal of Primatology 36, 223 (1995).	NA
Monachus schauinslandi	Bonness, Behavioral Ecology and Sociobiology 27, 113 (1990); Hiruki et al., Canadian Journal of Zoology 71, 458 (1993).	NA
Mungos mungo	Gilchrist, Behavioral Ecology 11, 1 (2006).	Hodge et al. 2011. Biology letters 7, 54 (2011).
Mus musculus	Ebensperger & Blumstein, in Rodent societies: an ecological and evolutionary perspective, Wolff, Sherman, Eds. (The University of Chicago Press, Chicago, 2007).	NA
Mustela erminea	Alterio, Ecography 21, 18 (1998); Hellstedt & Henttonen, Journal of Zoology 269, 205 (2006); Samson & Raymond, Mammalia 62, 165 (1998); Cuthbert & Sommer, New Zealand Journal of Zoology 29, 149 (2002).	NA
Mustela frenata	van Noordwijk & van Schaik, in Infanticide by Males and Its Implications, Van Schaik, Janson, Eds. (Cambridge University Press, Cambridge, 2000).	NA
Myodes glareolus	Ebensperger & Blumstein, in Rodent societies: an ecological and evolutionary perspective, J. O. Wolff, P. W. Sherman, Eds. (The University of Chicago Press, Chicago, 2007).	NA
Myotis myotis	Łupicki et al., Mammalia 74, 339 (2010).	NA
Nasalis larvatus	Murai et al., Primates 48, 117 (2007).	NA
Nasua nasua	Ebensperger, Biological Reviews 73, 321 (1998); van Noordwijk & van Schaik, in Infanticide by Males and Its Implications, Van Schaik, Janson, Eds. (Cambridge University Press, Cambridge, 2000).	Hirsch, Ethology 113, 446 (2007).

Neophoca cinerea	Le Boeuf & Campagna, in Infanticide and parental care, S. Parmigiani, F. vom Saal, Eds. (Harwood Academic Publishers, 1994), pp. 257-276; Higgins & Tedman, Marine Mammal Science 71, 617 (1990).	NA
Neotoma albigula	Topping & Millar, Behavioral Ecology and Sociobiology 43, 115 (1998).	NA
Neotoma cinerea	Escherich, American Zoologist 15, 821 (1975).	NA
Neotoma lepida	Blumstein, in Infanticide by Males and Its Implications, C. P. van Schaik, C. H. Janson, Eds. (Cambridge University Press, Cambridge, 2000)	NA
Neovison vison	Garcia-Diaz & Lizana, North-Western Journal of Zoology 9, 438 (2013).	NA
Nyctereutes procyonoides	van Noordwijk & van Schaik, in Infanticide by Males and Its Implications, Van Schaik, Janson, Eds. (Cambridge University Press, Cambridge, 2000); Drygala et al., Acta Theriologica 53, 111 (2008); Drygala et al., Wildlife biology 14, 457 (2008); Kowalczyk et al., Annales Zoologici Fennici 46, 291 (2009).	NA
Nycticeius humeralis	Kunz & Ebensperger, Acta Chiropterologica 1, 17 (1999).	NA
Ochotona curzoniae	Dobson et al., Behavioral Ecology 9, 622 (1998).	NA
Octodon degus	Ebensperger, Acta Ethologica 3, 89 (2001).	Ebensperger, Acta Ethologica 3, 89 (2001).
Odobenus rosmarus	Le Boeuf & Campagna, in Infanticide and parental care, S. Parmigiani, F. vom Saal, Eds. (Harwood Academic Publishers, 1994), pp. 257-276.	NA
Odocoileus virginianus	Sams et al., Journal of Mammalogy 77, 179 (1996).	NA
Onychomys torridus	Horner & Taylor, Journal of Mammalogy 49, 644 (1968).	NA
Oreamnos americanus	Gaillard et al., Annual Review of Ecology and Systematics 31, 367 (2000).	NA
Oryctolagus cuniculus	Künkele, Journal of Mammalogy 73, 317 (1992); Rödel et al., Ethology 114, 22 (2008).	NA
Oryx leucoryx	Harding, Oryx 41, 478 (2007).	NA
Otaria byronia	Campagna et al., Behaviour 107, 44 (1988).	NA
Otocyon megalotis	Lamprecht, Zeitschrift für Tierpsychologie-Journal of Comparative Ethology 49, 260 (1979); Malcolm, Journal of Zoology 208, 457 (1986); van Noordwijk & van Schaik, in Infanticide by Males and Its Implications, Van Schaik, Janson, Eds. (Cambridge University Press, Cambridge, 2000); Wright et al., Journal of Mammalogy 91, 437 (2012).	NA
Otolemur crassicaudatus	Buettner-Janusch, Folia primatologica 2, 93 (1964); Welker & Schaäfer-Witt, International journal of primatology 9, 509 (1988).	NA
Otolemur garnettii	Welker & Schaäfer-Witt, International journal of primatology 9, 509 (1988).	NA
Ovibos moschatus	Lent, Mammalian species 302, 1 (1988).	NA
Ovis aries	Gaillard et al., Annual Review of Ecology and Systematics 31, 367 (2000).	NA
Ovis canadensis	Festabianchet, Journal of Animal Ecology 58, 785 (1989); Festabianchet et al., Behavioral Ecology 5, 21 (1994); van Noordwijk & van Schaik, in Infanticide by Males and Its Implications, Van Schaik, Janson, Eds. (Cambridge University Press, Cambridge, 2000).	NA
Ozotoceros bezoarticus	Kunz & Ebensperger, Acta Chiropterologica 1, 17 (1999).	NA
Pan paniscus	Furuichi et al., in P. M. Kappeler, D. P. Watts, Eds., Long-term field studies of primates. (Springer-Verlag, Berlin Heidelberg, 2012), pp. 413-433.	NA
Pan troglodytes	Goodall, The chimpanzees of Gombe: patterns of behaviour. Harvard University Press, Cambridge, (1996); Townsend et al., Current Biology 17, R355 (2007).	NA

Panthera leo	Packer & Pusey, in Infanticide: Comparative and Evolutionary Perspectives, G. Hausfater, S. B. Hrdy, Eds. (Aldine, New York, 1984), pp. 31-42.	Packer & Pusey, in Infanticide: Comparative and Evolutionary Perspectives, G. Hausfater, S. B. Hrdy, Eds. (Aldine, New York, 1984), pp. 31-42.
Panthera onca	Soares et al., Genetics and Molecular Biology 29, 735 (2006).	NA
Panthera pardus	Hunter & Skinner, Transactions of the Royal Society of South Africa 56, 79 (2003).	NA
Panthera tigris	Hunter & Skinner, Transactions of the Royal Society of South Africa 56, 79 (2003).	NA
Papio anubis	Ebensperger, Biological Reviews 73, 321 (1998); Palombit, in Sexual Selection and Reproductive Competition in Primates: New Perspectives and Directions, C. B. Jones, Ed. (American Society of Primatologists, 2003), pp. 367-412.	Smuts, *Sex and Friendship in Baboons*. Routledge, (1985).
Papio cynocephalus	Collins et al., in Infanticide: comparative and evolutionary perspectives G. Hausfater, S. B. Hrdy, Eds. (Aldine: New York, 1984); Wasser & Starling, in Primate ontogeny, cognition and social behavior, J. G. Else, P. C. Lee, Eds. (Cambridge University Press, Cambridge, 1986), pp. 343-354; Shopland & Altmann, International Journal of Primatology 13, 61 (1987); Palombit, in Sexual Selection and Reproductive Competition in Primates: New Perspectives and Directions, C. B. Jones, Ed. (American Society of Primatologists, 2003), pp. 367-412.	Kleindorfer & Wasser, Behavioral Ecology and Sociobiology, 56, 328. (2004)
Papio hamadryas	Ebensperger, Biological Reviews 73, 321 (1998); Palombit, in Sexual Selection and Reproductive Competition in Primates: New Perspectives and Directions, C. B. Jones, Ed. (American Society of Primatologists, 2003), pp. 367-412.	NA
Papio papio	Ebensperger, Biological Reviews 73, 321 (1998); Palombit, in Sexual Selection and Reproductive Competition in Primates: New Perspectives and Directions, C. B. Jones, Ed. (American Society of Primatologists, 2003), pp. 367-412.	NA
Papio ursinus	Ebensperger, Biological Reviews 73, 321 (1998); Palombit, in Sexual Selection and Reproductive Competition in Primates: New Perspectives and Directions, C. B. Jones, Ed. (American Society of Primatologists, 2003), pp. 367-412; Brain, International Journal of Primatology 13, 593 (1992).	Cheney et al., 2006. In Reproduction and fitness in baboons: Behavioral, ecological, and life history perspectives. (Springer US 2006) pp. 147-176; Brain, International Journal of Primatology 13, 593 (1992).
Paraxerus cepapi	Blumstein, in Infanticide by Males and Its Implications, C. P. van Schaik, C. H. Janson, Eds. (Cambridge University Press, Cambridge, 2000).	NA
Peromyscus californicus	Blumstein, in Infanticide by Males and Its Implications, C. P. van Schaik, C. H. Janson, Eds. (Cambridge University Press, Cambridge, 2000); Ebensperger & Blumstein, in Rodent societies: an ecological and evolutionary perspective, J. O. Wolff, P. W. Sherman, Eds. (The University of Chicago Press, Chicago, 2007).	NA
Peromyscus leucopus	Blumstein, in Infanticide by Males and Its Implications, C. P. van Schaik, C. H. Janson, Eds. (Cambridge University Press, Cambridge, 2000).	NA
Peromyscus maniculatus	Blumstein, in Infanticide by Males and Its Implications, C. P. van Schaik, C. H. Janson, Eds. (Cambridge University Press, Cambridge, 2000).	NA
Peromyscus polionotus	Margulis et al., Animal Behaviour 69, 627 (2005); Kaufman & Kaufman, Journal of Mammalogy 68, 275 (1987); Foltz, American Naturalist 117, 665 (1981).	NA
Phacochoerus aethiopicus	Somers et al., Acta Theriologica 40, 257 (1995); van Noordwijk & van Schaik, in Infanticide by Males and Its Implications, Van Schaik, Janson, Eds. (Cambridge University Press, Cambridge, 2000).	NA
Phascogale tapoatafa	Rhind, Wildlife Research 29, 247 (2002).	NA
Phoca groenlandica	Le Boeuf & Campagna, in Infanticide and parental care, S. Parmigiani, F. vom Saal, Eds. (Harwood Academic Publishers, 1994), pp. 257-276.	NA

Phoca sibirica	Thomas et al., Mammalian Species, 1 (1982).	NA
Phoca vitulina	Le Boeuf & Campagna, in Infanticide and parental care, S. Parmigiani, F. vom Saal, Eds. (Harwood Academic Publishers, 1994), pp. 257-276.	NA
Phocarctos hookeri	Le Boeuf & Campagna, in Infanticide and parental care, S. Parmigiani, F. vom Saal, Eds. (Harwood Academic Publishers, 1994), pp. 257-276.	NA
Phodopus campbelli	Blumstein, in Infanticide by Males and Its Implications, C. P. van Schaik, C. H. Janson, Eds. (Cambridge University Press, Cambridge, 2000); Ebensperger & Blumstein, in Rodent societies: an ecological and evolutionary perspective, J. O. Wolff, P. W. Sherman, Eds. (The University of Chicago Press, Chicago, 2007).	NA
Phodopus sungorus	Blumstein, in Infanticide by Males and Its Implications, C. P. van Schaik, C. H. Janson, Eds. (Cambridge University Press, Cambridge, 2000).	NA
Phyllostomus hastatus	Bohn et al., Behavioral Ecology and Sociobiology 63, 1693 (2009).	NA
Phyllotis darwini	Ebensperger & Blumstein, in Rodent societies: an ecological and evolutionary perspective, J. O. Wolff, P. W. Sherman, Eds. (The University of Chicago Press, Chicago, 2007).	NA
Pithecia pithecia	Norconk, International journal of primatology 27, 653 (2006).	NA
Pongo abelii	Beaudrot et al., Behavioral Ecology and Sociobiology 63, 1549 (2009).	NA
Pongo pygmaeus	Beaudrot et al., Behavioral Ecology and Sociobiology 63, 1549 (2009).	NA
Potos flavus	Kays, Journal of Zoology 253, 491 (2001).	NA
Presbytis potenziani	Fuentes, International Journal of Primatology 23, 953 (2002).	NA
Presbytis thomasi	Steenbeek, in Infanticide by males and its implications, Van Schaik, Janson, Eds. (Cambridge University Press, Cambridge, 2000), pp. 153-177.	NA
Procolobus badius	Struhsaker & Leland, Zeitschrift fuer Tierpsychologie 69, 89 (1985).	NA
Propithecus diadema	Wright, International Journal of Primatology 16, 835 (1995); Erhart & Overdorff, International Journal of Primatology 19, 73 (1998).	NA
Propithecus edwardsi	Ebensperger, Biological Reviews 73, 321 (1998); Morelli, Behaviour 146, 499 (2009).	Morelli et al. Behaviour 146, 499 (2009).
Propithecus verreauxi	van Noordwijk & van Schaik, in Infanticide by Males and Its Implications, Van Schaik, Janson, Eds. (Cambridge University Press, Cambridge, 2000).	Erhart & Overdorff, International Journal of Primatology 29, 1227 (2008).
Proteles cristata	Koehler & Richardson, Mammalian Species 363, 1 (1990); van Noordwijk & van Schaik, in Infanticide by Males and Its Implications, Van Schaik, Janson, Eds. (Cambridge University Press, Cambridge, 2000); Kotze et al., Animal Behaviour 84, 1573 (2012).	NA
Pteronura brasiliensis	Mourao & Carvalho, Mammalia 65, 225 (2001).	NA
Pteropus hypomelanus	Kunz & Ebensperger, Acta Chiropterologica 1, 17 (1999).	NA
Pteropus vampyrus	Kunz & Ebensperger, Acta Chiropterologica 1, 17 (1999).	NA
Puma concolor	van Noordwijk & van Schaik, in Infanticide by Males and Its Implications, Van Schaik, Janson, Eds. (Cambridge University Press, Cambridge, 2000); Hunter & Skinner, Transactions of the Royal Society of South Africa 56, 79 (2003).	NA
Pygathrix bieti	Xiang & Grueter, American Journal of Primatology 69, 249 (2007).	NA
Pygathrix nemaeus	Angst & Thommen, Folia primatologica 27, 198 (1977).	NA
Pygathrix roxellana	Zhang et al., Folia Primatologica 70, 274 (1999); Qi et al., American Journal of Primatology 71, 670 (2009).	NA
Rangifer tarandus	Gaillard et al., Annual Review of Ecology and Systematics 31, 367 (2000).	Barrette & Vandal, Behaviour 97, 118 (1986).

Rattus norvegicus	Blumstein, in Infanticide by Males and Its Implications, C. P. van Schaik, C. H. Janson, Eds. (Cambridge University Press, Cambridge, 2000); Ebensperger & Blumstein, in Rodent societies: an ecological and evolutionary perspective, J. O. Wolff, P. W. Sherman, Eds. (The University of Chicago Press, Chicago, 2007).	NA
Rhabdomys pumilio	Schradin & Pillay, Journal of Comparative Psychology 117, 317 (2003).	NA
Rhinoceros unicornis	Dinerstein et al., Journal of Mammalogy 69, 813 (1988).	NA
Rhynchocyon chrysopygus	Rathbun, Mammalian species 117, 1 (1979).	NA
Saguinus fuscicollis	Tirado-Herrera et al., American Journal of Primatology 50, 153 (2000).	NA
Saguinus mystax	Culot et al., Primates 52, 179 (2011).	NA
Saguinus oedipus	Savage et al., American Journal of Primatology 38, 85 (1996).	NA
Saimiri oerstedii	Zimbler-DeLorenzo & Stone, American Journal of Primatology 73, 607 (2011).	NA
Saimiri sciureus	Hrdy, Advances in the Study of Behavior 6, 101 (1976).	NA
Sciurus carolinensis	Lane et al., Animal Behaviour 75, 1927 (2008).	NA
Semnopithecus entellus	Sugiyama, in Social communication among primates, S. A. Altmann, Ed. (University of Chicago Press, Chicago, 1967), pp. 221-236; Hrdy, Folia primatologica 22, 19 (1974); Hrdy, Advances in the Study of Behavior 6, 101 (1976).	Borries, Behavioral Ecology and Sociobiology 41, 139 (1997).
Speothos venaticus	Macdonald, Journal of Zoology 239, 525 (1996); van Noordwijk & van Schaik, in Infanticide by Males and Its Implications, Van Schaik, Janson, Eds. (Cambridge University Press, Cambridge, 2000).	NA
Spermophilus beecheyi	Ebensperger, Biological Reviews 73, 321 (1998).	NA
Spermophilus beldingi	Ebensperger & Blumstein, in Rodent societies: an ecological and evolutionary perspective, J. O. Wolff, P. W. Sherman, Eds. (The University of Chicago Press, Chicago, 2007).	NA
Spermophilus citellus	Ramos-Lara et al. Mammalian Species 46, 71 (2014).	NA
Spermophilus columbianus	Blumstein, in Infanticide by Males and Its Implications, C. P. van Schaik, C. H. Janson, Eds. (Cambridge University Press, Cambridge, 2000).	NA
Spermophilus franklinii	Blumstein, in Infanticide by Males and Its Implications, C. P. van Schaik, C. H. Janson, Eds. (Cambridge University Press, Cambridge, 2000).	NA
Spermophilus fulvus	Blumstein, in Infanticide by Males and Its Implications, C. P. van Schaik, C. H. Janson, Eds. (Cambridge University Press, Cambridge, 2000).	NA
Spermophilus parryii	Blumstein, in Infanticide by Males and Its Implications, C. P. van Schaik, C. H. Janson, Eds. (Cambridge University Press, Cambridge, 2000).	NA
Spermophilus richardsonii	Blumstein, in Infanticide by Males and Its Implications, C. P. van Schaik, C. H. Janson, Eds. (Cambridge University Press, Cambridge, 2000).	NA
Spermophilus townsendii	Blumstein, in Infanticide by Males and Its Implications, C. P. van Schaik, C. H. Janson, Eds. (Cambridge University Press, Cambridge, 2000).	NA
Spermophilus tridecemlineatus	Blumstein, in Infanticide by Males and Its Implications, C. P. van Schaik, C. H. Janson, Eds. (Cambridge University Press, Cambridge, 2000).	NA
Suncus murinus	Rissman, Journal of Experimental Zoology 4, 207 (1990).	NA
Suricata suricatta	Clutton-Brock et al., Proceedings of the Royal Society of London, Series B 265, 2291 (1998).	NA
Sus scrofa	Andersson et al., Applied Animal Behaviour Science 134, 184 (2011).	Andersson et al. Applied Animal Behaviour Science 134, 184 (2011).
Symphalangus syndactylus	Morino, Doctoral dissertation, Rutgers University-Graduate School-New Brunswick (2012).	NA

Tadarida brasiliensis	Kunz & Ebensperger, Acta Chiropterologica 1, 17 (1999); Knörnschild et al., PLoS One 6, e25001 (2011).	NA
Tamias striatus	Bergeron et al., Journal of Evolutionary Biology 24, 1685 (2011).	NA
Tarsius bancanus	Roberts, International Journal of Primatology 15, 1 (1994).	NA
Theropithecus gelada	Ebensperger, Biological Reviews 73, 321 (1998).	Dunbar, Behavioral Ecology and Sociobiology 7, 253 (1970).
Trachypithecus cristatus	Harding, Mammalian Species 42, 149 (2010).	NA
Trachypithecus poliocephalus	Zhao et al., Behavioral Ecology and Sociobiology 65, 1535 (2011).	NA
Trachypithecus vetulus	Ebensperger, Biological Reviews 73, 321 (1998).	NA
Tursiops truncatus	Patterson et al., Proceedings of the Royal Society, Series B 265, 1167 (1998).	NA
Ursus americanus	Ebensperger, Biological Reviews 73, 321 (1998); Samson, Canadian Journal of Zoology 79, 633 (2001).	NA
Ursus arctos	Ebensperger, Biological Reviews 73, 321 (1998); Wielgus & Bunnell, Biological Conservation 93, 145 (2000).	NA
Ursus maritimus	Taylor et al., Arctic 38, 303 (1985).	NA
Varecia variegata	van Noordwijk & van Schaik, in Infanticide by Males and Its Implications, Van Schaik, Janson, Eds. (Cambridge University Press, Cambridge, 2000); Baden et al., Behavioral Ecology and Sociobiology 67, 1937 (2013).	NA
Vulpes lagopus	Kruchenkova et al., Naturwissenschaften 96, 457 (2009).	NA
Vulpes velox	Kamler et al., Animal Behaviour 68, 83 (2004); Kitchen et al., Animal Behaviour 71, 1029 (2006).	NA
Vulpes vulpes	Packer & Pusey, in Infanticide: comparative and evolutionary perspectives., G. Hausfater, S. B. Hrdy, Eds. (Aldine, New York, 1984), pp. 31-42.	NA
Vulpes zerda	Lariviere, Mammalian Species 714, 1 (2002).	NA
Xerus inauris	Waterman, Ethology 101, 130 (1995).	NA
Zalophus californianus	Le Boeuf & Campagna, in Infanticide and parental care, S. Parmigiani, F. vom Saal, Eds. (Harwood Academic Publishers, 1994), pp. 257-276.	NA
Zalophus wollebaeki	Le Boeuf & Campagna, in Infanticide and parental care, S. Parmigiani, F. vom Saal, Eds. (Harwood Academic Publishers, 1994), pp. 257-276.	NA

B) Citations for population observation with details on female infanticide

The table lists the references with the observations on the characteristics of the killer and the victim and the circumstances of infanticide by females for the set of species for which this information was available. All references are listed in full below.

Species	Reference
Acomys cahirinus	Porter & Doane, Zeitschrift für Tierpsychologie 47, 225 (1978)
Aethomys namaquensis	Fleming & Nicolson, African Zoology 39, 123 (2004).
Apodemus sylvaticus	Gerlach & Bartmann, Behavioral Ecology 13, 408 (2002).
Arctocephalus gazella	Doidge et al. Journal of Zoology 449 (1984) ; Le Boeuf & Campagna, in Infanticide and parental care, S. Parmigiani, F. vom Saal, Eds. (Harwood Academic Publishers, 1994), pp. 257-276
Callithrix flaviceps	Hilário & Ferrari, Journal of Ethology 28, 195 (2010).
Callithrix jacchus	Melo et al. Folia Primatologica 74, 48 (2003).
Callithrix jacchus	Melo et al. Folia Primatologica 74, 48 (2003).
Callorhinus ursinus	Le Boeuf & Campagna, in Infanticide and parental care, S. Parmigiani, F. vom Saal, Eds. (Harwood Academic Publishers, 1994), pp. 257-276.
Canis dingo	Corbett. Ethology. 78, 177 (1988)
Canis latrans	Camenzind, in Coyotes: Biology, Behavior, and Management, M. Bekoff, Ed. (Academic Press, New York, 1978), pp. 267-294; Ebensperger, Biological Reviews 73, 321 (1998); van Noordwijk & van Schaik, in Infanticide by Males and Its Implications, Van Schaik, Janson, Eds. (Cambridge University Press, Cambridge, 2000).
Canis lupus	McLeod, Canadian Journal for Zoology, 68, 402 (1990)
Canis mesomelas	Jenner, PhD Thesis. University of Kent, Canterbury, UK (2008).
Canis simensis	SilleroZubiri et al., Behavioral Ecology and Sociobiology 38, 331 (1996); van Noordwijk & van Schaik, in Infanticide by Males and Its Implications, Van Schaik, Janson, Eds. (Cambridge University Press, Cambridge, 2000).
Clethrionomys glareolus	Ylonen et al. Annals Zoologica Fennici 34, 259 (1997)
Crocuta crocuta	White, Behavioral Ecology 16, 606 (2005)
Cynomys ludovicianus	Hoogland, Science 230, 1037 (1985)
Dicrostonyx groenlandicus	Mallory & Brooks, Biology of Reproduction, 22, 192 (1980)
Equus zebra	Lloyd & Rasa, Behavioral Ecology and Sociobiology, 25, 411 (1989)
Eulemur fulvus	Jolly et al., International Journal of Primatology. 21, 21 (2000)
Eulemur macaco	Andrews, Folia Primatologica, 69, 14 (1989)
Galea musteloides	Künkele & Hoeck, Ethology. 83, 316 (1989).
Halichoerus grypus	Anderson et al., Journal of Zoology 189, 407 (1979); Le Boeuf & Campagna, in Infanticide and parental care, Parmigiani & vom Saal, Eds. (Harwood Academic Publishers, 1994), pp. 257-276.
Heterocephalus glaber	Faulkes & Bennett, Trends in Ecology & Evolution, 16, 184 (2001).
Hyaena brunnea	Owens & Owens Nature 308, 843 (1984)
Lasiopodomys brandtii	Yu & Fang. Acta Theriologica Sinica, 23, 326 (2003)
Lemmus lemmus	Semb-Johansson et al., Oikos (1979): 246-260.
Lemur catta	Jolly et al, International Journal of Primatology. 21, 21 (2000)
Leontopithecus chrysomelas	De Vleeschouwer, et al. Folia Primatologica, 72, 1 (2001)
Leptonychotes weddellii	Le Boeuf & Campagna, in Infanticide and parental care, S. Parmigiani, F. vom Saal, Eds. (Harwood Academic Publishers, 1994), pp. 257-276
Lycaon pictus	Creel & Creel Animal Conservation 1, 1 (1998)
Macaca mulatta	Maestripieri. Behaviour, 131, 97 (1994)
Macaca nemestrina	Maestripieri. Behaviour, 131, 97 (1994)
Macaca radiata	Silk et al, Animal Behaviour, 29, 1106 (1981)
Macaca sylvanus	Paul & Kuester, Behavioral Ecology and Sociobiology 39,139 (1996)
Macaca tonkeana	Muroyama et al. International journal of primatology. 17, 219 (1996)

Marmota caligata	Patilet al., PloS one 10, e0119081 (2015).
Marmota flaviventris	Brody & Melcher, Animal Behaviour 33, 673-674 (1985).
Marmota marmota	King & Allainé, Canadian Journal of Zoology 80, 2137 (2002)
Megaderma lyra	Knörnschild et al. PloS one, 6, e25001 (2011)
Meles meles	Mallinson et al,. Philosophical Transactions of the Royal Society of London B: Biological Sciences 338, 393 (1992)
Meriones unguiculatus	Elwood & Ostermeyer, in: G. Hausfater, S.B. Hrdy (Eds.), Infanticide, Aldine, New York (1984), pp. 367–386
Meriones unguiculatus	Elwood & Ostermeyer, in: G. Hausfater, S.B. Hrdy (Eds.), Infanticide, Aldine, New York (1984), pp. 367–386
Mesocricetus auratus	Goldman & Swanson, Zeitschrift für Tierpsychologie. 37, 225 (1975)
Microtus agrestis	Agrell, Behavioral Ecology 6, 82 (1995)
Microtus canicaudus	Wolff et al. Journal of Mammalogy, 83, 947 (2002)
Microtus ochrogaster	Lonstein & De Vries, Physiology & Behavior, 66, 33 (1999)
Microtus pennsylvanicus	Ebensperger et al., Ethol Ecol Evol 12, 149 (2000)
Microtus townsendii	Boonstra, Ecology 59,242 (1978)
Mirounga angustirostris	LeBoeuf et al., Behaviour 43, 121 (1972)
Monachus schauinslandi	Le Boeuf & Campagna, in Infanticide and parental care, S. Parmigiani, F. vom Saal, Eds. (Harwood Academic Publishers, 1994), pp. 257-276
Mungos mungo	Hodge et al., Biology letters 7, 54 (2011)
Mus musculus	Manning et al. Animal Behaviour 50, 741 (1995)
Myotis myotis	Łupicki, et al., Mammalia, 74, 339 (2010)
Neophoca cinerea	Le Boeuf & Campagna, in Infanticide and parental care, S. Parmigiani, F. vom Saal, Eds. (Harwood Academic Publishers, 1994), pp. 257-276
Neotoma lepida	Fleming, Behavioral and Neural Biology 26, 41 (1979)
Nycticeius humeralis	Kunz & Ebensperger, Acta Chiropterologica 1, 17 (1999).
Odobenus rosmarus	Le Boeuf & Campagna, in Infanticide and parental care, S. Parmigiani, F. vom Saal, Eds. (Harwood Academic Publishers, 1994), pp. 257-276
Oryctolagus cuniculus	Künkele America Society of Mammalogists 73, 317 (1992)
Otaria flavescens	Le Boeuf & Campagna, in Infanticide and parental care, S. Parmigiani, F. vom Saal, Eds. (Harwood Academic Publishers, 1994), pp. 257-276
Otolemur crassicaudatus	Welker & Schaäfer-Witt, International journal of primatology 9, 509 (1988).
Otolemur garnettii	Welker & Schaäfer-Witt, International journal of primatology 9, 509 (1988).
Pan troglodytes	Pusey et al.,. International Journal of Primatology, 29, 949 (2008)
Panthera leo	Packer & Pusey, in: Infanticide: Comparative and Evolutionary Perspectives (1984), Eds: Hausfater & Hrdy, pp38
Papio cynocephalus	Kleindorfer & Wasser, Behavioral Ecology and Sociobiology 56, 328 (2004)
Papio ursinus	Cheney et al.: In Reproduction and fitness in baboons: Behavioral, ecological, and life history perspectives (pp. 147-176) (2006). Springer US; Brain International Journal of Primatology 13, 1992 (1992)
Peromyscus leucopus	Wolff & Cicirello, Behavioral Ecology 2, 38 (1991)
Peromyscus maniculatus	Wolff & Cicirello, Behavioral Ecology 2, 38 (1991)
Phacochoerus aethiopicus	Somers et al. Acta Theriologica 40,257 (1995)
Phodopus campbelli	Vella et al., Developmental psychobiology 46, 75 (2005)
Phodopus sungorus	Vella et al., Developmental psychobiology 46, 75 (2005)
Phyllostomus hastatus	Bohn et al., Behavioral Ecology and Sociobiology 63, 1693 (2009)
Phyllotis darwini	Ebensperger & Blumstein, in: Rodent societies: an ecological and evolutionary perspective, pp.267-279. (2007)
Propithecus edwardsi	Morelli et al. Behaviour 146, 499 (2009)
Pteropus hypomelanus	Kunz & Ebensperger, Acta Chiropterologica 1, 17 (1999).
Pteropus vampyrus	Kunz & Ebensperger, Acta Chiropterologica 1, 17 (1999).
Rattus norvegicus	Schultz & Lore, Journal of Comparative Psychology 107, 216 (1993)
Rhabdomys pumilio	Hill et al., Journal of Animal Ecology 84, 1497 (2015)

Speothos venaticus	Macdonald, Journal of Zoology 239, 525 (1996)
Spermophilus beecheyi	Trulio, Behavioral Ecology and Sociobiology 38, 97 (1996)
Spermophilus beldingii	Jenkins & Eshelman Mammalian Species 221, 1 (1984)
Spermophilus columbianus	Stevens, Canadian Journal of Zoology 76, 1183 (1998)
Suricata suricatta	Clutton-Brock et al., Proceedings of the Royal Society of London B: Biological Sciences 265, 2291 (1998)
Sus scrofa	Andersson et al., Applied Animal Behaviour Science, 134, 84 (2011)
Tadaria brasiliensis	Knörnschild et al. PloS one 6, p.e25001 (2011)
Vulpes lagopus	Kruchenkova e al., Naturwissenschaften, 96, 457 (2009)
Vulpes vulpes	Vergara, Canadian Field-Naturalist, 115, 170 (2001)
Zalophus californianus	Le Boeuf & Campagna, in Infanticide and parental care, S. Parmigiani, F. vom Saal, Eds. (Harwood Academic Publishers, 1994), pp. 257-276

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Supplementary File 2 for Lukas & Huchard: The evolution of infanticide by females in mammals

Credit for animal drawings used in Figure 1

All drawings were downloaded from PhyloPic: http://phylopic.org

Picture information is listed as:

Common name listed in figure (taxon identifier for picture on PhyloPic): Author

<u>Starting from top, clockwise:</u>

Old World primate (*Papio*): Uncredited

Hare (*Leporidae*): Sarah Werning

Squirrel (*Sciuridae*): Catherine Yasuda

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Bat (*Chiroptera*): Michael Keesey

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