

$$Pr\{M_3 \approx m \mid \text{not killed}\}$$

$$= \frac{\alpha^\nu e^{-(\alpha+1)m} m^{\nu-1}}{\Gamma(\nu)}$$

$$\int_0^\infty \frac{\alpha^\nu e^{-(\alpha+1)m} m^{\nu-1}}{\Gamma(\nu)} dm$$

$$= \frac{e^{-(\alpha+1)m} m^{\nu-1}}{\int_0^\infty e^{-(\alpha+1)m} m^{\nu-1} dm} = \frac{\Gamma(\nu)}{(\alpha+1)^\nu}$$

$$Pr\{M_3 \approx m \mid \text{not killed}\} = \frac{(\alpha+1)^\nu e^{-(\alpha+1)m} m^{\nu-1}}{\Gamma(\nu)}$$

"Prior"  
 $\nu, \alpha$

visit patch 3  
→  
don't get killed

"Posterior"  
 $\nu, \alpha+1$

$$E\{M_3\} = \frac{V}{\alpha} \quad \text{Prior}$$

After a visit to patch 3 and not getting killed

$$E_{\text{Post}}\{M_3\} = \frac{V}{\alpha+1}$$

Two states : Energy leaves  $x$   
Information  $\alpha$

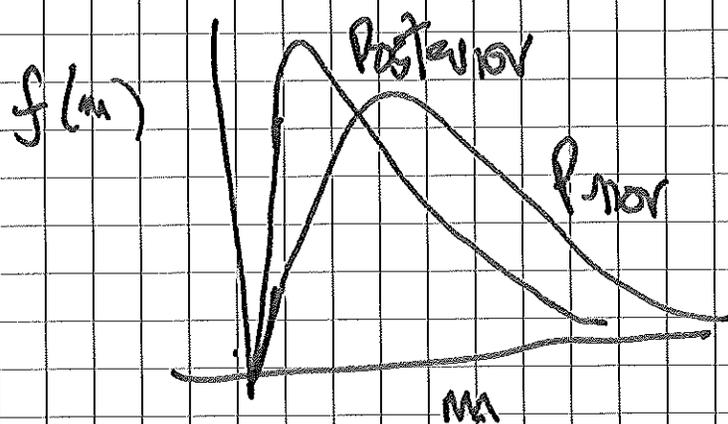
$$F(x, \alpha, t) = \max_i E\left\{ \Phi(x(\tau)) \mid X(t) = x, \right. \\ \left. \text{parameter for } M_3 \text{ is } \alpha \right\}$$

$$F(x, \alpha, T) = \Phi(x(T))$$

$$F(x, \alpha, t) = \max_i \left\{ V_i(x, \alpha, t) \right\}$$

$$V_2(x, \alpha, t) = e^{-m_2} \left[ \lambda_2 F(x - \alpha_2 + Y_2, \alpha, t+1) + (1 - \lambda_2) F(x - \alpha_2, \alpha, t+1) \right]$$

Visiting patch 2 cannot change the informational state



$$E\{M_3\} = \frac{2}{\alpha}$$

$$CV\{M_3\} = \frac{1}{\sqrt{2}}$$

$$V_3(x, \alpha, t) = \int_{m_3} e^{-m_3} \left[ \lambda_3 F(x - \alpha_3 + Y_3, \alpha, t+1) + (1 - \lambda_3) F(x - \alpha_3, \alpha, t+1) \right]$$

6.17

$$V_3(x, \alpha, t) = \int_0^{\infty} \alpha^\nu \frac{e^{-\alpha m}}{\Gamma(\nu)} m^{\nu-1} dm$$

$$e^{-m} \left[ \lambda_3 F(x - \alpha_3 + \gamma_3, \alpha + 1, t + 1) + (1 - \lambda_3) F(x - \alpha_3, \alpha + 1, t + 1) \right] dm$$

$$= \left[ \lambda_3 F(x - \alpha_3 + \gamma_3, \alpha + 1, t + 1) + (1 - \lambda_3) F(x - \alpha_3, \alpha + 1, t + 1) \right]$$

$$\int_0^{\infty} \alpha^\nu \frac{e^{-(\alpha+1)m}}{\Gamma(\nu)} m^{\nu-1} dm$$

$$V_3(x, \alpha, t)$$

$$= \left[ \lambda_3 e^{-\alpha} + (1-\lambda_3) e^{-\alpha} \right] \frac{\alpha^\nu}{\Gamma(\nu)} \int_0^\alpha e^{-(\alpha+1)u} u^{\nu-1} du$$

$$= \left[ \lambda_3 e^{-\alpha} + (1-\lambda_3) e^{-\alpha} \right] \frac{\alpha^\nu}{\Gamma(\nu)} \cdot \frac{\Gamma(\nu)}{(\alpha+1)^\nu}$$

$$V_3(x, \alpha, t) = \left[ \lambda_3 F(x - \alpha_3 + Y_3, \alpha+1, t+1) + (1-\lambda_3) F(x - \alpha_3, \alpha+1, t+1) \right] \left( \frac{\alpha}{\alpha+1} \right)^\nu$$

$$\frac{\alpha}{\alpha+1} < 1$$

$$E\{N_3\} = \frac{\nu}{\alpha} \text{ prior}$$



$$l^*(x, \alpha, t)$$

$$m_3 = \frac{\nu}{\alpha}$$

May 10 (noon) - Paper You Like

May 8

Monday May 13 - talk to your classmates

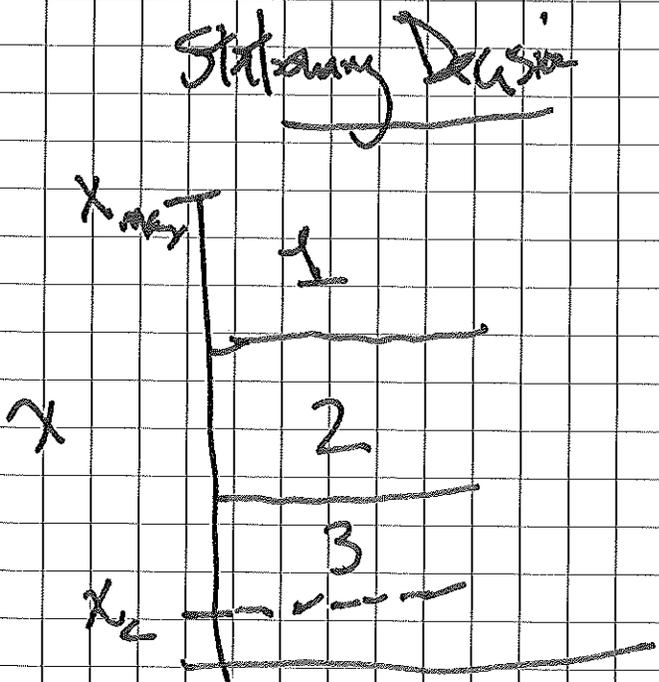
May 17 (midnight) - wake up to leave  
+ scientific paper

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## Informational Ecology - TLISHG

### Standard Patch Selection Model

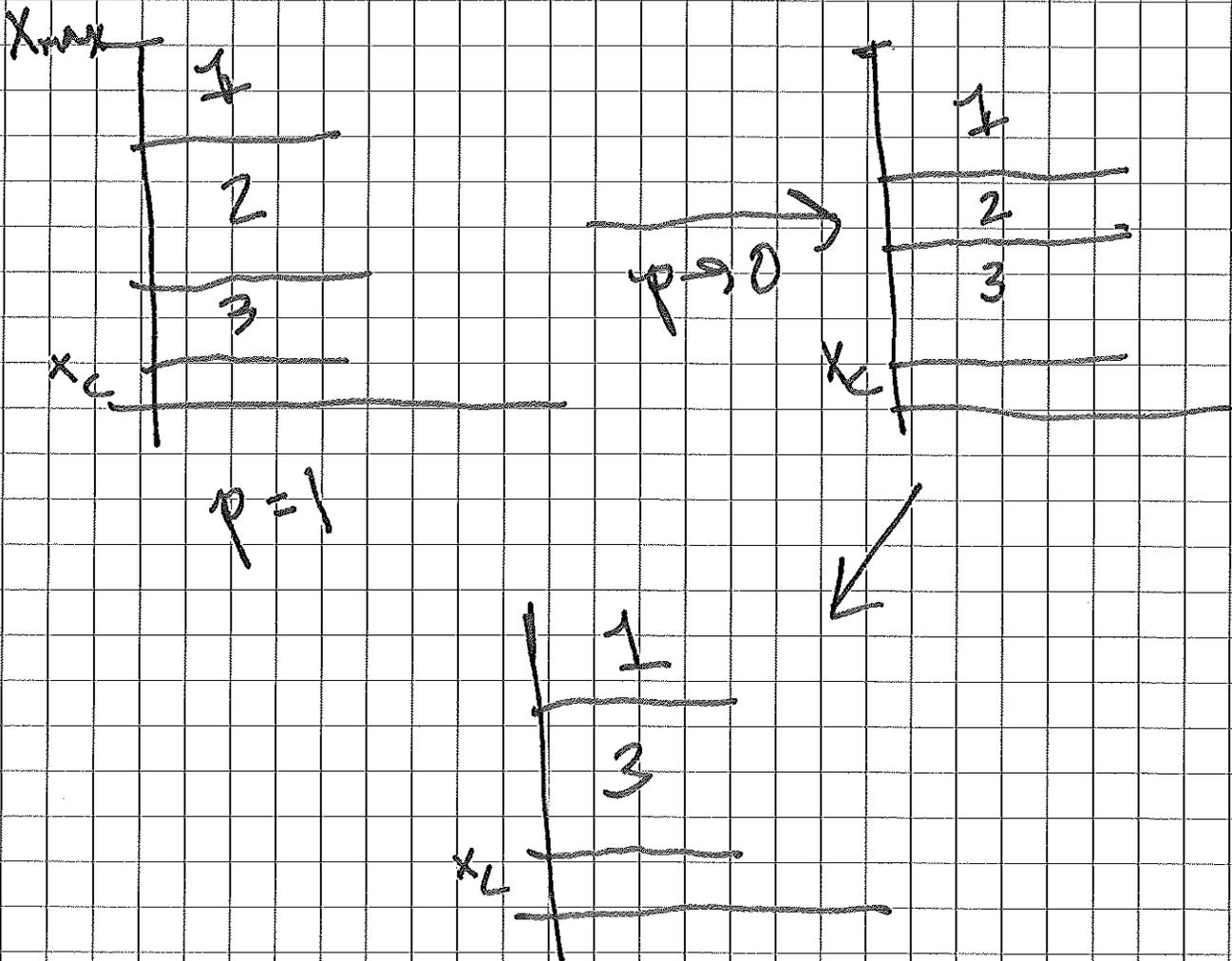
<u>Patch</u>	<u><math>\lambda_i</math></u>	<u><math>w_i</math></u>
1	0	0
2	0.4	0.004
3	0.6	0.0263



Suppose Peter's is now like this

$$m_3 = \begin{cases} 0.0203 & \text{(HPY) w.p. } p \\ = m_H & \\ 0.004 & \text{(LPY) w.p. } 1-p \\ = m_L & \end{cases}$$

Whether it is a HPY or LPY is fixed but not known to us forever



$$E\{\text{prob survival in patch } z\}$$

$$= p e^{-m_H} + (1-p) e^{-m_L}$$

SDP (Basic)

$$F(x, t) = \max_i \{V_i(x, t)\}$$

$V_1(x, t), V_2(x, t)$  are rote

What about  $V_3$

Choice 1

$$V_3(x, t) = e^{-m_H} \left[ \lambda_3 F(x - \alpha_3 + \psi_3, t+1) + (1 - \lambda_3) F(x - \alpha_3, t+1) \right]$$

Choice 2

$$V_3(x, t) = e^{-m_L} \left[ \begin{array}{c} \text{"} \\ \text{"} \end{array} \right]$$

Choice 3

$$V_3(x, t) = (p e^{-m_H} + (1-p) e^{-m_L}) \left[ \begin{array}{c} \text{"} \\ \text{"} \end{array} \right]$$

Strategy: ~~do~~ solve the SPP three times  
 (one for each choice) then do three forward  
 iterations to see which gives highest fitness  
 Forward simulations require choosing HPY or  
 LPY multiple times

Learning whether it is HPY or LPY

$$P\{HPY\} = p \quad \text{[start]} \quad \text{Prior}$$

Posterior

$$P\{HPY \mid \text{visited patch 3 and not killed}\}$$

$$= \frac{P\{\text{visited patch 3 and not killed} \mid HPY\} P\{HPY\}}{P\{\text{visited patch 3 and not killed}\}}$$

$$= \frac{e^{-m_H} p}{pe^{-m_H} + (1-p)e^{-m_L}} = p'$$

$$F(x, p, t) = \max E \left\{ \Phi(x(T)) \mid X(t) = x \right. \quad 8.4$$

current estimate  
for  $P_i \{HPV\} = p_i$

$$V_1(x, p, t), V_2(x, p, t) \sim \text{rate}$$

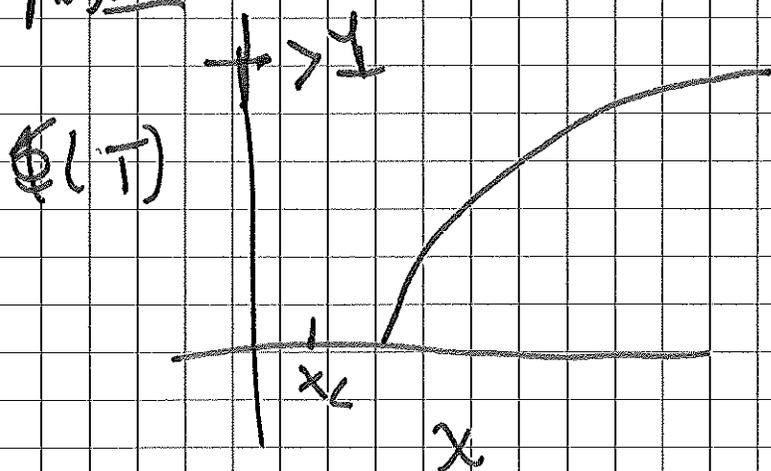
$$V_3(x, p, t)$$

$$= (p e^{-r_H} + (1-p) e^{-r_L})$$

$$\left[ \lambda_3 F(x - \alpha_3 + Y_3, p', t+1) \right.$$

$$\left. + (1 - \lambda_3) F(x - \alpha_3, p', t+1) \right]$$

Assume

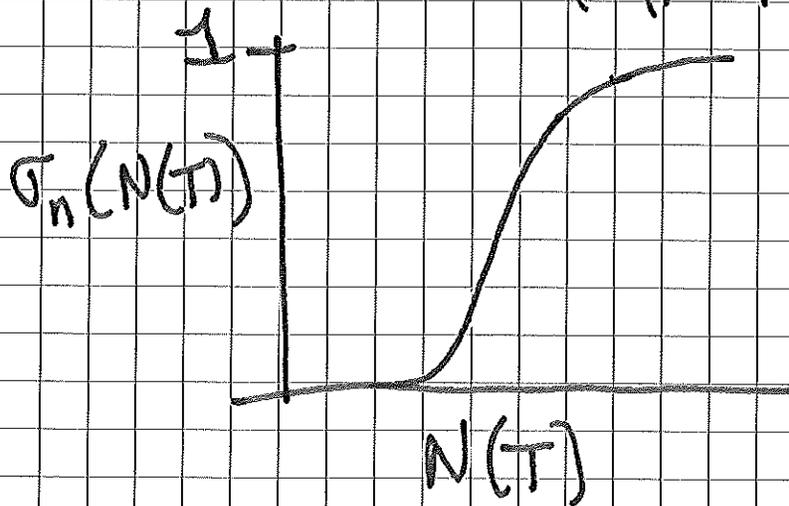


- $N_L$  (LPV)
- $N_H$  (HPV)
- $N_A$  (APV, etc.)
- $N_I$  (loan fra  
"fonta")

At T in any year

- Chick fledges successfully
- Mom has to survive the overwinter period

$$\sigma_n(N(T)) = P\{ \text{chick successfully fledges / parents at tree T are } N(T) \}$$



~~$$\sigma_p(X(T)) = P\{ \text{parent survives overwinter and successfully starts another nest / parents at tree T at } X(T) \}$$~~

# Parental Allocation

8.5

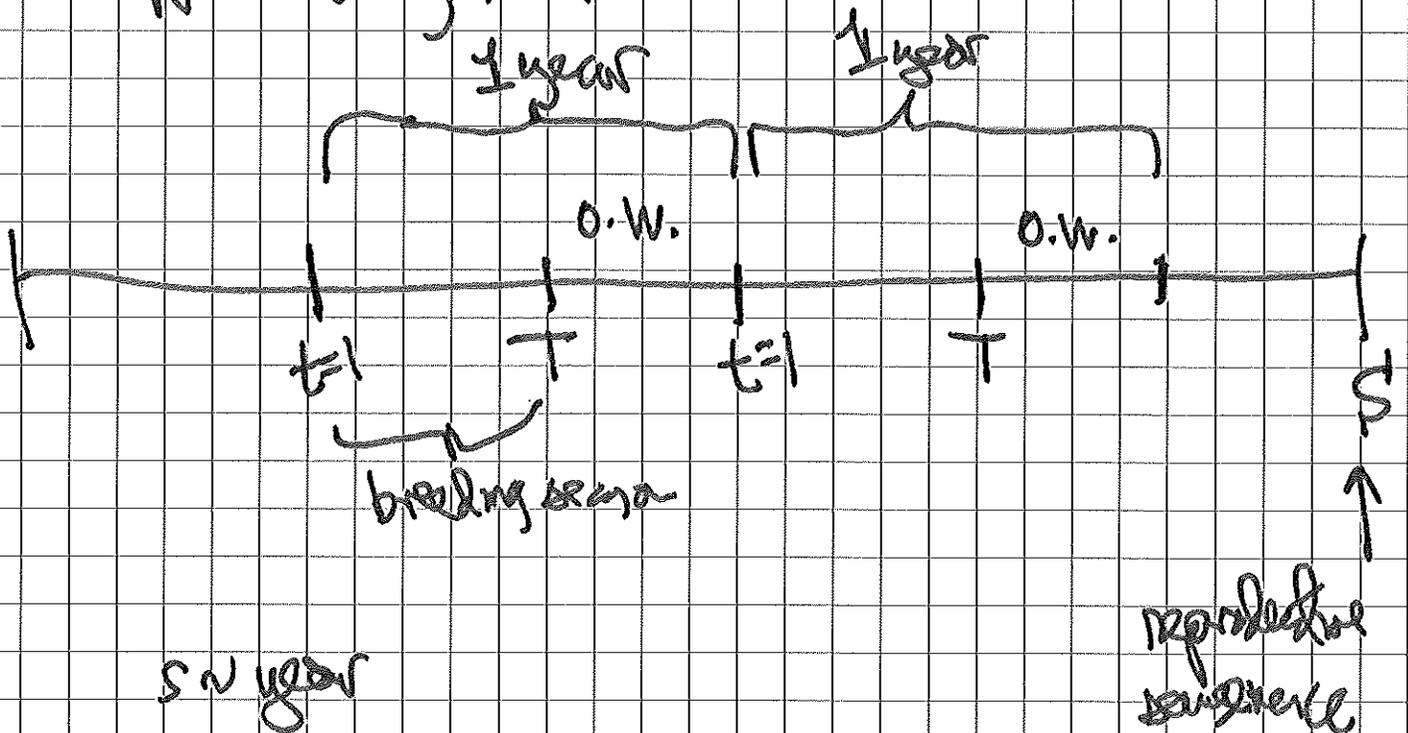
Long-lived seabird

1 baby/year

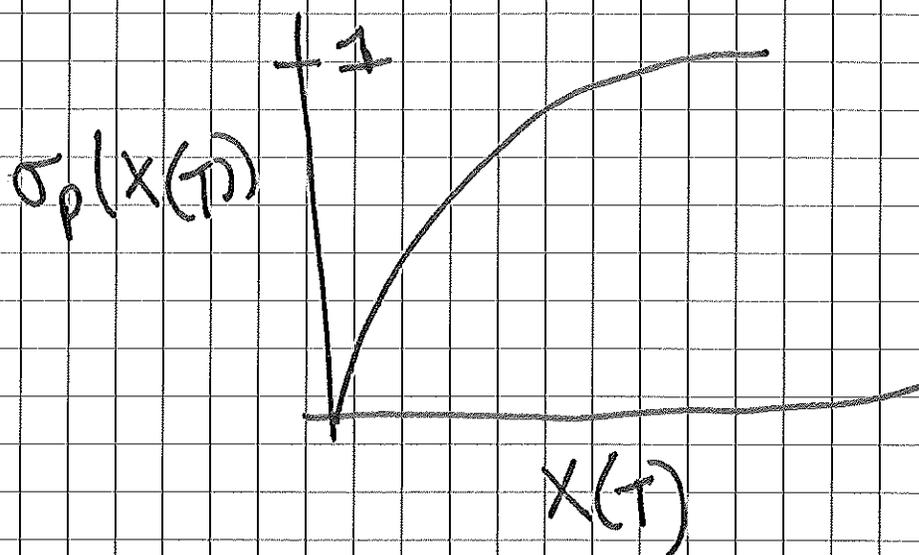
only one parent actually feeding

X ~ parental state

N ~ nesting state



$F(x, n, s, t) = \max E \{ \# \text{ of chicks produced} \}$   
between time  $t$  in ~~the~~ year  
 $s$  and ~~the~~ the time  
of senescence  $\{ X(t) = x, N(t) = n \}$



The final end condition

$$F(x, n, \frac{s}{T}, \frac{T}{T}) = \sigma_n(n) \leftarrow \text{Pr} \left\{ \text{her fledging survives} \right\}$$

In any other breeding year

$$F(x, n, s, T) = \sigma_n(n) \quad \text{initial mass of nestling}$$

$$+ \sigma_p(x) F\left(\frac{x}{1}, n, \frac{s}{1}, \frac{T}{1}\right)$$

her state at the  
start of a breeding season



Pseudo Code

Loop Over  $s$  (backwards in time)

Loop Over  $t$  (backwards in time)

Loop Over  $x \leftarrow$  Loop Over  $n$

If  $t \leq T \rightarrow$  sequential coupling

Else If ~~not~~  $t < T$

Loop over  $i$ , ask find  $food?$

N

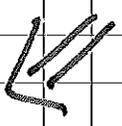
$V_i$  is given by  
 (A) in  
 the SDP

Y

Loop over  $g$   
 ( $0 \leq g \leq 1$ ) to  
 compute the best  
 allocation from (B)  
 in the SDP

$v^*(x, n, s, t)$

$p_i^*(x, n, s, t)$



Suppose there is predation of the nest,  $m_p(i)$

(8.10)

predation of the nest  $\Rightarrow$  man gives up for this year

$$F(x, n, s, t) = \max_i \left\{ e^{-m_i} e^{-m_p(i)} \left[ (1 - \lambda_i) F(x - \alpha_p, n - \alpha_n, s, t+1) \right. \right.$$

$$\left. \left. + \lambda_i \max_p F(x - \alpha_p + p Y_i, n - \alpha_n + (1-p) Y_i, s, t+1) \right] \right\}$$

$$+ e^{-m_i} (1 - e^{-m_p}) \left[ (1 - \lambda_i) F(x - \alpha_p, 0, s, t+1) \right.$$

$$\left. \left. + \lambda_i F(x - \alpha_p + Y_i, 0, s, t+1) \right] \right\}$$

20 May 2013

WEDS 22 MAY: NO CLASS, CODING DAY //

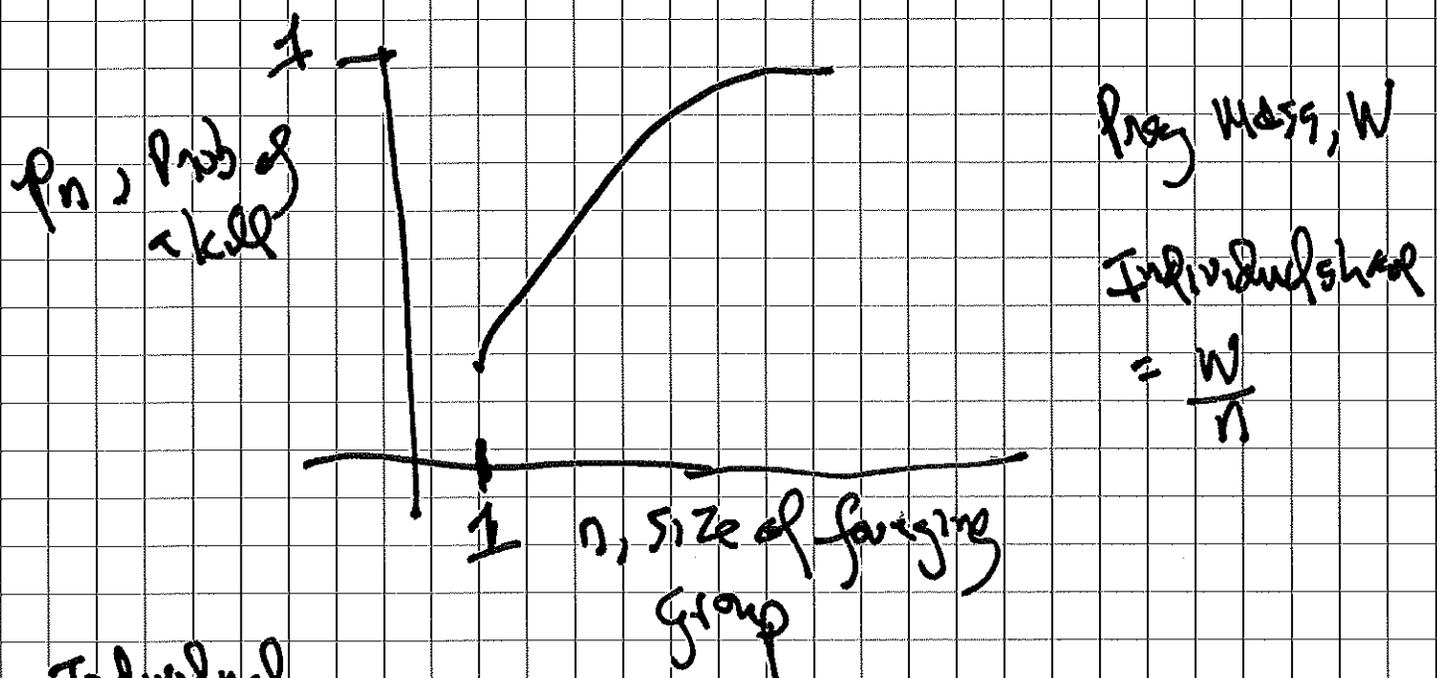
Mathematics & Sports

J.B. Keller

Warmup //

Squash Leader

Warmup for Dynamic Games: Group Foraging



Individual  
^ Feeding rate in a group of size  $n$ ,  $F_n = p_n \cdot \frac{W}{n}$

$$F_n = p_n \frac{W_n}{n} = E[\text{food share}]$$

$$V_n = \text{Variance} [\text{food share}]$$

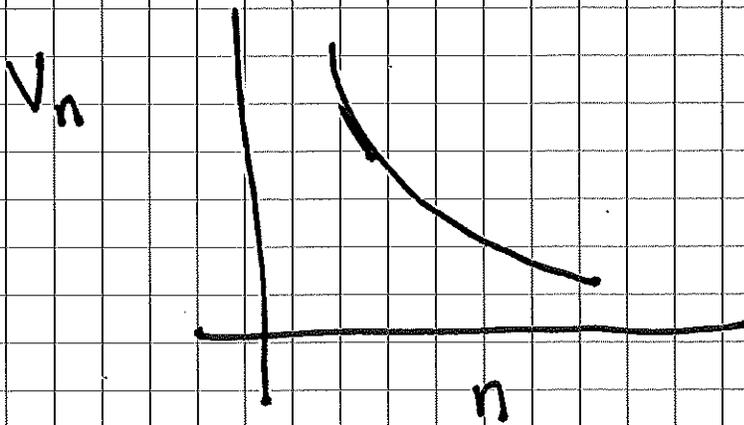
$$= p_n \left\{ \left( \frac{W}{n} \right)^2 \right\} - (F_n)^2$$

$$= p_n \left( \frac{W}{n} \right)^2 - p_n^2 \left( \frac{W}{n} \right)^2$$

$$= p_n (1 - p_n) \left( \frac{W}{n} \right)^2$$

Variance of a Bernoulli trial

$E\left\{ (\text{food share})^2 \right\}$



Food share =  $\begin{cases} W/n & \text{w.p. } p_n \\ 0 & \text{w.p. } 1-p_n \end{cases}$

Manged  
Clark 1988

Table 3.1  
Success rates for lion hunts\*

group size	T. Gazelle		Wildebeest & Zebra		Other	
	no. hunts	% success	no. hunts	% success	no. hunts	% success
1	185	15	33	15	31	19
2	78	31	17	35	11	9
3	42	33	16	13	5	20
4-5	42	31	16	37	4	25
6+	15	33	21	43	7	0

\*From Schaller 1972, Table 59.

### 3.1 The Serengeti Lion

Schaller (1972) observed a total of 523 chases of prey by Serengeti lions, and recorded the success rates for hunting groups of different sizes—see Table 3.1. Slightly more than half the hunts (274 out of 523) were undertaken by groups of lions; for zebra or wildebeest prey, nearly 70% of the hunts were by groups. With some exceptions, groups experienced a higher success rate than individuals. If, as a first approximation, we ignore the fact that females must usually share their kills with males and young, then the average individual food recovery per chase  $\bar{f}$  can be expressed as

$$\bar{f} = \frac{p_n \bar{W}}{n} \quad (3.1)$$

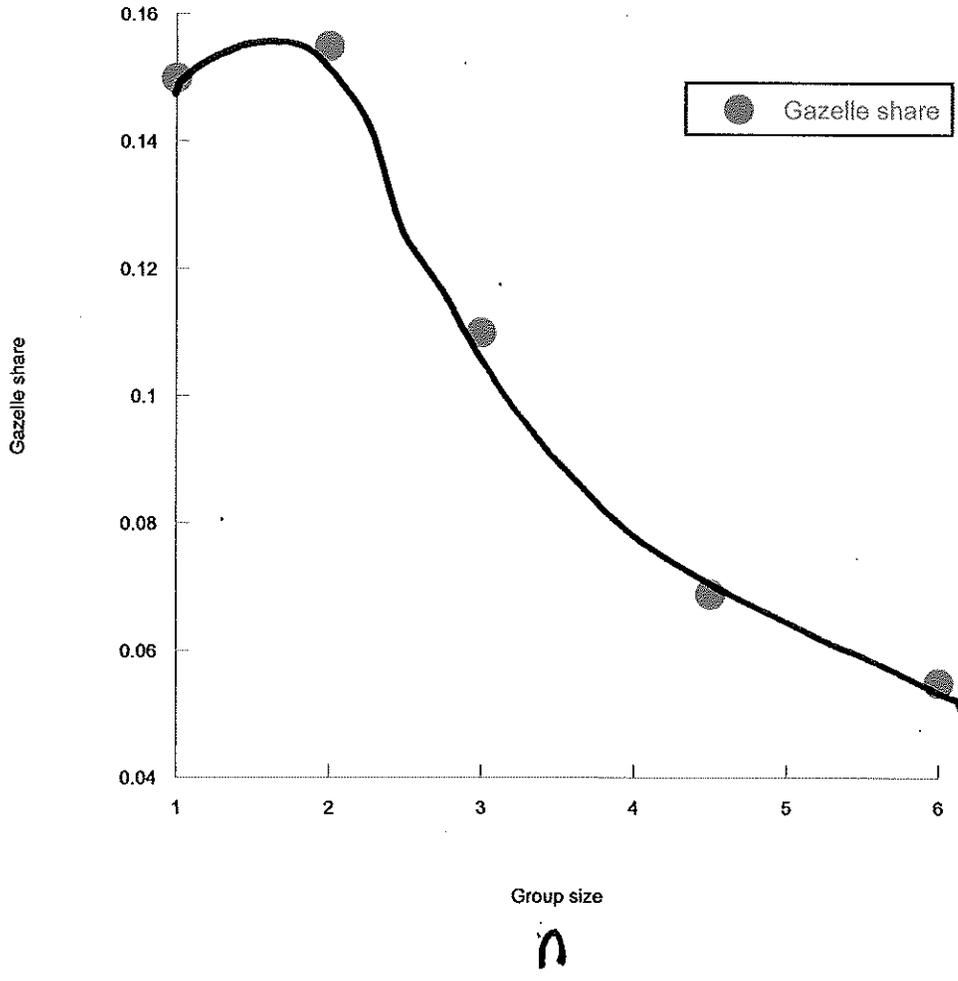
where  $n$  = hunting group size,  $p_n$  = probability of successful hunt, and  $\bar{W}$  = average weight of prey. Note from Table 3.1 that this measure of success gives a slight advantage to groups of size two (relative to single hunters) for Thomson's gazelle, and a somewhat larger advantage for wildebeest and zebra. Groups larger than two are never advantageous on these terms, yet larger groups are frequently observed (Table 3.2).

A more detailed analysis of average individual daily feeding rates as a function of hunting group size was given by Caraco and Wolf (1975), who included such additional features as multiple kills, scavenging by hyenas, and ecological circumstances

Thompson's Gazelle

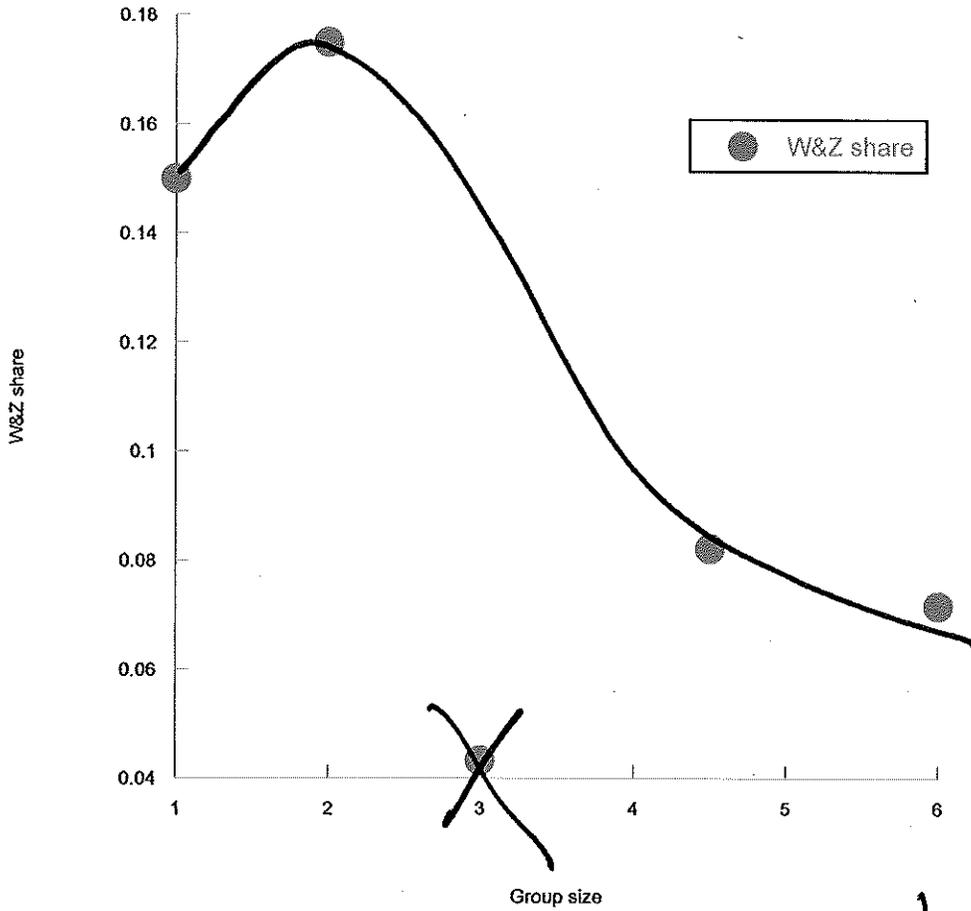
20.3

$$P_n = \frac{k}{n}$$



Group size  
n

Wildebeest and Zebra



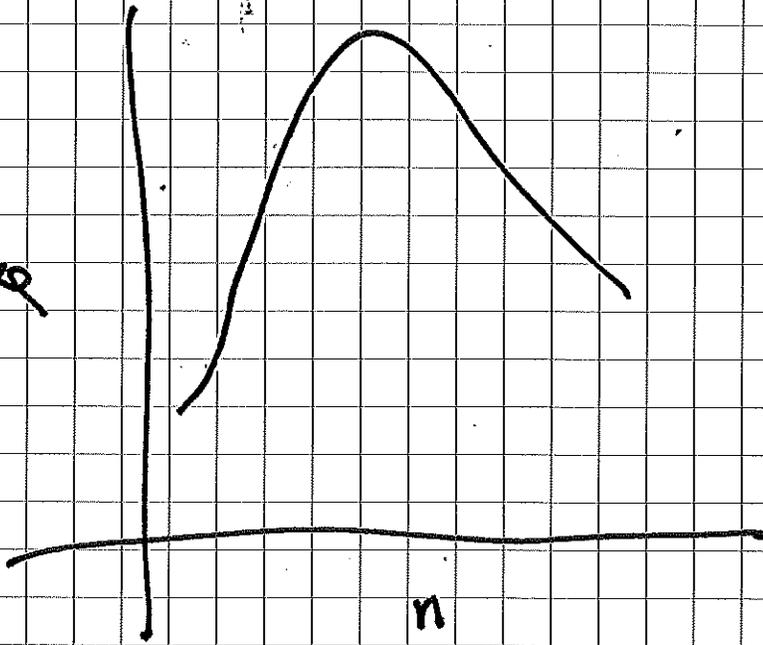
These suggest an optimal group size

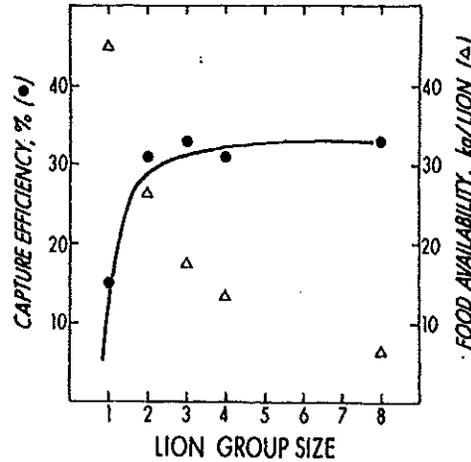
Casero and Wolf 1975

20.5

Av. Dat 109: 343 - 352

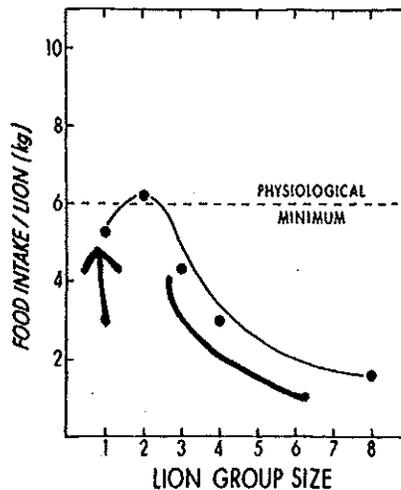
Food  
Intake





Gazelle

FIG. 1.—Capture efficiency and food availability per lion vs. lion group size. Solid line, showing efficiency of capture of Thomson's gazelle as a function of lion group size, has been visually fitted to observed data. Triangles indicate mean available prey biomass (kg) per lion per three captures (corrected for multiple kills) for each lion group size. Three chases approximate daily prey availability during dry season along woodlands-plains border. A daily average of three chases is predicted minimum for group of any size to physiologically sustain itself on Thomson's gazelle. Data from Schaller (1972).

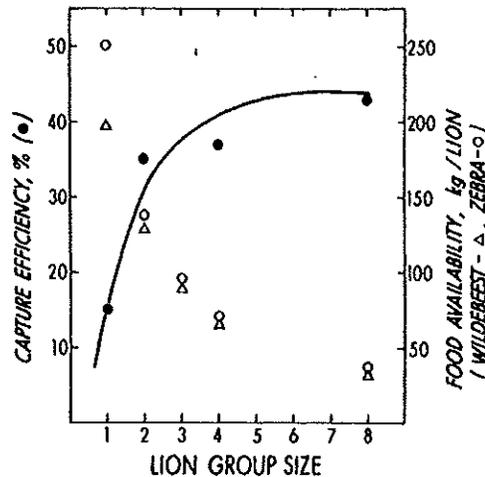


$n=2$  is optimal  
but also  
essential

FIG. 2.—Mean edible prey biomass (kg) per lion per three chases (predicted daily index) as a function of lion group sizes preying on Thomson's gazelle. Dashed line at intake of 6 kg represents daily physiological minimum requirement for an individual lion, males and females averaged.

intake is the greatest, and the individuals maximize their energetic benefit-to-cost ratio.

Schaller, citing a number of studies in addition to his own observations, concluded that adult male lions require an average of 7 kg of meat per day to remain healthy. Females require an average of 5 kg of meat per day as a physiological minimum. We employ 6 kg per lion as the daily minimum intake

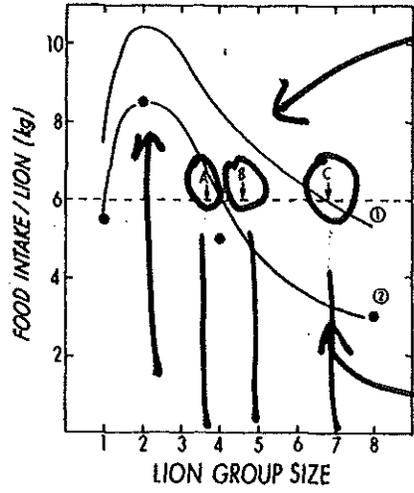


Wildebeest / Zebra

FIG. 3.—Capture efficiency and food availability per lion vs. lion group size. Solid line, showing efficiency of capture of wildebeest and zebra as a function of lion group size, has been visually fitted to observed data. Schaller's report of low capture efficiency for three lions has been omitted; we doubt that three lions have a lower capture efficiency than pairs. Triangles indicate mean available prey biomass (kg) per lion per wildebeest capture (corrected for multiple kills) for each lion group size. Circles represent similar calculations for lions preying on zebra. Data from Schaller (1972) and Kruuk (1972).

The actual mean availability per lion for these large prey animals incorporates several associated factors. Schaller estimated that 62.5% of the biomass is palatable to lions. Hyenas are ecologically very similar to lions and aggressively attempt to scavenge lion kills (Kruuk 1972). The combined observations of Schaller (1972) and Kruuk (1972) indicate that, if less than four lions share a carcass, lions lose about 10% of the meat they capture, as an average over all habitats. Four or more lions suffer negligible losses to scavengers. Additionally, Schaller found that a wildebeest or zebra carcass lasted 3 days on the average, and lions tended not to kill again until they had consumed their capture. Combining these observations and dividing the prey biomass by lion feeding-group size gives the expected mean intake available daily to each lion. For each group size of lions preying on wildebeest or zebra, we can calculate: mean edible weight (kg) per lion = mean carcass weight (kg) × capture efficiency (for each group size) × multiple-kill correction × palatability × loss to scavengers (for group sizes less than four) ×  $\frac{1}{3}$  mean carcass proportion consumed per 24 h ÷ lion group size. Figures 4 and 5, which are plots of the values as functions of lion group size, show the approximate daily food-intake curves and give reported mean group sizes for different habitats. We again assume that an individual's energetic expenditure per hunt is independent of foraging-group size and that hunting time budgets are equal. Two lions should have the greatest daily intake available and will receive the greatest reward for an equal energetic investment in hunting. However, groups with a mean of 1.0–4.0 lions still attain the minimum physiological daily requirement of 6 kg.

Wildebeest

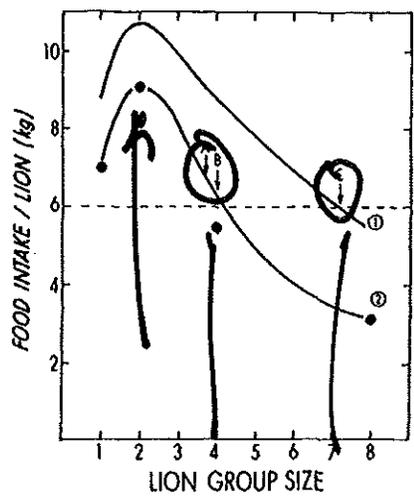


wet season

dry season

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).

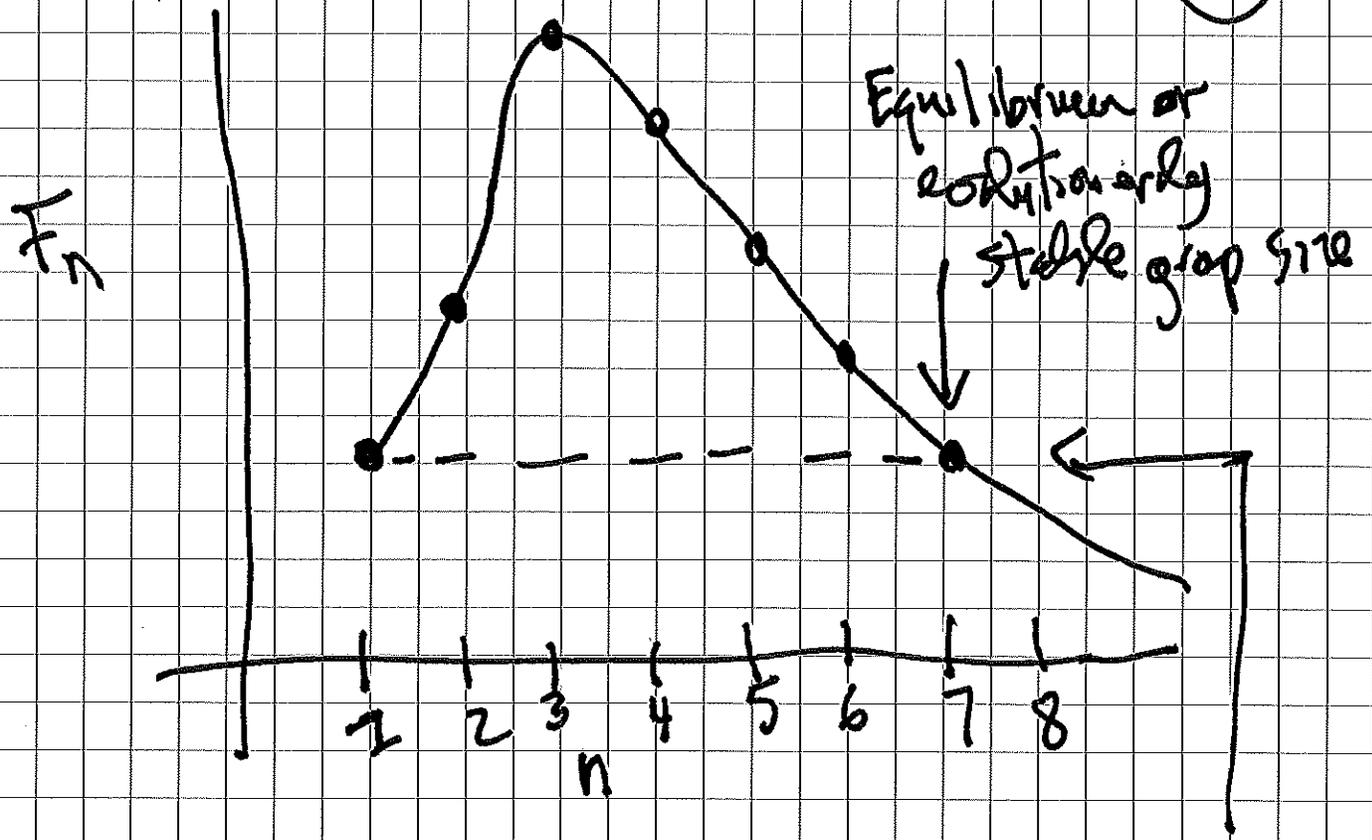
Zebra



William Feller  
 "Problems are not solved by ignoring them"

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).

20.8



Put lions on the landscape

"Two is good, three is better"

⇒ optimal group size

"Four is better than one"

"Still better than one"

No individual can do it in a way to give itself a higher rate of return

# Evolutionarily Stable Strategy (ESS)

20.1

W.D. Hamilton (1936-2000)

Nature's Oracle (U. Segerstrale)

John Maynard Smith (1920-2005)

Evolution and the Theory of Games (1982)

$I \sim$  behavior/strategy of our focal individual  
 $J \sim$  " " " rest of the population

$W(I, J)$  = fitness of the focal individual  
adopting strategy  $I$  in a population  
of  $J$ -strategists

$J$  is an ESS if

$W(J, J) \geq W(I, J)$  with the equality holding  
only when  $I=J$

(A Beautiful Mind S. Dasgupta) Nash Equilibrium

# Extraordinary Sex Ratio

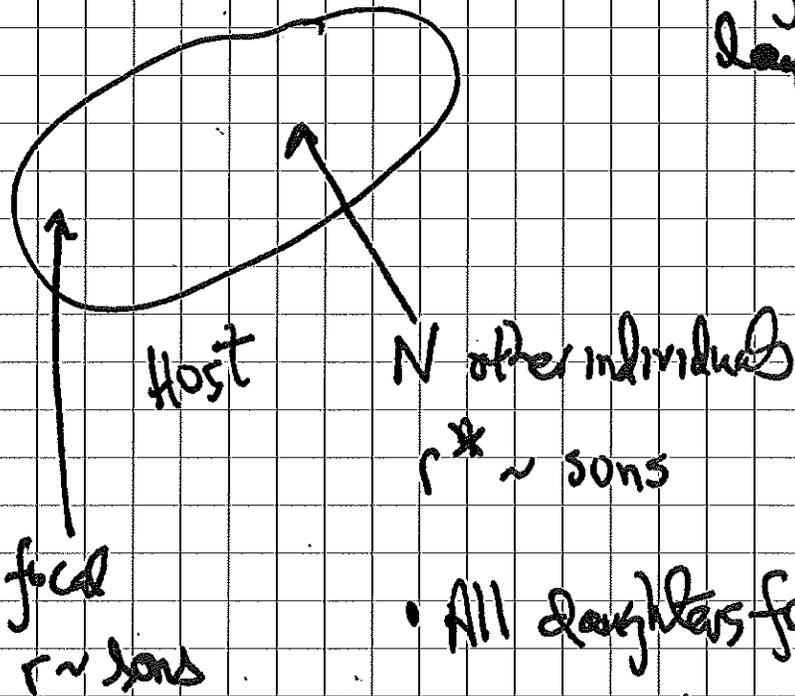
1930s R A Fisher argued sex ratios should be  $\sim 50:50$

## Insect Parasitoids

Highly skewed sex ratio

gregarious parasitoid  
lays  $\phi$  eggs

Local Mate Competition



- All daughters fertilized
- Sons compete for fertilizations

Fitness measure: grand offspring

20.11

N focal

daughters ♀ :  $C(1-r) \rightarrow C^2(1-r)$  grand offspring  
from daughters

sons ♂ :  $Cr$

Total number of daughters from this host

$$C(1-r) + N C(1-r^*)$$

↓  $\times C$  offspring / ♀

$$= C^2 [(1-r) + N(1-r^*)] \text{ grand offspring from this host}$$

Fraction of sons that she's produced

$$\frac{Cr}{Cr + NCr^*} = \frac{r}{r + Nr^*}$$

$$W(r, r^*) = c^2(1-r) + \frac{r}{r+Nr^*} \left[ c^2(1-r) + c^2 N(1-r^*) \right]$$

What does it mean that  $r^*$  is an ESS

$$W(r^*, r^*) \geq W(r, r^*) \quad \text{for any } r$$

with equality  
holding only  
when  $r = r^*$

To find  $r^*$  we set

$$\left. \frac{d}{dr} W(r, r^*) \right|_{r=r^*} = 0$$

- ① Find the derivative of  $W(r, r^*)$  wrt  $r$
- ② Set  $r = r^*$ , the derivative = 0
- ③ Solve for  $r^*$

2013

When ~~you~~ this is done, we get

$$r^* = \frac{N}{2(N+1)}$$

Hamiltonian ~~xx~~  
ratio

$$N \rightarrow \infty$$

$$N \rightarrow 0$$

$$r^* \rightarrow \frac{1}{2}$$

$$r^* \rightarrow 0$$

Fisher's result

What does this mean?

Make just enough son to  
fertilize all your daughters

20.14

- Games Against Conspecifics
- Predator-Prey Games

Quirk and Nagel (2000) pg 214 ff:

→ Frequency dependent predation.

Two comments

① P of survival in patch  $i$  =  $1 - m_i f_i$   
or  $e^{-m_i f_i}$

② Markov chain for forward iteration  
(no Monte Carlo simulation)

→ just think you're doing a Monte Carlo

29 May

## Timetable

Projects due to me by Jun 17 //

## Environment & Correlation

$E(t)$  = environment at time  $t$

$$= E_1, E_2, \dots, E_N$$

$$P_{ij} = P_i \{ E(t+1) = E_j \mid E(t) = E_i \}$$

$$P_j(t) = P_i \{ E(t) = E_j \}$$

$$P_1(t+1) = P_1(t)P_{11} + P_2(t)P_{21} + P_3(t)P_{31} + \dots + P_N(t)P_{N1}$$

$$P_2(t+1) = P_1(t)P_{12} + P_2(t)P_{22} + P_3(t)P_{32} + \dots$$

⋮

$$P_N(t+1) = P_1(t)P_{1N} + \dots$$

We write this as

$$\begin{pmatrix} I_1(t+1) \\ I_2(t+1) \\ \vdots \\ I_N(t+1) \end{pmatrix} = \begin{pmatrix} p_{11} & p_{21} & p_{31} & \dots & p_{N1} \\ p_{12} & p_{22} & & & \\ & & \ddots & & \\ & & & & p_{NN} \end{pmatrix} \begin{pmatrix} I_1(t) \\ I_2(t) \\ \vdots \\ I_N(t) \end{pmatrix}$$

↑  
vector

At least formally (this is also true)

$$\begin{pmatrix} I_1(t+\tau) \\ I_2(t+\tau) \\ \vdots \\ I_N(t+\tau) \end{pmatrix} = \begin{pmatrix} p_{11} & p_{21} & p_{31} & \dots \\ & \ddots & & \\ & & \ddots & \\ & & & \ddots \end{pmatrix}^\tau \begin{pmatrix} I_1(t) \\ I_2(t) \\ \vdots \\ I_N(t) \end{pmatrix}$$

e.g.

$$\begin{pmatrix} I_1(t) \\ \vdots \\ I_N(t) \end{pmatrix} = \begin{pmatrix} 0 \\ 1 \\ 0 \\ 0 \\ \vdots \end{pmatrix}$$

↔ being in environment 2 at time t

$$\begin{pmatrix} p_{11} & p_{21} & \dots & p_{N1} \\ & \ddots & & \\ & & \ddots & \\ & & & p_{NN} \end{pmatrix}^T$$

→ for purposes of SDP  
we can compute this  
once outside of the  
SDP

## BACK TO DYNAMIC STATE VARIABLE GAMES

A strategy  $J$  is an ESS if

$$W(J, J) \geq W(I, J) \text{ for all } I \text{ with equality holding only when } I=J$$

↑  
fitness of an individual  
playing strategy  
 $J$  against a field  
playing strategy  $J$

- Nash Equilibrium
- The ESS is the best response to the environment it creates

# Foraging with Interference Competition

29.3

$$\lambda_i(n_i) = \frac{\lambda_{i0}}{1 + \epsilon n_i} \quad V_i = \frac{V_{i0}}{1 + n_i}$$

↑  
number of other  
individuals in  
patch  $i$

↑  
strength of interspecific  
competition

If we know  $n_i$  then we get

$$F(x, \vec{n}_i, t) = \max_i \left\{ V_i(x, \vec{n}_i, t) \right\}$$

$$V_i(x, \vec{n}_i, t) = e^{-n_i} \left[ \lambda_i(n_i) F(x - \alpha_i, \vec{n}_i, t+1) + (1 - \lambda_i(n_i)) F(x - \alpha_i, \vec{n}_i, t+1) \right]$$

↓

$$x^*(x, \vec{n}_i, t)$$

But what of other individuals behavior?

29.4

Patch visitation strategy ( $i^*(x,t)$ ) of our focal individual is an ESS if it is the best response to the environment set up by other individuals using  $i^*(x,t)$

Suppose we give all the other individuals a strategy  $j^*(x,t)$  ← generator of decisions for the population

↓  
 $\lambda_i(t), Y_i(t)$  for each patch at each time by forward iteration

We'd now solve

$$F(x,t) = \max_i \left[ e^{-u_i} \lambda_i(t) F(x - \alpha_i + Y_i(t), t+1) + e^{-m_i} (1 - \lambda_i(t)) F(x - \alpha_i, t+1) \right]$$

If  $v^*(x,t)$  coming out of this SDP  
was equal to  $j^*(x,t)$  [the strategy going into  
the SDP] then we have the ESS.

If those don't match, then we can try replacing  
 $j^*(x,t)$  by  $v^*(x,t)$  and doing the Forward  
and Backward again.

But this can lead to oscillations in strategy space

J. M. McNamara "Errors" in Decision Making

(Clark and Mangel 2000, pg 220ff)

give a strategy to the population  $\Rightarrow \lambda_i(t), \psi_i(t)$  29.6

$$F(x,t) = \max_i V_i(x,t)$$

$$V_i(x,t) = e^{-\psi_i} \left[ \lambda_i(t) F(x - \alpha_c + \psi_i(t), t+1) + (1 - \lambda_i(t)) F(x - \alpha_c, t+1) \right]$$

let's let  $V^*(x,t) = \max_i V_i(x,t)$

We create

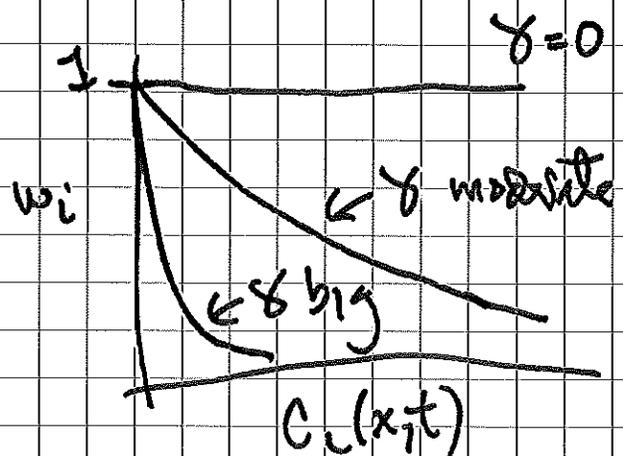
$$C_i(x,t) = V^*(x,t) - V_i(x,t)$$

fitness cost of being sub-optimal

Now let's set

$$w_i = e^{-\delta C_i(x,t)}$$

parameter



29.7

let

$$\mu_i(\gamma) = \frac{w_i}{w_1 + w_2 + w_3} = \text{pr} \{ \text{individual uses path } i \}$$

$$\begin{array}{l} \swarrow \\ \delta \rightarrow 0 \\ \mu_i \rightarrow 1/3 \end{array}$$

$$\begin{array}{l} \searrow \\ \delta \rightarrow \infty \\ \mu_i \approx 1 \\ \mu_i \approx 0 \text{ of } i \neq i^* \end{array}$$

$$\tilde{F}(x, t | \gamma) = E \left\{ \Phi(X(T)) \mid X(t) = x, \gamma \text{ is used to determine the } \mu_i \right\}$$

$$= \sum_{i=1}^3 \mu_i(\gamma) e^{-\mu_i} \left[ \lambda_i(t) \tilde{F}(x - \alpha_i + \gamma_i(t), t+1) + (1 - \lambda_i(t)) \tilde{F}(x - \alpha_i, t+1) \right]$$

The procedure is

- ① Specify  $\lambda_i(t), \gamma_i(t)$
- ② Solve the iteration equations for  $\tilde{F}(x, t)$   
This generates  $\lambda_i'$  (depending on  $\sigma, x, t$ )
- ③ Forward simulate once more. Generate  $\lambda_i''(t), \gamma_i''(t)$ .
- ④ If these  $\uparrow$  "equal"  $\lambda_i(t), \gamma_i(t)$ . Done  
Otherwise replace  $\lambda_i(t)$  by  $\lambda_i'(t)$   
 $\gamma_i(t)$  by  $\gamma_i'(t)$  and go back  
to step 2.

What does equal mean?

$$\sum_i \sum_t |\lambda_i(t) - \lambda_i'(t)|$$

3 June

PAM DWAC

H. Farnelo The Strangest Man

Predator Prey Bases in the Bering Sea

Killer whales (orcas)

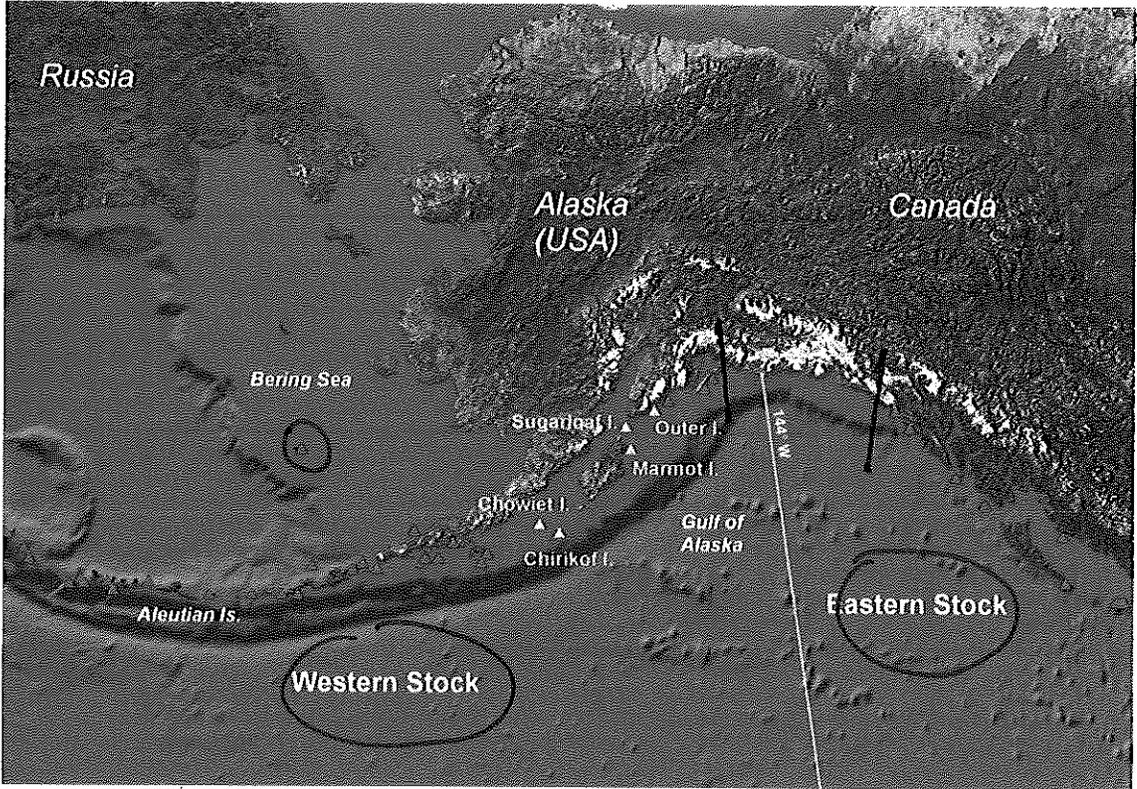
Stellar Sea lions

Wolff and Mangel *Ecol. Ecol. Research*

9:1293 (2007)

"

*Ecol Applic* 18:1932 (2008)



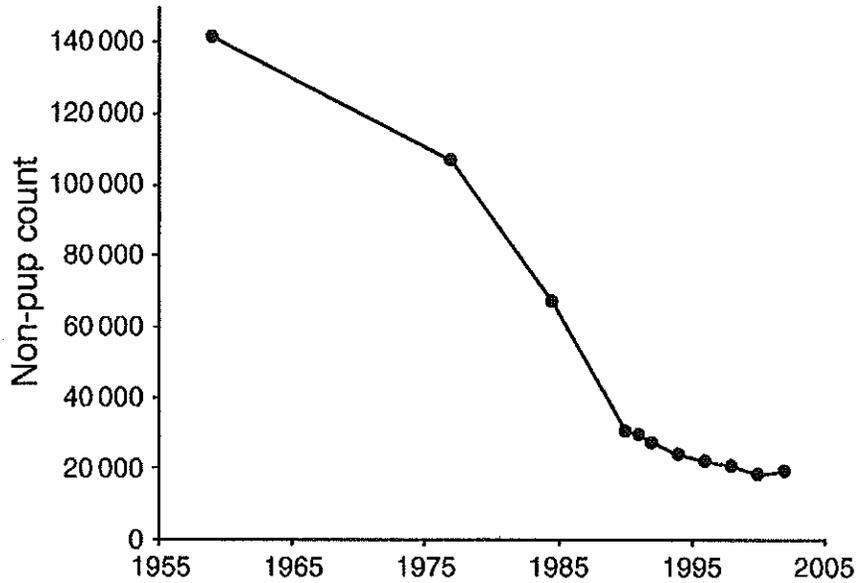
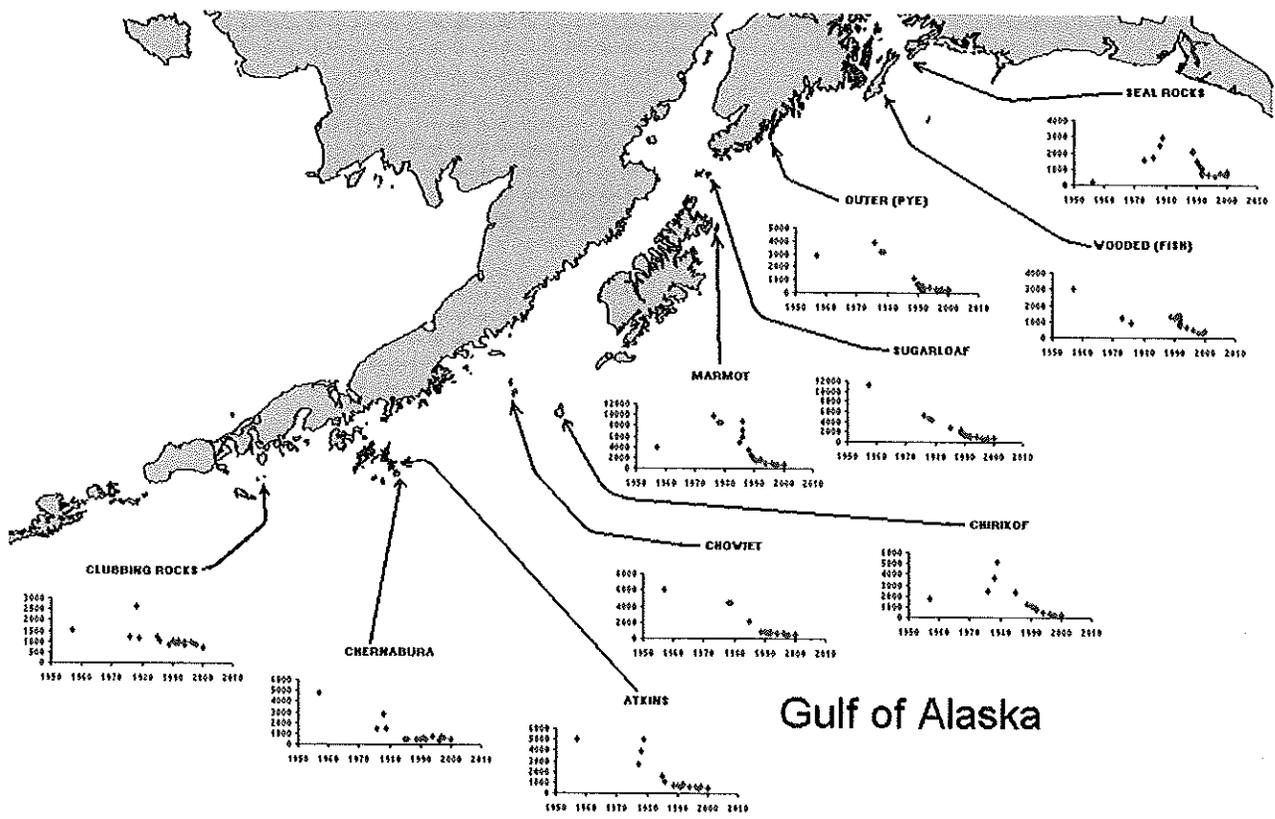


FIG. 1. Total non-pup counts for the western population of Steller sea lions (*Eumetopias jubatus*), ca. 1959–2002, showing the 11 years when range-wide totals were available (Merrick et al. 1987, National Marine Fisheries Service). The western population extends from 144° W longitude to the western tip of the Aleutian island chain. The sheer magnitude of the decline is obvious in this composite figure, but the spatial structure is not.



34

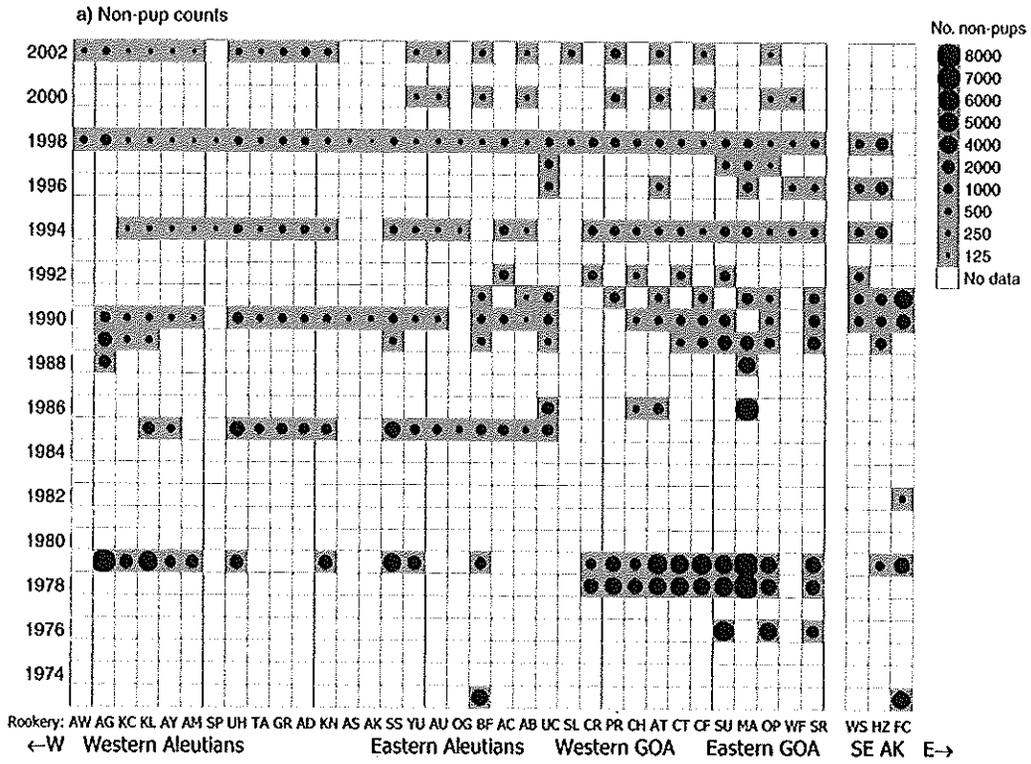


FIG. 2. Steller sea lion counts for individual rookeries in the Aleutian Islands, (GOA, Gulf of Alaska), and southeast Alaska (SE AK), 1973–2002. Even though not every population was censused in every year, many more data are available at this scale. Each column represents a rookery (see Appendix A: Table A1 for full rookery names); each row is a year. Panels (a) and (b) show non-pup and pup counts, respectively. Panel (c), in which the pup count has been divided by the non-pup count, provides an index of fecundity.

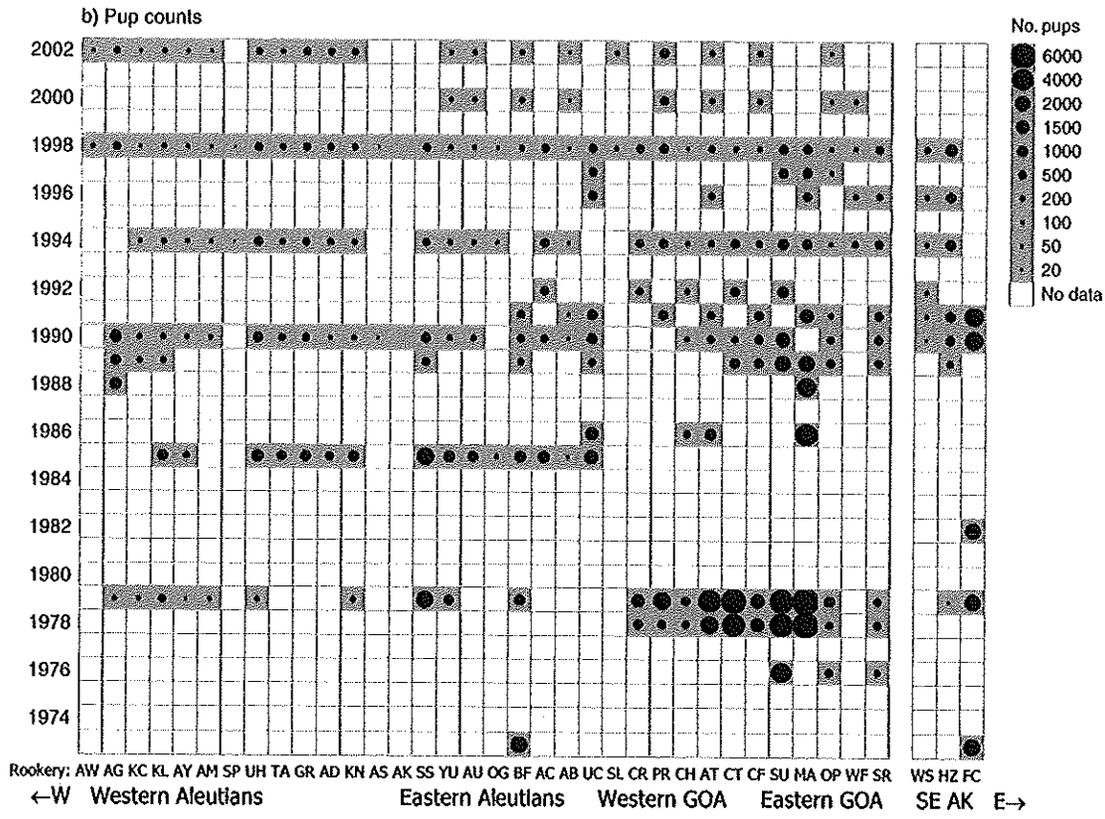


FIG. 2. Continued.

TABLE 1. The 10 hypotheses and their respective parameters.

Hypothesis	Parameter and mechanism of decline
Category I: insufficient prey availability	
$H_1$ : lower prey density $\rightarrow$ lower fecundity rate	$c_1$ , prey density increment per unit encounter rate; foraging shortfalls terminate pregnancy
$H_2$ : lower prey density $\rightarrow$ less pup recruitment	$c_2$ , prey density increment per unit encounter rate; foraging shortfalls cause pup starvation
$H_3$ : lower prey density $\rightarrow$ lower non-pup survival	$c_3$ , prey density increment per unit encounter rate; shortfalls cause non-pup starvation
Category II: unsuitable prey species composition	
$H_4$ : higher pollock fraction $\rightarrow$ lower fecundity rate	$c_4$ , exponent of non-pollock prey fraction in fecundity multiplier
$H_5$ : higher pollock fraction $\rightarrow$ less pup recruitment	$c_5$ , exponent of non-pollock prey fraction in pup recruitment multiplier
$H_6$ : higher pollock fraction $\rightarrow$ lower non-pup survival	$c_6$ , exponent of non-pollock prey fraction in non-pup survival multiplier
Category III: direct mortality due to fishing activities	
$H_7$ : more fishing activity $\rightarrow$ less pup recruitment	$c_7$ , pup mortality rate per fishery gear deployment within 20 km of rookery
$H_8$ : more fishing activity $\rightarrow$ lower non-pup survival	$c_8$ , non-pup mortality rate per fishery gear deployment within 20 km of rookery
Category IV: enhanced depredation by killer whales or sharks	
$H_9$ : fewer harbor seals (more predation) $\rightarrow$ less pup recruitment	$c_9$ , fraction of potential pup recruitment lost when harbor seal density $< h_{crit}$
$H_{10}$ : fewer harbor seals (more predation) $\rightarrow$ lower non-pup survival	$c_{10}$ , fraction of potential non-pup survival lost when harbor seal density $< h_{crit}$
$H_9, H_{10}$	$h_{crit}$ , harbor seal density below which sea lions become prey to killer whales

It's food

It's fishing

It's killer whales

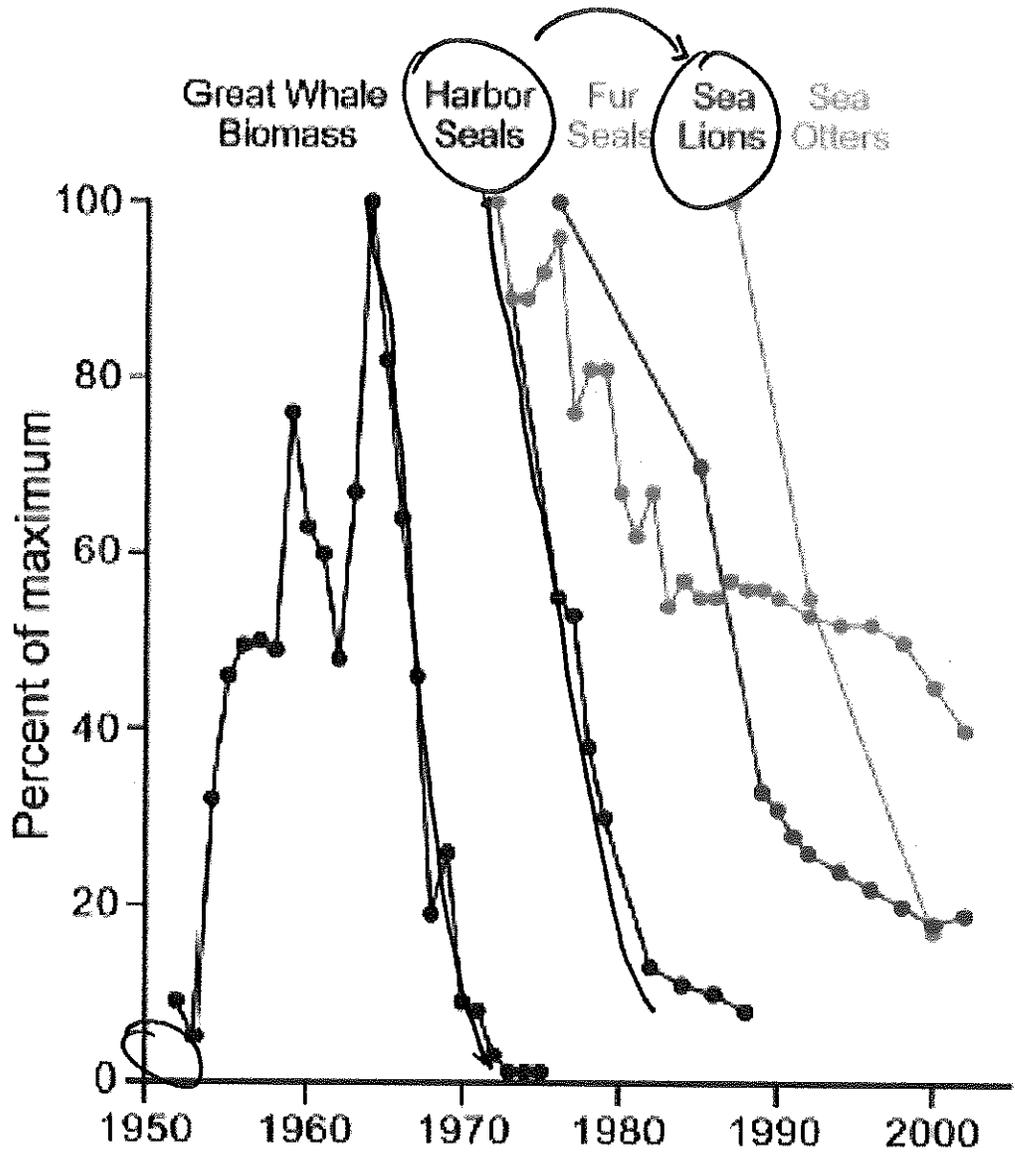


Fig. 2. The sequential collapse of marine mammals in the North Pacific Ocean and southern Bering Sea, all shown as proportions of annual maxima.

### Sequential megafaunal collapse in the North Pacific Ocean: An ongoing legacy of industrial whaling?

A. M. Springer<sup>a,b</sup>, J. A. Estes<sup>c</sup>, G. B. van Vleet<sup>d</sup>, T. M. Williams<sup>e</sup>, D. F. Doak<sup>f</sup>, E. M. Danner<sup>g</sup>, K. A. Forney<sup>h</sup>, and B. Pfister<sup>i</sup>

TABLE 2. Maximum likelihood estimates (MLE) and confidence intervals (based on area under the curve) for the parameters associated with the four supported hypotheses.

Hypothesis	MLE	95% confidence interval
$H_2$ : lower prey density → less pup recruitment	2 380 000	2 276 000–2 484 000
$H_4$ : higher pollock fraction → lower fecundity rate	0.053	0.0236–0.0824
$H_5$ : higher pollock fraction → less pup recruitment	3.67	3.312–4.028
$H_{10}$ : fewer HS (more predation) → lower non-pup survival	0.023	0.01816–0.02784

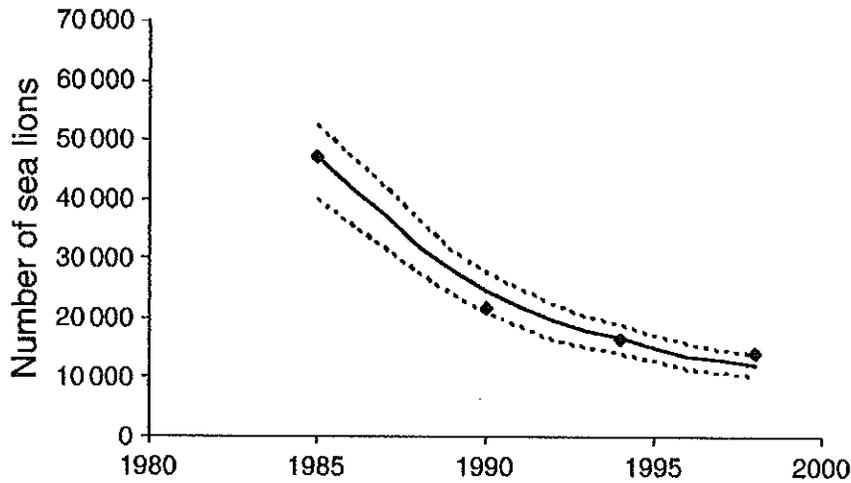


FIG. 11. Distribution of range-wide population trajectories for western Alaska, created using forward simulation and summed across the 28 rookeries for which 1985 counts were available or could be estimated by log-linear interpolation. The dotted lines are 1% and 99% quantiles of the 1000 simulation runs. The four diamonds show the observed counts, summed across the same 28 rookeries.

# Multi-trophic resource selection function enlightens the behavioural game between wolves and their prey

Nicolas Courbin<sup>1\*</sup>, Daniel Fortin<sup>1</sup>, Christian Dussault<sup>2</sup>, Viviane Fargeot<sup>1</sup> and Réhaume Courtois<sup>3</sup>

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## Summary

1. Habitat selection strategies translate into movement tactics, which reckon with the predator–prey spatial game. Strategic habitat selection analysis can therefore illuminate behavioural games. Cover types at potential encounter sites (i.e. intersections between movement paths of predator and prey) can be compared with cover types available (i) within the area of home-range-overlap (HRO) between predator and prey; and (ii) along the path (MP) of each species. Unlike the HRO scale, cover-type availability at MP scale differs between interacting species due to species-specific movement decisions. Scale differences in selection could therefore inform on divergences in fitness rewarding actions between predators and prey.

2. We used this framework to evaluate the spatial game between GPS-collared wolves (*Canis lupus*) versus caribou (*Rangifer tarandus*), and wolf versus moose (*Alces alces*).

3. Changes in cover-type availability between HRO and MP revealed differences in how each species fine-tuned its movements to habitat features. In contrast to caribou, wolves increased their encounter rate with regenerating cuts along their paths (MP) relative to the HRO level. As a consequence, wolves were less likely to cross caribou paths in areas with higher percentage of regenerating cuts than expected based on the availability along their paths, whereas caribou had a higher risk of intersecting wolf paths by crossing these areas, relative to random expectation along their paths. Unlike for caribou, availability of mixed and deciduous areas decreased from HRO to MP level for wolves and moose. Overall, wolves displayed stronger similarities in movement decisions with moose than with caribou, thereby revealing the focus of wolves on moose.

4. Our study reveals how differences in fine-scale movement tactics between species create asymmetric relative encounter probabilities between predators and prey, given their paths. Increase in relative risk of encounter for prey and decrease for predators associated with specific cover types emerging from HRO to MP scale analysis can disclose potential weaknesses in current movement tactics involved the predator–prey game, such as caribou use of cutovers in summer–autumn. In turn, these weaknesses can inform on subsequent changes in habitat selection tactics that might arise due to evolutionary forces.

**Key-words:** *Alces alces*, *Canis lupus*, managed Canadian boreal forest, multi-trophic analyses, predator-multi-prey behavioural game, *Rangifer tarandus*, search tactic, wolf–prey encounter

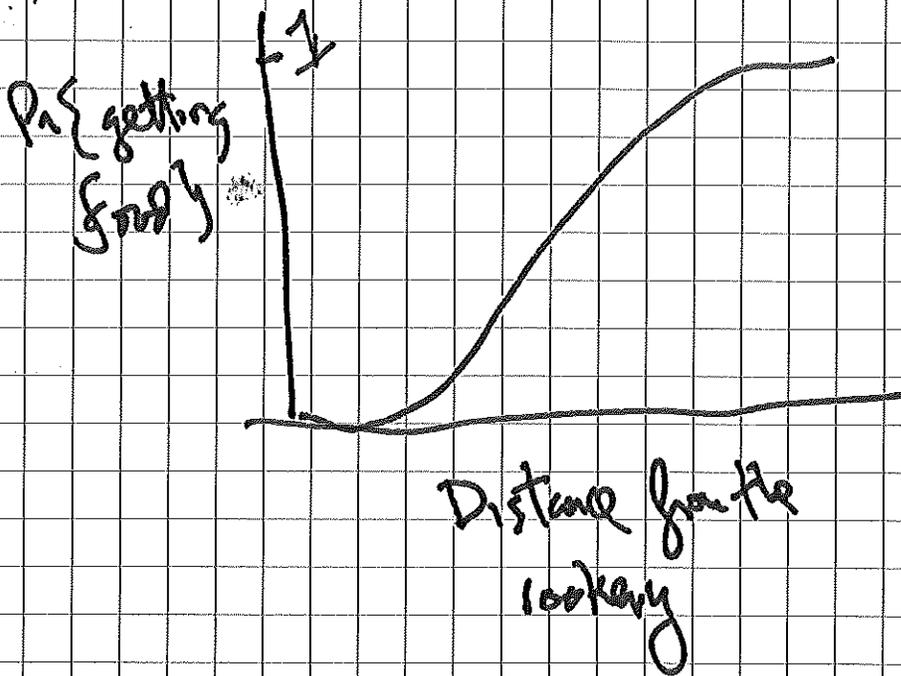
## Introduction

Predator–prey interactions are shaped by the habitat selection games taking place between them (Sih 1998;

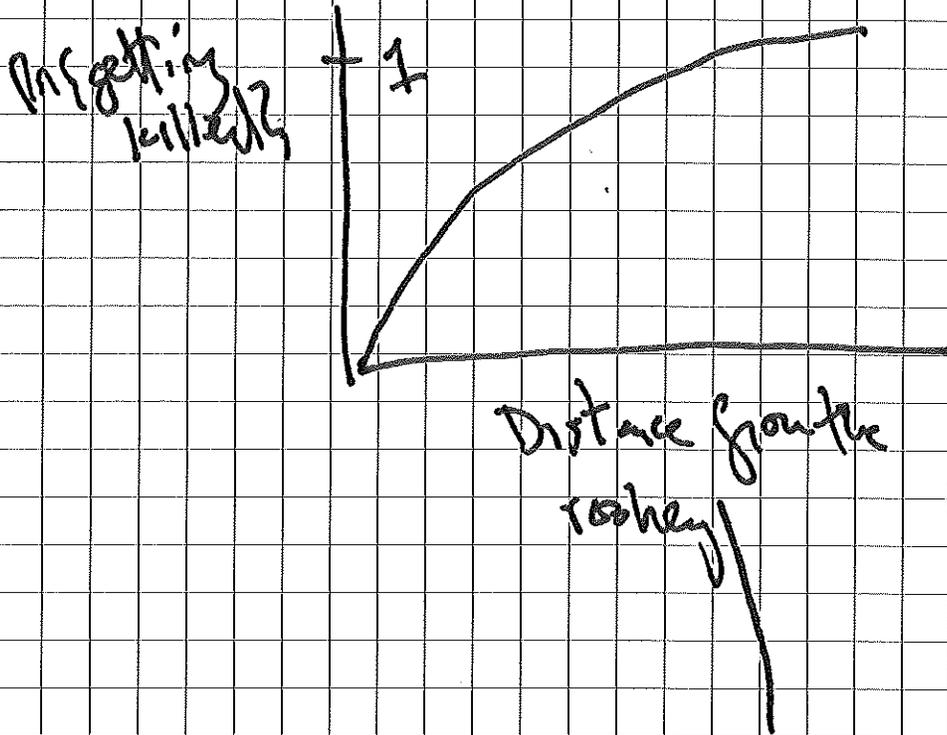
Lima 2002). Although most studies focus on the viewpoint of either the predator or the prey while considering the other group as motionless (Lima 2002), both predators and prey respond to one another's distribution and behaviour (Dupuch, Dill & Magnan 2009; Valeix *et al.* 2009). For example, many predators make selective use of

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3.16



(local depletion)



The predator/prey  
starvation  
trade off  
again!

(Infinite # of  
patches ~ spatial  
ecology)

3.11

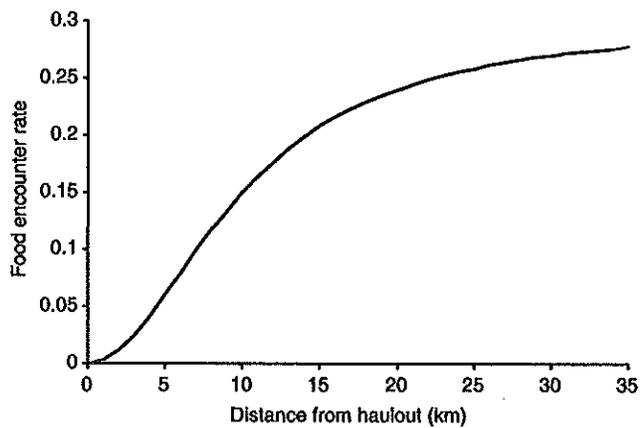


Fig. 2. Food encounter rate (for sea lions) as a function of distance from the haulout.

3,12

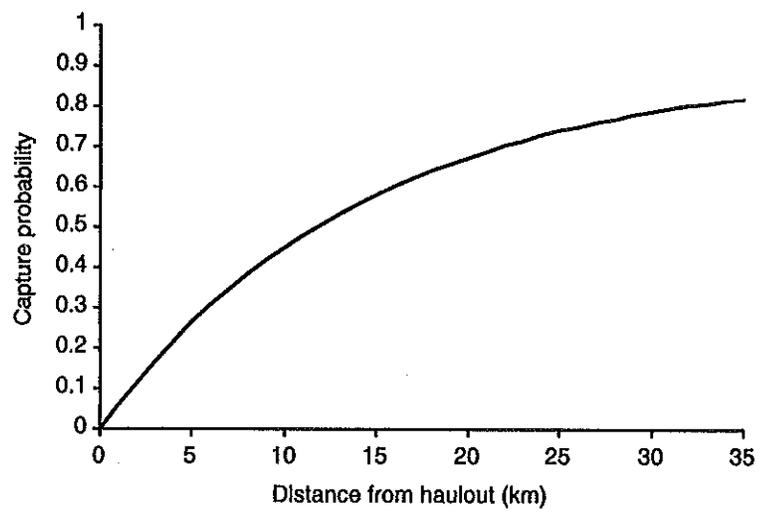


Fig. 1. Capture probability as a function of distance from the haulout.

3.13

Orcas

State

$X(t)$  = # days since he last meal  
 $f$  = maximum number of days that  
an orca can go without food

Environment

$T$  ~ time period of interest

$q(t)$  = length of daylight on day  $t$

$a$  ~ attack rate

$a q(t)$  = Number of attacks per day

$$p(d) = p_{\max} \left[ 1 - \left( \frac{1}{2} \right)^{d/c_p} \right]$$

=  $p_{\max}$  { successful capture at distance  $d$  from  
the haulout }

$$P_1 \{ \text{no stars captured today} \} \\ = (1 - p(a))^{a g(t)}$$

An aside

$$(1 - p(a))^{a g(t)} = \exp \left[ a g(t) \log(1 - p(a)) \right]$$

$$\left[ x = e^{\log(x)} \right] \quad \log(1+x) \approx x \quad [x \ll 1]$$

Replace  $\log(1 - p(a))$  by  $-p(a)$  to get

$$(1 - p(a))^{a g(t)} \approx \exp \left[ -a g(t) p(a) \right]$$

Reminds us of  $e^{-m_i} = P_1 \{ \text{survival when using path } i \}$

Fitness

$$O(x, t | d)$$

~~Pr~~ Pr { surviving to  $T$  | foraging  
for pellets at distance  
 $d$  from the kecol  
and  $X(t) = x$  deep since  
the last meal }

avoiding starvation 3.15

End condition

$$O(x, T | d)$$

$$= \begin{cases} 1 & \text{if } x \leq f \\ 0 & \text{otherwise} \end{cases}$$

DPE

$$O(x, t | d)$$

$$= \left(1 - (1 - p(d))^{a_g(t)}\right) O(\emptyset, t+1 | d)$$

$$+ (1 - p(d))^{a_g(t)} O(x+1, t+1 | d) I_{x+1 \leq f}$$

$$I_{x+1 \leq f} = \begin{cases} 1 & \text{if } x+1 \leq f \\ 0 & \text{if } x+1 > f \end{cases}$$

One additional twist: The area has a small change of mortality for the Steller per attack

$$e^{-i a_g T} = (e^{-i})^{a_g T}$$

$\uparrow$   $\leftarrow$  number of attacks over a season  
 $p_1$  { survive a single attack

Find metric for area fitness, to be optimized over  $a$  is

$$O(\phi, I/a, d) e^{-i a g T}$$

area optimal attack rate given starts  
the season full and still is a  
distance  $d$

area survives to  $T$  / avoiding starvation  
starting day 1 with  
deficit is patching distance  $d$   
from the haulout and uses attack  
rate  $a$

area avoiding a  
mortality inducing  
injury

[  $O(\phi, I/a, d)$  is better  
notation ]

This tells us

$a^*(d)$  = Given that Stellers are always at distance  $d$  this is the best attack rate for orcas.

We now need to find the "best" distance for Stellers  
 given the orca attack rate

Stellar SDP

Environment

$\gamma(d)$  = rate of food encounter at distance  $d$   
 $h$  = # hours orcas are present each day

6.1.2

$T \sim$  end time

$$F(x, T) = 0$$

J Morrison "The fitness and the end is always near"

↓  
Fat doesn't first

---

Once (Stochastic) Solutions

$$O(x, t | a, d)$$

$$= [1 - (1 - \mu(d))^{ag}] O(\emptyset, t+1 | a, d)$$

$$+ (1 - \mu(d))^{ag} O(x+1, t+1 | a, d) \mathbb{I}_{x+1 \leq f}$$

$$O(x, T | a, d) = \begin{cases} 1 & \text{if } x \leq f \\ 0 & \text{o.w.} \end{cases}$$

$O(\phi, 1 | a, d) = P\{ \text{an orca with no defect on day 1 survives to the end of the season} \mid \text{was struck by a whale straggler at distance } d \}$

Orca fitness  $(a, d)$

$$= O(\phi, 1 | a, d) e^{-i a d T}$$

$e^{-i}$   
 $\uparrow$   
 information

Maximize this over  $a$ , given  $d$



$a^*(d)$

$a^*(d)$

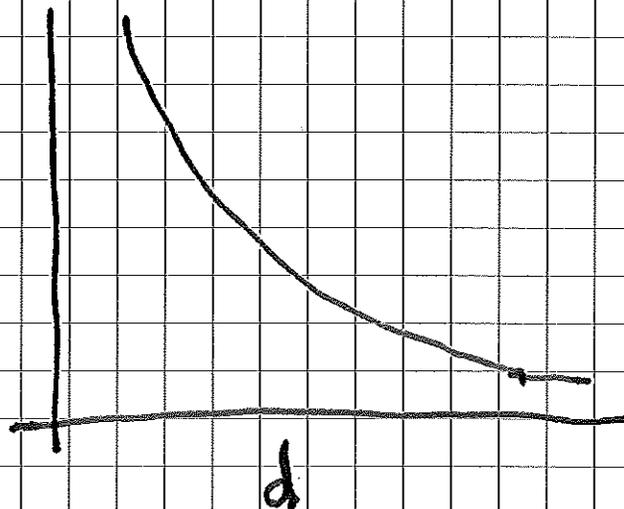


Table 1. Parameter values used in the model

Parameter	Value
Season duration (days)	$T = 180$
Number of hours available each day for hunting/foraging	$q = 12$
Maximum fasting period (days) for killer whales	$f_K = 12$
Maximum prey capture probability in attacks far from the haulout	$\mu_{\max} = 0.9$
Distance from haulout (km) where $\mu = \mu_{\max}/2$	$c_{\mu} = 10$
Probability of mortal injury for killer whales per attack	$i = 0.001$
Ratio of predators to prey	$r = 0.05$
Maximum fasting period (days) for sea lions	$f_S = 6$
Maximum food encounter rate (per hour) for sea lions far from the haulout	$Y_{\max} = 0.3$
Distance from haulout (km) where $Y = Y_{\max}/2$	$c_Y = 10$
Foraging time (hours) lost by all sea lions due to each attack	$h = 2$

## RESULTS

Figures 3 and 4 show the fitness surfaces for killer whales and sea lions at the start of winter. In Fig. 3, the dotted line (connecting vertical tangents of the fitness contours) corresponds to a killer whale's optimal attack rate strategy in response to the foraging distance used by sea lions. The predator's optimal strategy is to avoid unnecessary risk and decrease its attack rate when the prey are more vulnerable (further from the haulout). The dotted line in Fig. 4 similarly corresponds to a sea lion's optimal foraging strategy (distance from the haulout) in response to the attack rate chosen by killer whales. The line is U-shaped, reflecting a shifting trade-off between predation and starvation risk: At low attack rates, sea lions go where the food is, far from the haulout. At intermediate attack rates, the risk of predation drives them closer to the safety of the haulout. At high attack rates, so much foraging time is lost due to attacks that the animals must forage further out again to avoid starvation.

By choosing to forage in a more dangerous area, the sea lions are effectively reducing their level of anti-predator behaviour in response to elevated attack rates. This counter-intuitive result is actually quite general. We should expect reduced anti-predator behaviour in any situation where: (1) foraging time is limited, (2) predator attacks are frequent, and (3) foraging is interrupted by each attack. The same mechanism might explain Lima's (1986) observation of house sparrows decreasing vigilance in apparently dangerous settings.

The two response curves form the basis of a game played out over evolutionary time-scales (Fig. 5): Given a population of sea lions using a fixed foraging strategy (distance from the haulout), killer whales are predicted to evolve towards the corresponding attack strategy (rate) shown by the dashed line. Given that attack rate, the sea lions are predicted to evolve towards the corresponding foraging strategy (distance from the haulout) shown by the dotted line. In further iterations, the system eventually converges towards the stable point at the intersection of the two lines. This is a Nash equilibrium (Nash, 1950; Clark and Mangel, 2000).

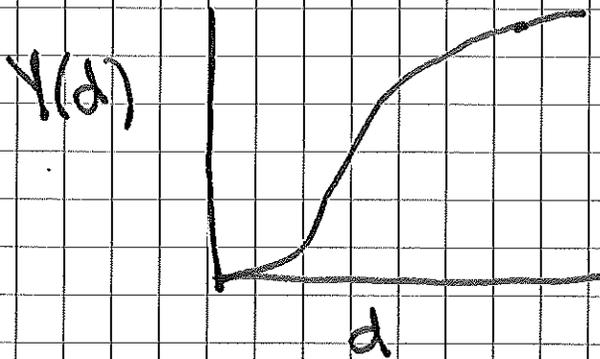
### Manipulating prey behaviour

When considering the game detailed in Fig. 5, one might ask what would happen if the predator were somehow able to make additional 'false attacks' without incurring the

## Stellus

1.3

$Y(d)$  = rate of food encounter at distance  $d$



## Effects of orcas on stellar foraging

$ah \sim$  # hours lost to foraging per orca attack

$g \sim$  # hours in a day

$a \sim$  # attacks/hr

$ag \sim$  attacks/day

$agh \sim$  hours lost to foraging per day when orcas attack at rate  $a$

$g - agh = g(1 - ah) =$  # hours available for foraging

Food is considered as a Poisson process with  
parameter

$$\lambda(d)q_b(1-ah)$$

so

$$\begin{aligned} P_n\{\text{Stellar finding no food in a day}\} \\ = e^{-\lambda(d)q_b(1-ah)} \end{aligned}$$

$Z(t)$  = # days a Stellar has gone without  
food on day  $t$

$g$  = maximum # days w.o. food before death

$S(z, t | a, d) = P_n\{\text{Stellar with } Z(t) = z$   
survives to time  $T$  | foraging  
at distance  $d$  and  
experiencing attack rate  $a\}$

End condition ~ "identical"

6.5

$$S(z, t | a, d)$$

$$= \left( 1 - e^{-Y(d)q(1-ah)} \right) S(\emptyset, t+1 | a, d)$$

$$+ e^{-Y(d)q(1-ah)} S(z+1, t+1 | a, d) \mathbb{I}_{z+1 \leq g}$$



$S(\emptyset, 1 | a, d) = P_1$  { given no predators,  $S$  will survive strobata for entire year when it freezes at distance  $d$  and experiences other rate  $a$  }

Steady state  $(a, d)$

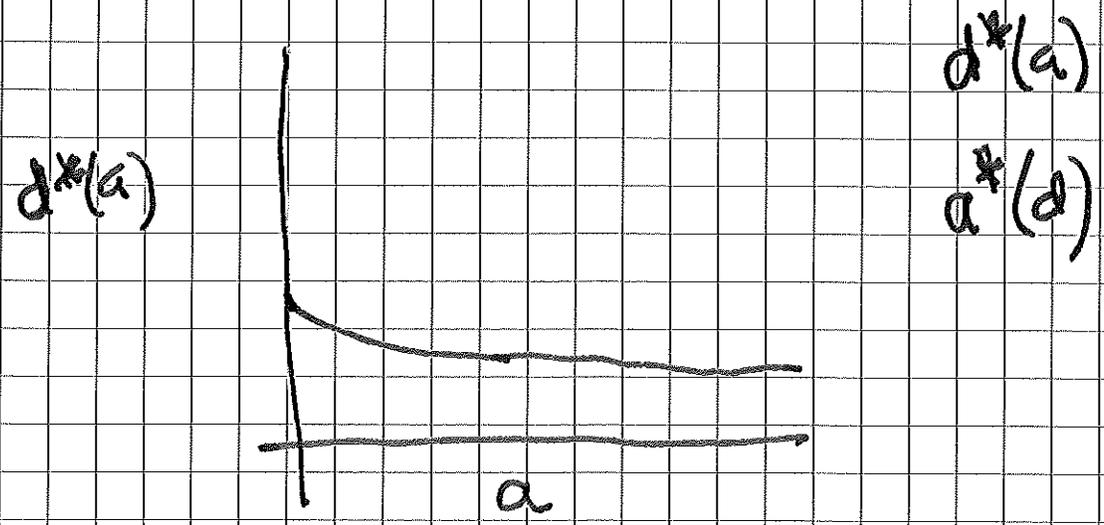
$$= S(\phi_1 | a, d) \left( e^{-\rho(d)} a \rho T \right) r$$

ratio of ovs  
to Steady

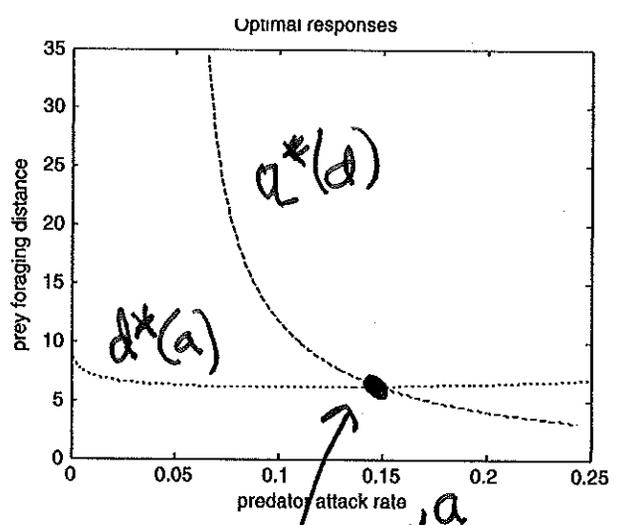
Maximize this over  $d$

given  $a$

$$d^*(a)$$



d



Best case  
 $a^* = 0.15$

Fig. 5. Curves showing the interaction between the predator response (dashed line) and the prey response (dotted line). Their intersection is a Nash equilibrium.

~~Neither over nor~~  
~~Stellers can do~~  
~~better~~

Each is doing the best response to the other's best response

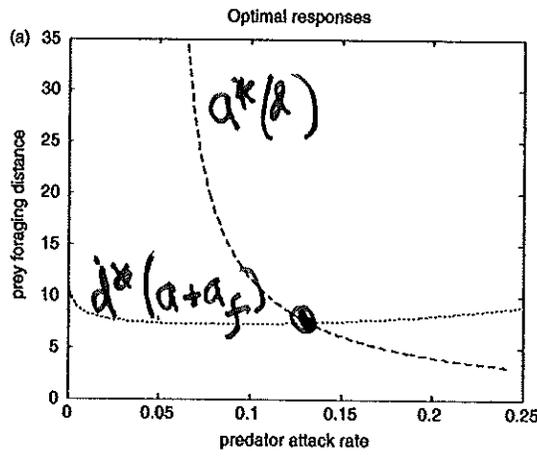
Kick's brilliant insight

What would happen if orcas did false attacks?

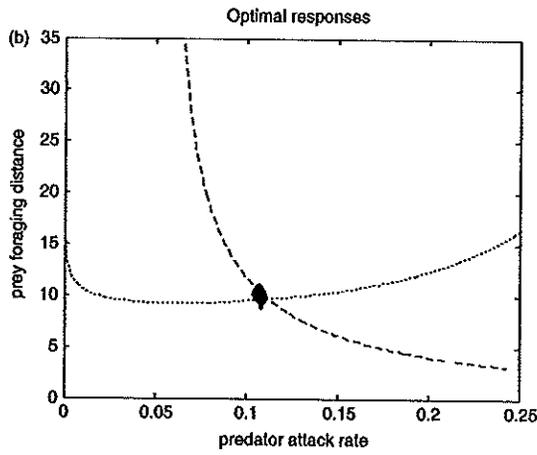
- orcas do not suffer the risk of injury
  - Stellers exhibit a fleeing response
- ⇒ best foraging time

6.8

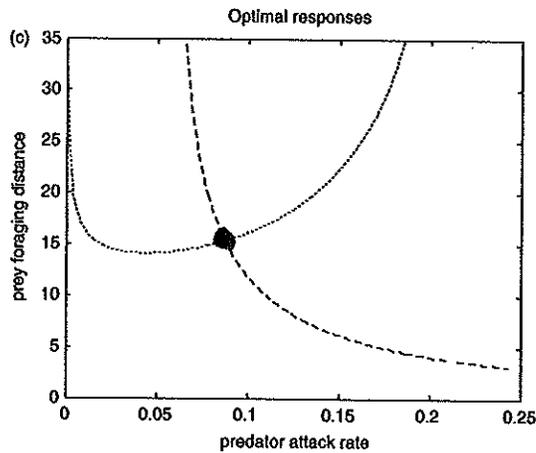
base 0.15/hr



false attack rate  
= 0.1/hr



0.2/hr



0.3/hr

Fig. 7. Predator (dashed)-prey (dotted) interaction curves: (a) 0.1 false attacks per hour, (b) 0.2 false attacks per hour, (c) 0.3 false attacks per hour.