

# HEB1330 : Primate Social Behavior

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November 10th, 2020  
Between-group conflict



# Between group conflict

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Populations fill the habitat

Groups are surrounded



# Overview

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- 1) What do groups fight over?
- 2) Who participates in intergroup conflict?
- 3) Imbalance of power hypothesis
- 4) Intergroup tolerance



**Reading:** Wilson et al 2014



# What do groups fight over?

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Resources	Females
“Defend” access to food or territory (14 spp, 19 studies)	“Defend” access to females (6 spp, 4 studies/reviews)
involves both sexes	involves mostly males
<i>Lemur catta</i> <i>Cebus capucinus</i> <i>Cebus olivaceus</i> <i>Saguinus mystax</i> <i>Saguinus fuscicollis</i> <i>Leontopithecus rosalia</i> <i>Colobus guereza</i> <i>Semnopithecus entellus</i> <i>Chlorocebus aethiops</i> <i>Cercopithecus mitis</i> <i>Cercopithecus diana</i> <i>Cercocebus galeritus</i> <i>Macaca fuscata</i> <i>Macaca silenus</i>	<i>Trachypithecus pileatus</i> <i>Papio anubis</i> <i>Papio cynocephalus</i> <i>Papio ursinus</i> <i>Papio hamadryas</i> <i>Gorilla gorilla</i>

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# What do groups fight over?

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Resources	Females
“Defend” access to food or territory (14 spp, 19 studies)	“Defend” access to females (6 spp, 4 studies/reviews)
involves both sexes	involves mostly males
HOWEVER they can fight for <i>both</i> resources and females	

# What do groups fight over?

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# PE Okavango Baboons

<https://www.youtube.com/watch?v=nAiZFhhHEXU>

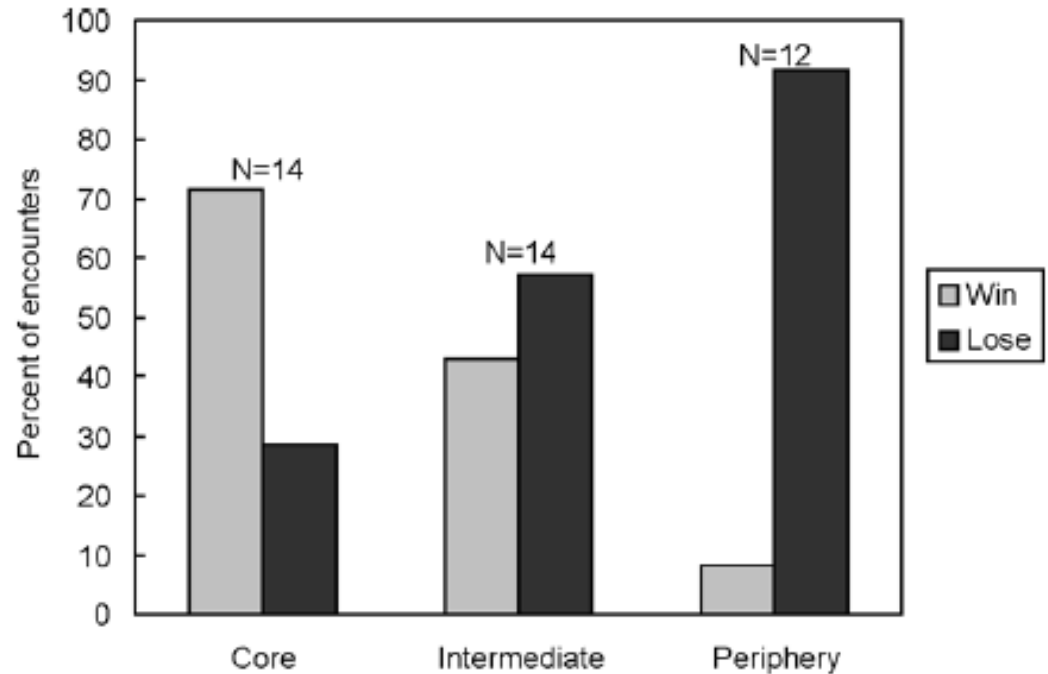


# Resource-Defense Aggression

- Defend access to food or territory
- Indicated by 'Home Field Advantage'

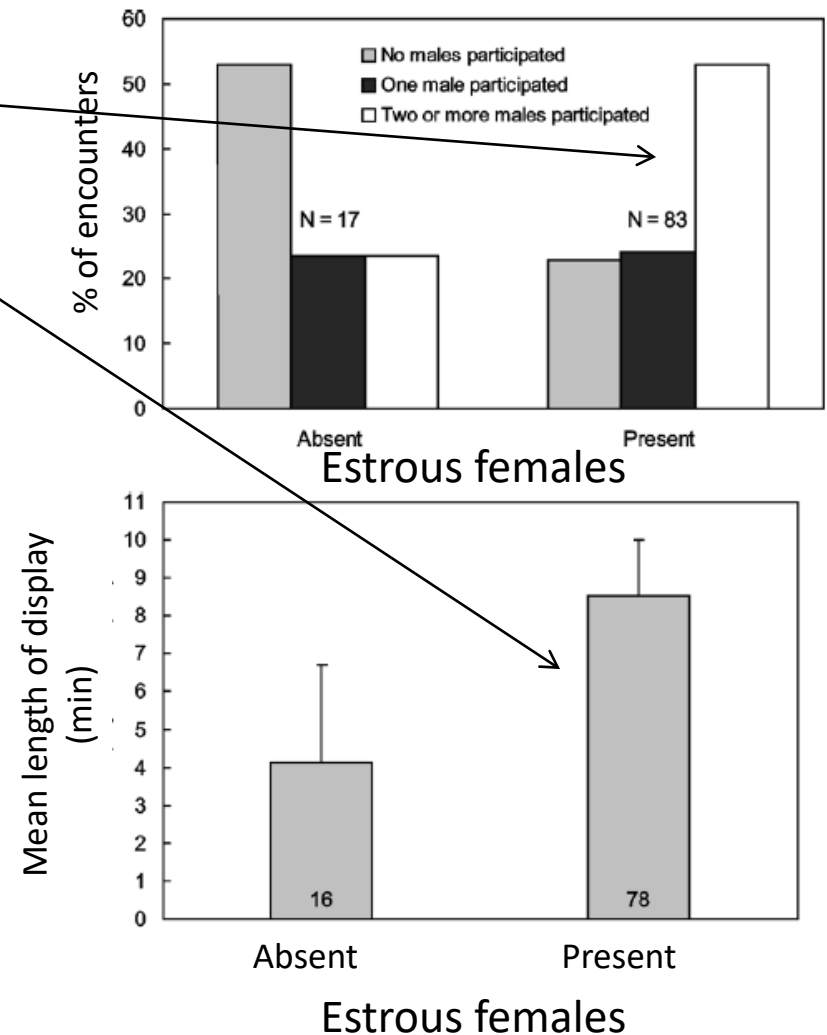
Core-Win; Edge-Lose

Lose: change course / retreat



# Female-Defense Aggression

- When there are more estrous females
  1. More males are aggressive
  2. Displays are twice as long
- High-ranking males are most active  
(they have the most to lose)



# Undefined context

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White-Faced Capuchin

Often it is not clear what primates are fighting over..

## REGULAR INTERGROUP FIGHTS

0/23 observations of one group attempting or succeeding at replacing another group at a feeding tree

- **NO CONTESTS DIRECTLY OVER FOOD**
- **CONTESTS NOT INFLUENCED BY FEMALE REPRODUCTIVE STATE**

<https://www.youtube.com/watch?v=B10dhfReWoY>

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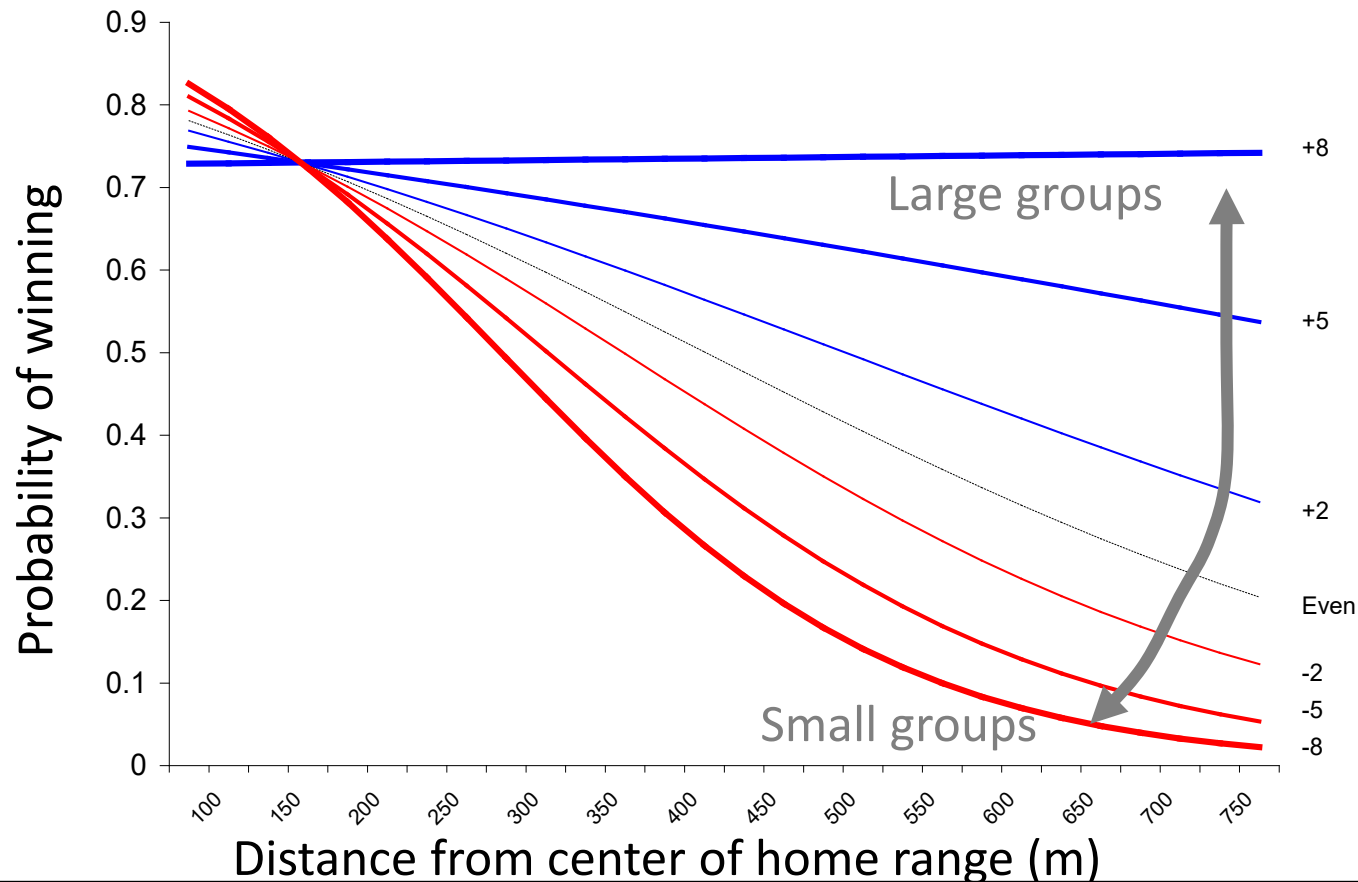


# What do groups fight over?

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Resources	Females	Status?
“Defend” access to food or territory (14 spp, 19 studies)	“Defend” access to females (6 spp, 4 studies/reviews)	“Defend” ability to win battles
involves both sexes	involves mostly males	
		What is the ultimate function?

# Inter-group Dominance Hypothesis



Winning groups were: -> larger

-> nearer center of home range

Looser groups : -> turned more often/ travel faster/ avoid border areas

# Inter-group Dominance Hypothesis



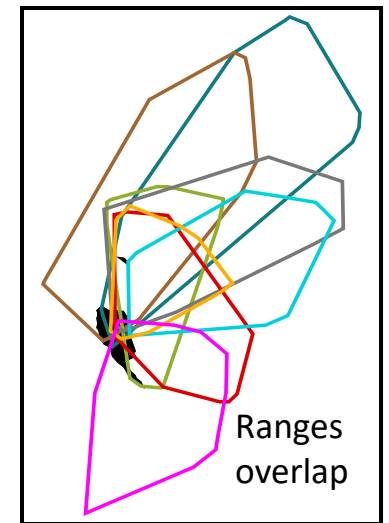
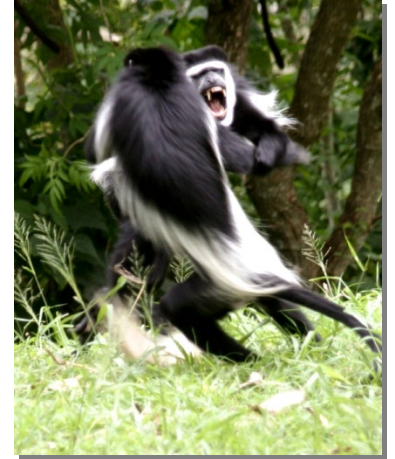
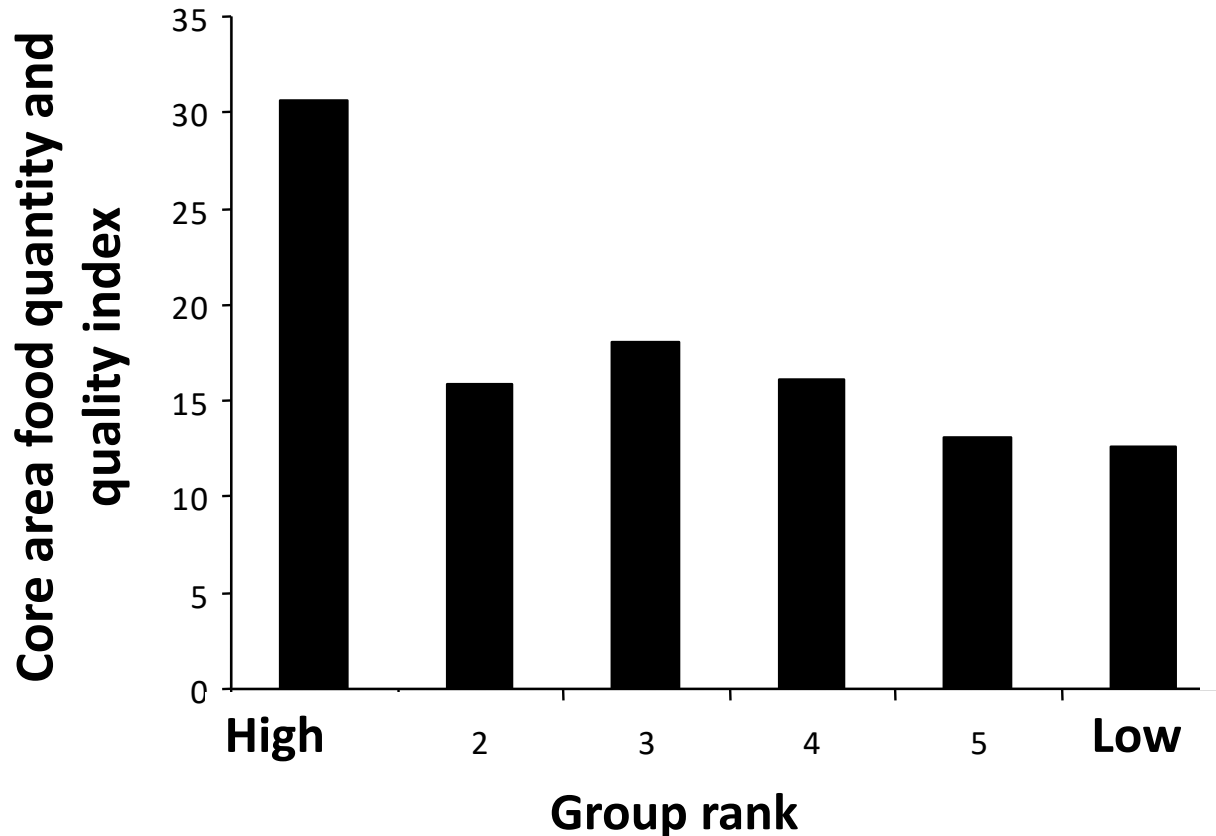
## **Inter-group Dominance Hypothesis**

- Groups use aggression to achieve dominance over their neighbors.
- Intergroup dominance promotes fitness by a variety of mechanisms, including access to more land and more females

# Inter-group Dominance Hypothesis

Dominant groups can have better food...

e.g. Black-and-white colobus (*Colobus guereza*)

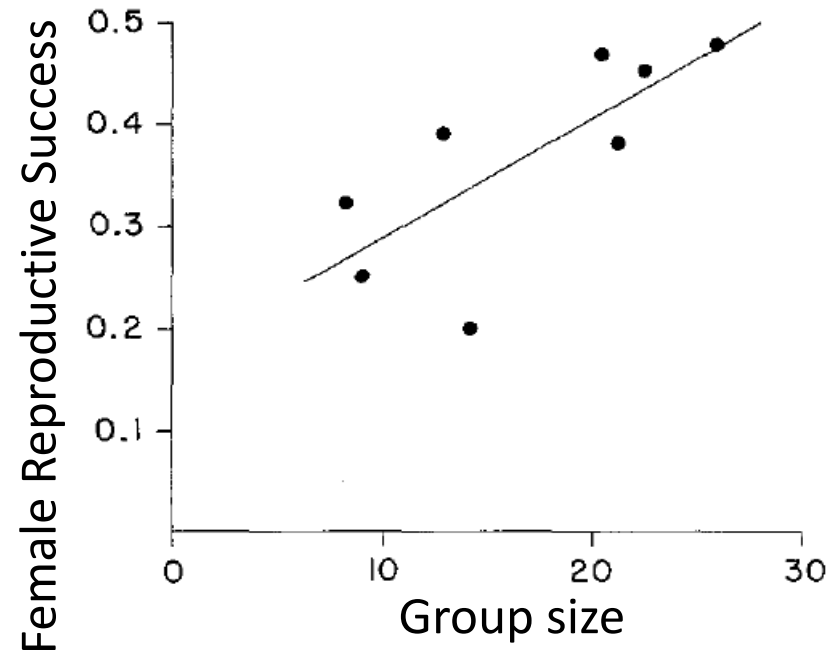
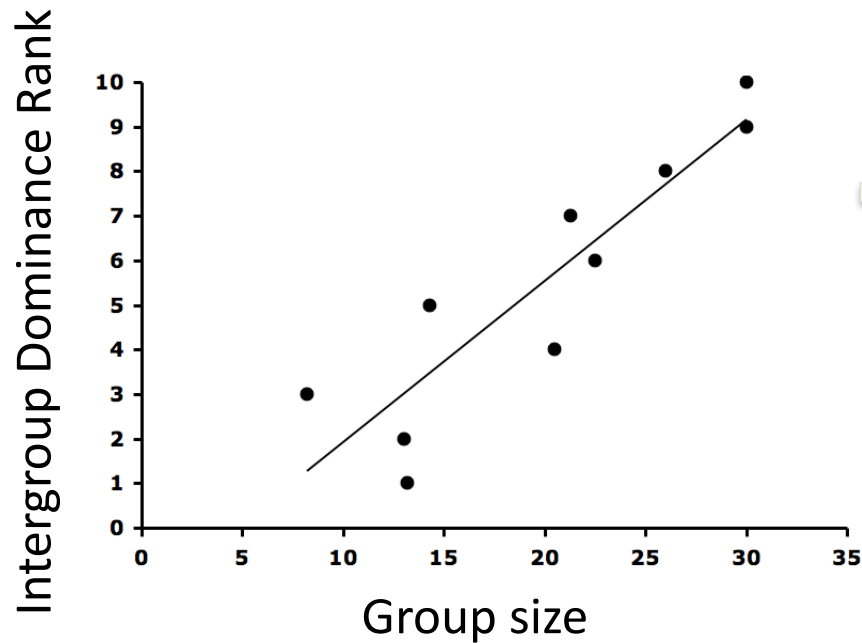




# Inter-group Dominance Hypothesis

Dominant groups can have high reproductive success...

e.g. Wedge-capped capuchins (*Cebus olivaceus*)



# What do groups fight over?

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Resources	Females	Dominance
“Defend” access to food or territory (14 spp, 19 studies)	“Defend” access to females (6 spp, 4 studies/reviews)	“Defend” ability to win battles
involves both sexes	involves mostly males	involves both sexes
promotes fitness by access to more land and more resources	promotes fitness by access to more females	promotes fitness to dominant group by a variety of mechanisms, including access to more land and more females

# Overview

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- 4) Intergroup tolerance



# Sex difference in participation

DEFEND  
MATES

DEFEND  
FOOD  
(territory)

ATTACK/KILL  
NEIGHBORS

...FF



...MM





# Sex difference in participation

Females tend to be involved (at least sometimes) in between-group aggression in female philopatric species

Species	Percent of Studies Reporting Female Participation	Number of Such Studies	Male Philopatry/ Female Transfer
<i>Lemur catta</i>	100	2	No
<i>Propithecus verreauxi</i>	100	2	No
<i>Cebus olivaceus</i>	100	1	No
<i>Papio cynocephalus</i>	28	5	No
<i>Macaca mulatta</i>	100	4	No
<i>M. fuscata</i>	100	1	No
<i>M. fascicularis</i>	100	1	No
<i>Cercopithecus mitis</i>	100	2	No
<i>C. aethiops</i>	57	7	No
<i>C. ascanius</i>	100	2	No
<i>Cercocebus albigena</i>	100	1	No
<i>Erythrocebus patas</i>	100	1	No
<i>Colobus guereza</i>	100	2	No
<i>Presbytis entellus</i>	67	6	No
<i>Alouatta seniculus</i>	100	1	Yes
<i>M. sylvanus</i>	0	1	No
<i>Ateles belzebuth</i>	0	1	Yes
<i>Papio hamadryas</i>	0	1	Yes
<i>Colobus badius</i>	0	2	Yes
<i>Pan troglodytes</i>	0	2	Yes
<i>Gorilla gorilla</i>	0	1	Yes

# Sex difference in participation

Female-philopatric primates: Females *can* lead intergroup fights

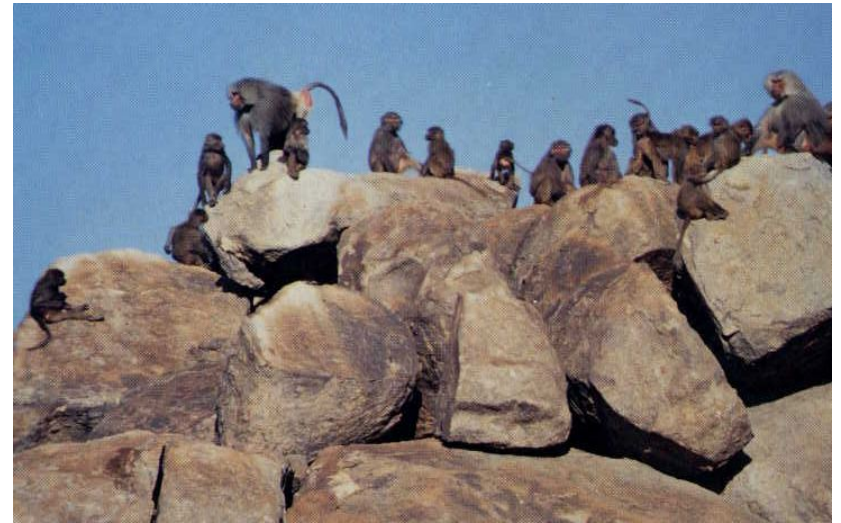


Rhesus macaques

# Sex difference in participation

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Male-philopatric primates: Males *always* lead intergroup fights



Hamadryas  
baboon



# Sex difference in participation

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**Fig. 1** Sitting among another band, a leader male (*left*) embraces the female he has retrieved from the standing male (*right*), who has his own female sitting in his shadow of attack. Note the challenging male provocatively touching the embraced female. Photo by Helga Peters 2007



# Individual difference in participation

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A **collective action problem** is a situation in which all individuals would be better off cooperating but fail to do so because of conflicting interests between individuals that discourage joint action

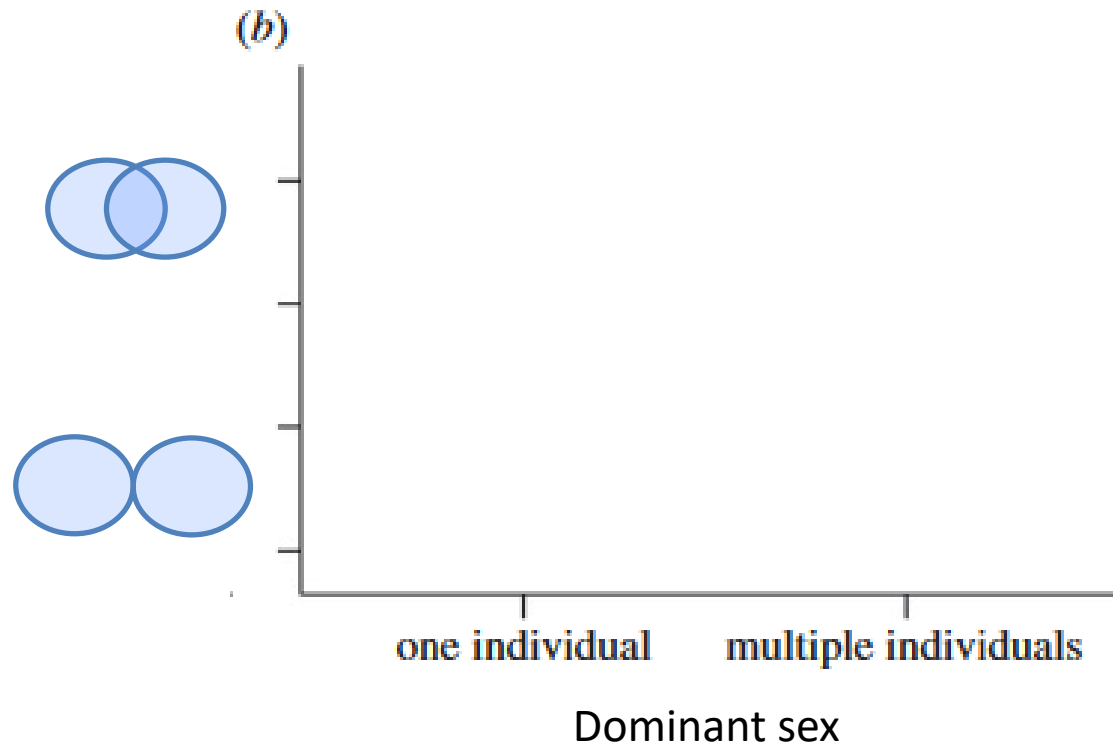


Defense of a common range provides a public good that is +/- equally shared between group members

# Collective action problem

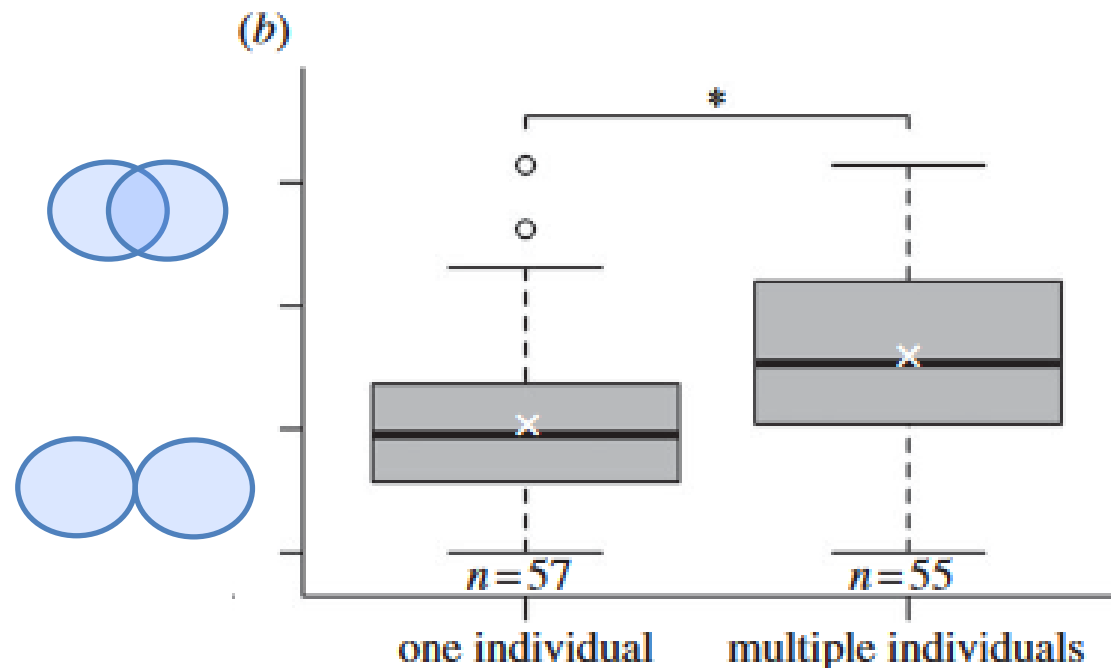
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Is there evidence of a collective action problem in territory defense?



# Collective action problem

Is there evidence of a collective action problem in territory defense?



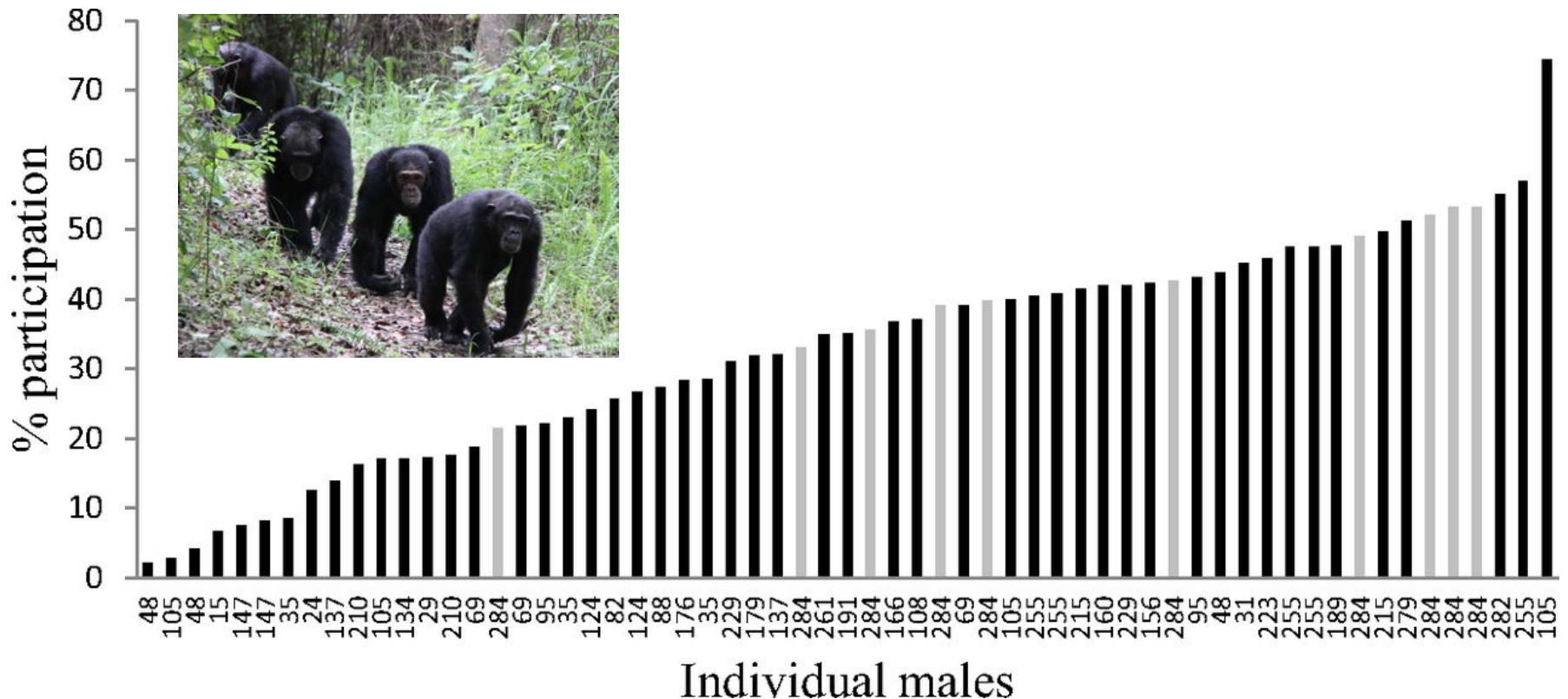
Collective territory defense in larger groups breaks down owing to increasing levels of free-riding

<https://www.youtube.com/watch?v=a7XuXi3mqYM>



# Collective action problem

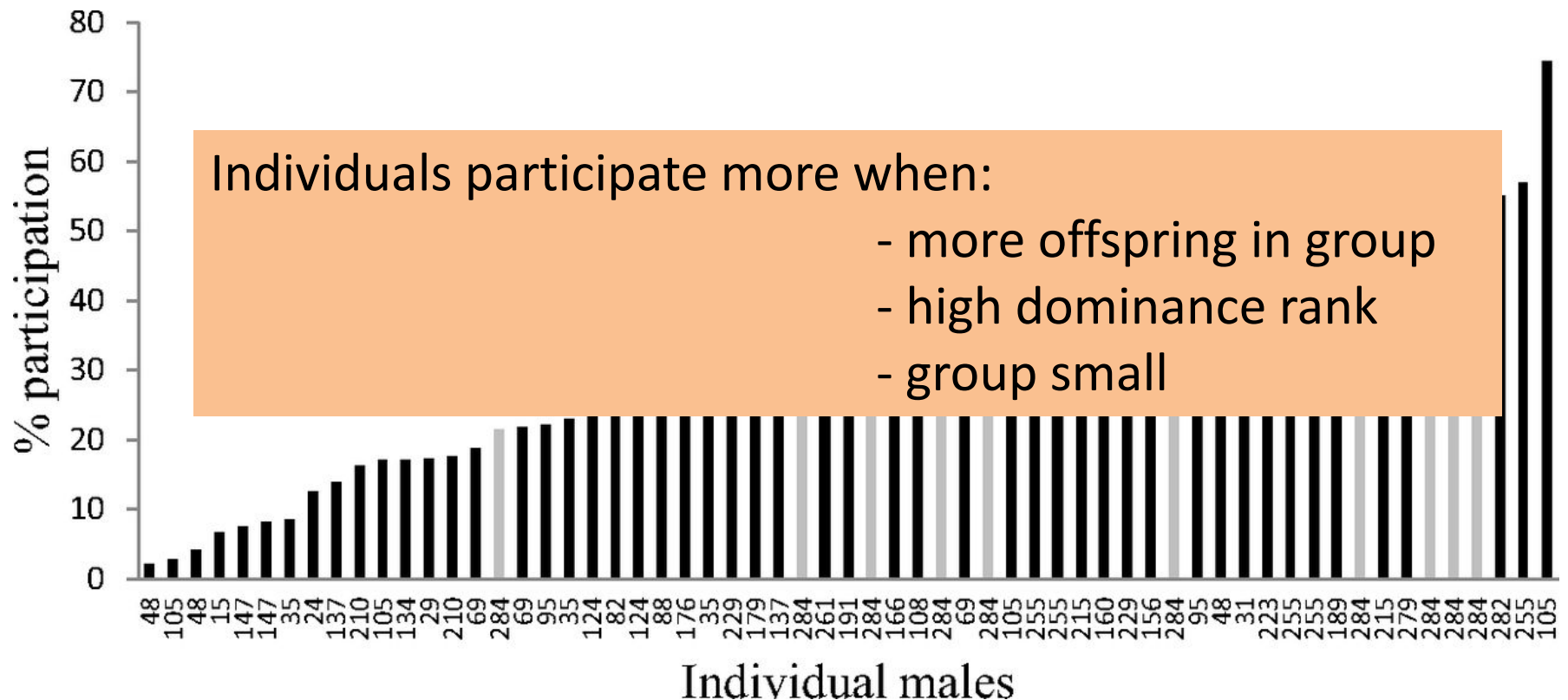
Collective action problems can be solved if some individuals gain more from public good and provide it as byproduct





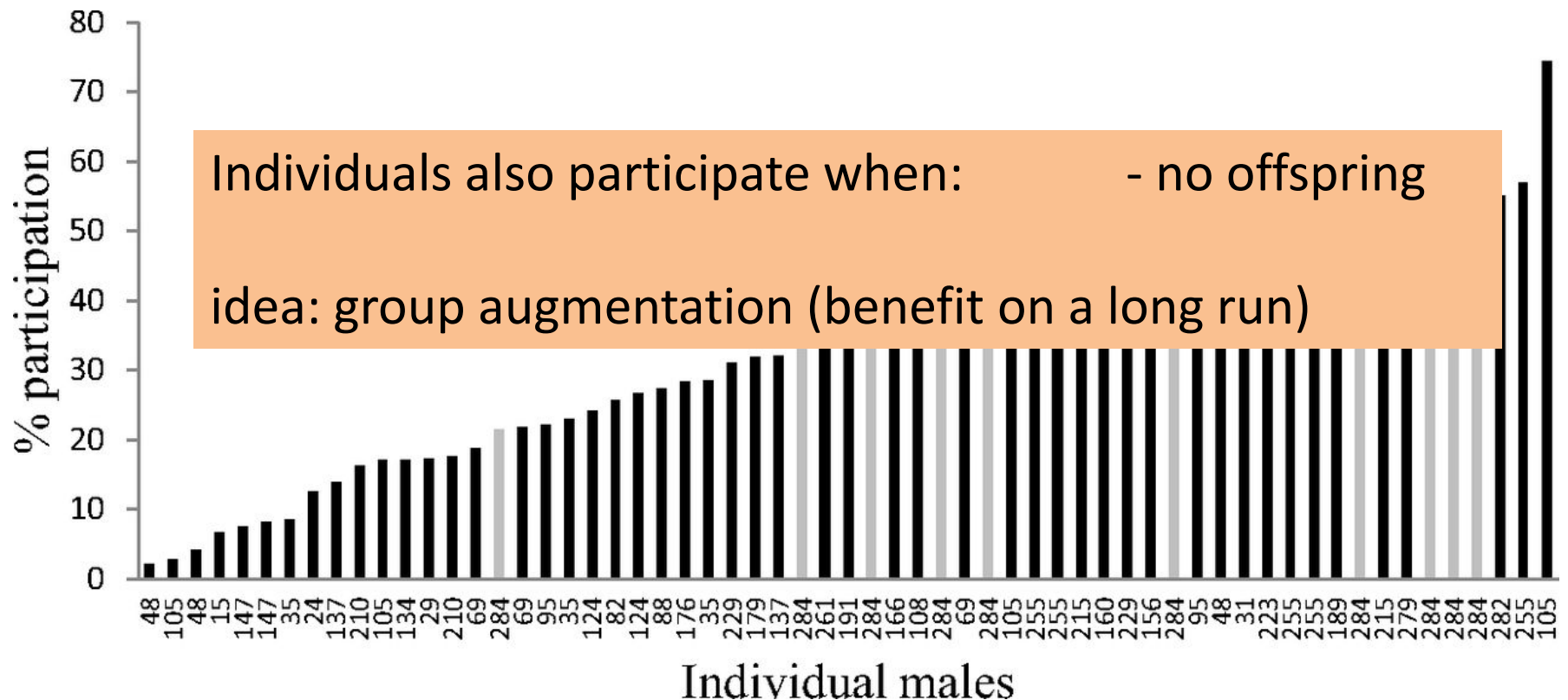
# Collective action problem

Collective action problems can be solved if some individuals gain more from public good and provide it as byproduct

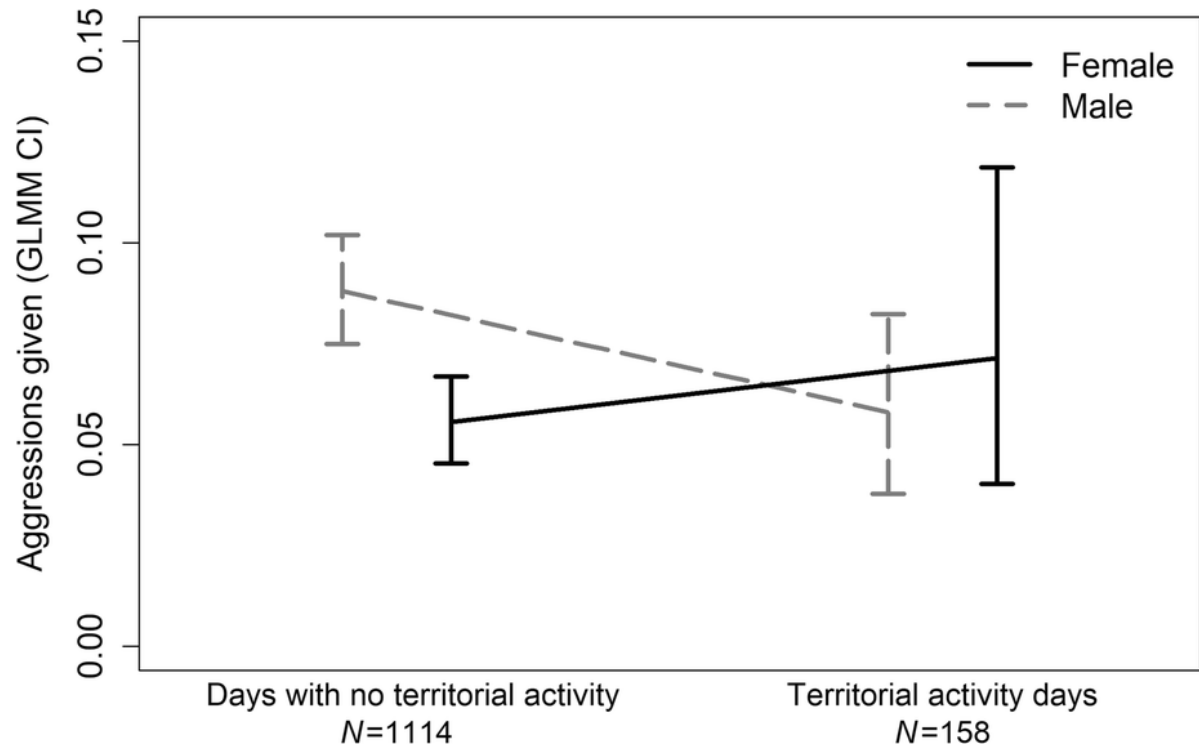


# Collective action problem

Collective action problems can be solved if some individuals gain more from public good and provide it as byproduct

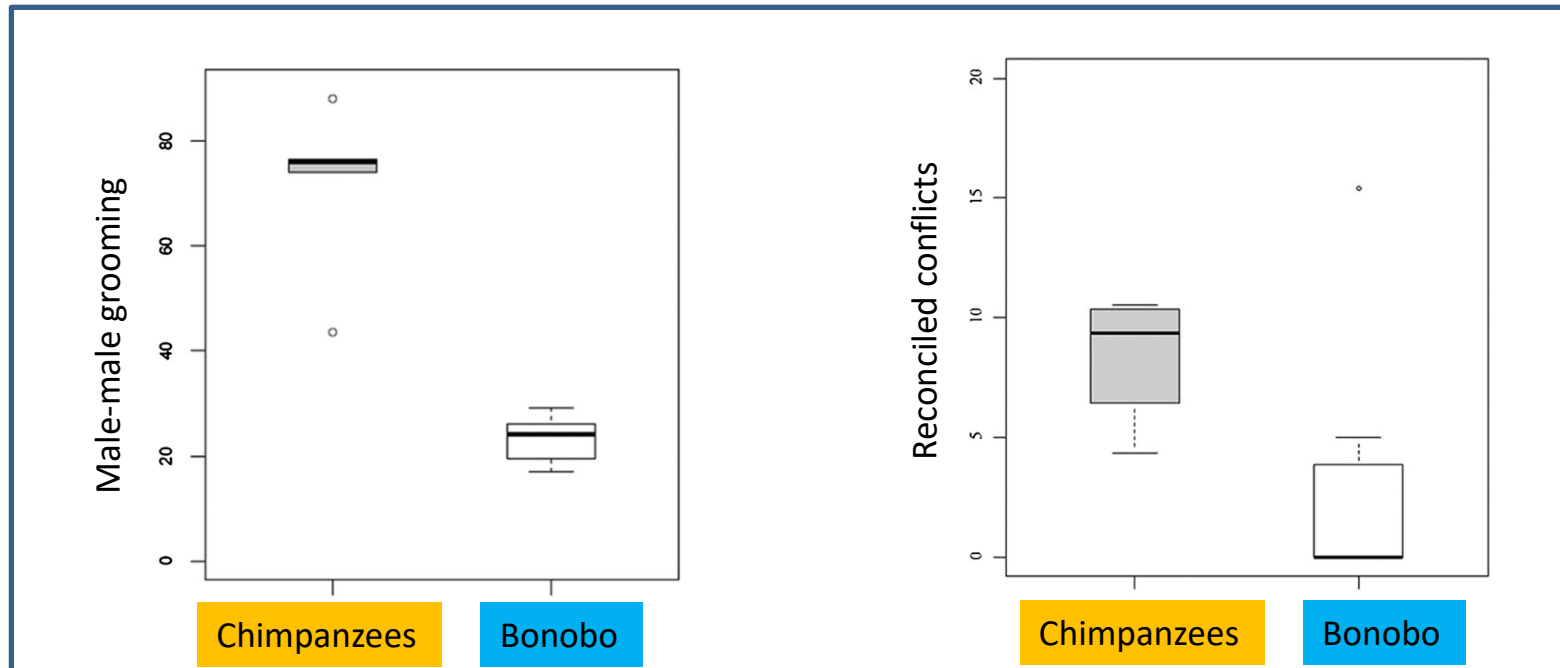


# In-group effects of between-group competition



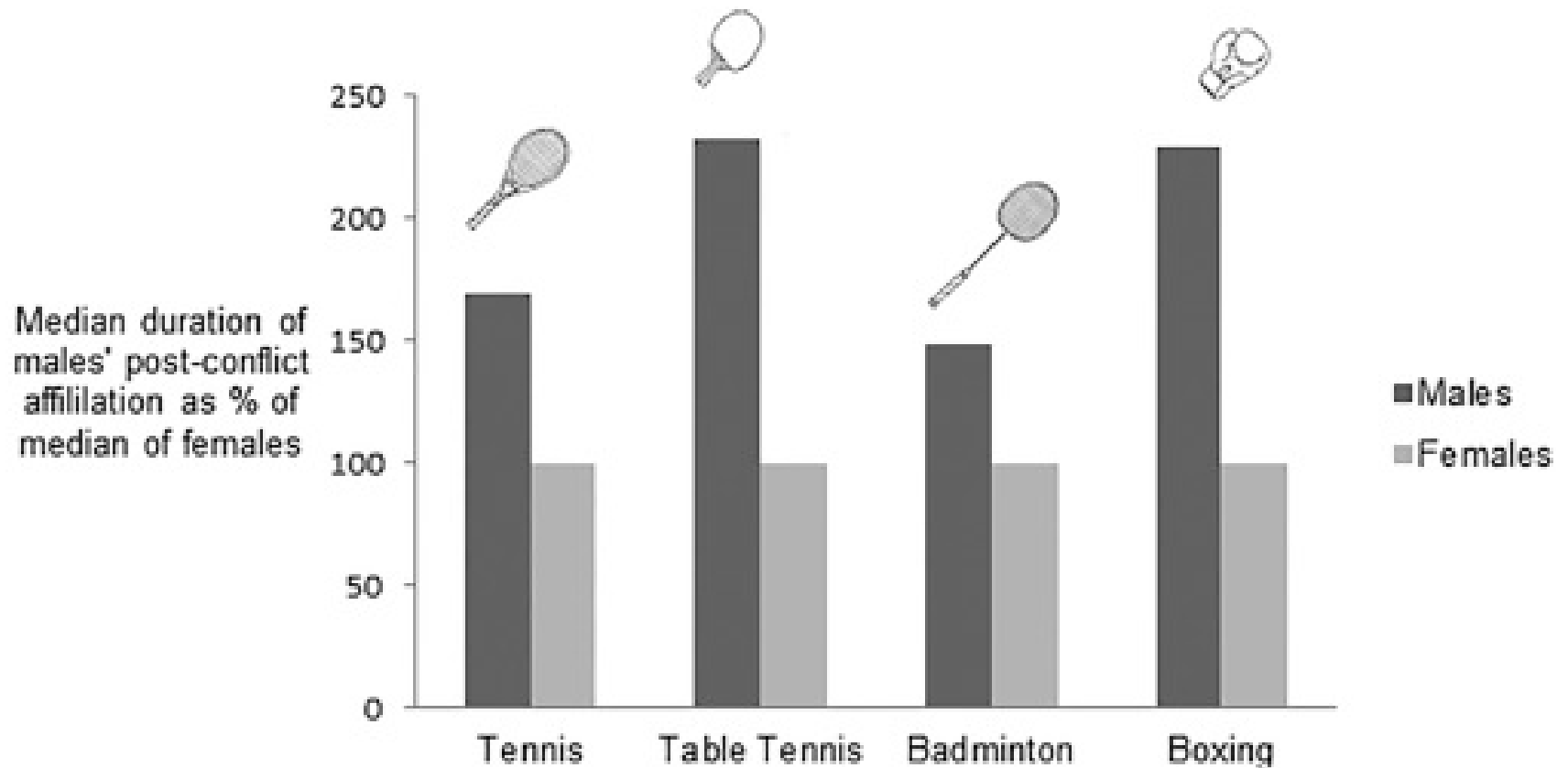
# In-group effects of between-group competition

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# In-group effects of between-group competition

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# Overview

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- 1) What do groups fight over?
- 2) Who participates in intergroup conflict?
- 3) Imbalance of power hypothesis
- 4) Intergroup tolerance



reading: xx

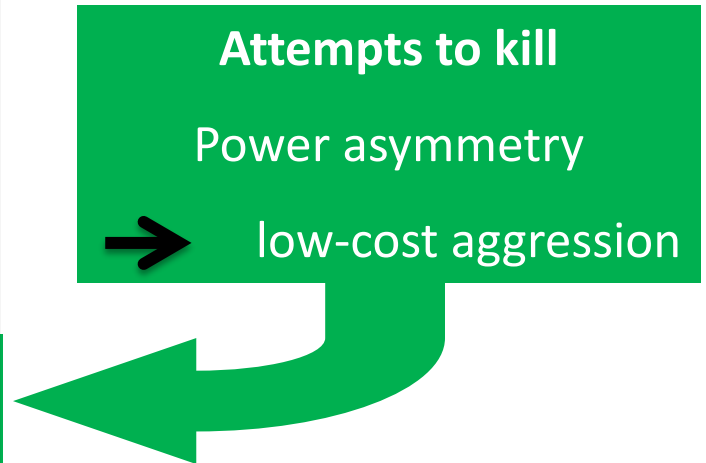
# Troop-living species: killing rare

- Little contact aggression in intergroup interactions
- Few coalitionary attacks on same-sex members of other groups.
- One explanation is that the groups are similar in size

# Community-living species: lethal raiding

found in species with 'parties' (temporary sub-groups, including lone individuals)

	<i>Stable troops</i>	<i>Parties (1-10)</i>
(1) Acoustic contact	✓	✓
(2) Approach-avoid	✓	✓
(3) Escalated battles	✓	✓
<b>(4) Opportunistic attack</b>		✓
<b>(5) Raid (pounce-&amp;-flee)</b>		✓



Troops: major imbalances of power are rare.



Communities: lone individuals vulnerable.

# Two Types of Between Group Aggression

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## 1. Balance of Power (mutual fear of intense aggression)

- Begins with mild threat
- Escalates slowly if at all
- Dangerous to attack ferociously
- Best to stop when opponent stops
- Both fighters survive

Multiple aggressors = Battles





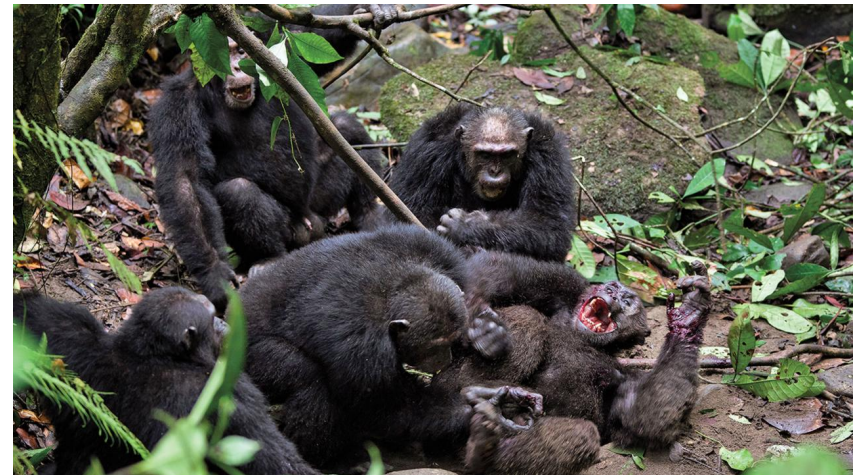
# Two Types of Between Group Aggression

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## 2. Imbalance of Power (aggressors are disinhibited)

- Begins with a strong attack
- Escalates rapidly
- No need to stop when opponent stops fighting
- Victims can die if the power imbalance is large
- Rare in the animal world

Multiple aggressors = Raids





# Imbalance of Power Hypothesis



Why do some primates form coalitions to kill?

Atomistic fission-fusion social organization (due to ecology)



Subgroups vary in size, so large parties may meet lone members of a neighboring group

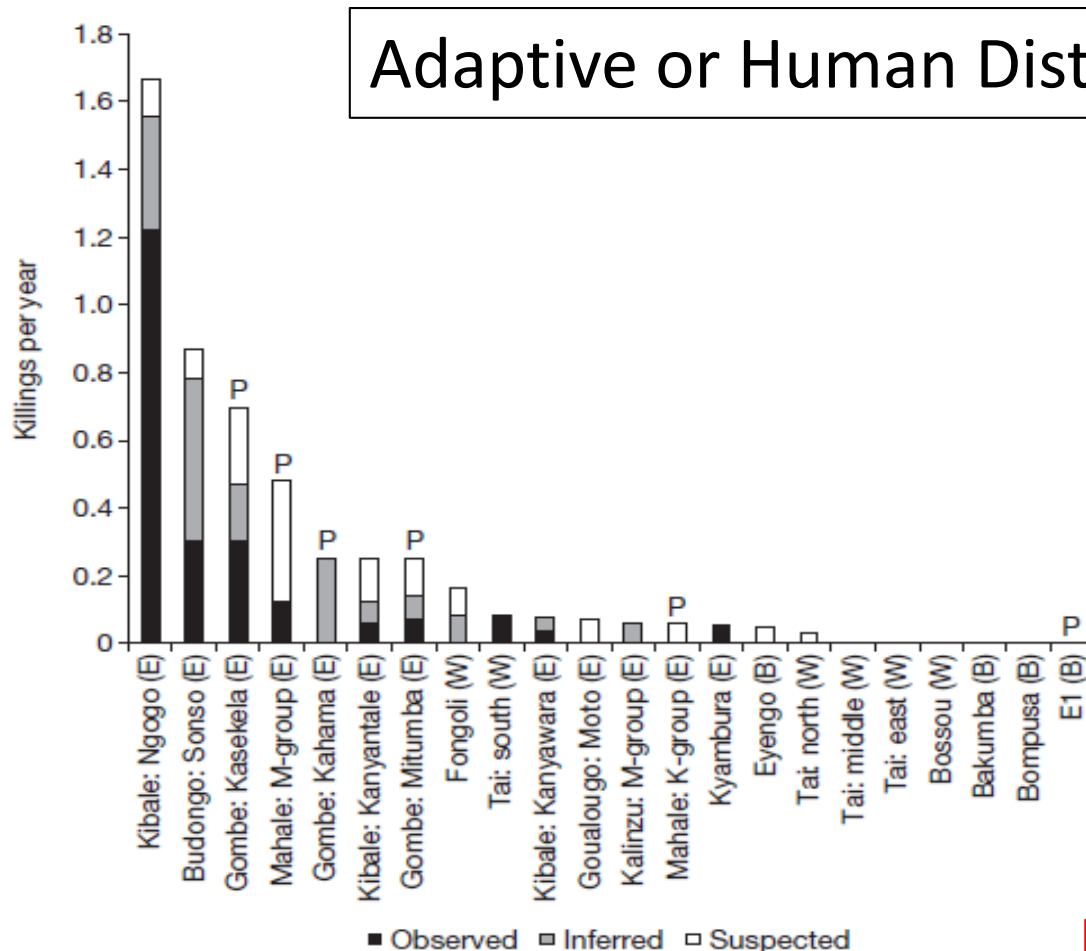


Asymmetrical distribution of power  
the dominant party can afford the cost of aggression



Attackers are never seriously damaged...  
Attack only when imbalance-of-power?

# Lethal Raiding in Chimpanzee



Adaptive or Human Disturbance?

Lethal aggression is NOT more common in:

- provisioned communities.
- communities that have been studied for a longer period.
- Communities that are more disturbed.

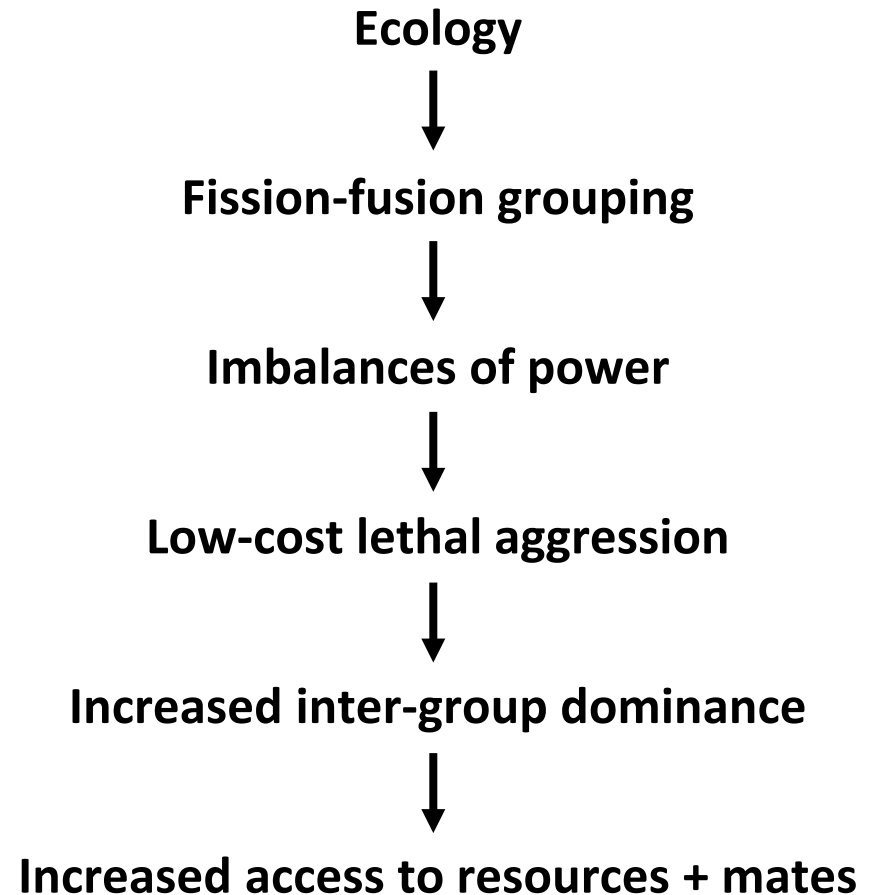
NOT HUMAN DISTURBANCE!

**Figure 1 | Number of victims killed per year by members of study communities.** Bars indicate the annual rate of observed (black), inferred (grey), and suspected (white) killings by each community for bonobos (B;  $n = 4$ ), eastern chimpanzees (E;  $n = 12$ ), and western chimpanzees (W;  $n = 6$ ). Communities with a history of provisioning are indicated by (P).



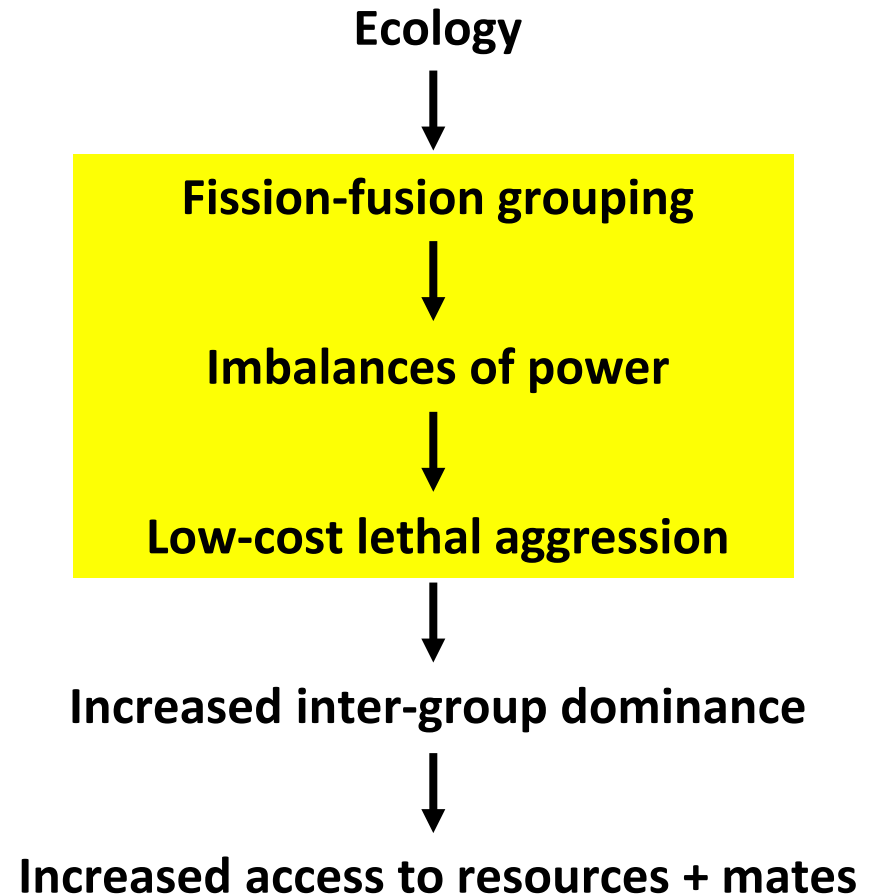
# Imbalance of Power Hypothesis

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# Imbalance of Power Hypothesis

**Prediction 1: Power asymmetry between opponents provokes attack**



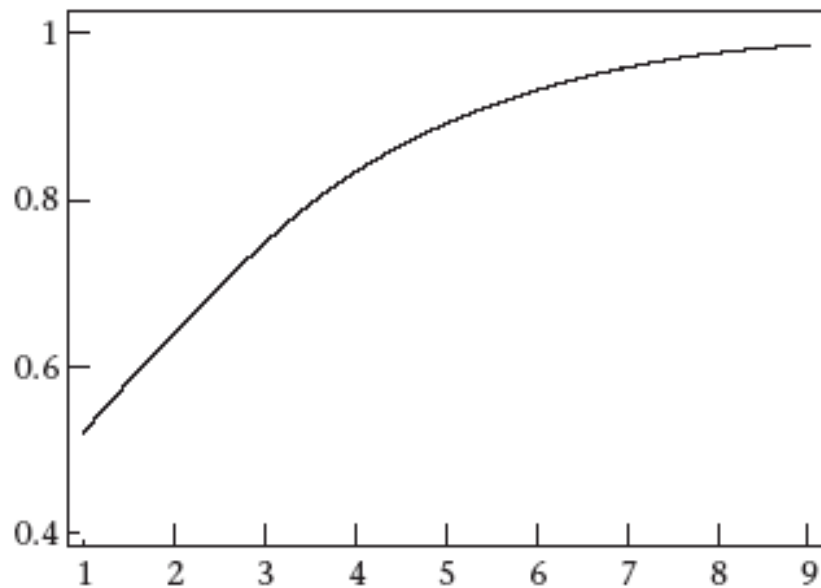


# Imbalance of Power Hypothesis

Prediction 1: Power asymmetry between opponents provokes attack



Probability of  
approaching the  
speaker



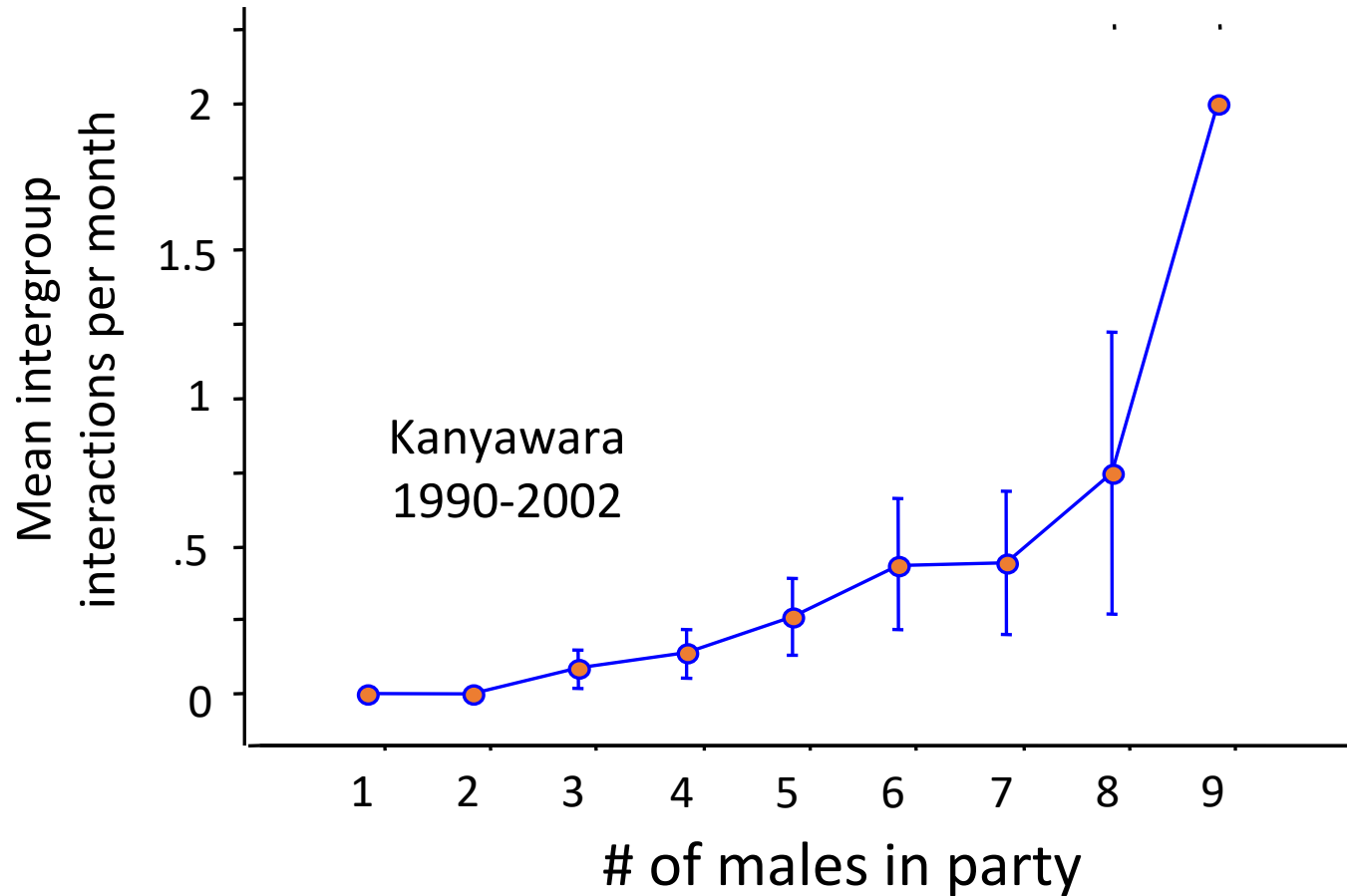
# of males in party



Playback  
experiments,  
Kanyawara

# Imbalance of Power Hypothesis

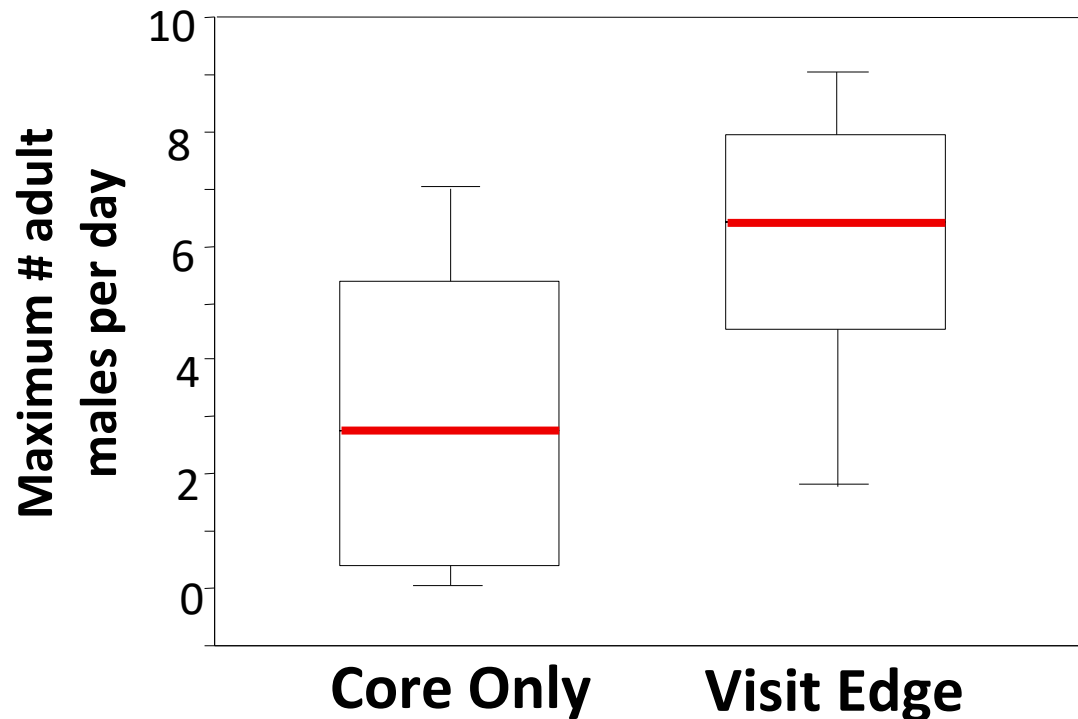
Prediction 1: Power asymmetry between opponents provokes attack



**Males in small parties avoid intergroup interactions**

# Imbalance of Power Hypothesis

Prediction 1: Power asymmetry between opponents provokes attack



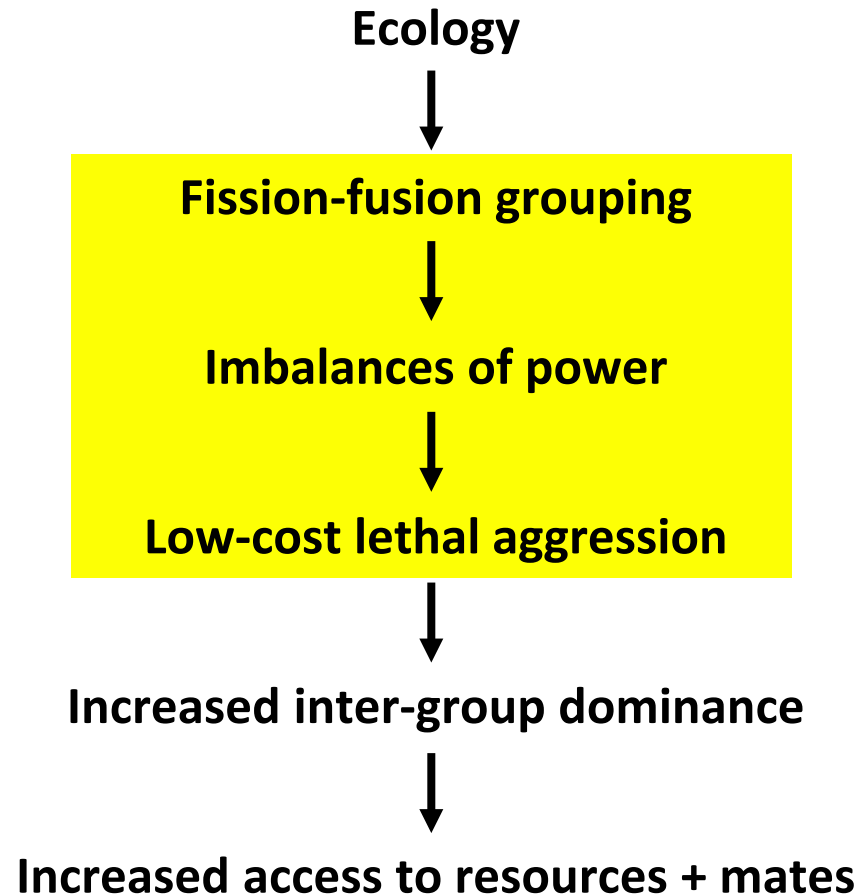
Males in small parties avoid territory edge (border zone)



Wilson (2001)

# Imbalance of Power Hypothesis

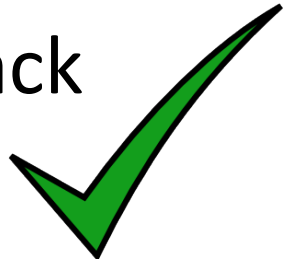
**Prediction 2: Power symmetry suppresses attack**



# Imbalance of Power Hypothesis

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## Prediction 2: Power symmetry suppresses attack



Battles: multiple fighters on each side



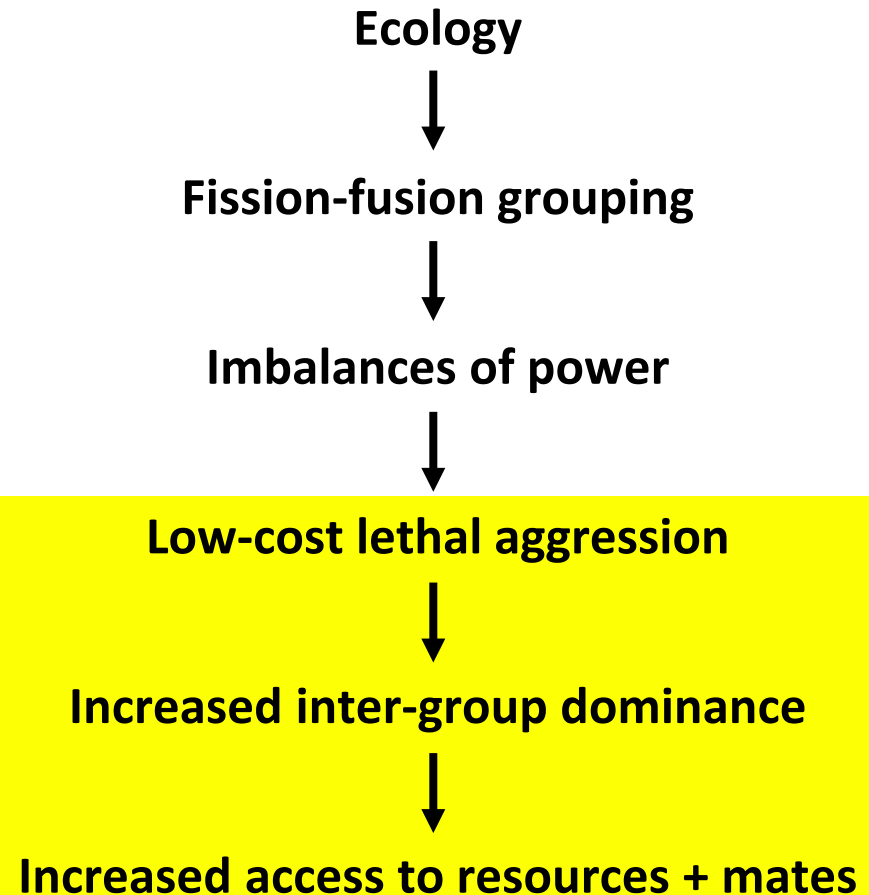
- Prolonged interactions (up to > 45 minutes)
- Mutual call, display, charge; little / no contact
- Repeated individual retreats and approaches
- High tension; much coalitionary behavior
- Ends in one or both parties withdrawing

**No deaths or serious injuries known in this context**



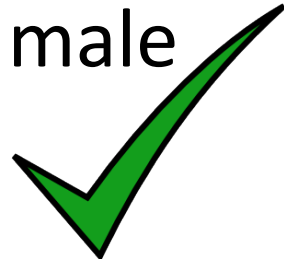
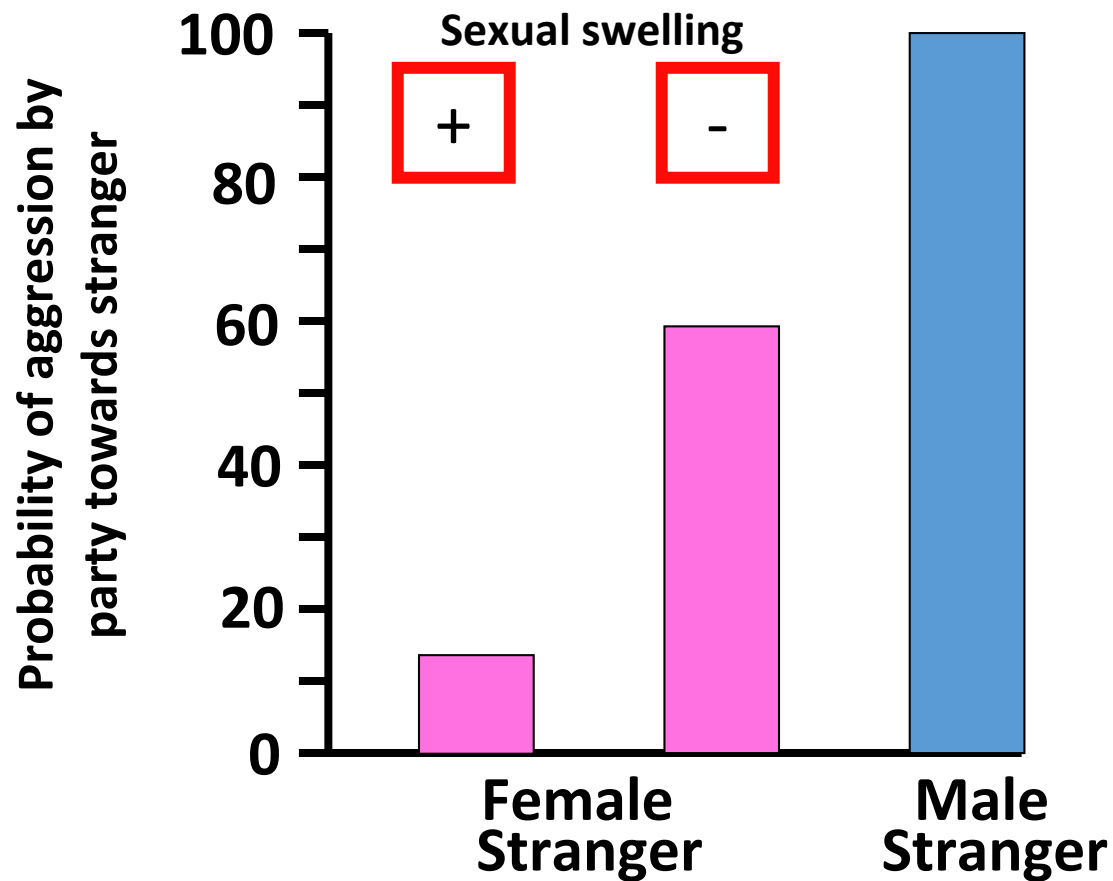
# Imbalance of Power Hypothesis

**Prediction 3: Victims of aggression tend to be male**



# Imbalance of Power Hypothesis

Prediction 3: Victims of aggression tend to be male

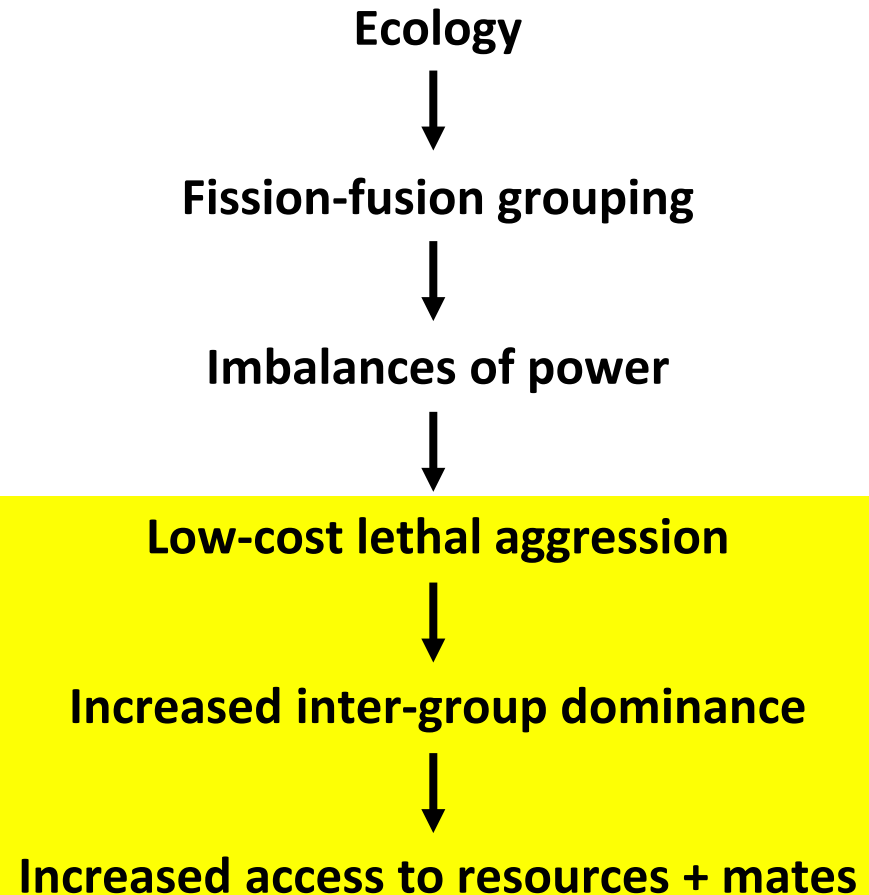


Gombe 1975-1992



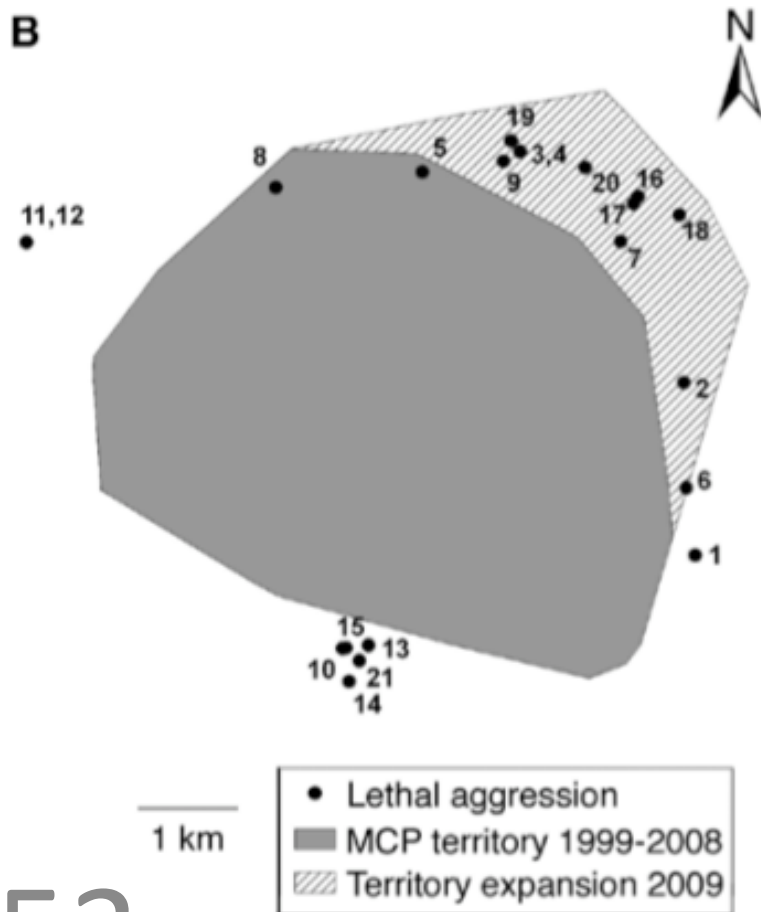
# Imbalance of Power Hypothesis

**Prediction 4: Inter-group dominance leads to increased resources**



# Imbalance of Power Hypothesis

**Prediction 4: Inter-group dominance → resources**

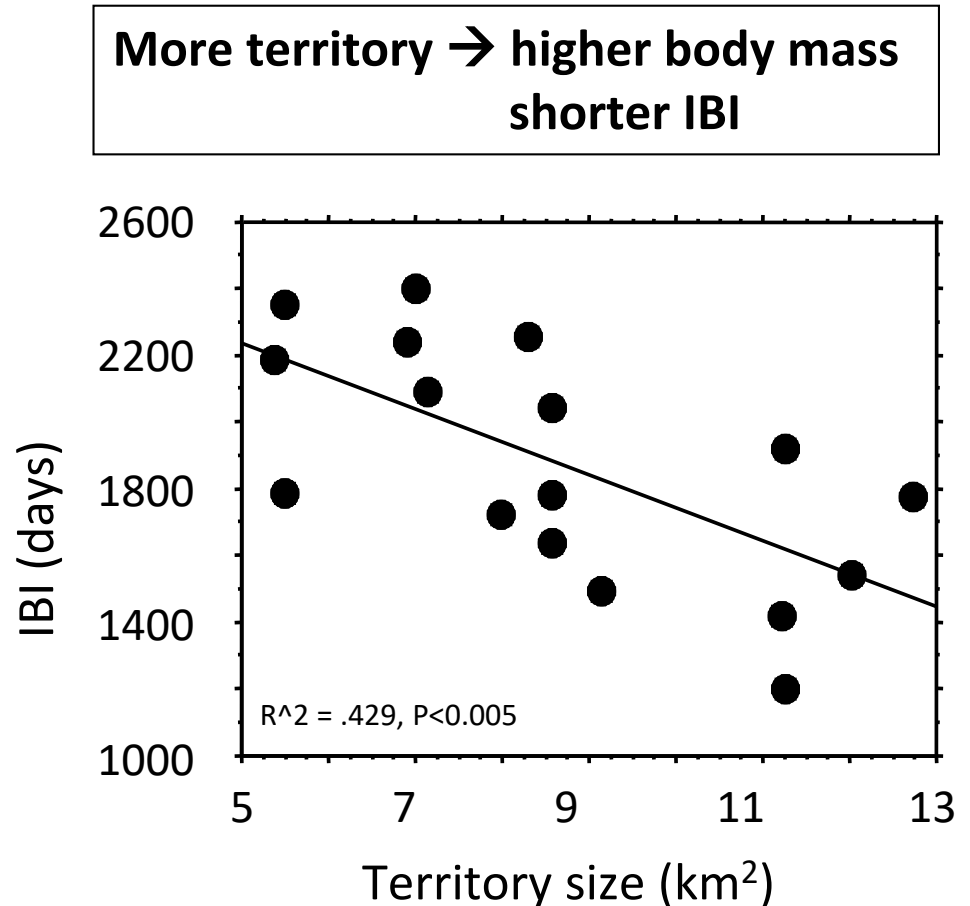
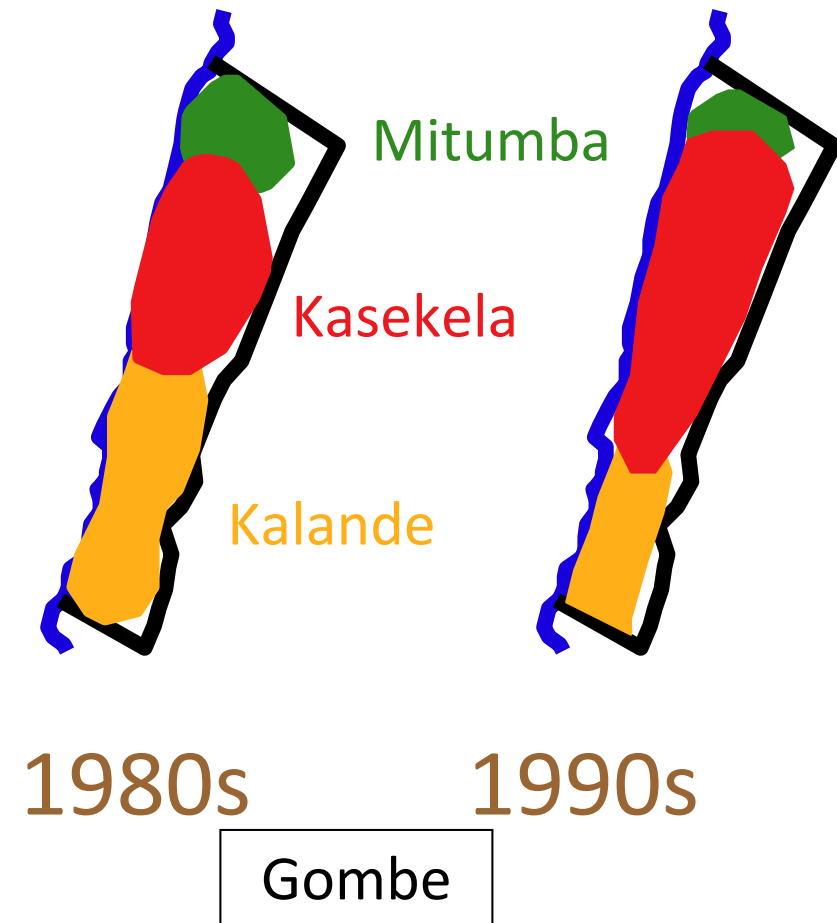


Ngogo Chimpanzees:

- Raiding results in more >20 kills
- Chimps occupy areas where kills occur

# Imbalance of Power Hypothesis

Prediction 4: Inter-group dominance → resources





# Imbalance of Power Hypothesis

**Prediction 4: Inter-group dominance → resources**



**Mahale, 1970s-1980s**

**1969-79 K-group community disappears ...**

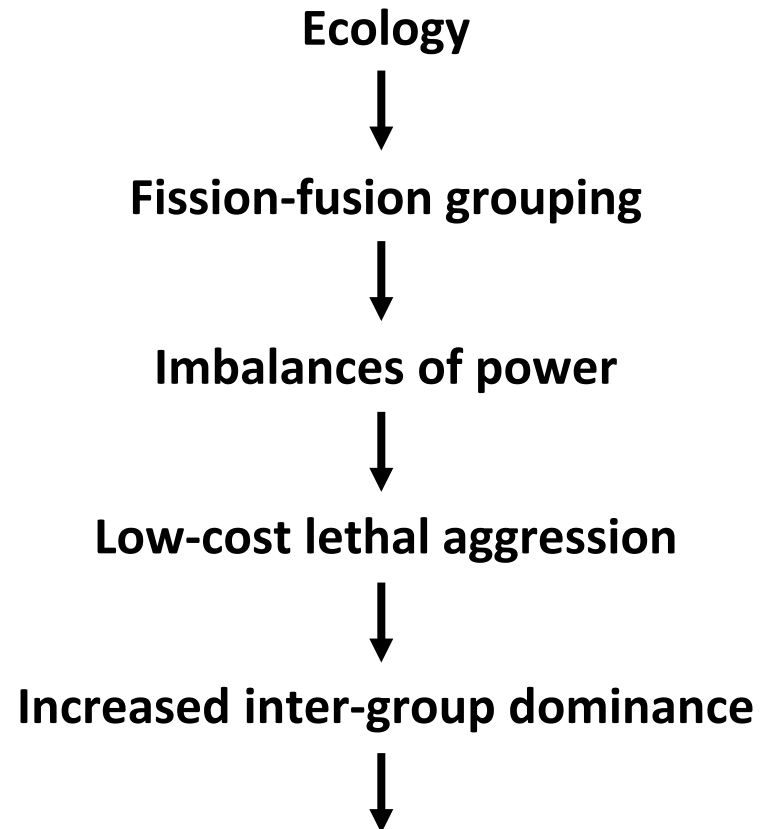
**M-group suspected to kill  $\geq 5$**

**K-group females join M-group (n = 6)**



T. Nishida

# Imbalance of Power Hypothesis



Ultimate Function



Increased access to resources + mates

# Lethal raiding in chimpanzees

Competing hypotheses for proximate cause

Generalized tendency.

Individual personality.

Mate competition.

Ecological stress.

Food contest.

Rival removal.



# Overview

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reading: xx

# Intergroup tolerance

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	Chimpanzees	Bonobos	Gorillas
Encounter duration	Hours	Up to several days	Up to several days
Occurrence of encounters (% of observation days)	3.33%–5%	0.2%–30%	WG: 2%
Lethal outcomes	Occur	Not reported	WG: not reported MG: occur
Patrolling and other territorial behavior	Occur	Not reported	Not reported
Coalitions formed among members of the same group	Occur	Occur	WG: not reported MG: occur
Coalitions formed among members of different groups	Not reported	Occur	Not reported
Copulation between groups	Occur	Occur	Not reported
Food sharing between groups	Not reported	Occur	Not reported
Grooming between groups	Not reported (except in the case of female visits)	Occur	Not reported



# Intergroup tolerance

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# Primate social behavior

## Summary

- Between-group aggression is present in almost every primate species
- How it is exhibited depends on social organization, philopatry and food abundance and distribution
- Need for allies promotes social complexity within groups, especially among the philopatric sex