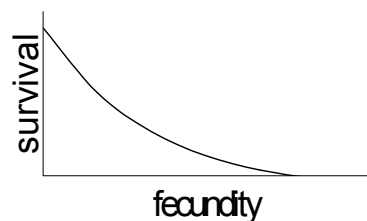


LIFE HISTORY THEORY - EXAM SAMPLE QUESTIONS AND PROBLEMS

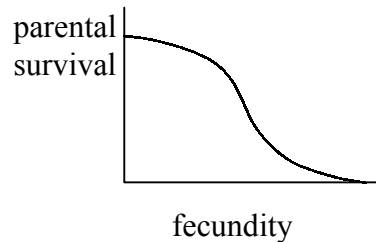
Questions: (ordered by the course programme, not by difficulty)

1. Can lifetime reproductive success (R) be used as a measure of fitness in exponentially growing populations? Why?
2. Mortality in the seed bank selects against dormancy. Why may dormancy evolve nevertheless?
3. Can the optimal clutch size be *larger* than the Lack clutch? (argue)
4. When comparing juvenile survival in broods of different sizes relying on natural variation in brood size, there is often no correlation between brood size (fecundity of the parent) and juvenile survival. Yet experiments with brood size manipulation often find a negative correlation. How do you explain the difference?
5. Consider a species that exhibits lekking, i.e., individuals collect at a mating place where males compete for the females and mate choice takes place. Predators often attack lekking individuals. How does increased mortality at lekking (i.e., appearance of a new predator) change the optimal fecundity? Assume that parental survival is traded off with fecundity, and density dependence need not be considered explicitly because it affects all individuals equally.
6. Can density dependent seedling mortality select for dormancy? What do you think of the claim, "Intermediate dormancy maximizes the equilibrium number of seeds and is therefore optimal"?
7. Consider an annual plant that has a total amount of resources R to produce seeds, such that it can make R/m seeds of size m . Survival of seeds depends on their size as in the Smith-Fretwell model. Assume that the habitat deteriorates such that the area suitable for germination shrinks and fragments, and consequently more seeds die because of landing outside the suitable area. Will this affect the optimal seed size?
8. Assume fecundity is traded off with parental survival only. The trade-off is convex:



What is the optimal fecundity?

9. Assume fecundity is traded off only with parental survival, whereas juvenile survival is constant. The shape of the trade-off is



By drawing lines of identical fitness ("iso-fitness lines"), show that both the semelparous and an iteroparous strategy may be locally optimal (i.e., better than other strategies with not too dissimilar fecundity).

10. Clutch size evolves to be smaller after a new cause of juvenile mortality appeared. There is no trade-off between clutch size and parental survival or clutch size and future reproduction of the parent or of its offspring. What is then a likely mechanism through which this new mortality selects for smaller fecundity? How would you test?

11. Will a nest predator affect the optimal clutch size if juvenile survival is the product of three independent factors, one depends only on clutch size, one depends on the presence of the predator, and one depends on population density? The predator does not harm the adults and density dependence affects only juvenile survival. (*Hint*: can you justify using the lifetime reproductive success, $R = \frac{ns_1(n)s_{pred}s_2(N)}{1-p}$, as a fitness measure?)

12. Explain briefly (no formulas) at least two different mechanisms that can explain the south-north trend found in avian clutch size.

13. Suppose that an experimenter kills some of the 5 years old individuals after reproduction, but does not harm the other age classes. How will this modify the optimal fecundity at ages 2, 5, and 6, and why?

14. Assume that a nest predator preferentially destroys the offspring of inexperienced one-year-old parents. How does this predator change the optimal fecundity at one year and at later ages?

15. Show that if the size of a population is constant, then at the stable age distribution the frequency of individuals always decreases with age.

16. Suppose that in an annual species, an individual born with size m can collect $R(m)$ amount of resources, which is then divided up to make $R(m)/m$ offspring of size m . The

offspring survive till reproduction with a constant probability s (no density dependence). Will decreasing offspring survival select for producing more (and smaller) offspring?

17. Since parents must allocate resources among their offspring, one expects a trade-off between offspring number and offspring quality (e.g. few large or many small offspring). Yet in nature offspring of high fecundity parents often have better quality. How can this be explained?

18. Assume that harvesting increases adult mortality but does not affect the juveniles. What kind of information do you need in order to predict whether harvesting will effect the optimal fecundity? (Suppose that density dependence affects all individuals equally and therefore need not be considered.)

19. *Reznick* (1982) found that in streams where juveniles suffer from predation, guppies lay less eggs than in streams where predators prefer large, adult guppies. How do you explain this difference?

20. Consider the model for the optimal age α at maturity we set up in the lectures that maximizes $m(\alpha)l_\alpha$. Assume that a new predator appears that consumes the eggs and hence causes an extra factor of mortality very early in life. Will this modify the optimal age at maturity? Why?

21. Assume that an annual species lives in a stochastic environment. Density dependence can be ignored because it acts in a strategy-independent way (i.e., all individuals are affected equally). Fecundity is traded off with juvenile survival. Some fluctuating environmental factor, such as weather, affects the survival of all juveniles independently of the number of their sibs, therefore juvenile survival equals $s_1(n) s_2(\xi_t)$, the product of a fecundity-dependent factor $s_1(n)$ and of a weather-dependent factor $s_2(\xi_t)$. Will the fluctuation have an effect on the optimal fecundity?

22. Assume that an annual species lives in a stochastic environment. Density dependence can be ignored because it acts in a strategy-independent way (i.e., all individuals are affected equally). Fecundity is traded off with juvenile survival. Some fluctuating environmental factor ξ_t , such as variable food supply, affects juvenile survival such that in good years, survival is higher ($\partial \ln s / \partial \xi > 0$) and the survival cost of fecundity is relieved ($\partial^2 \ln s / \partial \xi \partial n > 0$). Will the fluctuation increase or decrease the optimal fecundity as compared to the average environment? (*Hint*: first argue whether it is more important to be well adapted in relatively good years or in bad years. Then see what will be the optimum like in only those years that are important.)

23. Polyembryony is a pattern of development found in parasitoids in which a single egg laid into a host splits up into tens to hundreds of genetically identical siblings. In some cases, a subset of these siblings have a first larval instar that is specialised for fighting and killing other larvae but that cannot develop further. These fighting larvae appear to attack other larvae but not their sibs. Explain the adaptive value of this behaviour, and the

significance of the fact that the fighter larvae are genetically identical to those who benefit from their behaviour. (*This problem is taken from Stearns 1982.*)

Problems (all data are hypothetical and are constructed such that calculations are easy to carry out)

1. We are comparing an annual and a perennial species in two different environments. The perennial species reproduces each year, and its fecundity and adult survival is independent of age. Juvenile survival is density dependent, and is given by the same function $s(N)$ in both species. We measure the following life history parameters:

	environment 1	environment 2
n_A	10	5
n_P	2	2
p	0.9	0.5

Which environment favours the perennial species?

2. What is the long-term growth rate in a hypothetical population where the annual growth rate fluctuates such that $\lambda = 1$ in two-thirds of the years and $\lambda = 8$ in the remaining one third of the years?

3. In an experiment, clutch size is randomised across parents, and the survival of the offspring is measured. Suppose that we get

n	s
2	0.5
4	0.4
6	0.3
8	0.2
10	0.1

What is the (approximate) Lack clutch size?

4. In an experiment, clutch size is randomised across parents, and the survival of the offspring as well as of the parent is measured. Suppose that we get

n	s	p
2	0.5	0.8
4	0.4	0.8
6	0.3	0.5
8	0.2	0.2
10	0.1	0.1

What is the (approximate) optimal clutch size? (*Note*: in the table above, n is half the actual number of eggs, since we count female offspring only.)

5. We manipulated clutch size by adding or removing 2 eggs, and measured survival in the presence of a predator as well as with the predator excluded. The table shows the logarithm of survival probabilities:

	without predator	with predator
reduced	-0.5	-1
control	-0.75	-1.5
enlarged	-1	-2

Does predation modify the cost of fecundity?

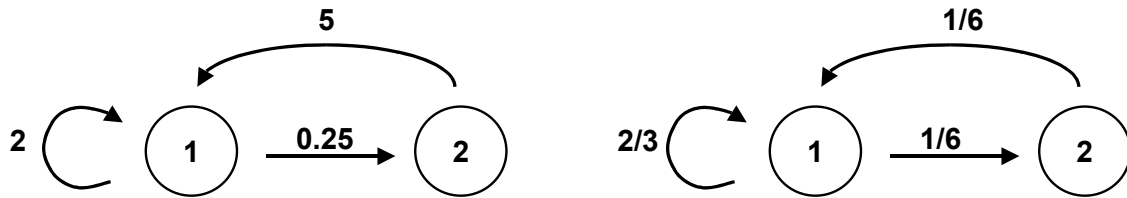
6. Draw the life cycle graph that corresponds to the Leslie-matrix below.

$$\begin{pmatrix} 0 & 2 & 3 & 0 \\ 0.7 & 0 & 0 & 0 \\ 0 & 0.5 & 0 & 0 \\ 0 & 0 & 0.2 & 0 \end{pmatrix}$$

7. Will the population with the Leslie-matrix below converge to a stable age distribution?

$$\begin{pmatrix} 0 & 2 \\ 0.8 & 0 \end{pmatrix}$$

8. The life cycle graph on the left shows the effective fecundities and the adult survival probability for an organism with maximum age of 2. In stable age distribution, there are 10 times as many one-year-old individuals than 2-year-old ones; the reproductive value of the 2-year-olds is twice as much as of the one-year-olds. The numbers on the right-hand graph are the elasticities that correspond to the life history data on the left.



What is the most effective way of increasing the population growth rate, and why?

- Increase the adult survival probability since this gives the smallest flow on the life cycle graph.
- Increase the effective fecundity (protect the offspring) of the one-year-old females because they are the most abundant.
- Increase the effective fecundity of two-year-old females because their reproductive value is the greatest.
- Increase the effective fecundity (protect the offspring) of the one-year-old females because this parameter is associated with the highest elasticity.

9. Recalculate the threshold value of $s(m-1)/s(m)$ for fratricide (=brood reduction by the offspring killing one of their brood-mates) in the brood reduction model we discussed, assuming that brood-mates are half sibs rather than full sibs. (*Hint*: between half sibs, the coefficient of relatedness is only 1/4.)

10. Should an offspring ever help its brood-mates by committing suicide? In the brood reduction model we discussed, calculate at least how large $s(m-1)/s(m)$ should be for suicide to be advantageous. (Assume that brood-mates are full sibs, and that brood size only affects the survival of the offspring but it has no effect on parental survival or future reproduction.)