40 MATING SYSTEMS AND PARENTAL CARE

Objectives

- Develop a game theory model of parental care and mating systems.
- Determine the environmental and biological conditions that lead to monogamy, polygyny, and polyandry.
- Examine which model parameters have significant impact on reproductive output for males and females.
- Verify the four evolutionarily stable strategies derived by Maynard Smith (1977).

Suggested Preliminary Exercise: Evolutionarily Stable Strategies

INTRODUCTION

You are well aware by now that there are fundamental differences between males and females of all species. From an evolutionary perspective, the goal is to produce as many offspring as possible that will, in turn, produce offspring. Males and females may have different strategies for doing this (Trivers 1972). Females, the egg producers, tend to invest a lot of energy in the production of gametes, while males invest much less in gamete production. In short, eggs are more "expensive" than sperm. For example, a human female typically produces only a few hundred viable eggs in her lifetime, whereas a human male can produce literally billions of sperm cells.

For many species, the production and propagation of gametes is the only parental investment. The fertilized egg, or zygote, is left to "sink or swim" on its own. But many other species nurture embryos through gestation and birth (almost exclusively the role of the female, though there are exceptions), and the offspring may require additional parental care in order to survive to reproductive age.

In some environments, both parents are needed to successfully rear young, while in other environments little or no care is needed. In cases where a single parent suffices to raise offspring, a male will maximize his fitness by fertilizing as many eggs as possible, leaving the parental care of his offspring to females. But if there are opportunities to mate with other, superior, males, a female should leave parental care to males to maximize her fitness! In situations where the young must be cared for, this sets up a "conflict" between the sexes because males and females differ with respect to behaviors that maximize fitness. All other things being equal, parents should maximize their fitness by fertilizing or producing as many eggs as possible, but if parental care enhances offspring survival, parents may maximize their fitness by providing care at the expense of additional matings. How can this conflict be resolved?

Mating Strategies

Mating strategies are often linked to the kind of parental care system that species employ. **Monogamy** is a mating system in which males and females form pair bonds, and often both care for the offspring. **Polygyny** is a mating system in which a male mates with several females. The female usually cares for the young while the male attempts to maximize his fitness by mating with as many females as possible. **Polyandry** is a mating system in which a female mates with several males. Males may care for the young while females attempt to maximize their fitness by mating with as many males as possible. And finally, **promiscuity** is a mating system free-for-all, in which either sex may care for the young and both males and females mate with many different individuals (Vehrencamp and Bradbury 1978; Alcock 2001).

Which mating system should be used to maximize fitness for males? Which mating system should be used to maximize fitness for females? Should parental care be given to the offspring? The answers to the questions depend, in large part, on the ecological conditions of a given environment, which affects how many parents are needed to ensure offspring survival, and how likely an individual will find another mate. But the strategy employed by a male or female also depends on the strategy adopted by the partner. For example, if the female cares for the young, and only a single parent is needed to raise offspring, the male may enhance his fitness by finding new females to mate with. But if the female does not care for the young, the male may enhance his fitness by attending the young himself. This type of conflict can be evaluated by **game theory** models, in which the different strategies played by the male and female collectively determine the evolutionary fitness gain.

A useful game theory model to resolve such conflict was developed by John Maynard Smith (1977). The model consists of two strategies: care for young (1) or desert young (0), that are chosen by both males and females. Thus, four "games" can be played: (1) both males and females care for young; (2) both males and females desert young; (3) the female cares for young and the male deserts; (4) the male cares for the young and the female deserts. Which of these games should be played depends on several parameters:

- P_0 = the probability of survival of eggs that are not cared for.
- P_1 = the probability of survival of eggs when one parent cares for young.
- P_2 = the probability of survival of eggs when two parents care for young.
- p = the probability of a deserter male finding a new mate.
- p' = the probability of a caring male finding a new mate.
- V = the number of eggs laid by a female deserter.
- v = the number of eggs laid by a female who cares for her young.

Thus, the model considers the value of parental care by one or two parents; the chance that males mate again; and how parental care affects the number of eggs the female can lay. We will assume that $P_0 \leq P_1 \leq P_2$, so that the probability of survival of eggs with parental care is never less than the probability of survival without parental care. We will also assume that $V \geq v$, so that females that care have less energy to allocate towards clutch size. Our final assumption is that p and p' do not depend on a male's parentage for a given clutch. Given these parameters, the fitness payoff for males and females can be determined as shown in Table 1.

For example, when both males and females care for the offspring, the female has a reproductive output equal to the number of eggs laid by a caring female (v) times the probability of young surviving when two parents offer care (P_2). But when a female cares but the male deserts, she has a reproductive output equal to the number of eggs laid per caring female (v) times the probability of young surviving when a single parent offers care (P_1). When both parents care for young, males have a reproductive output (fitness) equal that of the female ($v \times P_2$), but with the added benefits of remating with another female while still providing care to his first clutch ($v \times P_2 \times p'$). The equation v

Table 1. Fitness Payoff Parameters for Males and Females

	Female Fitness		Male Fitness	
	Female cares	Female deserts	Female cares	Female deserts
Male cares	$v \times P_2$	$V \times P_1$	$v \times P_2 + v \times P_2 \times p'$	$V \times P_1 + V \times P_1 \times p'$
Male deserts	$v \times P_1$	$V \times P_0$	$v \times P_1 + v \times P_1 \times p$	$V \times P_0 + V \times P_0 \times p$

$\times P_2 + v \times P_2 \times p'$ can be rewritten as $v \times P_2 \times (1+ p')$. When the female cares but the male deserts, his fitness is equal to that of a single-parent female ($v \times P_1$) plus the added benefits of remating with another female by deserting his clutch ($v \times P_1 \times p$). The equation $v \times P_1 + v \times P_1 \times p$ can be rewritten as $v \times P_1 \times (1 + p)$.

Evolutionarily Stable Mating Strategies

How do the two sexes resolve their conflicts? In this exercise, you'll set up a spreadsheet version of Maynard Smith's model and use it to explore the conditions in which different parental care systems are likely to evolve. There are four conditions that lead to a particular type of system. When these conditions are met, the strategy is called an **evolutionarily stable strategy** (**ESS** for short). In this case, the strategy played by the sexes is either "care" or "desert." A strategy is evolutionarily stable when, if all members of a population adopt it, then a mutant strategy could not invade the population and increase in frequency by natural selection (Maynard Smith 1982).

In order to arrive at ESS conditions, it's useful to first think about how the frequency of a particular strategy may change over time. We will let

- r = frequency of caring strategists (C).
- $s = 1 - r$ = frequency of deserter strategists (D).
- W(C), W(D) = fitness of caring and deserter strategists, respectively.
- E(C,C) = payoff to an individual adopting C (care) while the mate adopts C.
- E(C,D) = payoff to an individual adopting C while the mate adopts D (desert).
- E(D,D) = payoff to an individual adopting D while the mate adopts D.
- E(D,C) = payoff to an individual adopting D while the mate adopts C.

Because how well one sex fares depends on the strategies played by the opposite sex, we need to consider the fitnesses of each sex separately, while taking into account the frequency of C and D strategists in the opposite sex. Thus, calculations are needed for both sexes. For females, the fitness of players that engage in parental care is

$$W(\mathrm{C}) = [r_{\mathrm{m}} \times E(\mathrm{C,C})] + [s_{\mathrm{m}} \times E(\mathrm{C,D})] \qquad \text{Equation 1}$$

where r_m and s_m is the frequency of males that care and desert, respectively. The fitness of females that desert is

$$W(\mathrm{D}) = [r_{\mathrm{m}} \times E(\mathrm{D,C})] + [s_{\mathrm{m}} \times E(\mathrm{D,D})] \qquad \text{Equation 2}$$

Thus, you can see that the fitness of females depends on the strategies that males play as well as the frequency of each kind of strategist. The same equations work for males, except that we need to consider the frequencies of the female strategists in the population. To be clear, let's walk through an example. If we are interested in the fitness of a male that cares, we need to determine what his fitness is when he adopts a caring strategy and his mate also cares, E(C,C), and we need to determine what his fitness is when he adopts a caring strategy and his mate deserts, E(C,D). Suppose that 10% of females provide care to young while the remaining 90% desert. Thus, $r_f = 0.1$ and $s_f = 0.9$. If E(C,C) = 5 and E(C,D) = 3, then the fitness of caring males in the population is

$$W(\mathrm{C}) = [0.10 \times 5] + [0.90 \times 3] = 3.2$$

If a male adopts a deserting strategy, then we need to determine what his fitness is when he deserts and his mate also deserts, E(D,D), and we need to determine what his fitness is when he deserts but his mate cares, E(D,C). If E(D,D) = 0 and E(D,C) = 3, then the fitness of deserting males in the population is

$$W(\text{D}) = [0.10 \times 3] + [0.90 \times 0] = 0.3$$

In this example, males that provide care have higher fitnesses since $W(\text{C}) > W(\text{D})$, but how much this strategy increases in the next generation depends on the proportion of males playing each strategy. If a lot of individuals are playing the more successful strategy, then the trait will increase more quickly. We can calculate the mean fitness for males as

$$\overline{W} = \left[r_\text{m} \times W(\text{C})\right] + \left[s_\text{m} \times W(\text{D})\right] \qquad \text{Equation 3}$$

and the mean fitness of females as

$$\overline{W} = \left[r_\text{f} \times W(\text{C})\right] + \left[s_\text{f} \times W(\text{D})\right] \qquad \text{Equation 4}$$

Once we understand Equations 1–4, we can compute the frequency of a given strategy for a given sex in the next generation as

$$r' = \frac{r \times W(\text{C})}{\overline{W}} \text{ and } s' = \frac{s \times W(\text{D})}{\overline{W}} \qquad \text{Equation 5}$$

and we can show the change in the frequency with which each strategy is played for both males and females over time.

PROCEDURES

As Table 2 shows, there are four possible evolutionarily stable conditions (Maynard Smith 1982). The mating strategies that evolve depend on

- the value of parental care by one or two parents
- the chance that males mate again
- how parental care affects the number of eggs the female can lay

We will explore these conditions thoroughly in the exercise and try to make sense of their logic. The goal of this exercise is to develop a spreadsheet version of Maynard Smith's model and use it to explore the conditions in which different parental care systems are likely to evolve. As always, save your work frequently to disk.

Table 2. Conditions for the Four Evolutionarily Stable Mating Strategies of Maynard Smith (1982)

Strategy	Description	Conditions[a]
ESS 1	Female cares when	$vP_2 > VP_1$
Monogamy	Male cares when	$P_2(1 + p') > P_1(1 + p)$
ESS 2	Female deserts when	$VP_1 > vP_2$
Polyandry	Male cares when	$P_1(1 + p') > P_0(1 + p)$
ESS 3	Female cares when	$vP_1 > VP_0$
Polygyny	Male deserts when	$P_1(1 + p) > P_2(1 + p')$
ESS 4	Female deserts when	$VP_0 > vP_1$
Promiscuity	Male deserts when	$P_0(1 + p) > P_1(1 + p')$

[a]Conditions for an ESS are met when the inequality for the male and the female are *both* true.

INSTRUCTIONS	ANNOTATION

A. Set up the model and payoff parameters.

1. Open a new spreadsheet and enter headings as shown in Figure 1.

	A	B	C
1	***Parental Care and Mating Systems***		
2	**Based on Maynard Smith's (1977) game theory model**		
3			
4	**# of parents**	**Probability**	
5	0	P_0 =	0
6	1	P_1 =	0.1
7	2	P_2 =	0.9
8			
9	**Female behavior**	**# of eggs**	
10	Deserter	**V = desert =**	6
11	Care	**v = care =**	5
12			
13	**Male behavior**	**Probability of remating**	
14	Deserter	**p = desert =**	0.5
15	Care	**p' = care =**	0.5

Figure 1

2. Enter the variable values shown in cells C5–C7, C10–C11, and C14–C15.

The variables in the model include
- the probability of survival of eggs that are not cared for (P_0)
- the probability of survival of eggs cared for by a single parent (P_1)
- the probability of survival of eggs cared for by two parents (P_2)

(Remember that probabilities range from 0 to 1.)
For males, we also include
- the probability of mating again when the male deserts a nest (p)
- the probability of mating again when the male guards a nest (p')

For females, we must include
- the number of eggs laid per female when the female deserts the nest (V)
- the number of eggs laid per female when she cares for her young (v)

3. Graph the relationship between probability of survival of eggs as a function of the number of caring adults.

Use the XY scatter graph option and label your axes fully. Your graph should resemble Figure 2.

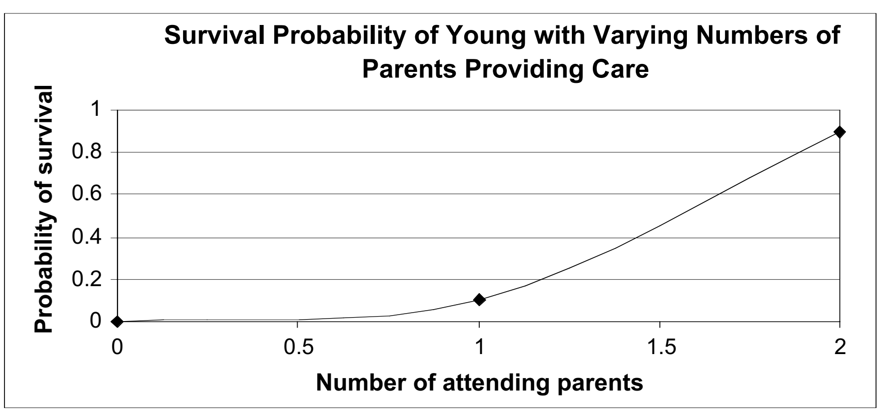

Figure 2

4. Set up new headings as shown in Figure 3.

Males and females can both employ one of two strategies: care or desert. Thus there are four fitness scenarios for each sex, depending on what strategy the mate plays. Cell I6 gives the fitness payoff for females that care when males also provide care, or *E*(C,C). Cell J6 gives the fitness payoff for females that desert while the male provides care, or *E*(D,C). Similarly, cell I11 gives the payoff for males that care when females also provide care, or *E*(C,C). Cell J12 gives the payoff to males that desert when their mates also desert, or *E*(D,D).

	H	I	J
4	**Female fitness matrix**		
5		***Female cares***	***Female deserts***
6	***Male cares***		
7	***Male deserts***		
8			
9	**Male fitness matrix**		
10		***Female cares***	***Female deserts***
11	***Male cares***		
12	***Male deserts***		

Figure 3

5. Enter formulae to compute the fitness payoffs for females in cells I6–J7 and males in cells I11–J12. Use the information in Table 1 to construct your formula.

Remember that the payoffs depend on which strategy is played by its partner. For a female that cares whose mate also cares, her payoff is the number of eggs laid per caring females × the probability of survival when both parents care for the young, or $v \times P_2$. The payoff formulae are given in Table 1, and the following formulae are based on the Table 1 equations.

Females:

- I6 **=C11*C7**
- I7 **=C11*C6**
- J6 **=C10*C6**
- J7 **=C10*C5**

Males:

- I11 **=C11*C7+C11*C7*C15** or **=I6+I6*C15**
- J11 **=C10*C6+C10*C6*C15** or **=J6+J6*C15**
- I12 **=C11*C6+C11*C6*C14** or **=I7+I7*C14**
- J12 **=C10*C5+C10*C5*C14** or **=J7+J7*C14**

6. Save your work.

B. Calculate initial female and male fitnesses.

We will track the fitnesses of males and females, as well as the frequencies in which individuals care (*r*) and desert (*s*) over a 20-year period, and determine which strategy evolves over time.

1. Set up fitness computations for females and males as shown in Figures 4 and 5, respectively.

	A	B	C	D	E
22		**Female fitness**			
23		Frequency of male strategy		Female fitness	
24	Time	Care	Desert	Care	Desert
25	0	0.1	0.9		

Figure 4

	F	G	H	I
22	Male fitness			
23	Frequency of female strategy		Male fitness	
24	Care	Desert	Care	Desert
25	0.9	0.1		

Figure 5

2. Set up a linear series from 0 to 20 in cells A25–A45.

Enter 0 in cell A25. Enter **=1+A25** in cell A26.
Select cell A26, and copy its formula down to cell A45.

3. Enter the starting frequencies of caring (r) males and deserting (s) males in cells B25–C25 as shown in Figure 4. Enter the starting frequencies of caring (r) and deserting (s) females in cells F25–G25 as shown in Figure 5.

Remember that r = frequency of caring (C) strategists and $s = (1 - r)$ = frequency of deserter (D) strategists. For now, enter the values shown in the figures. You will be able to change these starting frequencies later in the exercise. Cells B25–C25 give the frequency of male strategists at time 0. We need to know these frequencies in order to compute female fitness. Cells F25–G25 give the frequency of the female strategists at time 0. We need to know these frequencies in order to compute male fitness.

4. For year 0, enter formulae in cells D25 and E25 to compute the fitness, W, of females that care and desert. Refer to Equations 1 and 2 in the Introduction.

In cell D25 enter the formula **=$I$6*B25+$I$7*C25**.
In cell E25 enter the formula **=$J$6*B25+$J$7*C25**.
For the basis of these formulae, recall from Equation 1 that the fitness of females that care can be computed as

$$W(\mathrm{C}) = [r_\mathrm{m} \times E(\mathrm{C,C})] + [s_\mathrm{m} \times E(\mathrm{C,D})]$$

where r_m and s_m are the frequencies of males that care and desert, respectively. The fitness of females that desert (Equation 2) is

$$W(\mathrm{D}) = [r_\mathrm{m} \times E(\mathrm{D,C})] + [s_\mathrm{m} \times E(\mathrm{D,D})]$$

Your spreadsheet should now look like Figure 6.

	B	C	D	E
22	Female fitness			
23	Frequency of male strategy		Female fitness	
24	Care	Desert	Care	Desert
25	0.1	0.9	0.9	0.06

Figure 6

5. For year 0, enter formulae in cells H25 and I25 to compute the fitness, W, of males that care and desert.

In cell H25 enter the formula **=$I$11*F25+$J$11*G25**.
In cell I25 enter the formula **=$I$12*F25+$J$12*G25**.
Your spreadsheet should now look like Figure 7.

	F	G	H	I
22	Male fitness			
23	Frequency of female strategy		Male fitness	
24	Care	Desert	Care	Desert
25	0.9	0.1	6.165	0.675

Figure 7

6. Save your work.

C. Compute changes in fitnesses over time.

1. In cell B26, enter a formula to compute the frequency of a male caring strategy, r', in Year 1 for males. Refer to Equation 5 in the Introduction.

We entered the formula **=(B25*H25)/(B25*H25+C25*I25)** in cell B26.
The frequency of a caring strategy in the following generation is denoted by r'. Remember from Equation 5 that r' is calculated as

$$r' = \frac{r \times W(C)}{\overline{W}}$$

which is simply the fitness of males that care times the frequency of males that care divided by the mean fitness for males. Mean fitness of males, in turn, is calculated as

$$\overline{W} = \left[r_m \times W(C)\right] + \left[s_m \times W(D)\right]$$

2. In cell C26, enter a formula to compute the frequency of a male deserting strategy in year 1 for males.

In cell C26, enter the formula **=1-B26**.
The frequency of the deserting strategy in the following generation in denoted by s'. It can be computed as simply $1 - r'$.

3. Select cells D25–E25, and copy their formulae down 1 row.

	A	B	C	D	E
22		**Female fitness**			
23		Frequency of male strategy		Female fitness	
24	Time	Care	Desert	Care	Desert
25	0	0.1	0.9	0.9	0.06
26	1	0.503676471	0.496323529	2.514705882	0.302205882

Figure 8

4. In cell F26, enter a formula to compute r', the frequency of the caring strategy in year 1 for females.

Your spreadsheet should now look like Figure 8.
In cell F26 enter the formula **=(F25*D25)/(F25*D25+G25*E25)**.

5. In cell G26, enter a formula to compute s', the frequency of the deserting strategy in year 1 for females.

In cell G26 enter the formula **=1-F26**.

6. Select cells H25–I25, and copy their formulae down 1 row.

7. Select cells B26–I26, and copy their formulae down to row 45.

8. Save your work.

	F	G	H	I
22	**Male fitness**			
23	Frequency of female strategy		Male fitness	
24	Care	Desert	Care	Desert
25	0.9	0.1	6.165	0.675
26	0.992647059	0.007352941	6.706985294	0.744485294

Figure 9

D. Create graphs.

1. Graph the fitness of females that care and desert as a function of time (cells D24–E45).

Your spreadsheet should now look like Figure 9.

Figure 10

2. Graph the fitness of males that care and desert as a function of time (cells H24–I45).

Use the line graph option and label your axes fully. Your graph should resemble Figure 10. Use the line graph option and label your axes fully. Your graph should resemble Figure 11.

3. Save your work. Interpret your results. Why did a two-parent caring system evolve? Play around with the model and see if you can get another kind of mating system to evolve. (Change cells C5–C7, C10–C11, and/or C14–C15.)

Figure 11

E. Compute the ESS inequalities.

Finally, we are able to evaluate the inequalities provided in Table 2 to determine the conditions in which an evolutionarily stable strategy evolves. Remember, the inequalitites for both the female and male must be true in order for a given mating system to evolve as an evolutionarily stable strategy. We will enter formulae in cells B19–E20 to reflect the inequalities in Table 2. If the condition is true, we will have the spreadsheet return the word TRUE; if the inequality is false, we will have the spreadsheet return the word FALSE.

1. Set up new headings as shown in Figure 12.

	A	B	C	D	E
17		ESS 1	ESS 2	ESS 3	ESS 4
18		Both care	Male cares	Female cares	Neither cares
19	**Female inequality**				
20	**Male inequality**				

Figure 12

2. In cell B19, set up a formula to evaluate whether the inequality for females for ESS 1 is true or false

In cell B19 enter the formula **=IF(C11*C7>C10*C6,TRUE)**. An **IF** formula has three parts. The first part tells the spreadsheet to evaluate a condition. In our case, the condition is the ESS inequality derived by Maynard Smith (1982) for females that care for offspring. Females will care for offspring when $vP_2 > VP_1$. The second part tells the program what value to return if the condition is true. Since the word TRUE is entered, the spreadsheet will evaluate the inequality and return TRUE if the inequality is in fact true. Note that we left the third part off of this equation, which normally tells the spreadsheet what value to return if the condition is false. If the third part is not specified, the program will return the word FALSE by default.

3. Complete the table given in cells B19–E20 by entering formulae analogous to that in Step 2. Refer to Table 2 as you enter formulae.

Double-check your results with ours. The formulae we used are:

- B20 **=IF(C7*(1+C15)>C6*(1+C14),TRUE)**
- C19 **=IF(C10*C6>C11*C7,TRUE)**
- C20 **=IF(C6*(1+C15)>C5*(1+C14),TRUE)**
- D19 **=IF(C11*C6>C10*C5,TRUE)**
- D20 **=IF(C6*(1+C14)>C7*(1+C15),TRUE)**
- E19 **=IF(C10*C5>C11*C6,TRUE)**
- E20 **=IF(C5*(1+C14)>C6*(1+C15),TRUE)**

4. Save your work.

This table provides you a way to quickly determine if the inequalities for both males and females are true, and hence which parental care system is an ESS.

QUESTIONS

1. Fully interpret your graphical results and explain how the parental care system evolved. Is the system an ESS?
2. What parameter conditions are likely to lead to single-parent care (either social polyandry or polygamy)? Enter various values in your model and explore the outcomes.
3. What parameter conditions are likely to lead to social promiscuity?
4. Enter the following values in your spreadsheet.

	A	B	C
4	**# of parents**	**Probability**	
5	0	$P_0 =$	0
6	1	$P_1 =$	0.7
7	2	$P_2 =$	0.9
8			
9	**Female behavior**	**# of eggs**	
10	Deserter	V = desert =	10
11	Care	v = care =	5
12			
13	**Male behavior**	**Probability of remating**	
14	Deserter	p = desert =	1
15	Care	p' = care =	0

Which parental care system evolves? Evaluate the conditions in cells B19–E20. You should see that two ESSs are possible. Does the initial frequencies of *r* and *s* determine which parental care system is ultimately the most successful?

5. How does the environment affect P_0, P_1, P_2? How does the environment or characteristics of the population itself affect V, v, p, and p'?

6. The model you have built assumes that $P_2 > P_1 > P_0$. Why did we assume that $V \geq v$? Are these assumptions valid? Discuss the concept of trade-offs and constraints in your answer.

LITERATURE CITED

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