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10 **The evolution of infanticide by males in mammalian societies**

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30 **Short title:** The evolution of male infanticide in mammals

Abstract.

Male mammals may commonly kill conspecific offspring. The benefits of such infanticide to males, and its costs to females, likely vary across mammalian social and mating systems. Here
35 we use comparative analyses to show that infanticide primarily evolves in social mammals where reproduction is monopolized by a minority of males. It has not promoted social counter-strategies such as female gregariousness, pair-living, or changes in group size and sex-ratio but is successfully prevented by female sexual promiscuity, a paternity dilution strategy. These findings indicate that infanticide is a consequence, rather than a cause, of
40 contrasts in mammalian social systems affecting the intensity of sexual conflict.

One Sentence Summary

45 Infanticide by males is an evolutionary consequence, rather than a cause, of contrasts in mammalian social systems and reflects the intensity of sexual conflict.

Keywords: infanticide, mammals, phylogeny, social system, mating system, reproductive
50 skew, dominance tenure, polyandry

Main text

Infanticide by males is widespread in mammals and may represent the main cause of infant mortality in some populations (1). It has long been viewed as a sexually selected strategy that increases mating opportunities for killer males by shortening postpartum infertility in the victim's mother (2, 3). This is supported by natural observations across taxa showing that males target unrelated infants and often impregnate the victim's mother afterwards (1, 3, 4). Attempts to explain the taxonomic distribution of infanticide have however been mainly limited to investigations of the life-history correlates of male infanticide (5-8), showing that it rarely occurs where it does not accelerate the mother's return to sexual activity, as in seasonal breeders who cannot resume cycling before the next breeding season (8).

Several scenarios have linked the distribution of infanticide across species to the evolution of social organization and mating systems in mammals, and they remain largely untested or disputed (9, 10). According to the sexual selection hypothesis, the distribution of infanticide is expected to be modulated by contrasts in social systems that affect the intensity of male intrasexual competition (3, 5, 8). Male infanticide should thus be prevalent in species where a few males mate with multiple females and monopolize most reproductive opportunities. However, females may respond to infanticide by developing counter-strategies that may refine patterns of associations across species. Social counter-strategies may include the evolution of female sociality (6, 11, 12), of permanent male-female associations (13-15), or of changes in the group sex-ratio (6, 11, 12, 15) because females may form coalitions with other females or with resident males to defend their progeny against male invaders. Additionally, females may mate with multiple partners to confuse paternity and dissuade infanticide (6, 16, 17), which may thus be absent in species with pronounced sperm competition. The evolutionary arms race between the sexes driven by male infanticide has generated confusion and controversy regarding the role of infanticide in the evolution of mammalian societies, calling for more integrative studies.

Here we use information gathered on 260 mammal species including 119 species with, and 141 without infanticide (Figure 1) to identify how variation in social organization and mating systems may have favoured or prevented the evolution of infanticide by males using phylogenetic analyses (18). Specifically, we test if infanticide has primarily evolved in species where females breed throughout the year and some males have high reproductive monopoly, and if it has selected for social and sexual counter-strategies, including transitions towards

85 female gregariousness, permanent male-female associations, changes in group size or sex-
ratio or increases in female sexual promiscuity. We included infanticide records from wild
populations for which the killer was unambiguously identified as an adult male. Species for
which infanticide had never been observed were included only if natural observations on
90 females and juveniles were available over more than 3 reproductive seasons, to minimize the
risk of misclassifying them as “non-infanticidal”. The phylogenetic relatedness between
species was inferred from the updated mammalian supertree (19) and analyses were also
replicated in primates exclusively, which confirmed results obtained across mammals (see
supplementary results).

95 The distribution of male infanticide is closely associated with the absence of seasonal or
‘annual’ breeding (defined as an average inter-birth interval of 360-370 days). Infanticide
occurs in a majority of non-annual breeders (76% of 97 species), compared to 28% of 134
annual breeders ($\lambda=0.67$, $t=-4.0$, $p<0.001$). A long lactation (relative to gestation) and
the absence of a postpartum oestrus, two life-history traits affecting the time to cycling
100 resumption in mothers of killed infants, are also associated with male infanticide, though their
association disappears when controlling for annual breeding (for both traits, p as estimated by
MCMCglmm ($p\text{MCMC}$) >0.08 while $p\text{MCMC}$ for annual breeding <0.001). While previous
studies have used the ratio of the duration of lactation to that of gestation to estimate
infanticide risk (6-8), our results reveal that this association is weak: lactation exceeds
105 gestation in 25 of 45 mammal species with infanticide, and in 38 of 89 species without
infanticide. Other aspects of life-history were not associated with male infanticide (longevity:
 $n=210$ species, $p\text{MCMC}=0.08$; litter size: $n=230$ species, $p\text{MCMC}=0.07$; relative offspring
weight at birth: $n=191$ species, $p\text{MCMC}=0.59$), suggesting that infanticide evolution is not
determined by a species’ pace of life. Overall, the possibility for females to breed throughout
110 the year is the only life-history trait examined that significantly explains the distribution of
infanticide, confirming previous work and suggesting that infanticidal males gain extra
mating opportunities due to earlier cycle resumption of the victim’s mother in non-annual
breeders. Such males are thereby redirecting maternal investment from unrelated offspring
towards their own future offspring.

115

Comparing the occurrence of male infanticide across social systems, we find that males
commit infanticide more frequently in stable mixed-sex groups (66% of 112 species) than in
solitary species (40% of 78 solitary species, $p\text{AN}=0.01$), in species with female-only groups

(23% of 31 species, $p_{AN}=0.006$) and in pair-living species (18% of 39 species, $p_{AN}<0.001$).
120 Phylogenetic reconstructions confirm that variation in social organization is a key determinant
of the evolution of male infanticide, which is more likely in stable bisexual groups than in any
other social system (see supplementary table 1). In addition, social groups contain, on
average, 1 male per 2.5 females in species with male infanticide ($SD= 1.7$, $n=56$ species), but
only 1 male for 1.3 females in species without infanticide ($SD= 3.2$, $n=19$ species, Figure 2a;
125 $\lambda=0.47$, $t=-3.3$, $p=0.002$; this is not an effect of differences in group sizes, as group size
is similar in both sets of species: $p=0.28$). Phylogenetic reconstructions suggest that a biased
group sex-ratio is a determinant, rather than a consequence, of the evolution of male
infanticide: the strongest female biases are observed just before or at the transition towards
male infanticide, while there are few or no subsequent changes once infanticide has evolved
130 (see supplementary results).

In line with this, infanticide occurs more frequently where reproduction is monopolized by a
few males (Figure 2b): the median percentage of offspring sired by the alpha male is 67%
($SD=19.9$, $n=15$ species) in species with infanticide, compared to 35% ($SD=22.2$, $n=5$) in
135 species without ($\lambda=0.75$, $t=3.9$, $p=0.001$). Finally, males retain their dominant position
for shorter durations in species with infanticide (Figure 2c): on average, dominance tenure
covers two inter-birth intervals (if the females were to successfully wean each litter) ($SD=1.0$,
 $n=34$ species), compared to four in species without infanticide ($SD=1.2$, $n=6$) ($\lambda=0.0$,
 $t=-3.4$, $p=0.001$). These correlations hold after controlling for the effect of annual breeding,
140 which may also affect male ability to monopolize females (Supplementary Table 2). Overall,
these findings indicate that a high male monopolization potential favours transitions towards
infanticide by allowing males to maximize their reproductive output in systems where the
costs of holding dominance shorten their breeding tenures (20).

145 Male infanticide has been proposed to alter social evolution by favouring female
gregariousness or permanent male-female associations or by promoting a higher number of
resident males that may help mothers to protect their infants from male intruders. We found
no support for any of these scenarios. Infanticide risk is low in solitary species, the ancestral
mammalian social organization (9), and as such is unlikely to motivate evolutionary
150 transitions from a solitary lifestyle to other social organizations. Phylogenetic reconstructions
confirm that male infanticide is significantly more likely to evolve after transitions towards
group-living than in their solitary ancestors (see above). The presence of male infanticide

does not increase the likelihood of a transition from solitary living to social monogamy, to female gregariousness or to group living (see supplementary table 1). In addition, among
155 species living in stable bisexual groups, male infanticide is not linked to changes in the degree of female sociality (5.5 ± 5.1 females per group in 56 infanticidal species compared to 8.9 ± 4.0 in 13 non-infanticidal species; $p\text{MCMC}=0.93$). These findings indicate that infanticide by males did not trigger important transitions in mammalian social evolution. Population studies have nevertheless highlighted relationships between infanticide rates and group size (e.g., 21),
160 suggesting that the social consequences of infanticide may differ within populations versus across species, or that selection exerted by infanticide is insufficient at inducing major shifts in mammalian social organization.

Infanticide risk may also lead to the evolution of sexual counter-strategies by females, who
165 might prevent infanticide by mating with many males to dilute paternity (6, 16, 17). To test this hypothesis, we investigated evolutionary relationships between infanticide and testis size, an indicator of the intensity of sperm competition (22, 23). In support of the paternity dilution hypothesis, phylogenetic reconstructions indicate that relative testis size is larger in lineages in which more time has elapsed since the evolution of infanticide. State-dependent
170 diversification models (24) show that increases in testis size follow rather than precede transitions to infanticide as they are not detected on branches immediately before transitions to infanticide, suggesting that infanticide exerts directional selection on relative testis size (18). In addition, infanticide is subsequently lost in lineages where testes have grown large (Figure 3; $p\text{MCMC}=0.02$; see supplementary results), indicating that infanticide may
175 disappear where female attempts to prevent male sexual monopolization are successful.

Our findings support key predictions of the sexual selection hypothesis: males primarily kill the offspring of rivals in stable bisexual groups where a few males monopolize reproduction over short periods. Increased testis size following evolutionary transitions to infanticide and
180 secondary loss of infanticide in species with large testes suggests that female paternity dilution strategy efficiently reduces infanticide risk, and emphasizes the reversible nature of infanticide, which may appear and disappear according to the evolutionary arms race between the sexes. While past studies failed to find comparative evidence for sexual counterstrategies to infanticide (7, 16), our sample spanning all mammals, combined with phylogenetically
185 controlled analyses, and our focus on testis size to index female sexual promiscuity may explain divergent results.

Our analyses build on five decades of field observations to understand the distribution of species differences in the occurrence of infanticide by males across mammalian societies. The evolution of infanticide is largely determined by variation in the intensity of male-male contest competition and has not promoted major switches in mammalian social organization. However, it has impacted the evolution of mating systems by increasing female sexual promiscuity as a paternity dilution strategy. These findings suggest that the distribution of infanticide across mammals is a consequence of contrasts in social and mating systems, and closely reflects variation in the intensity of intra- and inter-sexual conflict.

195

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Figure legends

Figure 1: Distribution of male infanticide across mammals

Male infanticide has been reported for about half of all species in our sample (open circles) and seems to have evolved independently multiple times. It mostly occurs in social (dark grey branches), less in solitary (light grey branches), and least in monogamous species (black branches). Animal drawings are from phylopic.org (for full credit see (18)).

Figure 2: Infanticide is associated with polygynous mating systems

Male infanticide occurs in species in which (a) social groups contain more females per male, (b) dominant males obtain a higher share of reproduction in a given season, but (c) maintain their dominant position for shorter periods (here measured as the average number of inter-birth intervals).

Figure 3: Loss of male infanticide occurs in species with large testes

In some lineages in which males commit infanticide, testes appear to increase in size (relative to body mass) and subsequently, male infanticide is lost when testes are relatively large.

220

Figure 1

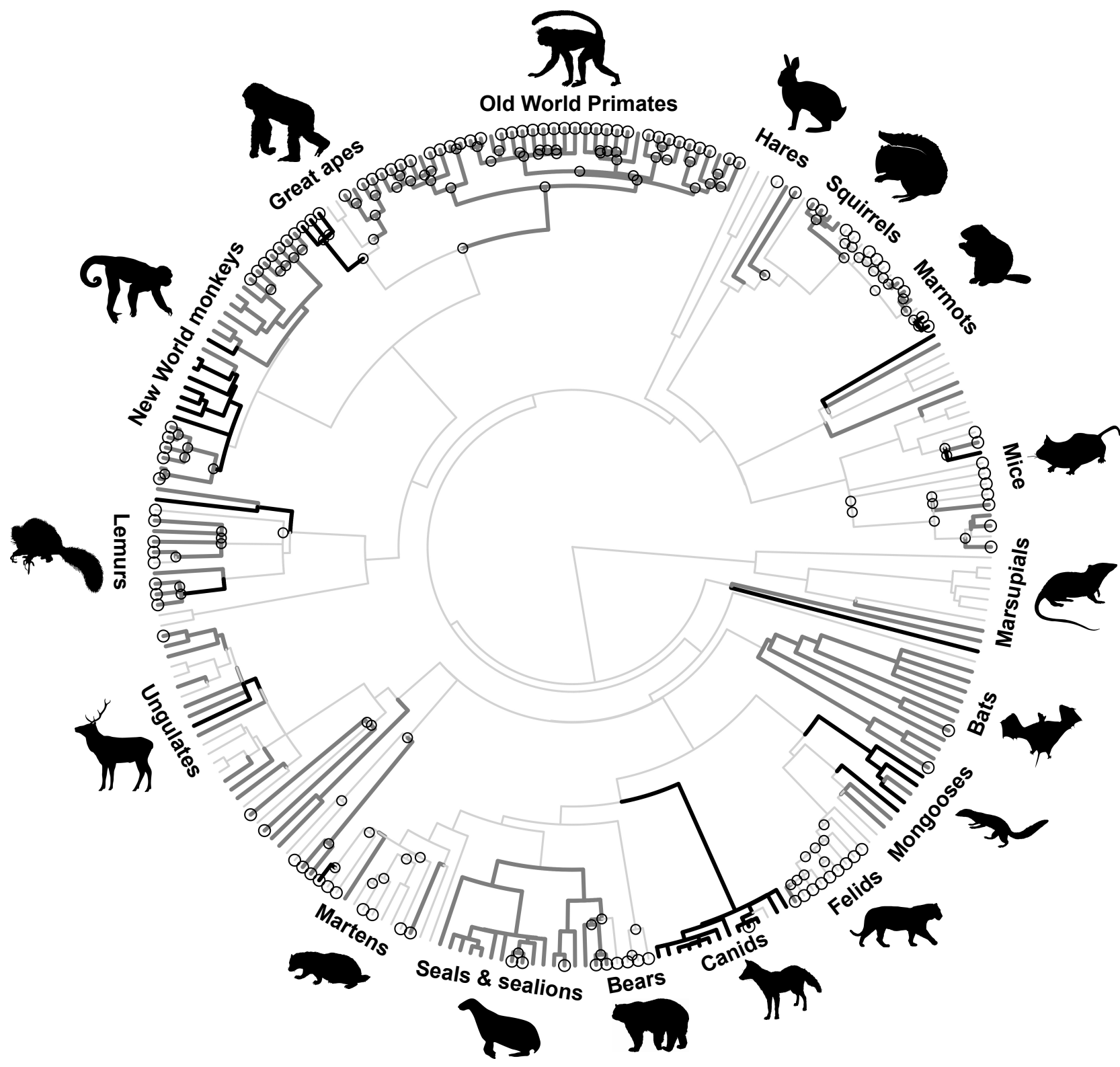
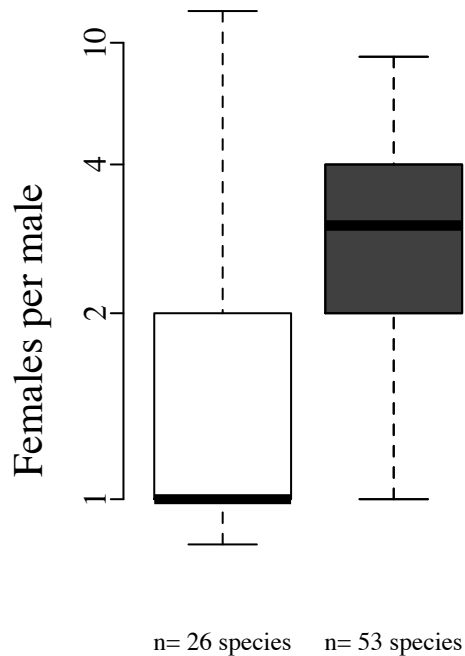
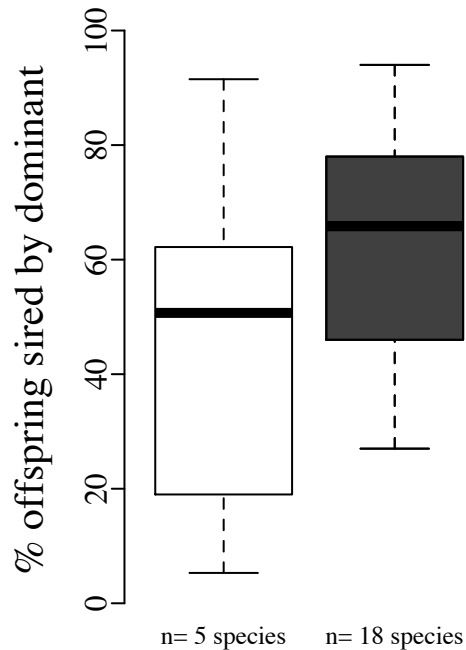


Figure 2**(a)****Sex ratio**

No Infanticide Infanticide

**(b) Reproductive skew**

No Infanticide Infanticide

**(c) Tenure length**

No Infanticide Infanticide

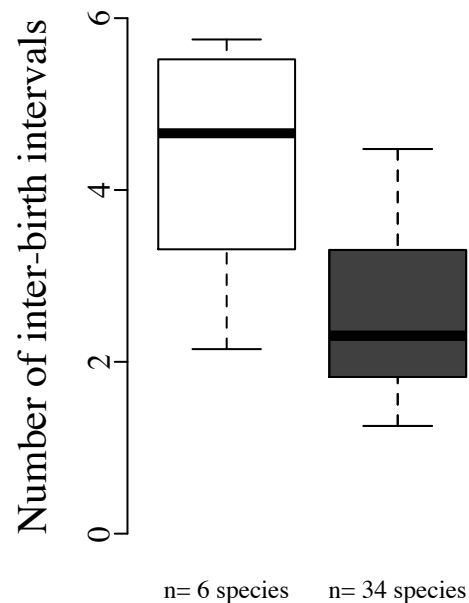
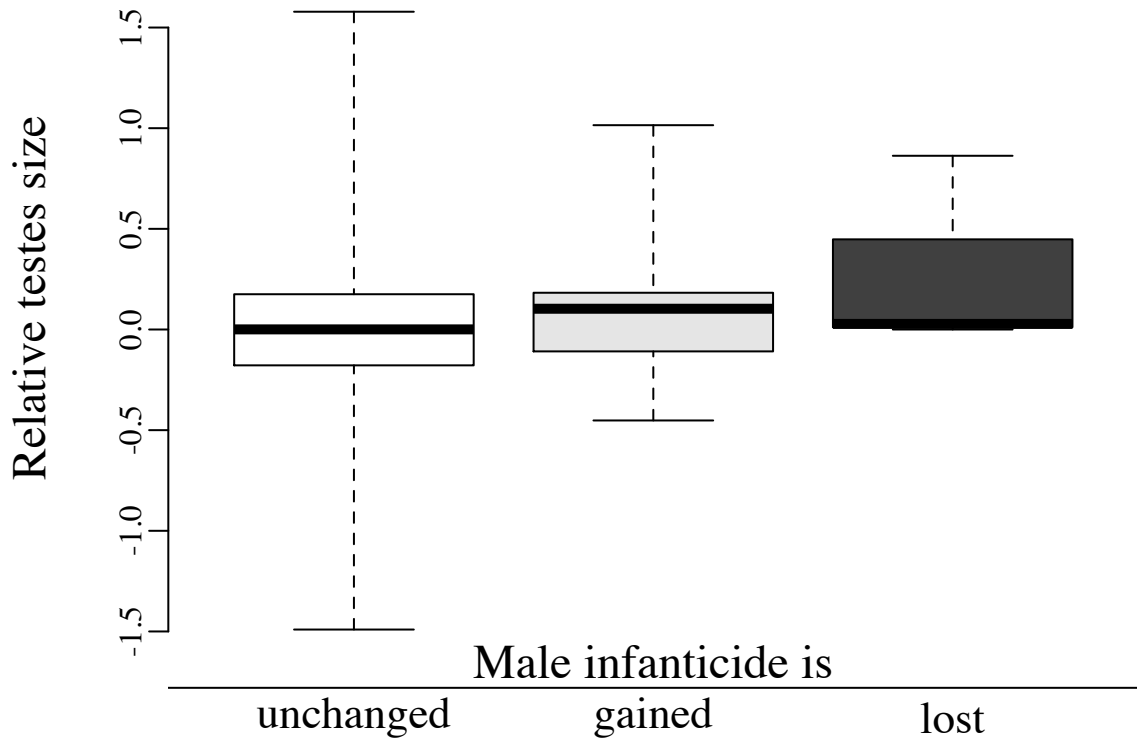


Figure 3



Supplementary Materials
for
The evolution of infanticide by males in mammalian societies

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This file includes:

Data and Methods (pages 1-6)

Supporting results for multivariate and the Ornstein-Uhlenbeck models (pages 6-7)

Credit for animal drawings used in Figure 1 (page 9)

Supplementary Table 1: inferences from Bayestraits' Discrete (page 10)

Supplementary Table 2: results from analyses run across all mammals (page 11)

Supplementary Table 3: results from analyses run across primates (page 12)

Supplementary Table 4: data on distribution of male infanticide (pages 13-22)

Data and Methods

To determine the taxonomic distribution of male infanticide, we relied on its observed distribution, which is documented for an increasing number of species that have been the focus of detailed and prolonged field studies. We took care to include only species in which this behaviour could have been observed in natural populations because they had been studied continuously over more than 3 reproductive seasons, including observations of females with unweaned juveniles, in order to minimize the risk of introducing noise in the data if some species were misclassified as "male infanticide absent" (see Supplementary Table 4). For the opposite, we only included a species as "male infanticide present" if the

data unambiguously showed that the individual committing infanticide was an adult male. From databases and reviews we extracted information on life-history (seasonal breeding, lactation and gestation length, inter-birth interval, longevity, body mass at birth, litter size [25-27] and postpartum oestrous [28]), on mating system (reproductive skew [22], length of dominance tenure in males [20], testis size as an index of multiple male mating by females [23,29-34]) and on sociality (social organization [9], group composition [20,35]). We classified the social organization of a species as solitary if breeding females tolerate the proximity of adult conspecifics only during the mating season; as monogamous if a single breeding female and a single breeding male share a territory, potentially including non-breeding offspring; as female-only groups where stable groups of breeding females associate permanently and males only join for mating; and as stable mixed-sex groups if two or more breeding females associate permanently with one or more male (9). Seasonal breeding was defined as an interbirth interval comprised between 360 and 370 days, and we used data on intra-annual variability in temperature (36) to verify that yearly breeding thus defined is associated with ecological seasonality (yearly variance in temperature 38.7, compared to 27.5 for non-seasonal breeders; $\lambda=0.92$, $t=-0.1$, $p<0.001$). We chose to exclude species reproducing always at the same season but less than once a year on average from the seasonally breeding species, as infanticide is likely to provide males with benefits in this context if a female resumes cycling one year earlier than she would if her infant was alive. We provide a full data file in text format at the Knowledge Network for Biocomplexity (<https://knb.ecoinformatics.org>).

We relied on the updated mammalian supertree (19) to reflect the phylogenetic relatedness between species. The tree was truncated to match our sample using functions of the package 'ape' (37) in the statistical software R (48). We resolved polytomies randomly for all analyses that require bifurcating trees, and repeated each analysis with three independent resolutions, which in all cases gave consistent results. Phylogenetic reconstruction of discrete traits were performed across trees with dated branch lengths, across ultrametric trees in which all tips have the same distance to the root and branch lengths are proportional to the number of descendants (39), and across trees in which all

branch lengths were transformed to equal one.

We used different approaches and methods to assess our hypotheses according to the type of prediction and data. Initially, we compared values of currently living species in which male infanticide is present to those in which male infanticide is absent without taking phylogeny into account by using Wilcoxon-tests. When assessing whether the distribution of a trait differed between species that were grouped into discrete categories while taking phylogeny into account, we used phylogenetic Anova as implemented in the R-package 'geiger' (40; indicated as pAN in the manuscript). We tested whether the presence or absence of infanticide explains variation in quantitative traits using phylogenetic generalized least squares regressions as implemented in the R-package 'CAPER' (41; indicated in the manuscript by listing the lambda-, t-, and p-value of the model) and examined whether changes in the traits most likely co-occur on the same branches by calculating phylogenetic independent contrasts using functions of the R-package 'ape'. To examine whether variation in continuous traits explained the distribution of infanticide across species we ran regression models in the R-package 'MCMCglmm' (42) that corrected for phylogenetic relatedness (indicated as pMCMC in the manuscript), using a fixed prior (43). The significance of factors in explaining variation in the dependent trait was assessed by the p-values (43). In addition to their presentation in the main manuscript, we also list all statistical results in Supplementary Table 2.

Both the phylogenetic generalized least squares regression and the MCMCglmm method estimate the extent of the phylogenetic signal, and thereby can correct for phylogeny to the appropriate degree (including the possibility of no phylogenetic signal). There are two traits, longevity and litter size, for which Wilcoxon tests returned a significant difference between species with and without infanticide that were not supported in analyses that controlled for phylogeny. We discuss these in the supplementary results below. In addition, to control for the possibility that some effects identified across all mammals might differ from patterns occurring within particular lineages of mammals, we repeated all analyses including only the 90 primate species in our sample. The significance of all the correlations reported are the same using the main dataset and the restricted,

primate-specific dataset (see Supplementary Table 3). However, when only including primate species, we do not have sufficient power to investigate the evolutionary sequence of changes in group sex ratio and testis size in relation to transitions towards presence or absence of male infanticide.

In order to decipher causal associations between two traits that could be coded as binary (absence versus presence) we compared inference models in Bayestraits Discrete (44, 45). In Discrete, we compared the evolution of male infanticide against the evolution of each type of social organization (solitary, socially monogamous, harem, multi-female multi-male group) in separate models. We first checked for each association whether models that assume a dependent evolution between male infanticide and a particular type of social organization were better supported compared to models that assume an independent evolution of the traits. If the inference suggested a dependent evolution, we ran further models to investigate the potential directionality of the association: first, we tested whether models in which transitions in social organization were constrained to occur at identical rate in both the presence and the absence of male infanticide were less supported (which would indicate that transitions in social organization might depend on the presence of male infanticide); second, we assessed whether models in which transitions in male infanticide were constrained to occur at equal rates independent of the social organization were less supported (which would indicate that the evolution of male infanticide depends on a particular type of social organization). We assessed significance between dependent and independent models by comparing the likelihood ratio statistic against a chi-squared distribution with four degrees of freedom (45); unconstrained models were considered to explain the data significantly better if the likelihood ratio statistic exceeded a chi-squared distribution with one degree of freedom.

To investigate causal relationships between male infanticide and continuous traits (testis size relative to body size and group sex ratio) we applied flexible Ornstein-Uhlenbeck models of trait diversification (24). Ornstein-Uhlenbeck models assume that a trait is under stabilizing selection toward a single or multiple adaptive optima. Specifically, we predicted that models that assume that relative testis size and group sex ratio evolve

towards different values in lineages in which male infanticide is present compared to absent are statistically better supported than models that assume that relative testis size and group sex ratio evolve independently of the presence or absence of male infanticide. We performed the Ornstein-Uhlenbeck model reconstructions using functions of the R-package 'OUwie' (46). We first reconstructed the evolution of male infanticide. Next, we assessed two possible ways in which the presence of male infanticide could influence either relative testis size or group sex ratios: first, the presence of infanticide could speed up or slow down the rate of change, but average values of testis size and sex ratio are about the same; second, while the rate of change is the same, the presence of male infanticide could be associated with a different peak value of testis size or sex ratio. Peak values, in comparison to averages, take into account the possibility that the value might only have been reached once male infanticide has been present for a sufficient amount of evolutionary time. Any association that shows that peak values of either testis size or group sex ratio differ between lineages in which male infanticide is either present or absent could however also be the consequence of the reversed directionality: male infanticide evolves in lineages in which either testis size or group sex ratio have already reached extreme values. To differentiate the direction of causality in such cases, we performed two further sets of analyses. First, we compared the estimated peak values to the observed average values for extant species which either do or do not show male infanticide. If infanticide evolves only when the value of a given trait is already high (or low) but does not subsequently influence the evolution of this trait, the average value is expected to be similar to the peak value, because infanticide evolves when the condition matches. If, in contrast, infanticide does influence the evolution of the trait, then the peak value should be more extreme than the average value observed in extant species, because these likely include a number of species where infanticide has only evolved recently and where the trait has not yet reached its peak value. Second, we checked whether directional selection favouring a different value of the trait had already started before infanticide evolved. For these analyses, we included the branches just before the nodes at which infanticide most likely first evolved, in lineages associated with the presence of male infanticide. If the presence of male infanticide leads to a shift in the peak

value, the inclusion of these additional branches should decrease or obscure any signal. If, alternatively, male infanticide only evolves in those lineages characterized by an extreme trait value, the inclusion of these additional branches should increase the strength of the signal. We report the results below.

Supplementary results

Inference of non-phylogenetic model differs from that of phylogenetic model

For longevity and litter-size, Wilcoxon-tests of the raw species values indicate a difference between species in which male infanticide is present as compared to absent. This difference does not hold in analyses controlling for phylogenetic relatedness. While including phylogenetic information could have introduced a bias if longevity and litter-size were to evolve in a more complex way than approximated by the shared co-ancestry between species, this scenario is unlikely because these two life-history traits generally show a strong phylogenetic signal. Instead, it appears that the association between male infanticide and longevity/litter-size is indirect, mediated by another trait that is approximated by the phylogenetic component and better explains the variance in longevity/litter-size. The factor mediating the relationship between male infanticide and longevity/litter-size is most likely group-living, which has a significant phylogenetic signal. This interpretation is supported by non-phylogenetic multivariate analyses which show that the presence of male infanticide no longer predicts variation in longevity/litter-size across species when controlling for the social organization (see Supplementary Table 2).

Analyses including only the primate species in our sample

The significance of all the correlations we report is the same when including only primate species in the analyses (90 of the 260 species are primates; see Supplementary Table 3). However, we do not have sufficient power with the more limited sample of species to investigate the evolutionary sequence of change of group sex ratio and testis size

in relation to transitions in male infanticide. Here, the AIC values of models assuming that species with male infanticide are associated with different values of group sex ratio and testis size compared to species in which infanticide is absent are within 1.5 of the AIC values of models assuming similar values. In addition, the multivariate analyses suggest that, in primates, annual breeding and postpartum oestrus is closely linked, and postpartum oestrus is a better predictor of male infanticide than is annual breeding.

Results of the Ornstein-Uhlenbeck model inferences

For both sex ratio and testis size, the presence of infanticide seems to be associated with different peak values, but not with different rates of evolution (in both cases, the likelihoods of these best supported models differ by >3 from the likelihoods of the next models assuming different peak values and different rates, and by >5 from the likelihood of the best supported models assuming equal peak values). These findings match the regression analyses comparing changes in the values of the traits. To disentangle causality, we compared peak values to average values among extant species and investigated whether changes in either sex ratio or testis size most likely originated before or after the transition towards male infanticide.

In contemporary species with male infanticide, the average group sex ratio is 1 male per 2.5 females, whereas it is 1 male per 1.3 females in species without infanticide; these values do not differ from peak values (1 male per 2.4 females in species with infanticide; 1 male per 1.6 females in species without infanticide). In addition, the strength of the association between male infanticide and group sex ratio increased when we included additional branches located immediately before the evolution of male infanticide, as shown by increases in the likelihoods of models supporting two different peak values, relative to models supporting similar peak values. The peak value of group sex-ratio changed to 1 male per 2.8 females in lineages with infanticide, and to 1 male per 1.2 females in lineages without infanticide.

In contemporary species with male infanticide, average relative testis size is 0.20 (indicative of relatively large testes for a given body size), whereas it is -0.02 in species

without infanticide; the peak value for species with infanticide appears much higher (0.48), whereas it is identical to the average relative testis size (-0.03) for species without infanticide, suggesting that the evolution of infanticide induces changes in testis size. In addition, the association between relative testis size and male infanticide disappeared when we included additional branches located immediately before transitions to male infanticide, confirming that changes in testis size follow, rather than precede, transitions to male infanticide: in this case the best supported model suggested that peak values for testis size were identical in lineages with or without infanticide.

These results suggest that a male-biased sex ratio is a cause for the evolution of infanticide, whereas testis size increases as a consequence of infanticide.

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

Starting from top, clockwise:

Old World primate (*Papio*): Uncredited

Hare (*Leporidae*): Sarah Werning

Squirrel (*Sciuridae*): Catherine Yasuda

Marmot (*Marmota monax*): Michael Keeseey

Mice (*Muridae*): Madeleine Price Ball

Marsupial (*Marsupialia*): Sarah Werning

Bat (*Chiroptera*): Michael Keeseey

Mongoose (*Herpestoidae*): Michael Keeseey

Felids (*Panthera*): Sarah Werning

Canids (*Canidae*): Michael Keeseey

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Marten (*Meles*): Uncredited

Ungulate (*Cervus*): Steven Traver

Lemur (*Daubentonia*): Uncredited

Great ape (*Gorilla*): Michael Keeseey

New World primate (*Cebus*): Sarah Werning

Supplementary Table 1: Inferences from Bayestraits' Discrete models investigating correlated evolution between male infanticide and social organization

Phylogenetic reconstructions that consider the evolution of male infanticide and social organization suggest that transitions to male infanticide depend on a social system involving bisexual groups (harem or multimale-multifemale). While male infanticide appears to evolve independently from social monogamy (and vice versa), transitions to male infanticide appear significantly more likely in lineages with bisexual groups. Changes in social organization do however not appear to be a consequence of male infanticide, as transitions to group living are equally likely when male infanticide is present or absent. The higher support for a dependent model in the case of group-living species appears to derive from this trait being evolutionarily stable, with transitions to this state much higher than losses of this state (regardless of the presence of infanticide). The values of delta log-likelihood represent the difference between the likelihood of the model presented and the likelihood of the best supported model (in all cases dependent and unconstrained), and values in bold with stars indicate models that are significantly less supported compared to this baseline model (based on a chi-square test comparison correcting for the difference in the number of parameters of each model).

Delta log-likelihood of a model assuming the evolution of both traits to be

	independent	dependent and unconstrained	dependent and transition rate of social organization to be equal whether infanticide occurs or not	dependent and transition rate of male infanticide to be equal in either social system
social monogamy versus solitary/gregarious/bisexual group	1.4	0		
group-living versus solitary/monogamous	7.7 **	0	0.5 in unconstrained dependent model transition rate to groupliving from infanticide <2 times lower	0.1 in unconstrained dependent model transition rate to infanticide from groupliving ~2 times higher
multi-female multi-male group versus solitary/monogamous/gregarious/harem	13.1 ***	0	1.2 in unconstrained dependent model transition rate to group living from infanticide <2 times lower	3.1 * in unconstrained dependent model transition rate to infanticide from group living ~3 times higher
harem versus solitary/monogamous/gregarious/multi-male	8.5 **	0	0.1 in unconstrained dependent model transition rate to harem from infanticide <2 times lower	3.3 * in unconstrained dependent model transition rate to infanticide from group living ~4 times higher

Supplementary Table 2: Summary of the results of the statistical analyses including all species.

The table presents for the non-phylogenetic Wilcoxon tests the test value W and significance value p , for phylogenetic Anova (PhyloAnova) the significance value p , for phylogenetic generalized least squares regression (PGLS) the most likely value for the transformation of the branch lengths $lambda$, whether this lambda value is significantly different from a value that reflects no phylogenetic signal ($p\ lambda = 0$) or a value that reflects that change occurs consistently over evolutionary time ($p\ lambda = 1$), for the MCMCglmm regression model the significance value p , and for multivariate regression models in MCMCglmm the significance values p for the two traits analysed simultaneously in one row.

	Non phylogenetic Wilcoxon		Phylo Anova	PGLS			MCMCglmm	
	W	p	p	$lambda$	$p\ (lambda = 0)$	$p\ (lambda = 1)$	t	$p\ (model)$
Seasonality	3496.5	<0.001	0.001					<0.001
Lactation/Gestation	5739	<0.001	0.07					0.002
Postpartum oestrus	1508	0.004	0.08					0.005
Longevity	6968.5	0.006		0.92	<0.001	<0.001	0.3	0.78
Litter size	5735	0.02		0.97	<0.001	<0.001	0.8	0.41
Offspring weight	4692	0.84		0.92	<0.001	<0.001	0.8	0.41
Sex ratio	109.5	0.01		0.37	0.07	<0.001	-3.3	0.002
Group size	161.5	0.45		0.56	0.02	0.01	-1.1	0.28
Females per group	285	0.23		0.24	0.01	<0.001	-1.2	0.25
Reproductive skew	66	0.01		0.75	0.16	0.02	-3.9	0.001
Tenure length	40.5	0.02		0	1	<0.001	-3.4	0.001
Testes size	2555.5	0.16		1	<0.001	1	-2.3	0.02
Solitary vs Monogamous	1852.5	0.001	0.001					
Solitary vs Groupliving	2037	0.01	0.01					
Monogamous vs Groupliving	3867.5	<0.001	<0.001					

Multivariate models in MCMCglmm

Seasonality	p<0.001	Lactation/Gestation	p=0.08
Seasonality	p<0.001	Postpartum oestrus	p=0.09
Groupliving	p=0.02	Longevity	p=0.24
Groupliving	p=0.04	Litter size	p=0.15
Seasonality	p=0.01	Male tenure length	p=0.004

Supplementary Table 3: Summary of the results of the statistical analyses including only primates.

The table presents for the non-phylogenetic Wilcoxon tests the test value W and significance value p , for phylogenetic Anova (PhyloAnova) the significance value p , for phylogenetic generalized least squares regression (PGLS) the most likely value for the transformation of the branch lengths λ , whether this λ value is significantly different from a value that reflects no phylogenetic signal ($p \lambda = 0$) or a value that reflects that change occurs consistently over evolutionary time ($p \lambda = 1$), for the MCMCglmm regression model the significance value p , and for multivariate regression models in MCMCglmm the significance values p for the two traits analysed simultaneously in one row.

	Non phylogenetic Wilcoxon		Phylo Anova	PGLS			MCMCglmm	
	W	p	p	λ	$p (\lambda = 0)$	$p (\lambda = 1)$	t	$p (model)$
Seasonality	316	<0.001	0.01					<0.001
Lactation/Gestation	334.5	<0.001	0.04					0.003
Postpartum oestrus	42	<0.001	0.01					<0.001
Longevity	564	0.28		0	1	<0.001	0.9	0.35
Litter size	410	0.01		1	<0.001	1	-0.6	0.53
Offspring weight	246	0.23		1	<0.001	1	-0.8	0.4
Sex ratio	86.5	<0.001		0.38	0.03	<0.001	-3.9	<0.001
Group size	69.5	0.2		0	1	0.03	-0.7	0.45
Females per group	217.5	0.8		0.35	0.03	<0.001	0.1	0.91
Reproductive skew	25	0.04		data for only 2 species in which infanticide is absent				
Tenure length	40.5	0.02		0	1	<0.001	-3.4	0.001
Testes size	203	0.44		1	0.06	1	-0.5	0.62
Solitary vs Monogamous	31.5	0.94	0.86					
Solitary vs Groupliving	48	0.006	0.003					
Monogamous vs Groupliving	730.5	<0.001	0.001					
Multivariate models in MCMCglmm								
Seasonality	p=0.02	Lactation/Gestation	p=0.06					
Seasonality	p=0.12	Postpartum oestrus	p=0.001					

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Supplementary Table 4: Data on infanticide occurrence

Species	MaleInfanticide	Reference
<i>Acinonyx_jubatus</i>	No	47
<i>Acrobates_pygmaeus</i>	No	48
<i>Aepyceros_melampus</i>	No	49
<i>Aethomys_namaquensis</i>	Yes	50
<i>Ailurus_fulgens</i>	No	51
<i>Alces_alces</i>	No	52
<i>Alouatta_caraya</i>	Yes	4
<i>Alouatta_guariba</i>	Yes	53
<i>Alouatta_palliata</i>	Yes	4
<i>Alouatta_pigra</i>	Yes	54, 55
<i>Alouatta_seniculus</i>	Yes	4
<i>Antechinus_stuartii</i>	No	56
<i>Antechinus_swainsonii</i>	No	65
<i>Antilocapra_americana</i>	No	16, 57, 58
<i>Antrozous_pallidus</i>	No	59
<i>Aotus_azarae</i>	No	60, 61
<i>Arctocephalus_forsteri</i>	No	62
<i>Arctocephalus_galapagoensis</i>	No	63
<i>Arctocephalus_gazella</i>	No	64, 65
<i>Arctocephalus_pusillus</i>	No	66
<i>Arctocephalus_tropicalis</i>	No	67
<i>Ateles_belzebuth</i>	Yes	68
<i>Ateles_geoffroyi</i>	Yes	68, 69
<i>Ateles_paniscus</i>	No	70, 71

Avahi_laniger	No	72
Bison_bison	No	16, 73, 74
Brachyteles_arachnoides	No	75
Brachyteles_hypoxanthus	No	76
Bunopithecus_hoolock	Yes	77, 79
Callimico_goeldii	No	79
Callithrix_flaviceps	No	80, 81
Callithrix_jacchus	No	81
Callorhinus_ursinus	No	4
Canis_dingo	No	82
Canis_latrans	No	4, 16
Canis_lupus	No	16, 83
Canis_mesomelas	No	16, 84
Canis_simensis	No	16, 85
Capreolus_capreolus	No	86
Cavia_aperea	No	4, 87
Cavia_intermedia	No	4
Cavia_magna	No	4, 88
Cavia_porcellus	No	4, 89
Cebus_apella	Yes	90
Cebus_capucinus	Yes	91
Cebus_nigritus	Yes	92
Cebus_olivaceus	Yes	4
Cercocebus_atys	Yes	4, 16
Cercocebus_galeritus	Yes	16
Cercocebus_torquatus	Yes	16, 93, 94
Cercopithecus_albogularis	No	95

<i>Cercopithecus_ascanius</i>	Yes	4
<i>Cercopithecus_campbelli</i>	Yes	96
<i>Cercopithecus_mitis</i>	Yes	4
<i>Cervus_elaphus</i>	No	97
<i>Chalinolobus_gouldii</i>	No	98
<i>Cheirogaleus_medius</i>	No	99, 100
<i>Chiropotes_albinasus</i>	No	101
<i>Chiropotes_satanas</i>	No	101
<i>Chlorocebus_aethiops</i>	Yes	102, 103
<i>Colobus_guereza</i>	Yes	4
<i>Colobus_vellerosus</i>	Yes	12
<i>Connochaetes_taurinus</i>	No	104
<i>Crocidura_russula</i>	No	105
<i>Crocuta_crocuta</i>	No	106
<i>Cuon_alpinus</i>	No	107
<i>Cynictis_penicillata</i>	No	108
<i>Cynomys_gunnisoni</i>	No	7
<i>Cynomys_leucurus</i>	No	109
<i>Cynomys_ludovicianus</i>	Yes	7
<i>Cynomys_parvidens</i>	Yes	110
<i>Cynopterus_brachyotis</i>	Yes	111
<i>Cystophora_cristata</i>	No	112
<i>Dasyurus_hallucatus</i>	No	113
<i>Dasyurus_viverrinus</i>	No	113
<i>Diceros_bicornis</i>	No	114
<i>Dicrostonyx_groenlandicus</i>	Yes	7
<i>Didelphis_virginiana</i>	No	115

Dolichotis_patagonum	No	116
Enhydra_lutris	Yes	117
Eptesicus_fuscus	No	118
Equus_caballus	Yes	16
Equus_zebra	Yes	119, 120
Erythrocebus_patas	Yes	121
Eubalaena_australis	No	122
Eulemur_fulvus	Yes	123
Eulemur_macaco	Yes	123, 124
Eumetopias_jubatus	No	125
Felis_catus	Yes	126
Galea_monasteriensis	No	127
Gazella_dorcas	No	128
Giraffa_camelopardalis	No	129, 130
Gorilla_beringei	Yes	4
Gorilla_gorilla	Yes	131
Halichoerus_grypus	Yes	132
Haplemur_griseus	No	133
Helogale_parvula	No	134, 135
Herpestes_sanguineus	No	136, 137
Heterocephalus_glaber	No	138
Hippopotamus_amphibius	Yes	139
Hippotragus_equinus	No	140
Hyaena_brunnea	No	141
Hyaena_hyaena	No	142, 143
Hylobates_lar	Yes	14
Lagothrix_lagotricha	No	144, 145

Lasiopodomys_brandtii	Yes	7
Lemur_catta	Yes	123, 146
Leontopithecus_rosalia	No	147
Leopardus_pardalis	Yes	47
Lepilemur_edwardsi	Yes	148
Leptonychotes_weddellii	No	149
Lepus_americanus	No	150
Lophocebus_albigena	No	151
Lophostoma_silviculum	Yes	152
Loris_lydekkerianus	No	153, 154
Loris_tardigradus	No	153, 155
Loxodonta_africana	No	156, 157
Lycaon_pictus	No	158
Lynx_canadensis	Yes	47
Lynx_pardinus	Yes	159
Macaca_arctoides	Yes	160
Macaca_fascicularis	Yes	4
Macaca_mulatta	Yes	161
Macaca_nemestrina	Yes	16
Macaca_nigra	Yes	16
Macaca_radiata	Yes	4
Macaca_silenus	Yes	16
Macaca_sinica	Yes	162
Macaca_sylvanus	Yes	4
Macaca_thibetana	Yes	163
Macaca_tonkeana	No	164
Macropus_giganteus	No	165

Madoqua_kirkii	No	166
Mandrillus_sphinx	Yes	167
Marmota_caligata	Yes	110
Marmota_caudata	Yes	7
Marmota_flaviventris	No	7
Marmota_marmota	Yes	4
Marmota_monax	No	168
Martes_americana	No	169
Martes_pennanti	No	169
Megaderma_lyra	No	152
Meles_meles	No	4
Mellivora_capensis	Yes	171
Mephitis_mephitis	Yes	172
Microcebus_murinus	No	173, 174
Microtus_arvalis	Yes	175
Microtus_canicaudus	No	7
Microtus_pennsylvanicus	Yes	110
Microtus_townsendii	No	7
Mirounga_angustirostris	Yes	176, 177
Mirounga_leonina	Yes	178
Monachus_schauinslandi	Yes	179, 180
Mungos_mungo	No	181
Mustela_erminea	No	182
Mustela_frenata	Yes	16
Myodes_glareolus	Yes	110
Myotis_myotis	No	183
Nasalis_larvatus	Yes	184

Nasua_nasua	Yes	4
Neophoca_cinerea	Yes	185
Neotoma_albigula	No	186
Neotoma_cinerea	No	187
Neotoma_lepida	No	7
Neovison_vison	Yes	188
Nyctereutes_procyonoides	No	189-191
Ochotona_curzoniae	No	192
Octodon_degus	No	193
Odobenus_rosmarus	No	194
Odocoileus_virginianus	No	195
Onychomys_torridus	No	196
Oreamnos_americanus	No	197
Oryctolagus_cuniculus	No	198
Oryx_leucoryx	Yes	199
Otaria_byronia	Yes	200
Otocyon_megalotis	No	201
Ovibos_moschatus	No	202
Ovis_aries	No	197
Ovis_canadensis	No	203
Ozotoceros_bezoarticus	No	204, 205
Pan_paniscus	No	206
Pan_troglodytes	Yes	207, 208
Panthera_leo	Yes	209
Panthera_onca	Yes	210
Panthera_pardus	Yes	47
Panthera_tigris	Yes	47

Papio_anubis	Yes	4
Papio_cynocephalus	Yes	211
Papio_hamadryas	Yes	211
Papio_ursinus	Yes	4, 213
Paraxerus_cepapi	Yes	7
Peromyscus_leucopus	Yes	7
Peromyscus_maniculatus	Yes	7
Peromyscus_polionotus	No	214, 215
Phacochoerus_aethiopicus	No	216
Phascogale_tapoatafa	No	217
Phoca_groenlandica	No	194
Phoca_sibirica	No	218
Phoca_vitulina	No	194
Phocarcos_hookeri	Yes	219, 220
Phodopus_sungorus	Yes	7
Phyllostomus_hastatus	No	221
Pithecia_pithecia	No	222
Pongo_abelii	No	223
Pongo_pygmaeus	No	223
Potos_flavus	No	224
Presbytis_potenziani	No	71
Presbytis_thomasi	Yes	225
Procolobus_badius	Yes	226
Propithecus_diadema	Yes	227, 228
Propithecus_edwardsi	Yes	4, 229
Propithecus_verreauxi	Yes	16
Proteles_cristata	No	230

Pteronura_brasiliensis	Yes	231
Pteropus_hypomelanus	No	232
Pteropus_vampyrus	No	232
Puma_concolor	Yes	47
Pygathrix_bieti	Yes	233
Pygathrix_roxellana	Yes	234, 235
Rangifer_tarandus	No	197
Rhabdomys_pumilio	Yes	236
Rhinoceros_unicornis	Yes	237
Rhynchocyon_chrysopygus	No	238
Saguinus_fuscicollis	No	239
Saguinus_mystax	No	240
Saguinus_oedipus	No	241
Saimiri_oerstedii	No	242
Saimiri_sciureus	Yes	243
Sciurus_carolinensis	Yes	244
Semnopithecus_entellus	Yes	245
Speothos_venaticus	No	246
Spermophilus_beecheyi	No	4
Spermophilus_beldingi	Yes	110
Spermophilus_columbianus	Yes	7
Spermophilus_franklinii	Yes	7
Spermophilus_parryii	Yes	7
Spermophilus_richardsonii	No	7
Spermophilus_townsendii	Yes	7
Spermophilus_tridecemlineatus	Yes	7
Suricata_suricata	No	247

Sus_scrofa	No	248
Symphalangus_syndactylus	Yes	249
Tadarida_brasiliensis	No	111, 152
Tamias_striatus	No	250
Theropithecus_gelada	Yes	4
Trachypithecus_cristatus	Yes	251
Trachypithecus_poliocephalus	Yes	252
Trachypithecus_vetulus	Yes	4
Tursiops_truncatus	Yes	253
Urocyon_cinereoargenteus	No	254
Ursus_americanus	Yes	4, 255
Ursus_arctos	Yes	4, 256
Ursus_maritimus	Yes	257
Varecia_variegata	Yes	258
Vulpes_lagopus	Yes	259
Vulpes_velox	No	260, 261
Vulpes_vulpes	No	209
Vulpes_zerda	No	262
Xerus_inauris	No	263
Zalophus_californianus	No	194