Biology 352, Spring 2019 **Exam Number__KEY__**

Second midterm exam

Part 1. Very short answer, worth 20% of the exam.

Point values for each in parentheses

1-1) Match the following terms used in behavioral ecology with the appropriate topics of behavioral study listed to the right (you may apply more than one topic to a term and some topics may not be represented; 8 pts).

Terms		**Topics**
g	Iteroparity	a) Optimality Modeling
a	Patch residency time	b) Game Theory
g	W = M • P • L	c) "Passive" grouping
c	Selfish Herd	d) "Active" grouping
c	Ideal Free Dispersion	e) Territoriality
b	Hawk vs. Dove	f) Evolution of sexual reproduction
e	Intruder Pressure	g) Life History Theory
e	Economic Defensibility	

1-2 What is the most likely behavioral explanation for why animals might be distributed uniformly within a habitat (2 pt)? ***Territoriality or other expression of dominance that excludes others from an area***

1-3) Excluding monogamously breeding birds, give two clear, real-life examples of species in which unrelated individuals defend a group territory (2 pts)

The most obvious example, from readings: the Striped Parrotfish. Others: Pied-wagtails, male lion groups

1-4) Describe the three basic patterns of animal dispersion found in nature (2 pts).

1) ***Random*** 2) ***Grouped/Clumped*** 3) ***Uniform/Spread out***

Which is the ***least*** common? ***Random***

1-5) Describe a mechanism of group formation that decreases *per capita* risk of predation and give an example. (3 pts). ***Several possible answers: Predator saturation (cicadas, herring); confusion (e.g. starlings); cooperative defense (buffalo, elephant); more eyes/ears (ostrich).***

1-6) List the four basic assumptions of the Ideal Free Model of dispersion (2 pts):

1) ***Resources are patchy***
2) ***Animals have "perfect knowledge" of their environment***
3) ***Animals are free to move among resource patches***
4) ***Animals are identical (no competitive advantages to certain individuals***

What are the two basic predictions of this model (2 pts)?

1) ***All individuals receive equal resource intake on all patches***
2) ***The number of individuals present in patches is proportional to patch quality***

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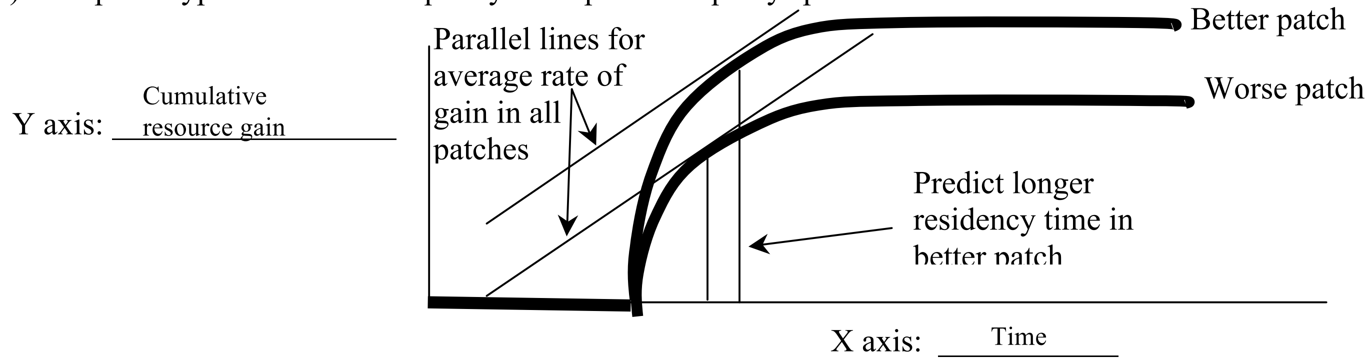
Part 2 (Short answer) worth 13 pts each (39 % of grade)

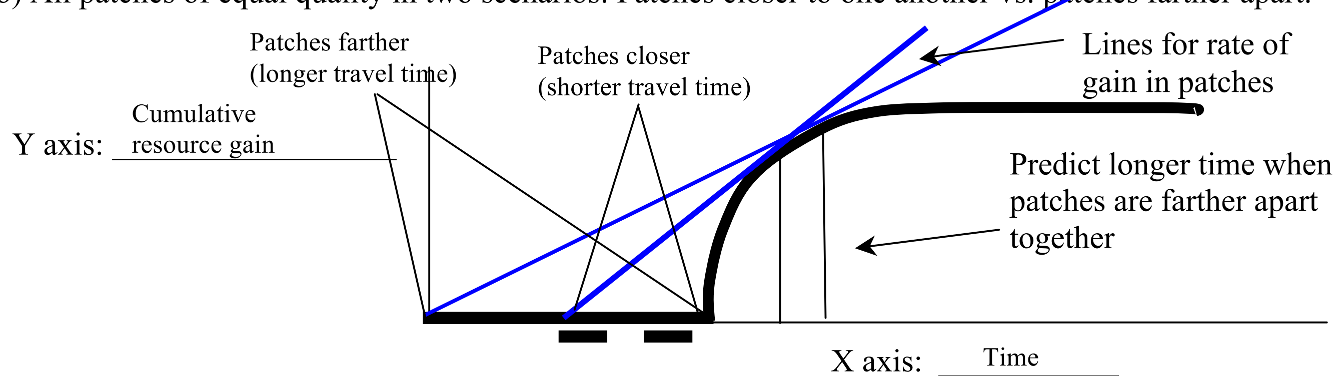
(NOTE: *answer 3 of the 4 questions*)

2-1) Using a graphical "diminishing returns" model of resource consumption, predict the relative patch residency times (shorter or longer) for a forager under the following two conditions: Label *all* appropriate components and axes and be clear about your predictions regarding patch residency time with reference to your graphs.

a) Two patch types that differ in quality… all patches equally spaced from one another



b) All patches of equal quality in two scenarios: Patches closer to one another vs. patches farther apart.



2 - 2) Describe, mathematically, the switching point between specialist and generalist feeding as a function of search time for an animal that has the choice of two prey items that differ in the following ways:

Prey type 1 has an energetic value of E_1, handling time of H_1, and search time of S_1
Prey type 2 has an energetic value of E_2, handling time of H_2, and search time of S_2

The decision to switch from specialization (only eat the more profitable prey) and generalization (eat both prey types) will occur when the search time for the more profitable prey becomes high enough to make including the less profitable prey in the diet. Presuming, in the example above, that Prey type 1 is more profitable (i.e., $E_1/H_1 > E_2/H_2$) then switching would occur when the payoff of Prey 1, $E_1/(H_1 + S_1)$ becomes less than the payoff of Prey 2: E_2/H_2.

Setting $E_2/H_2 > E_1/(H_1 + S_1)$ and solving for S_1:

$$(H_1 + S_1) * E_2/H_2 > E_1$$

$$(H_1 + S_1) > E_1(H_2/E_2)$$

$$S_1 > E_1(H_2/E_2) - H_1$$

So, as a function of the search time for Prey 1, switching is predicted when $S_1 > (E_1 * H_2/E_2) - H_1$

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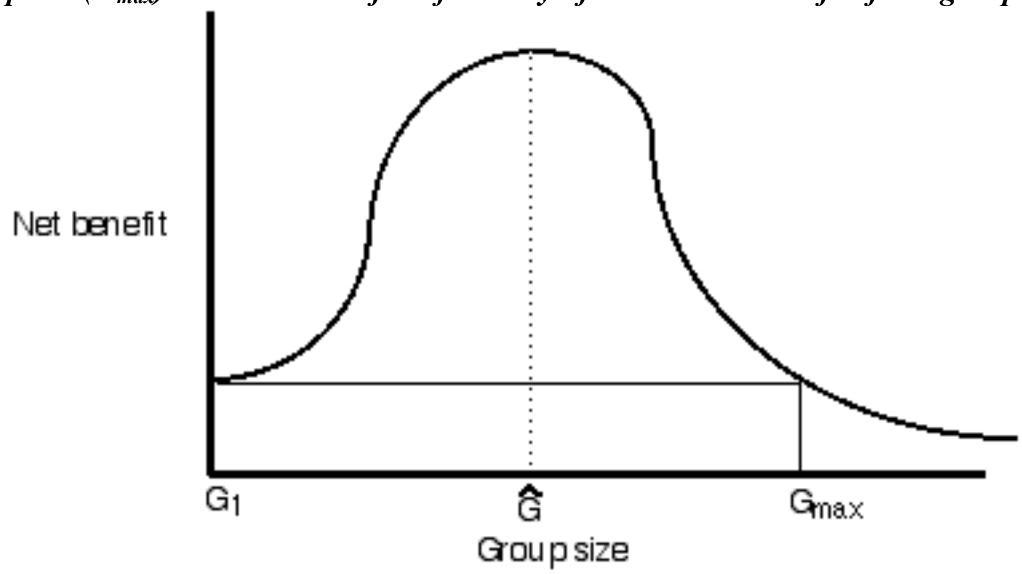
Part 2 (continued)

2 - 3) Briefly describe an "active mechanism" of grouping that increases the effectiveness of acquiring food. Then, draw the expected general relationship between group size and per capita benefits for this situation and, based on your plot, clearly identify the "optimal group size" and the expected maximum size of groups. Be sure to label all parts of your figure clearly and in detail, including axes.

There are a number of possibilities here: Reduced path overlap, facultative prey response, risk minimization, and information transfer are examples from lecture. Any "active" grouping is going to produce a humped shape curve similar to the one drawn below. Optimal group size would be the size that provides the highest per capita benefit (Ê) however, if group members are unable to exclude others, then the group may become larger up to the point (G_{max}) where the benefits of solitary life exceed the benefits from group living.



2-4) Define and give a real-life example of a kinesis and a taxis. For each, describe a pattern of dispersion (grouped, spread out, random) that might result, with clear justification for your answer.

A kinesis is a non-directional movement or action in response to an environmental stimulus. For example wood lice show an increased level of randomly directional movement in drier environments. This tends to produce groups in areas of moisture as individuals slow down and thus stay together more than they would in drier areas.

A taxis is a directional movement or action towards or away from an environmental stimulus. There are many examples possible. Any taxis towards a stimulus will produce aggregations at the source of the stimulus, (e.g. moths aggregating at a streetlight). Uniform distributions might also occur if the stimuli occur in a uniform distribution, although under such circumstances, we might expect uniformly distributed groups.

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Part 3 (Short essay answer) worth 25 pts each (50% of grade)

Answer <u>one</u> of the next <u>two</u> questions (3-1A or 3-1B)

3 – 1A Baby songbirds typically die without some provisioning of food. Nestling survival is often directly related to the rate at which parents can deliver food to the nest. Consider the following scenario associated with variable levels of food availability and parental care for a hypothetical species of songbird.

In most years, food availability allows a single parent (male or female) to successfully rear two nestlings. If both parents provide food then four nestlings typically survive. Additional mating opportunities are negligible for both sexes. In occasional years of higher food abundance (which are unpredictable), feeding by both parents again results in the successful rearing of four offspring, while care by a single parent (male or female) allows three nestlings to survive. In these good years there is also a 50% chance that a non-caring parent will find another mate and produce another brood of three successful nestlings. Based on these payoffs, describe in as much detail as possible (i.e., **quantitatively**), *the expected patterns of parental care and mating system* you would observe in the two different kinds of years (i.e., average vs. higher food availability). Assume that males and females are equal with regards to the costs of parental care, the probability of finding other mates, and the expectation of future reproductive success.

Since males and females are effectively equal, this problem can be solved using Game Theory. In normal years, the payoff matrix would look like:

	Feed	***Don't Feed***
Feed	4	2
Don't Feed	2	0

Because "Feed" always provides the best payoff, irrespective of what the mate does, this is a pure ESS for "Feed". Biparental care with strict monogamy will be expressed

In "good" years, the matrix would be different. Here, the payoff of not feeding, while your partner feeds is 4.5 (3 + 1.5) because of the added probability (0.5) of reproductive success from mating again (3): 3 x 0.5 = 1.5

	Feed	***Don't Feed***
Feed	4	3
Don't Feed	4.5	1.5

This is a mixed stable ESS, with the proportion of "feed" calculated as: (3-1.5)/((3-1.5)+(4.5-4)=1.5/2=0.75 Thus, an individual is expected to help feed 75% of the time and not feed 25% of the time. The selection for "not feeding" at some times leads to a small, but meaningful level of polygyny during good years.

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3 – 1B) The Barred Hamlet, a simultaneously hermaphroditic fish, can produce both eggs and sperm at the same time. Individuals employing a “hermaphrodite” strategy allocate most of their resources to female function (i.e., to making eggs), producing just enough sperm to fertilize the eggs of another individual employing the same strategy. By spawning together, two “hermaphrodites” will, on average, fertilize 180% more eggs than if they allocated all of their energy to egg production. In a population of these fish, a mutant “male” strategy emerges in which an individual produces many more sperm and just enough eggs (10% of what a “hermaphrodite” produces) to make a partner release all of their eggs. These individuals have more energy to swim around and will, on average, be able to find and mate with three hermaphrodites during the daily spawning period. Assuming that all individuals are of equal size and competitive ability, what is the evolutionary fate of the mutant “male” strategy… will it successfully invade the population and, if so, to what extent?
Answer with as much detail as possible and show all your work.

This is a classic game theory problem with the following properties:

Player A (left side)
Player B (top side)

	herm.	*male*
herm.	P_{11}	P_{12}
male	P_{21}	P_{22}

Strategy 1: spawn as a hermaphrodite (herm.) allocate 90% eggs, 10% sperm
Strategy 2: spawn as a male (male) allocate only 9% eggs (10% of herm).

Payoffs (expected reproductive success): all payoffs judged relative to 100 % allocation towards eggs

	1.8	*0.99*
	2.97	*0.18*

P_{11} (both act as hermaphrodites) = eggs produced by each = 0.9 + 0.9 = 1.8

P_{12} (Player A is hermaphrodite, B is male) = eggs produced by hermaphrodite + eggs produced by male = 0.9 + 0.09 = 0.99

P_{21} (Player A is male, B is hermaphrodite = (3 x eggs produced by hermaphrodites) + (3 x eggs produced by “male”) = 3 x 0.9 + 3 x 0.09 = 2.7 + 0.27 = 2.97

P_{22} (both are male) = 2 x eggs produced by male (0.1 of 0.9) = 2 x 0.09 = 0.18

This is a mixed, stable ESS and the frequency of playing hermaphrodite can be calculated from: $f = (P_{12} - P_{22})/((P_{12} - P_{22})+(P_{21} - P_{11}))$ yields the following:
$(0.99 – 0.18)/[(0.99 – 0.18) + (2.97 - 1.8)] = 0.81/(0.81 + 1.17) = 0.44$

		●
	●	

So, we expect a fish to play “hermaphrodite” 44% of the time and “male” 56% of the time (a behavioral polymorphism) or 44% of the fish should play hermaphrodite all the time and 56% should play male all the time (genetic polymorphism).

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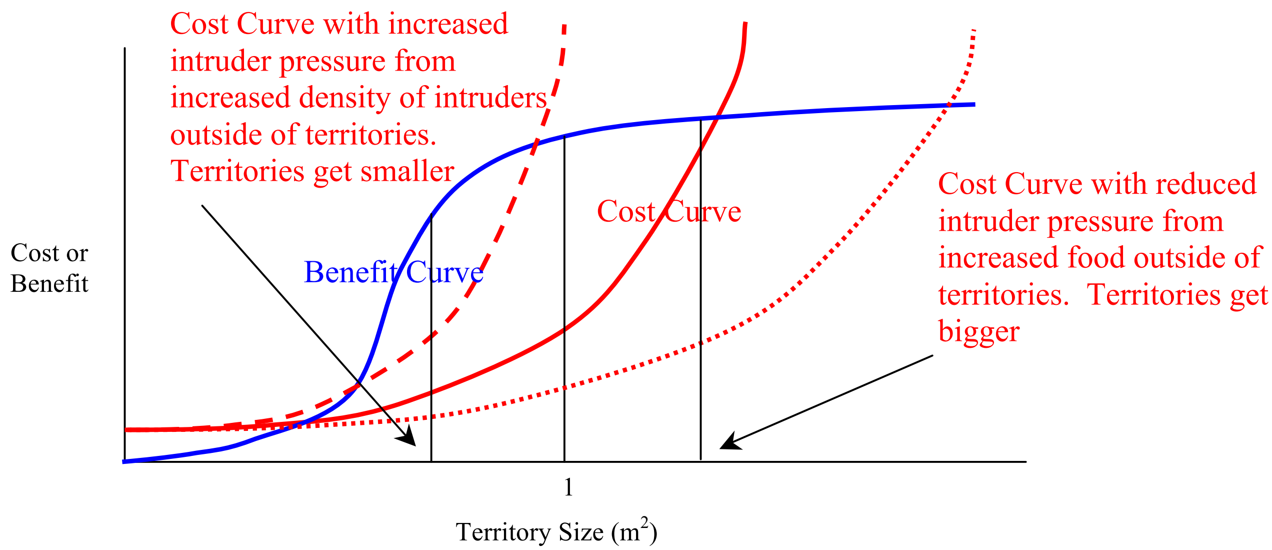
Part 3 (continued)

Answer one of the next two questions (3-2A or 3-2B)

3 – 2A) You are studying the dispersion of herbivorous damselfish on a reef and find that territorial individuals defend exclusive-use feeding territories from non-territorial conspecifics that are 1 m^2 in size. You want to study how the costs and benefits of territoriality influence dispersion in this habitat. Using the axes provide below, begin by drawing the hypothetical cost and benefit curves associated with the defense of different sized territories for a range of territories that are, and are not, economically defensible. Be sure to label your curves clearly and denote the size(s) of territories that are expected.

Next, assume that these fish are net benefit maximizers, and use this information to provide a scale for the x axis.



Upon further study, you find that algal standing crops inside territories are 10g of algae/m^2, which is roughly twice the level found outside of territories. The density of non-territorial damselfish is 2 fish/m^2. Based on this information, you decide to do some experiments.

In the first experiment, you augment food levels outside the territory so they are now 7.5 g of algae/m^2. Based on the curves you have drawn previously, what is the predicted effect of this experiment and why?

Intruder pressure is measured as $R_I/D_I – R_O/D_O$ where R is resource density and D is density either inside (I) or outside (O) of the territory. Thus, in the original situation, intruder pressure should be 10/1 - 5/2 = 7.5. If food is augmented to 7.5 g of algae/m^2 then this changes to 10/1 – 7.5/2 = 6.25. With lower intruder pressure you would get decreased costs of defense, shifting the cost curve (red) to the right and larger territories are predicted.

In the second experiment you add a school of non-territorial fish to the reef so that their density is now doubled. As before, what is the predicted effect of this experiment and why why (again, you may use the graph, but be sure to justify your answer with detail)

Now Intruder Pressure will increase, as the density of individuals outside territories is higher. The cost curve will shift to the left and territories are expected to shrink.

3 – 2B) A territorial songbird is killed during the night by a weasel. The weasel promptly goes to sleep in some nearby bushes. The following morning, a neighboring bird has the opportunity to expand his territory to include the now vacant neighboring area. There is a 55% chance that he will be able to invade this new area without a contest and a 45 % chance he will have to fight for the territory with another neighbor.

If he gets the new territory without a fight, there is a 70% chance that he will simply move into the new area and fail to notice the sleeping weasel... as a result, he too will be killed the following night. If he does notice the weasel however, he can successfully drive it away from the area and thus double his current reproductive output.

If he fights for the new territory, there is a 60 % chance that he will win and, despite the costs of fighting, increase his reproductive output by 30 %. If the neighbor wins, however, the costs of fighting will lead to a 20 % reduction in reproductive output. In either case, the fighting birds will wake the weasel, who will leave the area completely because of all the commotion.

Given these probabilities and assuming that current reproductive output relates directly to fitness with no other costs or benefits of moving or staying, should the male attempt to take over the vacant territory?

This is an optimality problem. To answer, you must compare current reproduction (r) with expected reproduction if the male invades the vacant territory. The expected payoff can be calculated from the probabilities associated with different costs and benefits:

There are two probabilities associated with taking over the new area:

1) Uncontested (p= 0.55) or

2) With a fight ((1 - p) = 0.45).

The payoff if uncontested is calculated as:

30% probability of doubling and 70% chance of death (future reproductive output = 0), or:

0.3(2r) + 0.7(0r) = 0.6r

The payoff with a fight is calculated as:

60% prob of increase in r by 30% and 40% prob of decrease by 20%,

0.6 (r + 0.3r) + 0.4 (r - 0.2r) = 0.6(1.3r) + 0.4(0.8r) = 0.78r + 0.32r = 1.1r

Clearly, fighting is better than getting the territory uncontested (because of the high probability of not detecting the stoat in the uncontested scenario), but the question asks about the decision to take over or not take over, not whether to fight or not to fight (which is given as a fixed probability).

If the male invades, his expected payoff is the payoff of doing so without a fight (1) or with a fight (2) multiplied by the appropriate probability:

0.55(0.6r) + 0.45(1.1r) = 0.33r + 0.495r = 0.825r

Since 0.825r is less than r then the expected payoff of invading is less than current reproductive output.

Thus: DON'T TAKE OVER