Economics of the Family

Equilibrium Group Size and Genetic Relatedness

Stable Groups of Non-Relatives (***r* = 0**)

And

Stable Groups of Relatives (***r* > 0**)

Require Group-Membership Benefits

Fitness, Inclusive Fitness (*Direct* + *Indirect*)

Advantages of Group Membership

1. Groups **Discover** Food *Clumps* Faster than Solitaries

    Spatially Heterogeneous Resources

    Discovery by One Group Member Means Feeding Opportunity for Others

    "Information Center" Hypothesis

2. Enhanced **Capture** & **Consumption** of Food

    Carnivore Groups Take Larger Prey than Solitaries

    Success per Capture Attempt Greater for Group

    Groups Repel Scavengers (Overcome Territory Defense)

Larger Group May Also Increase Local Competition (*Cost*)

3. Groups **Reduce** Time/Energy **Costs** of Foraging

Time Allocation to Vigilance

Social Spiders, Less Energy Web Maintenance

4. Group Feeding Increases **Offspring Survival**

Helpers Assist Parents in Feeding New Offspring

Communal Nursing

Relatedness Important

5. **Protection** from Predation

"Many Eyes" and Vigilance

"Confusion Effect" During Escape

Repelling Predators, Protect Offspring

"Dilution Effect"

Cultural Transmission of "Danger"

6. Mate Discovery

Larger Groups, Mixed Lineages

Mammals: Males Disperse

Birds: Females Disperse

Males & Limited Territories

Costs of Group Membership

1. Resource Competition

2. Exposure to Contagious Pathogens, Parasites

3. Attraction of Predators

4. Aggression, Dominance Interference

5. Competition for Breeding Opportunities

Aggregation Economy: Advantage to Grouping

Small Groups: Net Benefits Increase

Large Groups: Competitive Costs May Dominate

Equilibrium Group Size

Rules of Entry

1. *Free Entry*: Solitaries Join or Not
2. *Group-Controlled Entry*: Invite or Not

Interaction, Conflict

Non-Relatives First ($r = 0$)

Second, Relatives ($r > 0$)

Relatedness' Impact on Equilibrium Group Size
Depends on Entry Rule

Aggregation Economy

G: Group Size, Approximate as Continuous

W(G): Individual's Direct Fitness, Group Size = $G \geq 1$

$$\left(dW(G)/dG\right)_{G=1} > 0$$

Fitness Increases in *G* at Small *G*

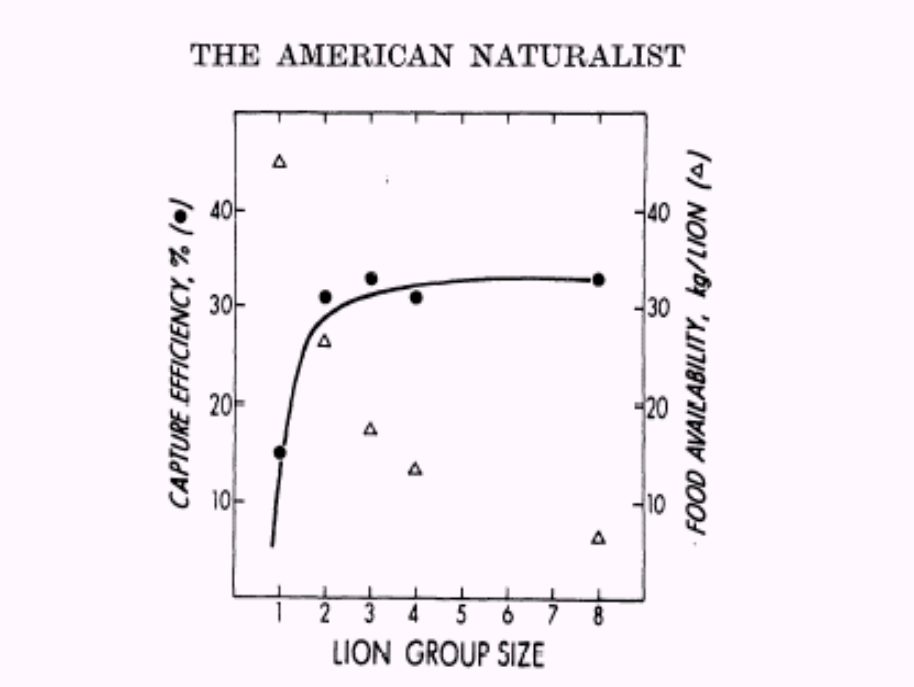
$$\left(dW(G)/dG\right)_{G=G^*} = 0; \quad \left(d^2W(G)/dG^2\right)_{G=G^*} < 0$$

Individual Fitness Maximal at $G = G^* > 1$,
"Optimal" Group Size

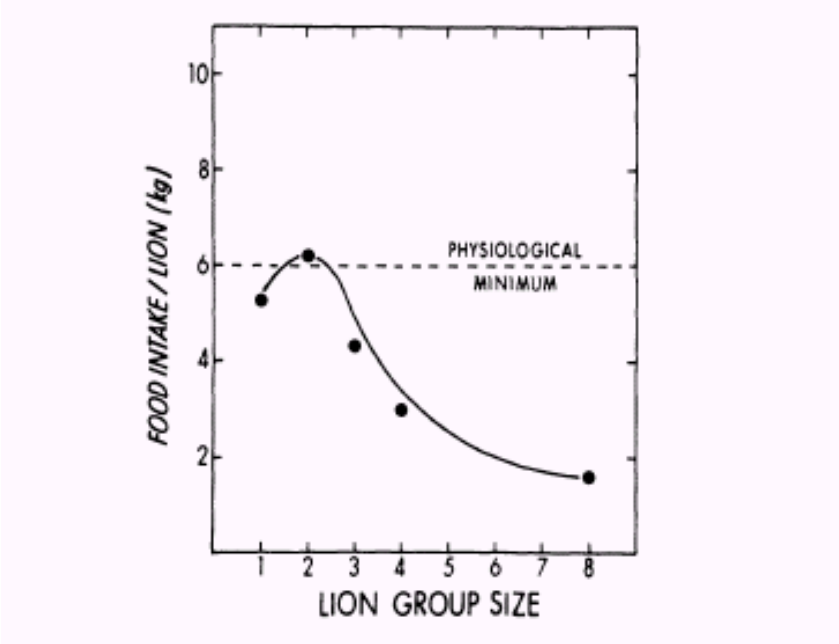
$$\left(dW(G)/dG\right)_{G>G^*} < 0; \quad \lim_{G \to \infty} W(G) < W(1)$$

Fitness Decreases in G, G > G*;
Very Large Groups, Fitness < Solitary's Fitness

Fitness Function "Peaked"



Lions Hunting Thomson's Gazelle



Aggregation Economy: Food Intake/Day

$G^* = 2$; Observe Mean $G = 1.5$ to 2

Lions Hunting Wildebeest & Zebra

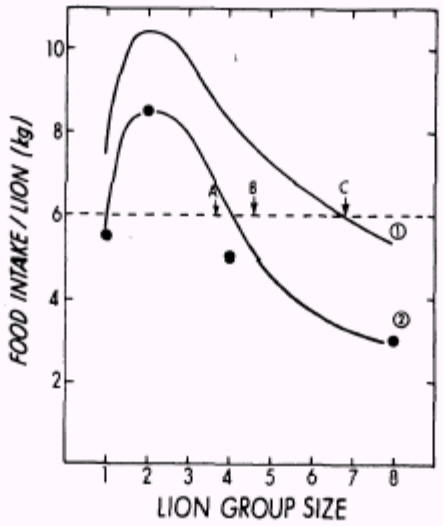


FIG. 4.—Mean edible prey biomass (kg) per lion per chase per 24 h as a function of lion group sizes preying on wildebeest. Line 1 shows hypothesized wet-season intake in woodlands-plains border region, where vegetation cover increases lion capture efficiencies. Line 2 gives same calculations for eastern plains and western woodlands, when wildebeest are available prey. Dashed line at intake of 6 kg represents daily physiological minimum requirement for an individual lion, males and females averaged. Observed mean lion group sizes (Schaller 1972) are given for eastern plains (*A*), western woodlands (*B*), and border region (*C*).

Lion Aggregation Economy: Wildebeest Prey

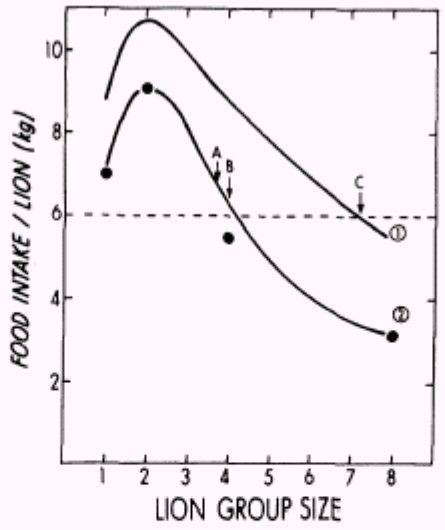
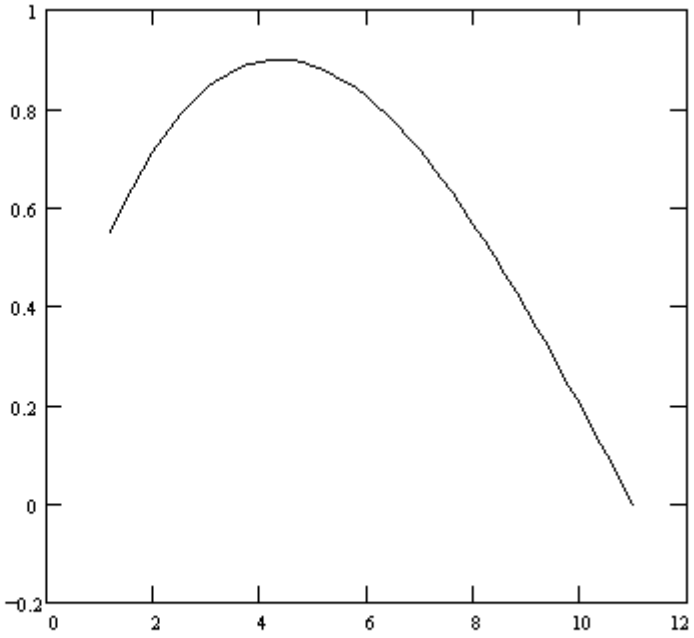


FIG. 5.—Mean edible prey biomass (kg) per lion per chase per 24 h as a function of lion group sizes preying on zebra. Line 1 shows hypothesized wet-season intake in woodlands-plains border region, where vegetation cover increases lion capture efficiencies. Line 2 gives same calculation for eastern plains and western woodlands, when zebra are available prey. Dashed line at intake of 6 kg represents daily physiological minimum requirement for an individual lion, males and females averaged. Observed mean lion group sizes (Schaller 1972) are given for eastern plains (*A*), western woodlands (*B*), and border region (*C*).

Lion Aggregation Economy: Zebra Prey

Survival =

W(G)



Group Size G

Aggregation Economy

W(G) Increases at $G = 1$

G^* 4.353, *W(G)* Maximal $G = 4$

Large *G*, $W(G) < W(1)$

What Group Size Predict?

Rules of Entry

Free Entry: Solitaries Decide to Enter Group
Or Remain $G = 1$

Solitaries Enter Group at No Cost

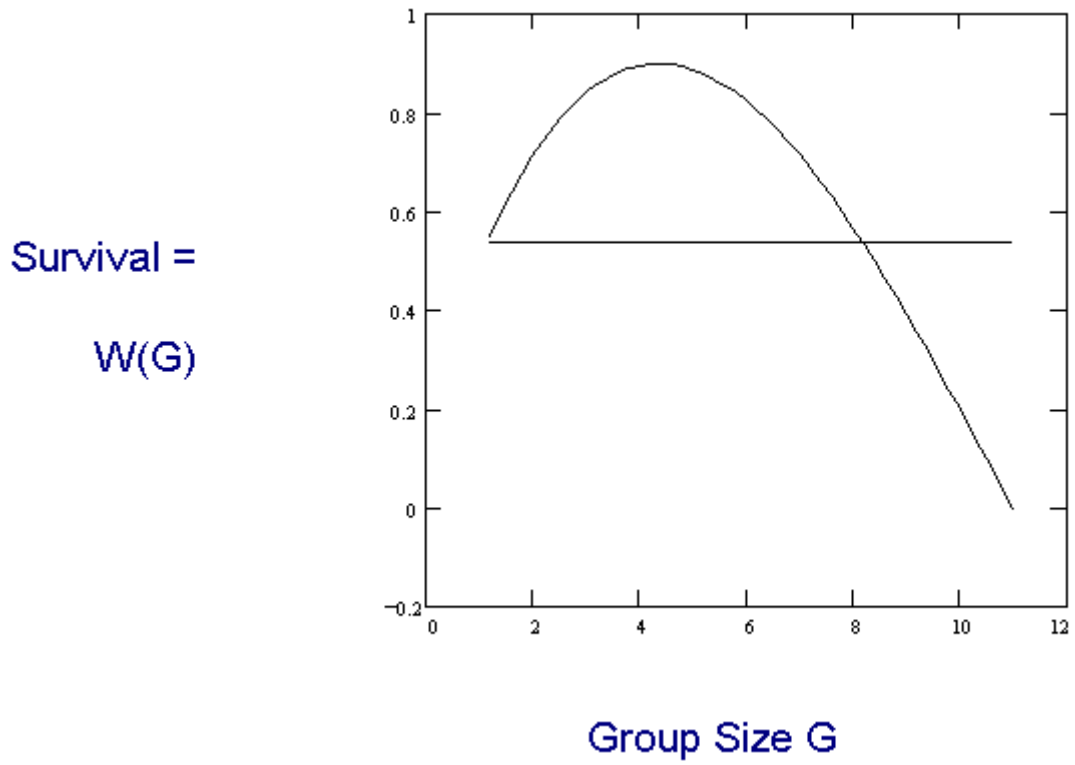
Assume $r = 0$

Free Entry: Individual Should Join Group of G,
Group Becomes $(G + 1)$,
If Individual's Fitness Increases

Solitary: Join G If $W(G + 1) > W(1)$;

Do Not Join If $W(G + 1) < W(1)$

Free Entry Group Size Increase to **Equilibrium** G^,
Where Solitaries Stop Joining



$W(G)$ Peaked; $W(G = 1)$ Horizontal

Solitaries Join $G = 7$, Since $W(8) > W(1)$

Solitaries Do Not Join $G = 8$, Since $W(9) < W(1)$

Equilibrium Group Size $G\hat{} = 8$, Under Free Entry

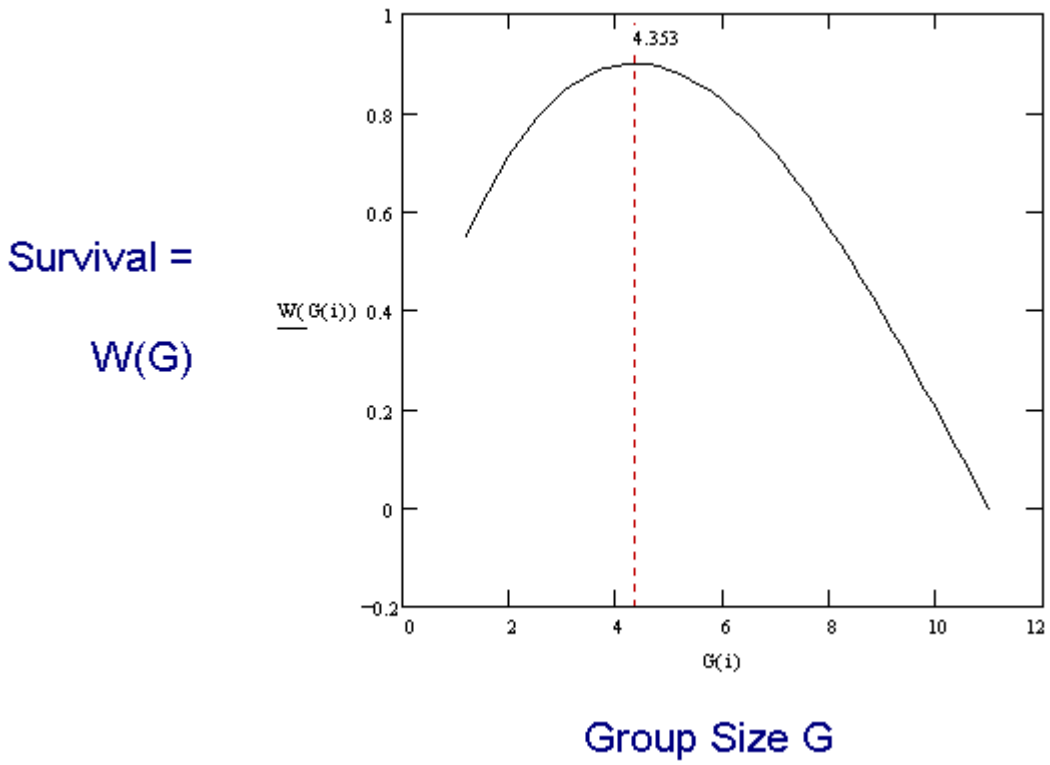
Group-Controlled Entry:

Group Members Recruit When $G < G^*$

Prevent Joining When $G = G^*$

(Evict Member If $G > G^*$)

Group-Control: Group Increases to Optimum G^*, Where W(G) Maximal



Group Control Maximizes Direct Fitness of Mutualistic Group Members; $G = 4$

See Results for *Non-Relatives*

Relatedness

Effects on Self: $\mathbf{E_S}$

Effects on Relatives: $\mathbf{E_R}$

Relatedness *r*, Average Over Relatives

Actions: *Join* or *Remain Solitary* Under Free Entry

Recruit or *Repel* Under Group-Controlled Entry

Action Increases Inclusive Fitness:

$\boldsymbol{r\,E_R + E_S > 0}$ Hamilton's Rule Generalized

Indirect, Weighted + Direct
Components of Inclusive Fitness

Free Entry to Group of Relatives

Join Until Group Size Large Enough That Increase by
One More Member Would Reverse
Hamilton's Inequality

$G < G^*$ Joiner & Group Benefit from Increase

$G^* < G < G^\wedge$ Joining Increases Solitary's Direct Fitness,
But Decreases Indirect Fitness

Group Size Can Never Exceed G^, Equilibrium Group Size
for $r = 0$

Free-Entry: Predict **Group Size** Same or **Smaller**
As Relatedness Increases

Group-Controlled Entry by Relatives

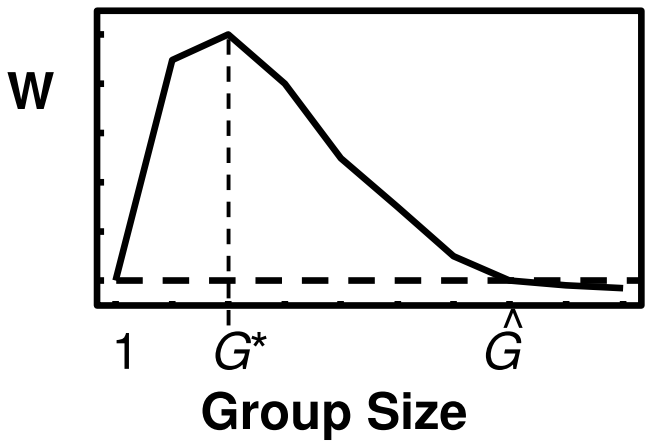
$G < G^*$ Recruit

$G = G^*$; Recruiting Decreases Direct Fitness,
But Increases Indirect Fitness

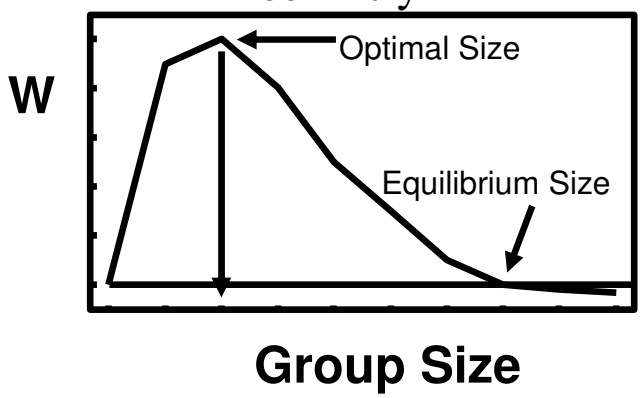
Group Control: Equilibrium with Relatedness

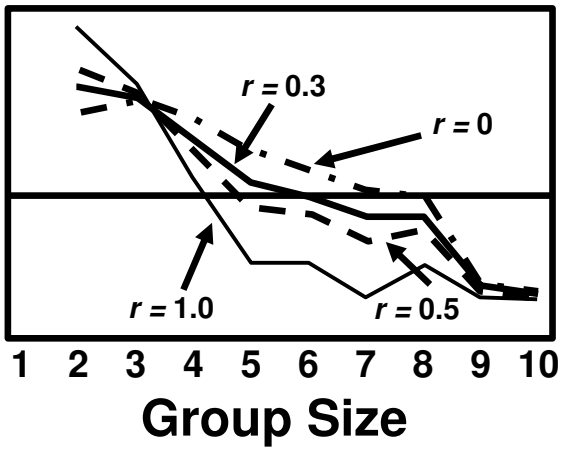
$G^* <$ Equilibrium $< G\hat{}$

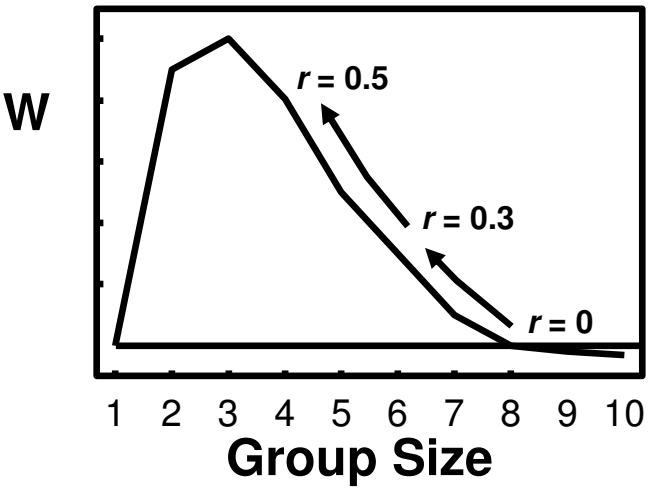
Group-Control: Predict **Group Size** Same or **Larger**
As Relatedness Increases



Free Entry


W
Optimal Size
Equilibrium Size
Group Size


r = 0.3
r = 0
r = 1.0
r = 0.5
1 2 3 4 5 6 7 8 9 10
Group Size


W
r = 0.5
r = 0.3
r = 0
1 2 3 4 5 6 7 8 9 10
Group Size

Group Controlled Entry