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EVOLUTIONARY BIOLOGY BIOS 30305 EXAM #2 FALL 2017

There are **3** parts to this exam. Use your time efficiently and be sure to put your name on the top of each page.

Part I. True (T) or False (F) (2 points each)(30 pts. total)

1)	Nearly all living animal lineages, including chordates, evolved during the Cambrian period.	**T**	F
2)	In small captive populations, doubling the effective size of the population maintains twice the amount of additive genetic variation.	**T**	F
3)	Assortative mating in a population can break up non-random associations of alleles across multiple loci.	T	**F**
4)	Quantitative Trait Loci (QTLs) are genomic regions that contain genes, or are linked to genes, that contribute to population differences in phenotype.	**T**	F
5)	The Classic View of speciation is based on the idea that postzygotic isolation evolves more rapidly in sympatric species.	T	**F**
6)	Bright orange bill color in many bird species is used by females as an indicator of immune function.	**T**	F
7)	Ecological situations that require rapid evolution are likely to favor asexual reproduction.	T	**F**
8)	The Red-Queen Hypothesis may explain the evolution of recombination in large eukaryotic genomes.	**T**	F
9)	The rate of adaptation depends on both the strength of selection and on the heritability of traits.	**T**	F
10)	Ring species demonstrate the development of instantaneous reproductive isolation among adjacent populations.	T	**F**
11)	Mate provisioning is an example of an indirect benefit driving the evolution of female preference.	T	**F**
12)	Similar ecological conditions can lead to parallel evolution of similar phenotypes.	**T**	F
13)	Character displacement prevents divergence between closely related species when there are unexploited niches available.	T	**F**

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14) Antagonistic-Pleiotropy among fitness traits can maintain genetic variance for fitness in natural populations **T** **F**

15) Haldane's Rule suggests that when there is an asymmetry between male and female hybrid fitness it is typically the homogametic sex that has reduced fitness. **T** **F**

Part II. Multiple Choice (3 points each)(30 pts total).

16) Which of the following statement(s) is/are **TRUE**,

A. Sexual selection is stronger in monogamous species.
B. A highly skewed breeding sex ratio can generate strong sexual selection.
C. Male-Male interactions reduce the variance in reproductive success.
D. Variance in reproductive success influences the opportunity for sexual selection.
E. A and D
F. B and D

17) One form of the Good-Genes model for the evolution of female choice is the handicap principle. Which of the following statements is **NOT TRUE** under the handicap principle?

A. Handicaps are examples of honest signals since there is a true cost to elaborate male traits.
B. Females who mate with males carrying an exaggerated trait will have female offspring with decreased fitness.
C. The bigger the handicap, the higher the genetic quality of the male carrying the trait.
D. Female preference for exaggerated male traits can lead to a genetic correlation between preference and trait.

18) Which of the following statement(s) about character displacement is/are **TRUE**?

A. Character displacement can promote rapid divergence among closely related species.
B. Character displacement is the divergence of male and female traits involved in sexual selection.
C. Character displacement can constrain divergence into occupied niches.
D. A and B.
E. A and C.

19) What is the best definition of sexual selection?

A. Selection related to any aspect of offspring production.
B. Selection that arises as a consequence of competition for access to mates.
C. Selection on the form and structure of gametes.
D. Selection that results in any type of difference between the sexes.

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20) Anisogamy refers to,

A. A positive relationship between body size and fecundity.
B. A non-random mating process in which one sex competes for the other.
C. An asymmetry in the size of gametes, with one small type and one large type.
D. Variation in the ratio of testes weight to body weight in primates with different mating systems.

21) Which one of the following is **NOT** a prezygotic reproductive isolating mechanism?

A. Mating occurs, but no gametes are transferred.
B. The backcross or F_2 has reduced viability.
C. Mating occurs, gametes are transferred, but fertilization does not take place.
D. Populations are infected with different strains of the bacteria *Wolbachia* causing reciprocal male sterility.

22) Which of the following statements is **NOT TRUE**?

A. The selection differential is the covariance between phenotype and relative fitness.
B. The selection differential is the difference between the mean of selected parents and the mean of the base population prior to selection.
C. The selection differential is the difference between the mean of the offspring of selected parents and the mean of the offspring of all parents.
D. The selection differential is equal to the response to selection divided by the heritability.

23) Epistatic interactions are an important component of which of the following?

A. The build up of postzygotic reproductive isolating mechanisms.
B. The phenotypic covariance between half-sibs.
C. The almost universal observation of inbreeding depression in natural populations following the mating of related individuals.
D. A and C.

24) Which of the following statements best describes the three phases of Wright's Shifting-Balance model of movement between peaks in an adaptive landscape?

A. Migration followed by random genetic drift and selection towards a new fitness optima.
B. Selection towards a new fitness optima followed by random genetic drift and migration.
C. Random genetic drift followed by selection towards a new fitness optima and migration.
D. The appearance of a rare beneficial mutation followed by selection towards a new fitness optima and migration.

25) Which of the following provides evidence for reinforcement?

A. Premating isolation between the two species is higher in areas where they are sympatric vs. areas where they are allopatric; postzygotic isolation is strong in all crosses.

B. Postzygotic isolation between two species is higher in areas where they are sympatric vs. areas where they are allopatric; premating isolation is the same in allopatric and sympatric populations.

C. Premating isolation between the two species is higher in sympatry than allopatry; there is no postzygotic isolation in any cross.

D. Both A and C.

This question was not worded well. The correct answer is **A**. A number of you chose **C** (or **D**). The problem with **C** is that if there is no postzygotic isolation (i.e., no deficit in hybrid fitness) then there is no reinforcing selection to avoid this deficit. However, I counted this one as correct as it does reflect the early development of prezygotic isolation shown in the Coyne & Orr *Drosophila* data.

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Part III. Short Answer (40 pts. total) Be concise and to the point, short focused answers are better than long rambling ones.

26. One of the most amazing transitions in the fossil record is the sudden appearance of diverse metazoan organisms in the Cambrian period about 530 MYA. This phenomenon is often referred to as the "Cambrian Explosion", however, some researchers have questioned whether it was really an "explosion" or more like a "slow burn". (12 points)

A. Which view do you think is more appropriate? Support your answer with information from class. (4 points)

You could argue either viewpoint in this answer and receive full credit as long as you support your arguments. While it is certainly true that the diverse array of forms in the Cambrian period appear suddenly in the fossil record around 530 MYA, the origin of metazoans certainly precedes this time frame. Two observations are particularly relevant. The somewhat enigmatic Ediacaran fauna data back as early as 640 MYA. We do not know with any certainty how these forms are connected to the later forms in the Cambrian, but they certainly predate the start of the Cambrian. Additionally, there are a number of estimates of the origin of modern phyla based on molecular clocks that suggest a divergence time much earlier than the Cambrian. One study by Wray et al. (1996) suggests that the major metazoan groups may have diverged between 1.0-1.2 BYA. Taken together these results suggest that the diversification that led to the "Cambrian Explosion" began much earlier and that a "slow burn" may be a more appropriate view.

B. The diversification of metazoan groups in the Cambrian period is a classic Adaptive Radiation. What **two (2)** factors contribute to an Adaptive Radiation? List and explain these **two** factors and **provide an example for each factor from the Cambrian radiation.** (4 points for each – 2 for the factor and 2 for the example)

Two factors suggested by the paleontologist G. G. Simpson that play a role in adaptive radiations are:

1) **ECOLOGICAL OPPORTUNITY** - Can be the result of the invasion of unoccupied territory, or the extinction of a competitor opening up an available niche. The main feature is the availability of unoccupied niches. When there is open niche space for species to diversify into, mechanisms like character displacement can rapidly promote diversification.

An example of ecological opportunity in the Cambrian is the development of trophic levels in the ecological community. For the first time there are predators, prey, etc, changing the number and nature of niches and opening up new unexploited niche space. Credit was also given for mention of an increase in O_2 or phosphorus levels leading to novel niches. The invasion of land was not given credit since this occurred after the Cambrian period.

2) **KEY INNOVATION** - The evolution of a novel trait can lead to an adaptive radiation by opening up new niches and exposing organisms to novel selection pressures promoting divergence.

An example of a key innovation contributing to the Cambrian explosion is the evolution of developmental genes such as the *Hox* genes. The *Hox* genes are key developmental regulators of body segmentation and would certainly have evolved prior to the diversification in body plans we observe in the Cambrian fauna. Another example is the evolution of hard body parts. The

evolution of wings, lungs, amniotic eggs and other vertebrate characteristics were not given credit since these key innovations occurred after the Cambrian period.

27) Female preference for male traits can drive the evolution of exaggerated male traits. List ***and*** explain **three** (**3**) theories for the evolution of female preference. (9 points)(3 pts for each)

There are a number of possible answers to this question. These include:

1) **Direct Benefits** (i.e., mate provisioning, nuptial gifts) that increase female fitness
2) **Indirect Benefits**:

Good-genes Model: the key element of this model is preference by females for males that are carrying high fitness genes

Handicap Principle: this model is an example of "honest signaling" by males advertising high-fitness genes that overcome a fitness handicap. The main indirect fitness benefit for females is in daughters that inherit these high-fitness alleles.

Fisherian Runaway Process: this model requires a genetic correlation between female preference and male trait. This process begins with a pattern of assortative mating that leads to linkage disequilibrium between preference and trait alleles.

Sexy-son Hypothesis: one way to couch the runaway process that emphasizes that the indirect fitness benefit to females is sons with exaggerated traits and a mating advantage

3) **Antagonistic Coevolution:** An alternative to the Good-genes Model is based on Sexual Conflict. Just like the Good-genes models the genetic correlations created by assortative mating can lead to a runaway process.

4) **Sensory Bias:** Pre-existing preferences that are "hard wired" due to the sensory machinery in females.

Any three of these was acceptable. Full credit was not given if Good Genes & Handicap principle, or Sexy-son and Fisherian Run-away were used together since they are not distinct from one another. For each, a reasonable explanation was required.

Bonus (1 pt): Which of these theories best explains the *origin* of female preference?

This question was evaluated based on what you had down for the first part. Sensory Bias most directly addresses the question of the origin of female preference since it does not require selection at all. Among the others, anytime there are direct benefits the selection pressure on females will be the highest since there is a direct effect on her individual fitness. Antagonistic coevolution also directly affects the female's fitness so this one would be next. All the other categories are an indirect benefit and are more applicable to the evolution of female preference and male trait *after* they are established in a population. Among these, a good genes model is the best choice.

28) For your summer internship you are in charge of managing a Ring-tailed Lemur population in Madagascar and you begin to gather quantitative genetic data. When single-parent vs. offspring body size are plotted in this population, the data yield a linear regression with a slope of

0.25. The mean mass of all adults in this population is 5 kilograms. In this lemur population there is strong selection on body size and only the largest 25% of these adults breed. If the mean mass of all breeding adults is 6 kilograms, *what is the expected mean mass of all adults in the following generation?* (9 points)

The slope of a single parent – offspring regression is equal to ½ the heritability.

$h^2 = 2(0.25) = 0.5$ (2 points)

The selection differential (S) is equal to the difference between the mean of the selected parents and the mean of the base population. In this case, the base population has a mean of 5 kilograms, and the selected parents are the largest 25% of all individuals with a mean of 6 kilograms.

S = 6 - 5 = 1 kilogram (3 points)

The response to selection is then,

$R = h^2S = (0.5)(1) = 0.5$ kilograms (3 points)

In the next generation the mean mass equals the mean in the prior generation plus the response to selection.

5 + 0.5 = 5.5 kilograms (1 point)

29) In evolutionary theory the cost of sexual reproduction is commonly referred to as the ***two-fold cost of sex***. Explain the **two (2)** parts of the two-fold cost of sex. (10 points)

First cost: Demographic Cost. Since asexual females produce only females and sexual females produce both females and males, the asexual lineage has a 2-fold advantage over the sexual lineage in terms of potential population growth. (2 points – 1 pt. for identifying the cost and 1 pt. for an explanation)

Second cost: Genetic cost. Sexual individuals only pass ½ of their alleles to their offspring while asexual individuals pass along all their alleles. Big benefit to asexuality when you think about evolution as a change in allele frequencies over time and fitness as the transmission of an individual's genes to the next generation. (2 points – 1 pt. for identifying the cost and 1 pt. for an explanation)

Other costs to sexual reproduction were given partial credit included the cost of finding mates, the risk of sexually transmitted diseases, and the inability to maintain a multilocus genotype, etc.

Asexual reproduction is clearly beneficial since it avoids the "two-fold cost of sex". So why is sexual reproduction so common in nature? Explain **three (3)** benefits of sexual reproduction that offset the advantages of asexual reproduction. (2 points for each)

The three major categories of benefits to sexual reproduction are:

Combination of multiple beneficial mutations. In asexual lineages multiple beneficial mutations must occur in the same background sequentially. This takes time. Sexual lineages can bring multiple mutations together into the same genetic background rapidly via recombination and the inheritance of a single copy of the genome from each parent.

Ability to remove deleterious mutations. Sexual individuals can produce haploid gametes that harbor a reduced load of deleterious alleles. They can make offspring that have higher fitness than themselves. This ability can avoid the action of Muller's Rachet and the inevitable mutation meltdown that asexual lineages are prone to because of the accumulation of deleterious mutations.

Recombination and independent assortment generate tremendous amounts of genetic variation that is the fuel for evolution by natural selection. In changing environments, or in the presence of parasites and pathogens, sexual lineages have a big advantage over asexual lineages. They can adapt faster.

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Extra Work Space:

Section 1	_____/30
Section 2	_____/30
Section 3	_____/40
Total	_____/100