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Letter to the editor   Open Access

Lower risk of male infanticide in multilevel primate societies

DEAR EDITOR,

Male infanticide is considered a severe manifestation of sexual conflict in non-human primates during male takeover or male dominance changes. Males engaging in infanticide may obtain fitness benefits, but at the cost of female reproductive outcomes. Consequently, females have developed various anti-infanticide counterstrategies, such as coalitions, dispersal, and promiscuity. However, the effectiveness of such strategies in primate societies remains unclear. Here, we conducted comparative phylogenetic analysis across 38 populations of 26 primate species and found that both total infant mortality due to infanticide and mortality of at-risk infants during male takeover or dominance changes are reduced in multilevel societies. These findings provide empirical evidence that the effectiveness of female counterstrategies varies across mating systems and/or social organizations and suggest that male-driven infanticide may be an important selective force for the evolution of multilevel societies.

Male-directed infanticide is a severe form of sexual conflict in non-human primates (Lukas & Huchard, 2014; Palombit, 2015). During social disruption, such as changes in dominance or resident status, an adult male may kill an unrelated infant to shorten the inter-birth interval of the mother and enable the male to sire an infant sooner than if he waited for the female to return to a reproductive state, thereby increasing his reproductive success compared to non-infanticidal males. However, these fitness benefits occur at the cost of female reproductive outcomes. Therefore, females have developed various anti-infanticide counterstrategies. Females may seek and maintain relationships with proctor males to ensure protection from infanticide (Palombit, 2015), as observed in monogamous (Opie et al., 2013) and uni-male multi-female societies (Palombit, 2015). In multi-male multi-female societies, females may protect against potential infanticide by mating with multiple adult males in their social group to confuse paternity (Palombit, 2015). Additionally, females may escape by transferring to another social group or avoid potential infanticidal males until their infants are weaned (Xiang et al., 2022). Females may also form coalitions with other females to defend against infanticidal males (Palombit, 2015). Although promiscuity, escape, and coalitionary defense have been reported in females in various species, few studies have investigated the effectiveness of such strategies in terms of mortality of at-risk infants during male takeover or dominance changes.

Given that the costs and benefits of male infanticide and potential female counterstrategies are shaped by social interactions of same- and opposite-sex individuals (Lukas & Huchard, 2014), the resolutions to sexual conflict expressed in male infanticide may vary across social organizations and mating systems (Clutton-Brock, 1989). Specifically, the availability of alternative mating partners has a marked effect on the success of inducing paternity confusion. Additionally, female-female relationships or bonds determine coalition formation within a group and the transfer of tolerance between groups/units. As females have limited mating partner options and infrequent interactions with females from other groups/units, male infanticide is common in uni-male societies after male replacement. For males to gain siring benefits through infanticide, they must monopolize females against other males over an extended period. Thus, the low ability of males to monopolize mating in multi-male multi-female societies results in rare male infanticide. However, the extent to which the effectiveness of female counterstrategies differs across social organizations or mating systems remains uncertain. Furthermore, comparative phylogenetic analysis is necessary to identify the patterns of divergence in adaptive evolution.

In multilevel societies, female primates live in core social units (one male units, OMU), which consist of one adult male and multiple females. Multiple OMUs associate and forage together in larger social bands, unlike in uni-male and multi-male societies (Xiang et al., 2022). While Qi et al. (2020) observed that females may mate with extra-group males to reduce the risk of infanticide, Xiang et al. (2022) suggested that the availability of social interactions may increase the effectiveness of female counterstrategies in multilevel societies. As male-female and female-female interactions can develop both within and between social units, we propose that females in multilevel societies will exhibit more counterstrategies compared to multi-male and uni-male societies. We also hypothesize that more counterstrategies will be associated with lower total infant mortality due to male-driven infanticide and lower mortality of at-risk infants. Additionally, we predict that the effectiveness of female counterstrategies against male infanticide will be greater in multilevel societies compared to uni- and multi-male societies.

In the current study, we conducted a comprehensive review of existing literature pertaining to male infanticide and female counterstrategies. We selected those studies that reported total number of births and number of newborns who died from

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assumed or witnessed infanticide during a fixed period. Our search was based on previous reviews of primate species in which infanticide has been reported and in which females and males form stable associations. We independently searched Web of Science and other search engines (up to July 2022) to identify relevant literature, and cross-checked all entries. We classified species into three categories based on social organization or mating system: i.e., uni-male (including monogamous and polygamous), multi-male, and multilevel societies (uni-male units nested within a larger band). We collected data from 38 populations of 26 species, including uni-male societies (15 populations of 11 species), multi-male societies (18 populations of 13 species), and multilevel societies (five populations of four species, Supplementary Table S1). Additionally, we searched for information regarding: (i) average proportion of offspring born that were fathered by extra-group males (promiscuity strategy); (ii) formation of female-female coalitions during within-group aggressive interactions (coalitionary defense strategy); and (iii) successful transfer of females who gave birth in one social group to another social group (female transfer strategy). The rates of extra-group paternity reported in these studies ranged from 0% to 57% and were heavily skewed, with no extra-group paternity recorded in half of all species. We transformed these rates into a binary variable, indicating whether extra-group paternity had or had not been recorded.

For comparative analyses, we used the updated mammalian supertree (Lukas & Huchard, 2014) to estimate phylogenetic relatedness among the sample species. To assess whether total infant mortality from male infanticide and mortality of at-risk infants were lower in multilevel societies, we ran a generalized linear mixed model using the MCMCglmm function (Lukas & Huchard, 2014) in R. We included species identity as a random factor and phylogenetic relatedness among species as a covariance matrix. We specified a broad prior (V=1, nu=0.001) and set the number of iterations to 1 000 000, with a burn-in of 200 000 and a thinning of 100. We tested whether the occurrence of each of the three counterstrategies was associated with reduced infant mortality from infanticide and with type of society using generalized linear squared regression models. Specifically, we estimated the extent of similarity among species due to shared phylogenetic history using maximum-likelihood estimates of the lambda-transformation of the covariance using the corPagel function in the ape package (Lukas & Huchard, 2014).

Our results indicated that females in multilevel societies relied on more counterstrategies, with 2.25±0.52 (mean±standard deviation (*SD*)) counterstrategies in five species with multilevel societies, compared to 1.4±0.86 counterstrategies in 11 species with multi-male societies and 1.0±0.94 counterstrategies in nine species with uni-male societies (Figure 1A) (controlling for phylogenetic relatedness; estimate for difference to multi-male societies: −0.13, standard error 0.35, P=0.702; estimate for difference to uni-male societies: −0.63, standard error 0.37, P<0.05). Survival of offspring was also positively correlated with the number of female counterstrategies against male infanticide (Figure 1B,

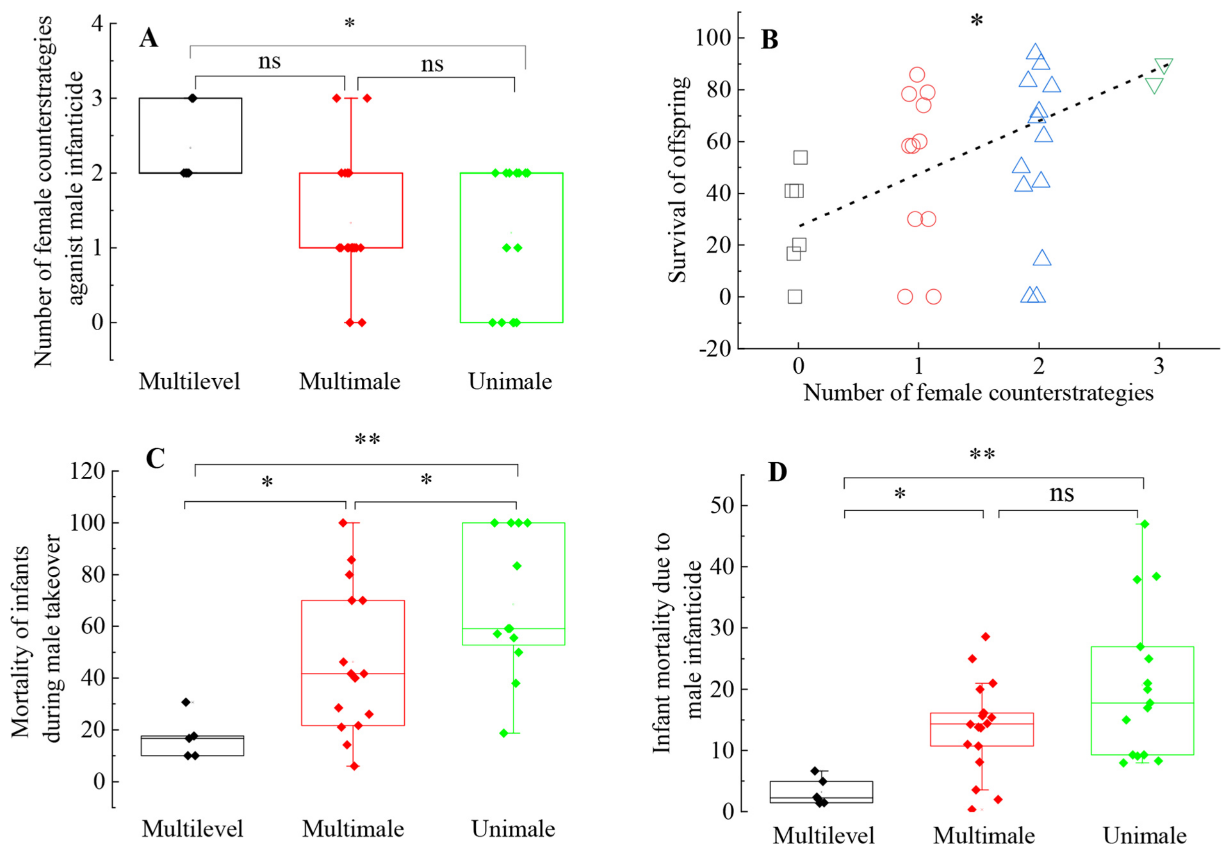

Figure 1 Interspecies/population variation in female counterstrategies and demography through male infanticide in 38 populations of 26 species among uni-male, multilevel uni-male, and multi-male societies

A: Females in multilevel societies rely on more counterstrategies. B: Survival of offspring is positively correlated with number of female counterstrategies. C: Mortality of related infants is lower in multilevel societies compared to other social systems. D: Total infant mortality due to male infanticide in multilevel societies is lower than that in other social systems. ns: Not significant; *: P<0.05; **: P<0.01.

controlling for phylogenetic relatedness; estimate for combined strategies: −0.04, standard error 0.02, *P*<0.05).

Across the 38 populations, 15% of all offspring were killed by males (range 0.3%–47%). In about one third of these populations, infanticide accounted for more than half of all observed infant deaths, confirming that male-driven infanticide is a major influence on female reproductive success (total infant mortality in these populations ranged from 10% to 71%, median 32%). On average, total infant mortality due to male infanticide was 3% across the six multilevel society populations, 15% across the 17 multi-male multi-female society populations, and 23% across the 16 uni-male society populations. Controlling for species identity and phylogenetic similarity, regression analysis indicated that at-risk (of infanticide) infants experienced lower mortality rates in multilevel societies than in the other social systems (Figure 1C, estimate for difference to multi-male societies: 0.81 (95% CI 0.76–0.95), *P*<0.05; estimate for difference to uni-male societies: 0.60 (95%CI 0.7–0.89), *P*<0.01; estimate for difference between multi-male and uni-male societies: 0.49 (95%CI 0.45–0.86), *P*<0.05). Total infant mortality due to male infanticide was also lower in multilevel societies compared to the other social systems (Figure 1D, estimate for difference to multi-male societies: 0.88 (95% CI 0.79–0.98), *P*=0.02; estimate for difference to uni-male societies: 0.80 (95% CI 0.70–0.89), *P*<0.01).

Our study revealed that multilevel societies, where females have the opportunity to engage in social interactions within and between different units, exhibit multiple female counterstrategies against male-driven infanticide. Notably, both mortality of at-risk (of infanticide) infants and total infant mortality due to male infanticide were significantly lower in multilevel societies. A decade-long field study of golden snub-nosed monkeys (*Rhinopithecus roxellana*) found that females in multilevel societies employ a range of responses to protect non-weaned offspring from infanticidal males, including mating with males outside their OMU, forming defensive coalitions with other females in the same OMU, and successfully transferring to other OMUs (Xiang et al., 2022). These results suggest the importance of social constraints in shifting the balance of sexual conflict toward females or toward males and in enhancing the effectiveness of female counterstrategies. Therefore, these findings support the hypothesis that female counterstrategies may vary across population mating systems or social organizations (Clutton-Brock, 1989). Overall, this empirical evidence enhances our understanding of the complex interplay between social structure, reproductive strategies, and infanticide in non-human primates.

Our study also highlights possible implications for the evolutionary pathway leading to multilevel societies in primates. Previous research has suggested that ecological conditions influenced the original ancestral multi-male multi-female groups of African papionins (gelada, Guinea, and hamadryas baboons), which underwent an internal fission process resulting in the formation of multilevel societies (Xiang et al., 2022). However, studies on Asian colobines (genus *Rhinopithecus*) suggest that multilevel societies resulted from the aggregation of several OMUs into a large band (Qi et al., 2014). Although we could not identify whether some social factors that resulted in group fission in African papionins occurred here, our study demonstrated that male infanticide may be an important selective force in the evolution of multilevel societies. Natural populations of snub-nosed monkeys often experience high infant mortality during their first winter, given the extreme high altitude and latitude habitats (Yu et al., 2022), and have a long interbirth interval (Xiang & Sayers, 2009; Xiang et al. 2017). Additional deaths from male infanticide may reduce population stability and survival in the uni-male societies, because the mortality of high risk (of infanticide) infant resulting from male takeover or dominance changes is generally higher (Figure 1C), and total infant mortality due to male infanticide is also higher than occurs in the multilevel society (Figure 1D). Therefore, multilevel societies may counteract the tendency toward high infant mortality due to male infanticide. Our results provide support for the hypothesis proposed by Nunn & van Schaik (2000) that infanticide is a more important selective agent than ecology in primate social evolution, with Opie et al. (2013) also arguing that infanticide places selective press on monogamous societies.

SCIENTIFIC FIELD SURVEY PERMISSION INFORMATION

Before we conducted this study, we obtained approval from the Institutional Animal Care and Use Committee of the Institute of Zoology, Chinese Academy of Sciences, and the State Forestry and Grassland Administration.

SUPPLEMENTARY DATA

Supplementary data to this article can be found online.

COMPETING INTERESTS

The authors declare that they have no competing interests.

AUTHORS' CONTRIBUTIONS

M.L. and H.J.P. designed the project. Y.L.X. and Y.Y. compiled the data and conducted the analyses. Y.L.X., Y.Y., and H.J.P. wrote the paper. All authors read and approved the final version of the manuscript.

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REFERENCES

Clutton-Brock TH. 1989. Review lecture: mammalian mating systems. *Proceedings of the Royal Society B:Biological Sciences*, **236**(1285): 339−372.

Lukas D, Huchard E. 2014. The evolution of infanticide by males in mammalian societies. *Science*, **346**(6211): 841−844.

Nunn CL, van Schaik CP. 2000. Social evolution in primates: the relative roles of ecology and intersexual conflict. *In*: van Schaik CP, Janson CH. Infanticide by Males and Its Implications. Cambridge: Cambridge University Press, 388–420.

Opie C, Atkinson QD, Dunbar RIM, et al. 2013. Male infanticide leads to social monogamy in primates. *Proceedings of the National Academy of Sciences of the United States of America*, **110**(33): 13328−13332.

Palombit RA. 2015. Infanticide as sexual conflict: coevolution of male strategies and female counterstrategies. *Cold Spring Harbor Perspectives Biology*, **7**(6): a017640.

Qi XG, Garber PA, Ji WH, Huang ZP, Huang K, Zhang P, et al. 2014. Satellite telemetry and social modeling offer new insights into the origin of primate multilevel societies. *Nature Communications*, **5**: 5296.

Qi XG, Grueter CC, Fang G, et al. 2020. Multilevel societies facilitate infanticide avoidance through increased extrapair matings. *Animal Behaviour*, **161**: 127−137.

Xiang ZF, Sayers K. 2009. Seasonality of mating and birth in wild black-and-white snub-nosed monkeys (*Rhinopithecus bieti*) at Xiaochangdu, Tibet. *Primates* **50**(1): 50–55.

Xiang ZF, Yang WJ, Qi XG, et al. 2017. An examination of factors potentially influencing birth distributions in golden snub-nosed monkeys (*Rhinopithecus roxellana*). *PeerJ*, **5**: e2892.

Xiang ZF, Yu Y, Yao H, et al. 2022. Female countertactics to male feticide and infanticide in a multilevel primate society. *Behavioral Ecology*, **33**(4): 679−687.

Yu Y, He G, Li DY, et al. 2022. Climate change challenge, extinction risk, and successful conservation experiences for a threatened primate species in China: golden snub-nosed monkey (*Rhinopithecus roxellana*). *Zoological Research*, **43**(6): 940−944.