## Bio 608 Problem Set - Fall 2007

1. Consider the following hypothetical game, which is sort of a 2-player producer-scrounger game. Animals form pairs and harvest resources on their territories. Let the resource value of a territory be V. If two producers get the territory, they share V; i.e. they each get V/2. Scroungers are incapable of harvesting resources themselves, so if they share a territory, they each get 0. If a Producer shares a territory with a Scrounger, the Producer gets proportion p of V; whereas, the Scrounger gets the remainder (i.e. proportion (1-p) of V). So the payoff matrix looks like this (payoffs are to players along the rows, given an opponent who plays a strategy in the columns):

	Producer	Scrounger		
Producer	V/2	p V		
Scrounger	(1- <i>p</i> ) V	0		

Using your vast knowledge of game theory, your job is to determine the evolutionarily stable strategy, or ESS.

Let f equal the frequency of Producers at the ESS, and solve for f in terms of p. How does the ESS depend on p, if at all? Are there conditions that favor a mixed ESS or genetic polymorphism versus a pure ESS? If so, what are they? (Hint: consult your notes on the Hawk-Dove game.)

First, check to see if P &/or S are pure ESS's by using stability criterion 1 (i.e. I is an ESS if E(I,I) > E(J,I), or if I is a better reply to itself than is J). P is an ESS if

 $E(P,P) \ge E(S,P),$ 

which is true if p > 0.5. If p = 0.5, then

E(P,P) = E(S,P),

in which case we need to consider stability criterion 2: is E(I,J) > E(J,J)? Because

 $E(P,S) \rightarrow E(S,S),$ 

P is an ESS when p = 0.5. Thus P is a pure ESS if  $p \ge 0.5$ . S is never an ESS because,

E(S,S) < E(P,S).

A mixed ESS or a genetic polymorphism is possible if p < 0.5 (in which case neither P nor S are pure ESS's). Let f be the frequency of P at the ESS. Producer fitness is given by

 $W_{P} = f E(P,P) + (1-f) E(P,S),$ 

and Scrounger fitness is given by

 $W_{s} = f E(s,P) + (1-f) E(s,s).$ 

At the ESS,  $W_P = W_S$ ; therefore, we set the two fitnesses equal to one another, substitute in the payoffs, and solve for f in terms of p. When we do this, we find that at the ESS,

f=2p.

Interestingly, Scroungers can only persist in this game if they get more resources than Producers when they share territories with Producers.

 Consider the Ideal Free Distribution. You have a habitat with five patches (i.e. mechanical bird feeders) in an aviary with 200 hungry foragers (i.e. birds). The 5 patches distribute bird seed at the following rates: Patch A, 5 units per minute; Patch B, 10 units per minute; Patch C, 15 units per minute; Patch D, 20 units per minute; and Patch E, 50 units per minute.

# What is the predicted Ideal Free Distribution of foragers among patches?

10 foragers in Patch A, 20 foragers in Patch B, 30 foragers in Patch C, 40 foragers in Patch D & 100 foragers in Patch E.

### What is the average feeding rate within and among patches? 0.5 units of food per forager per minute

#### Show the graphical solution to this problem.

The graphical solution is a bivariate plot of Patch Reward Rate (Y) versus Foragers Per Patch (X). The IFD line contains 2 points as (X,Y) coordinates: the origin (0,0), and the bivariate mean (40,20). See graph below.



The rationale for the origin is that a patch with zero food should attract zero foragers. The rationale for the bivariate mean is that at the IFD, the average reward rate within and among patches equals the average reward rate for the whole environment. The average reward rate for the whole environment equals, YBar divided by XBar, which equals the slope of the line. Thus, the IFD predicted number of foragers in each patch lie on this line at the given patch reward rates. 3. Consider the following cohort life table, with 5 age classes (0, 1, 2, 3, 4), the following numbers in each age class,  $n_x$ , and the following schedule of birth,  $m_x$ . (Hint: import into Excel and use formulas)

x	n <sub>x</sub>	l <sub>x</sub>	S <sub>x,x+1</sub>	m <sub>x</sub>	l <sub>x</sub> m <sub>x</sub>	R <sub>x</sub>
0	67523			0		
1	2113			0		
2	276			166		
3	133			166		
4	0			-		

Fill in the missing columns in the table ( $I_x$ ,  $s_{x,x+1}$ ,  $I_xm_x$ , and  $R_x$ ). Below is the table with all the values filled in.

x	n <sub>x</sub>	l <sub>x</sub>	S <sub>x,x+1</sub>	m <sub>x</sub>	l <sub>x</sub> m <sub>x</sub>	R <sub>x</sub>
0	67523	1	0.031293	0	0	1.005494
1	2113	0.031293	0.13062	0	0	32.13157
2	276	0.004087	0.481884	166	0.678524	245.9928
3	133	0.00197	0	166	0.32697	166
4	0	0	-	0	0	0

## Plot a graph of $R_x$ versus x.

Next follows the graph of  $R_x$  vs x.



Imagine a mutation that increased fecundity by 10% at age 2, but reduced survival from age 2 to age 3 by 10%. Would such a mutation be favored by natural selection? Why or why not (show your calculations)? If a mutation increased  $m_2$  by 10%, but reduced  $s_{2,3}$  by 10%, the table would change as follows. The changed values are in bold (note: I built in the 10% reduction in  $s_{2,3}$  by reducing  $n_3$  to 119.7).

x	n <sub>x</sub>	l <sub>x</sub>	S <sub>x,x+1</sub>	m <sub>x</sub>	l <sub>x</sub> m <sub>x</sub>	R <sub>x</sub>
0	67523	1	0.031293	0	0	1.04065
1	2113	0.031293	0.13062	0	0	33.25499
2	276	0.004087	0.433696	182.6	0.746377	254.5935
3	119.7	0.001773	0	166	0.294273	166
4	0	0	-	0	0	0

These adjustments translate into a *relative* gain of 10% in  $l_2m_2$  and a *relative* loss of 10% in  $l_3m_3$ . Such a mutation would be selectively advantageous, however, because the *absolute* gain in  $l_2m_2$  exceeds the *absolute* loss in  $l_3m_3$ . This is reflected in a higher  $R_0$ , the net replacement rate, for the mutant than for the wild type. Subsequent mutant  $R_xs$  are also higher, except the last age class, when  $R_x = m_x$ . The changes to the  $R_x$  versus x graph are indicated in red.

Where on the following graph (Ensminger 2007) does this tradeoff take place?



The tradeoff is represented in Amanda's figure between arrows D and E.