

Lions and tigers and humans, oh my!

Including human predation of primates in primate behavioral ecology.

KATHERINE H. BANNAR-MARTIN
Department of Anthropology, University of Texas at Austin

PREDATION ON PRIMATES

- Predation is often invoked as a strong selection pressure on animal behavior and a key factor influencing group size.¹⁻³ Primate anti-predator strategies include large group sizes, aggressive defense, alarm calling, and concealment.⁴
- However, human predation has largely been omitted from models and studies of primate anti-predator strategies. Consequently, few data are available on primate behavioral reactions to human predation.
- Yet primates are expected to employ anti-predator strategies that are predator-specific,⁵⁻⁹ and human predators are different in their use of projectile weapons, cursorial hunting, coursing, and ambush hunting (Figure 1).^{9,10}

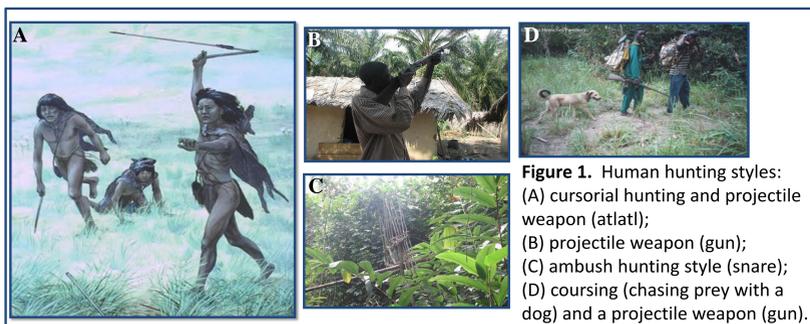


Figure 1. Human hunting styles: (A) cursorial hunting and projectile weapon (atlatl); (B) projectile weapon (gun); (C) ambush hunting style (snare); (D) coursing (chasing prey with a dog) and a projectile weapon (gun).

- Human predators preferably target larger primate species and have higher kill rates.^{3,11} Humans have been predators of primates for hundreds of thousands of years^{12,13} and rates of human predation have been steadily increasing,^{14,15} making it a common source of predation pressure on extant primate communities.
- Given that many primate populations studied today experience some level of human predation,¹⁶ empirical tests of socioecological theory include populations under current or recent human predation pressure without making explicit the level of hunting that does or does not exist at the study site.

GROUP SIZE AND PREDATION

- Optimal group size is a balance between the costs and benefits of living in large groups.^{17,18}
- Large groups are thought to provide three major advantages in reducing individual vulnerability to predation: (1) improved predator detection, (2) reduced per capita risk of capture, and (3) occasional defense.¹⁹
- However, human predators are hard to detect (can ambush and hunt from a distance),²⁰ can kill multiple individuals of a group at a time (undermining the benefits of dilution),²¹ and communal defense against human predators is rarely documented.
- Consequently, different group size optima exist for primates experiencing human predation instead of just nonhuman predation (Figure 2).

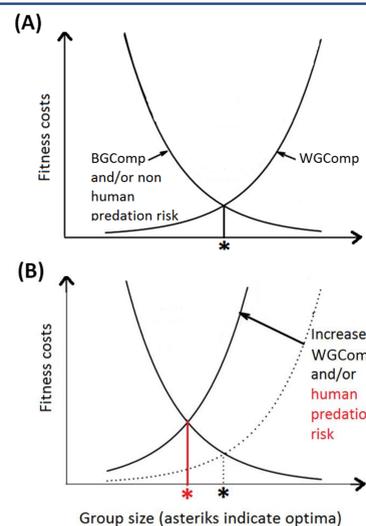


Figure 2. Predicted effects of predation risk, within group competition (WGComp) or between group competition (BGComp) on optimal primate group size and fitness costs. (figure modified from 22)

(A) The optimum group size is large enough to minimize the fitness costs of non human predation risk and WGComp, and maximize the group's ability to minimize BGComp.
(B) With human predation of primates, group size is expected to decrease to favor concealment. The optimal group size is the largest group size that can minimize the fitness costs of WGComp while maximizing the group's ability to defend its resources in BGComp and evade human predators.

RESEARCH QUESTIONS

- Do primates under human predation pressure favor visual and auditory concealment?
- Do primates under human predation pressure have smaller group sizes?
- Do smaller group sizes alter the predictions of socioecological models^{19,23-25}?



METHODS

- Extensive Web of Science, and Google Scholar literature search for peer-reviewed publications on changes in primate behavior and primate group size with human predation/hunting compared to areas with no human predation.
- Noted whether behaviors around predators differed between areas with no human predation and areas with human predation.
- Changes in group size (increases or decreases) for hunted versus non-hunted areas (of the same forest) were assigned a sign value to statistically evaluate with a sign test²⁶ the direction of the group size change with human predation. Neutral or nonsignificant changes (n=3) in group size were not included.
- Predicted and observed modified group size optima were included in socioecological models of female relationships^{19,23-25} to investigate if new group size optima alter any of the predictions of these socioecological models.

1. IS CONCEALMENT COMMON IN HUNTED AREAS?

Table 1. Predicted primate concealment strategies against human predators, which decrease the likelihood of being detected, and whether those strategies are supported empirically for human predation.

Strategies for Concealment	Strategy used with human predation?
Decreased use of alarm calls	Yes ^{7,27,28} and No (calls made at a distance) ⁷
Use of higher vertical strata	Yes ²⁹
Smaller groups	Yes ^{4,21,30-37}
Freezing (remaining still)	Yes ³⁸
Nocturnality /Lunarphobia	Unknown

2. IS GROUP SIZE SMALLER IN HUNTED AREAS?

- Small groups are more common than large groups in hunted areas versus non-hunted areas (Figure3).

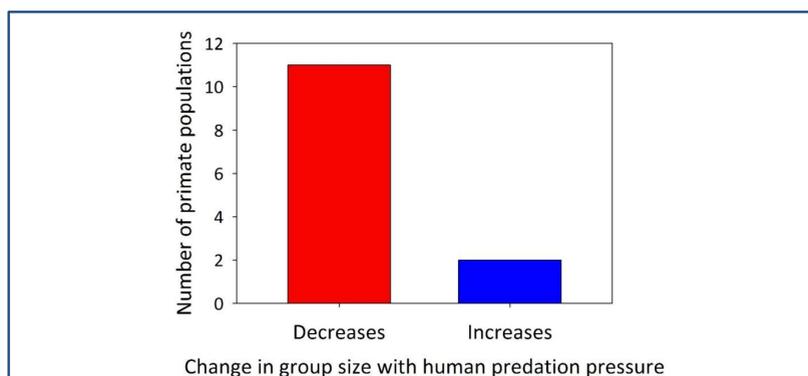


Figure 3. Number of primate populations with decreasing^{4,21,30-37} or increasing^{5,39} group size with human predation pressure. N=13 (12 species). Sign test, $p < 0.05$.

3. IMPLICATIONS FOR SOCIOECOLOGICAL MODELS?

Table 2. Socioecological model of female relationships^{19,23-25} (white background) with group size predictions and revised female relationships with human predation pressure added (blue background). Group sizes are predicted as responses to predation risk, and changes in group size are relative to the original predictions. Text in blue are predictions that differ from the original models with explanations below.

Human pred.*	Non-human pred.* ²⁴	Group size	WGC** ¹⁹	BGC*** ¹⁹	Female dispersal ¹⁹	Female relationships ¹⁹
<i>Clumped food resources</i>						
Absent	High	Large	High	Low	Rare	Nepotistic & despotic
High	High	Medium	High	Low	Rare	Nepotistic but tolerant ^A
High	Low	Small	Low	Low	Common	Egalitarian ^B
Absent	Low	Medium	High	High	Rare	Nepotistic but tolerant
High	Low	Medium	High	High	Rare	Nepotistic but tolerant
High	High	Small	Low ^C	High	Rare	Nepotistic but tolerant
<i>Dispersed food resources</i>						
Absent	High	Large	Low	High	Rare	Egalitarian
High	High	Medium	Low	High	Rare	Egalitarian
High	Low	Small	Low	Low	Common ^D	Egalitarian
Absent	High	Large	Low	Low	Common	Egalitarian
High	High	Medium	Low	Low	Common	Egalitarian
High	Low	Small	Low	Low	Common	Egalitarian

*pred.= predation
**WGC= Within group contest competition
***BGC= Between group contest competition

- Relationships become tolerant as group size decreases relaxing the intensity of WGC.
- WGC is low due to small group size. Females can disperse as risks are relaxed with low non-human predation, and human predators have a lower likelihood of detecting a single dispersing individual. Egalitarian female relationships result.
- WGC is low because group size is small.
- Females can disperse because resources are dispersed and group size is small, relaxing BGC.

CONCLUSIONS

- YES**, primates favor auditory and visual concealment with human predators (Table 1).
- YES**, primate group sizes decrease with human predation (Figure 2).
- YES**, smaller group size optima with human predation change some of the predictions of socioecological models (Table 2).
 - Female relationships become more tolerant/egalitarian and female dispersal is more common with human predation.
- Primates DO employ anti-predator strategies that are specific to human predators.
- Humans live everywhere primates live,¹⁰ therefore the amount and potential for human predation needs to be evaluated before a study of "natural" primate behavior occurs.

FUTURE DIRECTIONS

- Primate responses are likely to change with species, habitat, and population density. Regional and phylogenetic differences are also likely to exist with primates that evolved in varying degrees and histories of sympatry with humans.
- More studies are needed to evaluate the full range of effects human predation can have on primate behavior.

ACKNOWLEDGEMENTS

I would like to thank Dr. Rebecca Lewis, Dr. Anthony Di Fiore, Dr. Mariah Hopkins, Kim Valenta, Amber Heard-Booth and Kelsey Ellis for providing invaluable advice.

WORKS CITED

Please see attached sheet.