PH.D. PROGRAM IN BIOLOGY - THE CITY UNIVERSITY OF NEW YORK
FIRST EXAMINATION - ECOLOGY, EVOLUTION AND BEHAVIOR
FALL 1991

Session I. Short factual questions. Answer 10 of the following 16 questions. At least one paragraph should be used to answer question. USE A SEPARATE PAGE FOR EVERY QUESTION!!!!!!

Questions 1-9. Define what is meant by the following terms and cite appropriate examples of each (each term counts as a separate question) :

1. test of homology
2. reticulate evolution
3. apparent competition
4. ecotype
5. founder effect
6. relic taxon
7. polyandry

8.. index of consistency (Give an example of a hypothetical data matrix with an index of 1.0 and another matrix with an index of 0.5.)

9. nominal taxon (also explain how the taxon came into existence)

10. List criteria by which a population nay be recognized as being overexploited. Discuss the characteristics which may be observed and explain the relative value of each criteria.

11. What is the relationship between the amount of effort which may go into a given reproductive event and the selection for semelparity.

12. Distinguish between heritability (broad sense) and heritability (narrow sense). Which of these measures can be used to predict the response to selection and why?

13. What is concerted evolution, and what are two genetic mechanisms that can lead to concerted evolution?

14. What is a circadian clock and what types of behaviors may be regulated by it?

15. Differentiate between territory and home range.

16. Select any one vertebrate behavioral trait. Generate 2 ultimate and 2 proximate questions about the origin of this trait.

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Session II. Longer factual essays. Answer two of the four questions.

1. Patterson (1981) has stated that, '-instances of fossils overturning theories of relationship based on Recent organisms are very rare, and may be non-existent." Gauthier et al. ' (1989) Ann.Rev. SVS. Ecol. have challenged this view. Discuss the viewpoints of these investigators and state the case pro and con for the necessity of having fossil forms for classification.

2. The essence of the MacArthur and Wilson (1961) 'equilibrium theory of island biogeography' is that the number of species on an island is determined by a balance between immigration and extinction, and that this balance is dynamic, with species continually going extinct and being replaced (through immigration) by the same or by different species. From this theory the following predictions could be made:
a. The number of species on an island should eventually become roughly constant through time.
b. This should be a result not of stasis, but of continual turnover of species, with some becoming extinct and other immigrating.
c. Large islands should support more species than small islands.
d. Species number should decline with increasing remoteness of an island.

However, some of these predictions could be made without reference to the equilibrium theory. State which of the above predictions could be made without reference to the equilibrium theory and discuss alternative hypotheses which would account for these non-equilibrium theory based predictions.

3. What is the "adaptationist programme'-? Review and discuss the concepts of this program as applied to population genetics and systematics.

4. Discuss differences and similarities in the development of singing behavior in one or more types of song bird. Cite specific references in your discussion wherever possible.

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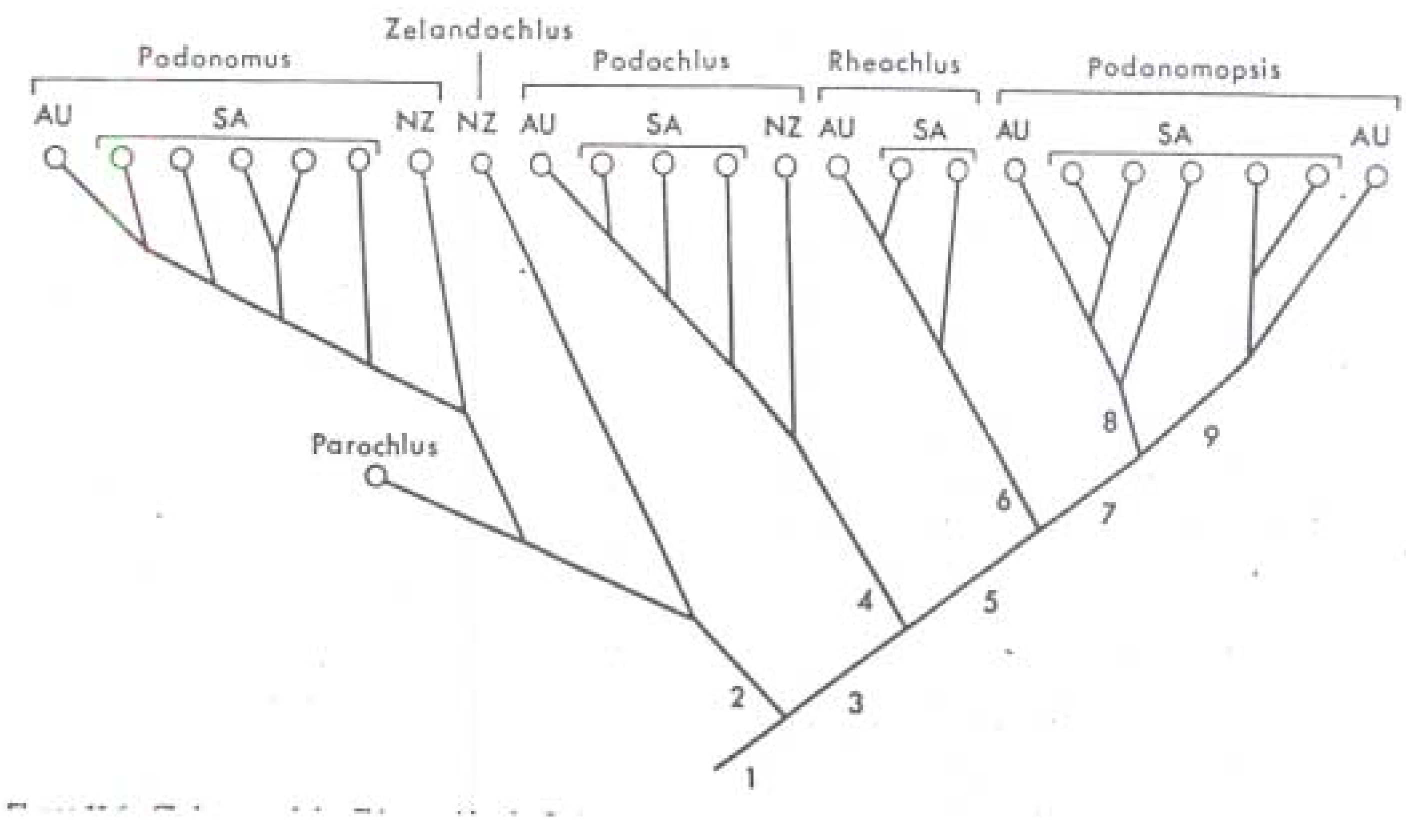
Session III. Data analysis. Select one of the four questions.

1. The diagram below is a cladogram of chironomid (midge) species of four genera in the tribe Podonomini, which their geographic occurrence in Australia (AU) , South America (SA) , and New (NZ). These data have been recently interpreted:

> **"**Given that the Australian groups all stand out as comparatively young apomorphic offshoots of older hierarchies in southern South America and that they appear apomorphic by comparison with their closest relative, it is logical to conclude that their occurrence in Australia is due to Gondwanic expansion by ancestral species via (or from) East Antarctica before Australia because separated from East Antarctica in the Eocene."

What is the logical principle that allows this interpretation? State an alternative principle that allows an alternative interpretation. What possible evidence might convince you that one alternative is correct and the other wrong?



2.

The gall-making tephritid fly Eurosta solidaginis induces a spheroid gall on the stem of the goldenrod species Solidago altimissa and S. gigantea. Sympatric populations of these plants often support large populations of this well-known insect. A study was designed to provide a comparative analysis of the influence of the host plant on the ecology and life history factors of the insect. Factors under investigation were its survivorship, influence of gall size (which is the insect's only source of food) , and vulnerability of the gall-maker to natural enemies. Note that the gall-maker, with a single generation per year, is attacked by two other insects, the parasitoid wasp, Eurytoma gigantea, and the inquiline (meaning living in the same gall) beetle, Mordellistena unicolor, and two bird predators, Picoides pubescens (downy woodpecker) and Parus atricapillus (black-capped chickadee).

Three randomized belt transects (2 m x 40 m) were sampled in the early spring such that all ramets of both host plant species were examined and the frequency and state of all galls determined and analyzed. The survivorship and causes of mortality were determined for each individual. However, in some cases, it was impossible to determine the fate of the gall insect and those particular individuals was classified as unknown.

Refer to the following three pages where one table and six figures summarize the data obtained. Consider these observations and results and develop an essay to respond to the following questions. Wherever appropriate, please indicate and interpret the appropriate statistical test which would have been required to yield the results obtained. Prepare your essay as a discussion of the results provided and conclusions considering the following points.

1. Discuss the relationship between host plant species, gall size and gall-maker size. Do larger galls increase the size of the gall-maker because of the increased food supply?

2. In what manner does gall size influence gall-maker mortality? Be sure to specify each of the causes of mortality in your discussion. Also indicate any differences in mortality between the two host plant species.

3. What are the implications of higher larval weight in the 6. maker larvae on future population growth of this species?

4. What factor(s) appear most important in determining the success of the wasp parasitoid, Eurytoma gigantea, and similarly, what factors appear most important in affecting bird predation?

5. What would you suggest as the next step in continuing this line of research?

Table 1. Larval biomass and gall diameter for galls from two host plants

Host plant	n	$\bar{x}$	SD
Larval biomass (mg)[a]			
S. altissima	66	50.4	11.2
S. gigantea	44	39.9	9.5
Gall size (mm)[b]			
S. altissima	66	21.3	2.2
S. gigantea	44	23.5	2.3

[a] $t = 5.11$; $P < 0.001$.
[b] $t = 4.84$; $P < 0.001$.

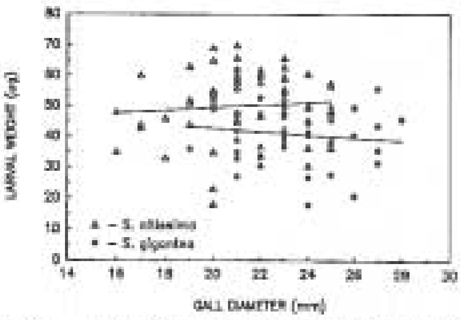


Fig. 1. Linear regression of larval weights over gall diameters. Neither regression slope was significantly different from zero: *S. altissima*, $y = 36.12 + 0.67x$; *S. gigantea*, $y = 53.84 - 0.50x$.

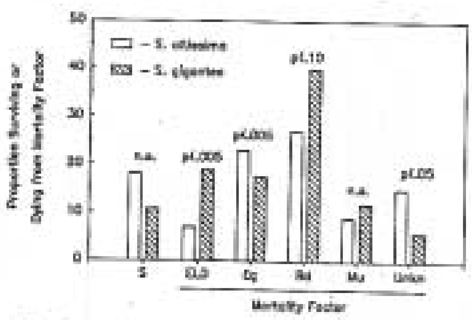


Fig. 2. Proportion of gallmakers surviving, or dying from specific mortality factors, on the two host plants. Abbreviations as follows: S, surviving gallmaker larvae; ELD, early larval death; Eg, attack by *Eurytoma gigantea*; Bd, bird attack; Mu, attack by *Mordellistena unicolor*; Unkn, death to unknown causes.

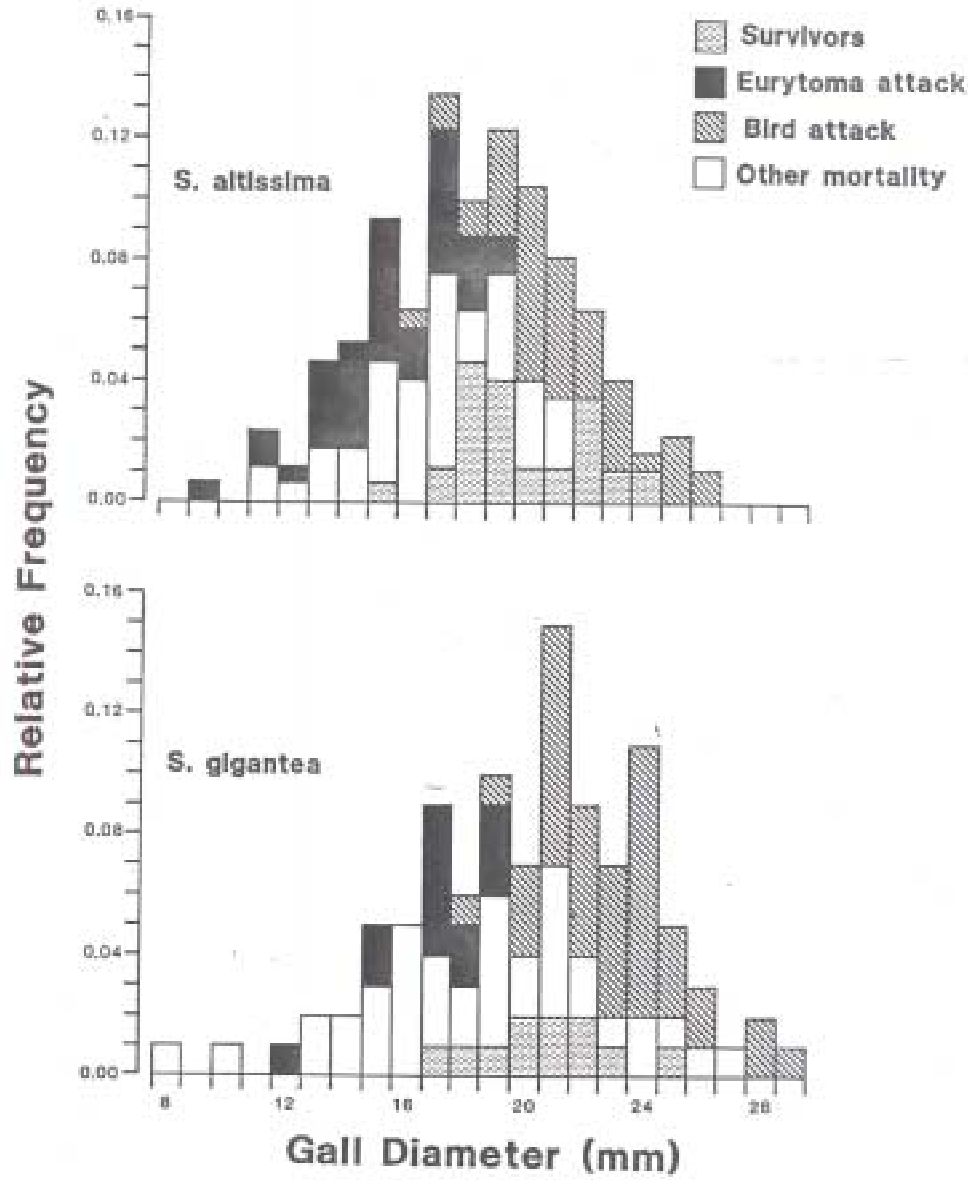


Fig. 3. Frequency histograms of gall sizes on the two host plants.

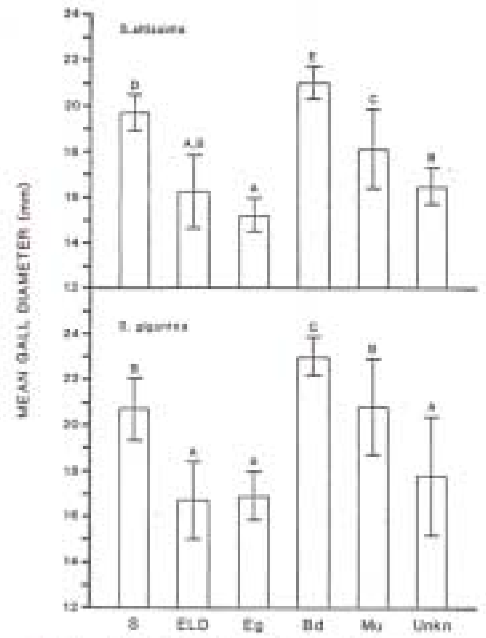


Fig. 4. Mean diameters of galls containing surviving *Eurosta*, or where killed by specific mortality factors; abbreviations as in Fig. 2. Galls from different hosts analyzed separately. Means noted with the same letters do not significantly differ.

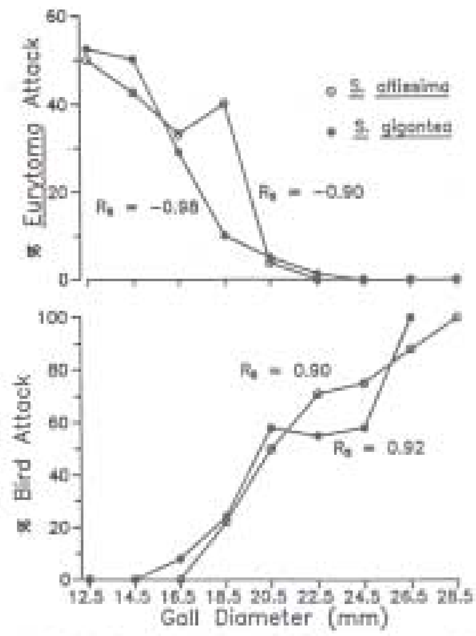


Fig. 5. Size-dependent attack by *Eurytoma* and by birds on galls from the two host plants. Attack rates calculated after excluding ELD galls, because they did not contain gallmaker larvae.

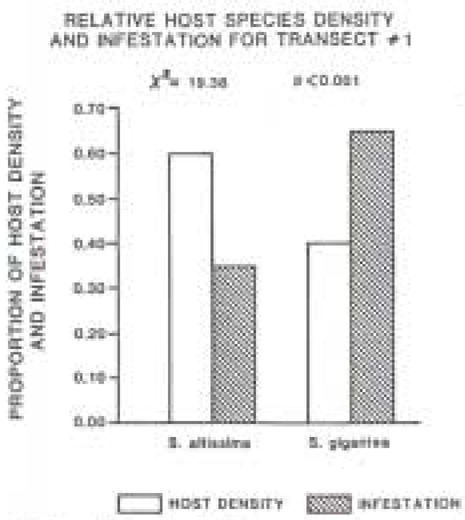


Fig. 6. Proportion of galls on each species compared with the proportion of stems of each in transect 1 (see text).

Session III Question 3

The occurrence of reproductive isolation is often an important step on the road to speciation especially in animals Postzygotic isolation i.e. hybrid sterility or inviability is common among species in the genus *Drosophila*, where it often affects only one sex among the hybrids It is sometimes possible to examine the genetics of postzygotic isolation in Drosophila using genetically marked stocks and backcrosses between the fertile hybrids of the parent species.

Orr and Coyne (Genetics, 1989, 121: 527-537) investigated the role of the X chromosome in causing sterility in hybrids between members of the *Drosophila virilis* group (Figure 1). They crossed *D. virilis* strains containing a recessive visible mutants on the X chromosome (Table 1) to strains of other species which were all wild-type for the X. When possible, these crosses were done in both directions, i.e. the *D.* virilis mutant stock was used in separate crosses as the male or the female parent. They then scored the fertility of the hybrid miles and females noting the eye color phenotype as an indication of the species source of the X chromosome (or chromosomes) [males are XY, females are XX.

Examine the tables below and answer the following questions. (It may help you to diagram the genotypes of the crosses):

1. What effects does the source of X chromosomes have on male fertility on female fertility? Are, the effects on male and female fertility in the same or different directions?

2, The authors use the G or χ^2 tests to examine the statistical significance of fertility differences. What do these tests measure, how are they similar and/or different, and why might you prefer (or require) the use of one test or the other? Which of the tests shown in Table 5 are χ^2 tests?

3. Table 6 shows the results of an attempt to "map" sterility-causing loci to two portions of the X chromosome, marked by the y and as genes. What conclusions can you reach about the effects of the two chromosome regions on fertility?

4. Do you think hybrid sterility has evolved only once in this group, or more than once? Why?

5. In the footnote to Table 5, the authors note that for backcrosses to non-virilis species, they cannot test for heterogeneity but only for deviations from in expected 1:1 ratio of the genotypes (this is because they must test-cross the backcross progeny to determine their genotype and thus they cannot test the genotypes of sterile females). How does testing against the 1:1 ratio (vs. doing a heterogeneity test) change the number of degrees of freedom in a G or χ^2 test,

III·3 (cont)

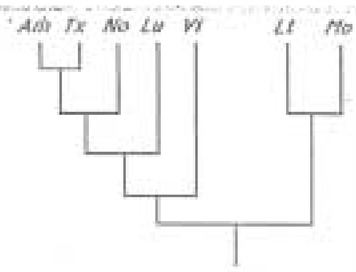


FIGURE 1.—Phylogeny of the *D. virilis* group. This phylogeny is based on concordant electrophoretic, morphological and karyotypic characters (see text). Am = *americana*, Tx = *texana*, No = *novamexicana*, Lu = *lummei*, Vi = *virilis*, Lt = *littoralis*, Mo = *montana*.

TABLE 1

Strains used in this study

Drosophila virilis *white*	A strain constructed by introgressing the Bowling Green *white* eye color allele [map position 1-105; ALEXANDER (1976)] into a wild-type strain of *D. virilis* and reextracting the mutant
yellow, apricot	*yellow* (*y*) at 1–2.9 and *apricot* (*ap*) at 1–136.0 (ALEXANDER 1976). As the *X* is about 170 map units long, each half is marked with a mutation
D. americana	Myrtle Beach State Park, South Carolina (Bowling Green Strain 15010-0951.00); Red Cloud, Nebraska (obtained from L. THROCKMORTON)
D. lummei	Finland (15010-1011)
D. novamexicana	San Antonio, New Mexico (15010-1031.8)
D. texana	Morrilton, Arkansas (15010-1041.23)
D. littoralis	Merlingen, Switzerland (15010-1001)
D. montana	Mount Hood National Forest, Oregon (15010-1021.19)

TABLE 2

Fertility of males and females in pure species

Species	Sex	Fertile	Total	Proportion fertile
virilis w	Male	207	211	0.98
	Female	81	81	1.00
virilis y, ap	Male	208	216	0.96
	Female	74	74	1.00
texana	Male	203	207	0.98
	Female	79	79	1.00
lummei	Male	154	156	0.99
	Female	68	69	0.96
americana	Male	167	185	0.90
	Female	78	80	0.98
novamexicana	Male	204	205	0.99
	Female	113	113	1.00
littoralis	Male	174	185	0.94
	Female	85	88	0.97

TABLE 3

Fertility of hybrid F_1 and backcross males

Parental cross	*X* chromosome genotype	Fertile	Total	Proportion fertile	*G* value
VT	*w*	129	195	0.66	60.7**
TV	w^+	199	209	0.95	
(VT)V	*w*	142	150	0.95	54.9**
	w^+	103	167	0.62	
(VT)T	*w*	98	116	0.84	13.9**
	w^+	192	199	0.96	
VA	*w*	185	200	0.92	6.3*
AV	w^+	210	215	0.98	
(VA)V	*w*	212	220	0.96	1.4
	w^+	200	213	0.94	
(VA)A	*w*	141	154	0.92	1.0
	w^+	181	192	0.94	
VLu	*w*	154	162	0.95	2.5
LuV	w^+	198	202	0.98	
(VLu)V	*w*	196	197	0.99	6.6*
	w^+	208	215	0.95	
(VLu)Lu	*w*	202	206	0.98	0.7
	w^+	197	206	0.96	
VN	*w*	15	229	0.07	162.1**
NV	w^+	43	44	0.98	
(VN)V	*w*	206	209	0.99	201.6**
	w^+	108	144	0.43	
(VN)N	*w*	33	152	0.22	163.4**
	w^+	153	172	0.89	
VLi	*w*	23	144	0.16	
(VLi)V	*w*	40	74 (13)	0.54	54.8**
	w^+	0	74 (43)	0.00	

In this and Tables 4–6, species names are abbreviated as follows: V = *virilis*, A = *americana*, T = *texana*, N = *novamexicana*, Lu = *lummei*, Li = *littoralis*, M = *montana*. In crosses, the species abbreviation for females is presented first, then males [*e.g.*, VT = *virilis* ♀ × *texana* ♂; (VT)V = F_1♀ (*virilis* ♀ × *texana* ♂) × *virilis* ♂]. In the (VLi)V cross, the number in parentheses refers to the number of immotile males with no mature, differentiated sperm. All *G* statistics are from heterogeneity *G* tests.

* $P < 0.05$; ** $P < 0.001$.

TABLE 5

Fertility of hybrid F_1 and backcross females

Parental cross	X chromosome genotype	Fertile	Total	Proportion fertile	G or χ^2
VT	w/w^+	86	87	0.99	1.28
TV	w/w^+	109	113	0.97	
(VT)V	w/w	107	109	0.98	14.48**
	w/w^+	116	136	0.85	
(VT)T	w/w^+	105			0.01
	w^+/w^+	104			
VA	w/w^+	89	89	1.00	2.91
AV	w/w^+	90	93	0.97	
(VA)V	w/w	121	123	0.98	4.68*
	w/w^+	120	129	0.93	
(VA)A	w/w^+	63			6.84*
	w^+/w^+	37			
VLu	w/w^+	58	60	0.97	0.00
LuV	w/w^+	118	122	0.97	
(VLu)V	w/w	91	91	1.00	11.57**
	w/w^+	106	120	0.88	
(VLu)Lu	w/w^+	106			7.59*
	w^+/w^+	68			
VN	w/w^+	88	89	0.99	0.78
NV	w/w^+	69	69	1.00	
(VN)V	w/w	125	127	0.98	17.45**
	w/w^+	78	94	0.83	
(VN)N	w/w^+	89			0.01
	w^+/w^+	88			
VLi	w/w^+	14	16	0.88	
(VLi)V	w/w	44	53	0.83	0.68
	w/w^+	50	65	0.77	

All G and χ^2 statistics are heterogeneity statistics (SOKAL and ROHLF 1981), except in the backcross to non-*virilis* species (*e.g.*, (VT)T). In backcrosses to non-*virilis* species, female genotypes are recognizable only by progeny testing (see text). Therefore, we can report only the number of viable/fertile females of each genotype. For these crosses we test the observed numbers of w/w^+ and w^+/w^+ females against an expected 1:1 ratio.

* $P < 0.05$, ** $P < 0.001$.

TABLE 6

Dissection of X-effects in cross between *D. virilis* and *D. novamexicana*

Cross	Sex	Genotype	No. fertile	Total	Proportion fertile
(VN)V	Male	y, ap	193	201	0.96
		y, ap^+	60	150	0.40
		y^+, ap	113	121	0.93
		y^+, ap^+	82	200	0.41
	Female	y, ap	67	68	0.99
		y, ap^+	60	62	0.97
		y^+, ap	89	91	0.98
		y^+, ap^+	67	96	0.70
(VN)N	Male	y, ap	13	46	0.28
		y, ap^+	96	118	0.81
		y^+, ap	7	58	0.12
		y^+, ap^+	109	139	0.78

F_1 female hybrids between *D. virilis yellow, apricot* females and *D. novamexicana* males were backcrossed to either parental species and recombinant and nonrecombinant offspring scored for fertility. Female offspring were not scored in the backcross to *D. novamexicana* because all females produced in this cross are fertile.

Session III question 4

EEB Data Analysis Question 4 1991

Read the introduction and background information given below, and examine Figures 1-6. Explain your conclusions regarding the behavior of the birds, and discuss the results in terms of optimality theory.

Introduction

For wading birds feeding in estuaries, the time available for feeding is limited by tidal cycles, and competition for food is often severe. Individuals which are unable to gather enough food are likely to die, especially during the winter. Optimal foraging theory would predict that fitness would be increased by efficient foraging, and that natural selection would favor individuals with feeding behaviors that yield the greatest possible energetic return for the time and energy spent in foraging.

Background Information

This data analysis question derives from a series of field observations on the size of mussels taken by oystercatchers throughout the year. You are given the following information and definitions regarding the study and its results:

1) Oystercatchers: have three techniques for opening mussels: stabbers stab at the junction between the two mussel valves ventral hammerers strike the ventral surface of the mussel dorsal hammerers strike the dorsal surface of the mussel

2)Biomass: was used as a measure of the caloric value of mussel flesh eaten.

3)Mussels: exhibited an annual cycle of tissue loss and regeneration. Between February and April, the biomass of large mussels fell by as much as 50%

4)Handling Time: defined as the time elapsed between the first blow or stab and the swallowing of the last piece of flesh.

5)Profitability: defined as the biomass of flesh ingested per unit of handling time.

6) Relative Risk: the likelihood that a mussel of a given size class would be taken once it was encountered by a bird. As calculated in this study, it represents a measure of feeding preference that was independent of the number of mussels in each size class.

Data to be Analyzed

The foraging behavior of the oystercatchers was observed throughout the year, yielding the following data:

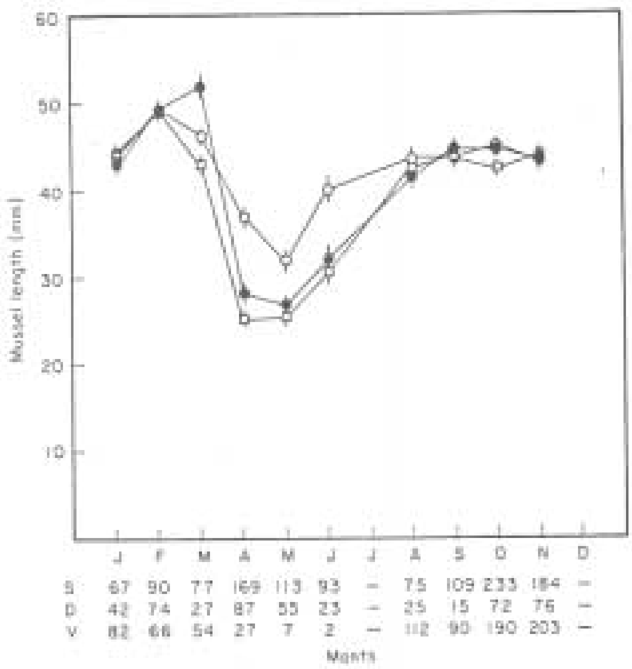


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Figure 1.

Figure 1. The length (± SE) of mussels taken by oystercatchers throughout the year. Stabbers (S, □), dorsal hammerers (D, ●), ventral hammerers (V, O). Numbers are sample sizes.

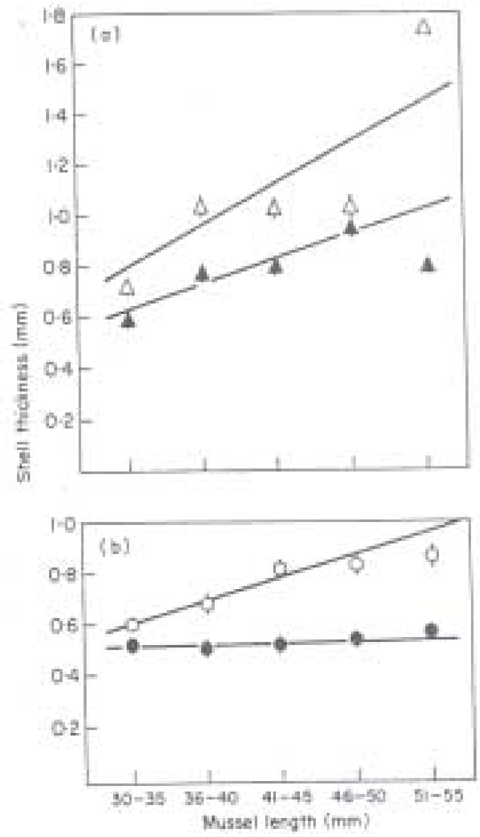

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Figure 2.

Figure 2. Selection for shell thickness by (a) ventral and (b) dorsal hammerers. Mussels eaten by oystercatchers (●, ▲) and collected from the bed of the estuary (O, Δ). Linear regressions: ventral shell thickness of mussels eaten by ventral hammerers Y = 0.076-0.0208X, N = 73, r^2 = 0.46; ventral shell thickness of mussels on bed Y = 0.194-0.0296X, N = 73, r^2 = 0.37; dorsal shell thickness of mussels eaten by dorsal hammerers Y = 0.494-0.0009X, N = 131, r^2 = 0.10; dorsal shell thickness of mussels found on the bed Y = 0.089-0.016X, N = 131, r^2 = 0.14.

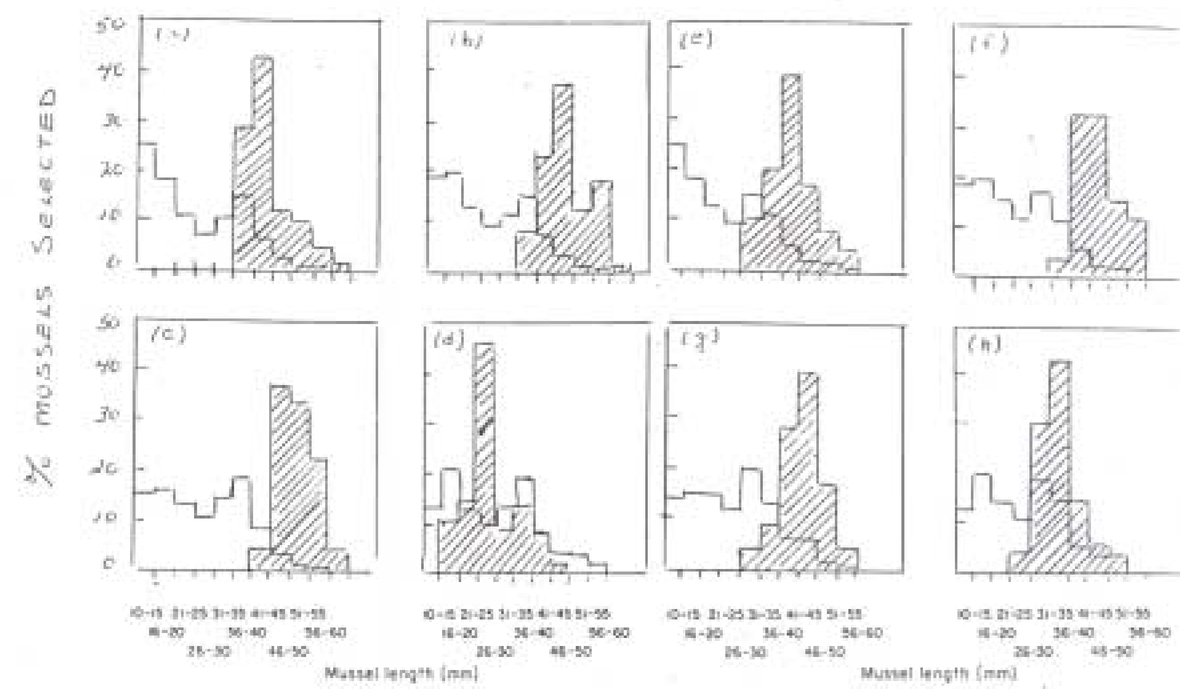

Figure 3. Comparison of observed size selection with that predicted by random foraging. (a)-(d) Dorsal hammerers: January to April; (e)-(h) ventral hammerers: January to April. Observed (▨), predicted (□) based on densities of thin-shelled mussels [i.e. mussels with shell thickness of < 0.6 mm for dorsal hammerers and < 0.8 mm for ventral hammerers]. Sample sizes for January-April: observed dorsal hammerers 42, 74, 27, 55; observed ventral hammerers 82, 66, 54, 27. Observed versus predicted distributions compared using the Kolmogorov-Smirnov two-sample test; all comparisons significantly different at $P < 0.001$, except dorsal hammerers in April ($P < 0.05$) and ventral hammerers in April (NS).

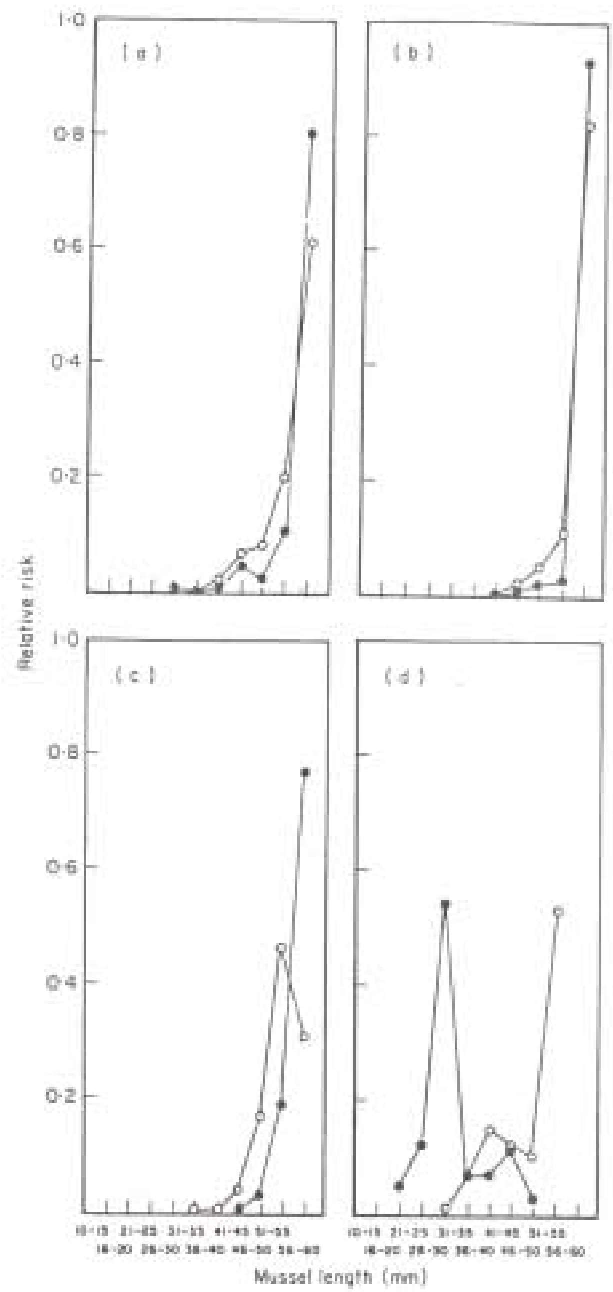

Figure 4. Relative risk of being taken for mussels of different lengths. (a)-(d) January to April. Dorsal hammerers (●), ventral hammerers (O).

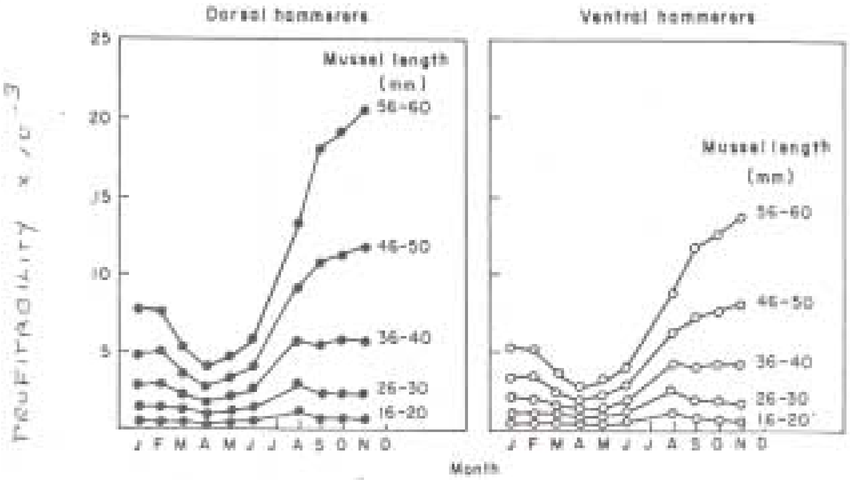

Figure 5. Changes in the profitability of mussels throughout the year. Profitability = g AFDW/s handling time, where AFDW = ash free dry weight, s = seconds.

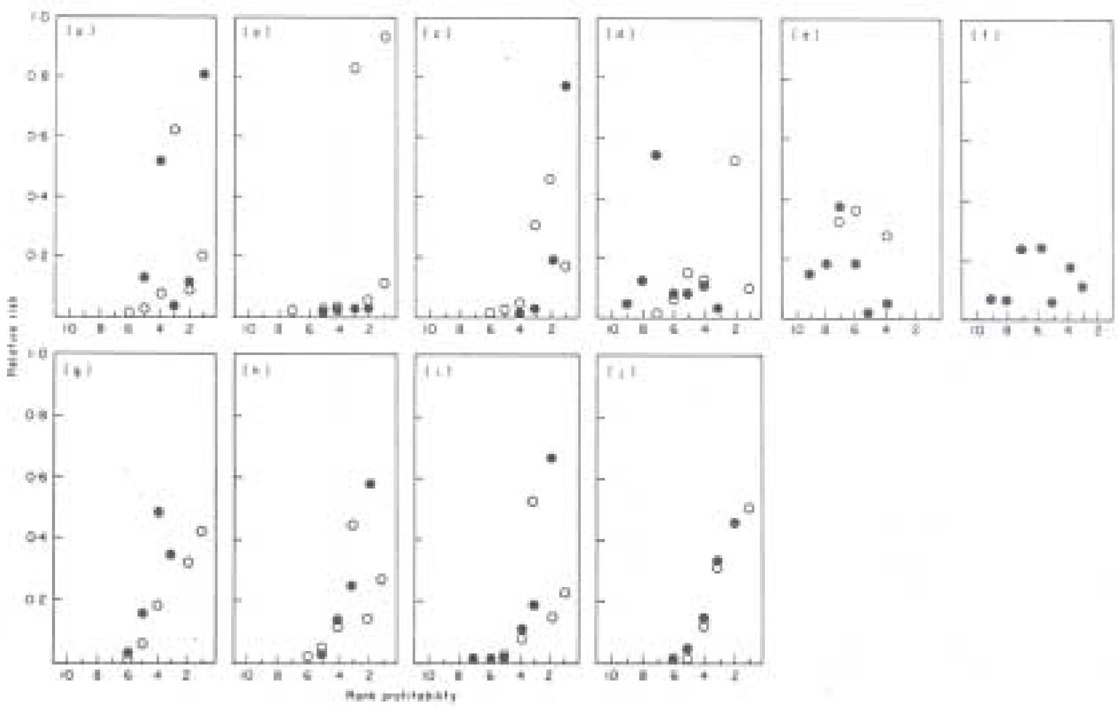

Figure 6. The relationship between relative risk of being taken and profitability. Dorsal hammerers (●), ventral hammerers (O). (a)-(f) January-June, (g)-(j) August to November. 1 = most profitable class, 10 = least profitable class.

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Session IV. Research Proposal

Choose one of the following topic areas for your research and carefully develop each of the following in your proposal:

a) What are the critical questions you are asking?
b) What field and/or lab methodologies would you use to examine the question? What are the assumptions in using these techniques.
c) What sort of data do you anticipate collecting?
d) How would you organize and analyze the data?

1. You have decided to attempt to determine the phylogenetic relationships among some major groups of non-vertebrate organisms using a molecular or chemical approach. Design a research project that will examine no more than 12 species. List the groups that you intend to sample and justify your choices. What molecular or chemical approaches will you use and why? How do you intend to analyze your data?

2. The waters of the coastal zone of the New York Bight contain resident fish populations as well as seasonal migrants. In an effort to explain the ability of these waters to support large populations of resident and migrant fish, two major hypotheses have been put forward. The first states that there is, in these waters, sufficient quantity and diversity of potential food organisms so that the migrant and resident fish populations are never in competition for food even if they preferentially feed *on* the same food items. The second hypothesis states that there is sufficient diversity in the feeding repertories of these fish populations so that either or both migrants and residents can switch from preferred to alternative food items and thus avoid serious competition. Select one of these hypotheses for testing, and design a research proposal which will attempt to falsify your chosen hypothesis.

3. Laboratory analysis of a series of 25 fixed, adult specimens of species x , taken from a single locality, during one field season by an experienced field worker, reveals an absence of males. Design a research project to distinguish among the various possible causes of this apparent skewed sex ratio.

4. Some lizards defend feeding territories. Suppose that juvenile lizards, despite their smaller size, were guarding territories larger than those defended by most adults. Two hypotheses for this difference are that 1) juveniles are forced into suboptimal habitat and therefore need to defend a larger area to obtain sufficient food, and 2) juveniles need to defend more space because they are growing actively and need to eat more than adults, which need only to maintain their body weight. How might you test the competing ideas experimentally?