ET Week 3 – The lizard project

Exercise Liz 1 (Games lizards play):

The American lizard species *Uta stansburiana* has three male morphs differing in the colour of their throats: orange (O), blue (B) and yellow (Y).

The O-morph is biggest, and O-males are very aggressive, defending large territories. B-males also defend territories, but these are quite small, since B-males spend most of the time guarding their females to prevent extra pair copulations. Y-males do not have territories. They strongly resemble females, both in appearance and in behaviour. These males are "sneakers": they enter foreign territories and try to "steal" fertilisations, by copulating with any unguarded female they encounter.

In direct competition with blue males, orange males have a competitive advantage since they are bigger and stronger. In competition with yellow males, however, orange males have a disadvantage: they spend a lot of time defending and extending their territory and can therefore not efficiently guard their females against sneakers. Blue males, in contrast, guard their females against sneaking and therefore have a competitive advantage when confronted with yellow males. Competitive relationships are therefore cyclic: orange dominates blue, blue dominates yellow, and yellow dominates orange. This is also apparent from the frequencies of the various types: If the orange morph is common in a certain year, yellow males have a selective advantage. As a consequence, the yellow morph will become common in the following year. Once yellow males are common, blue males have an advantage, leading to an increase in their frequency. One year later, orange males profit from the commonness of blue males, and so on (see the figure below).

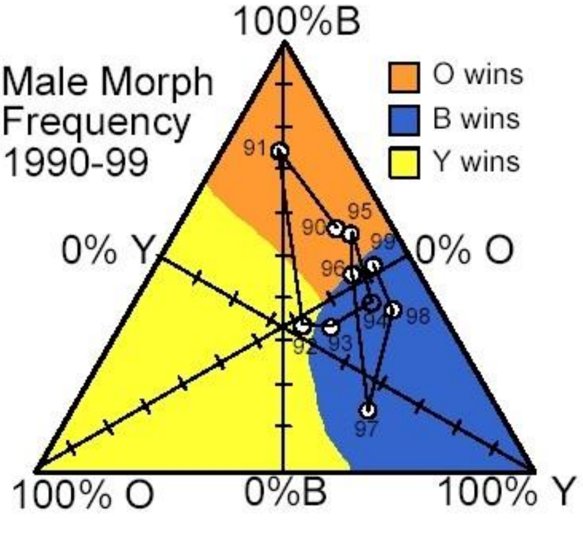
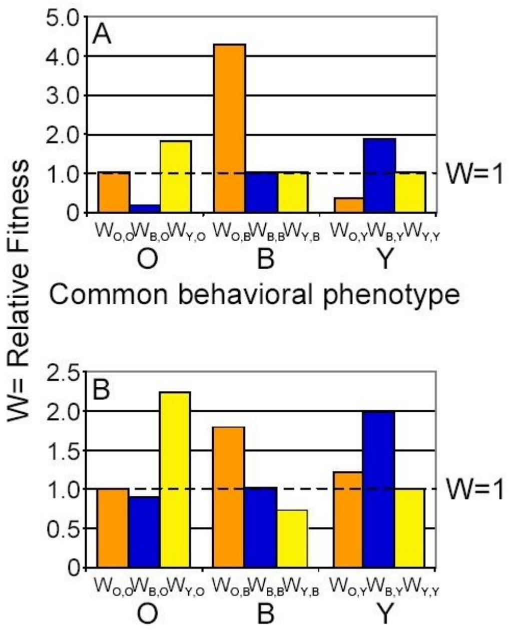


Figure 1. Among-year changes in the frequency of adult male colour morphs. Combined data from Sinervo & Lively (1996) and Sinervo (2001).

Barry Sinervo and his coworkers (see http://bio.research.ucsc.edu/~barrylab/) estimated the fitness of the different morphs in two ways: (A) on basis of the number of copulations a male had depending on the morphs of the males in adjacent territories (Sinervo & Lively 1996, Nature 380, 240-243), and (B) by a parentage analysis based on molecular markers (Sinervo 2001, Genetica 112-113, 417-434). The results are represented in the two graphs below.



(a) Before going on, you should first read the article by Sinervo & Lively (1996). Convince yourself that graph (A) above corresponds to Figure 4a of that article. Show that these data can – up to some rounding – be translated into the following “payoff matrix”:

	Y	**B**	**O**
Y	1.0	1.0	2.0
B	2.0	1.0	0.1
O	0.3	4.0	1.0

How have the fitness values in the matrix been determined? Why are all the diagonal elements equal to 1.0?

(b) Based on the fitness values in (a), Sinervo & Lively then make theoretical predictions on the dynamics of the system (see their Figure 4b). These predictions are based on the replicator dynamcis:

$$p_i' = p_i \cdot \frac{F_i(p_1, p_2, p_3)}{\overline{F}(p_1, p_2, p_3)} \tag{1}$$

where p_i and p_i' are the frequencies of morph *i* in the present and in the next generation, respectively, while F_i and $\overline{F}$ denote the fitness of morph *i* and the mean fitness of the population, respectively. Calculate the fitness of the three morphs and the mean fitness of the population for the special case $p_Y = 0.2,\ p_B = 0.3,\ p_O = 0.5$. Which morph has the highest fitness?

(c) Simulate the dynamics of the lizard game with the help of an Excel worksheet. Show that the system converges to an equilibrium at which all three morphs have the same fitness. [You can try to find this equilibrium analytically, by solving the equations $F_Y = F_B = F_O$. This can be done mathematically or (with some creativity) with the Excel function GoalSeek.] Does mean fitness increase in the course of evolution?

(d) Compare the simulation results with the empirical results of Sinervo (Figure 1 above). The empirical findings can also be found in the Excel file **Ex ET11 - Lizard data.xlsx**. In this file, the empirical findings and the model predictions are plotted in the same graph. Check whether the model predictions plotted agree with your own predictions. Do you agree with Sinervo and Lively that the model provides a satisfactory explanation for the pattern found in nature? Why/why not?

(e) Repeat your simulations, but now for the improved fitness estimates by Sinervo (2001; see graph (B) above). Do they yield a better fit to the data?

(f) Sinervo and Lively model the dynamics of the system by means of the replicator dynamics. We have seen before that the replicator dynamics implicitly presupposes *asexual* reproduction. Of course, Sinervo and Lively are aware of the fact that their lizards reproduce sexually. What is their main argument for using the replicator dynamics nevertheless? Are you convinced by their argument?

Exercise Liz 2 (Mendelian lizards):
In the late 1990's, Sinervo came to the conclusion that the replicator dynamics does not represent his lizard system in an adequate way. Let us therefore investigate how the dynamics of the lizard system changes by assuming Mendelian inheritance. There are different ways to do so, and you should implement the scenarios (a) to (c) below (on the following page). For each scenario, you should address the following points:

- Run simulations with different starting conditions. Plot the evolutionary trajectories of the frequency distribution of the three morphs in triangular co-ordinates (*i.e.*, a simplex). Describe for each scenario in a few words how the dynamics looks like and to what extent the simulations agree with the field patterns observed by Sinervo and colleagues.
- Do you observe sustained oscillations under all circumstances? If oscillations do not occur, try to give an explanation.
- For each of the three scenarios estimate the heritability of morph colour by means of a regression analysis (as in Sinervo & Lively 1996). Is morph heritability affected by the frequency distribution of morph alleles? Does it matter how the colour morphs are encoded, that is, which numbers represent the various morphs?

After having considered all three scenarios, you should address the following topics:

- Which of the two payoff matrices yields the better predictions? Does your answer depend on the genetic scenario considered?
- To what extent does genetic detail matter for the course and outcome of evolution? Will it ever be possible to understand the lizard system without knowing the underlying genetics?
- Which of the models considered (including the replicator dynamics) do you prefer? Why? More generally, when having to decide between two models would you prefer the one that makes the more realistic assumptions or the one that makes better-fitting predictions? Is it possible to test the model assumptions and the model predictions? How?

(a) Consider first the situation that the three lizard morphs (i.e., the three phenotypes) are encoded by a single gene locus with two alleles *A* and *a*. You then have three genotypes that might correspond to the three phenotypes *Y*, *B* and *O*. It may be of importance which of the three morphs corresponds to a homozygote genotype (*AA* or *aa*) and which corresponds to the heterozygote *Aa*. Consider therefore all three possibilities:

(1) $AA = O,\ Aa = Y,\ aa = B$
(2) $AA = B,\ Aa = O,\ aa = Y$
(3) $AA = Y,\ Aa = B,\ aa = O$

(b) In 1998, Sinervo claimed to have good evidence for a different genetic model. In this model he considers a gene locus with three alleles *y*, *b* and *o*. There are now six genotypes; the three homozygotes *oo*, *yy*, *bb* and the three heterozygotes *ob*, *by*, *yo*. According to Sinervo, the three homozygotes correspond to the three morphs in an obvious way (*oo* = *O*, *yy* = *Y*, *bb* = *B*). Moreover, allele *o* is dominant over *b* (*ob* = *O*), *b* is dominant over *y* (*by* = *B*), and *y* is dominant over *o* (*yo* = *Y*). Hence, rather miraculously, the dominance pattern at the genetic level perfectly matches the behavioural dominance at the phenotypic level (*O* beats *B* beats *Y* beats *O*...).

(c) In the meantime, Sinervo had to acknowledge that the model in (b) is too nice to be true. You can make the model in (b) more realistic by considering partial dominance. The heterozygote *ob*, has a tendency h_{ob} to develop into an orange morph and a tendency $1-h_{ob}$ to develop into a blue morph. The model is then determined by the three dominance parameters h_{ob}, h_{by} and h_{yo}, and the model in (b) corresponds to the special case $h_{ob} = h_{by} = h_{yo} = 1$.

Exercise Liz 3 (Females enter the picture: the *r*-*K* game):

The females of *Uta stansburiana* also have different morphs. Yet here there are only two morphs: orange (O) and yellow (Y). Sinervo showed that orange-throated females produce large clutches of small eggs while yellow-throated females produce smaller clutches of large eggs. In evolutionary ecology, a reproductive strategy that is based on a high growth rate (which is often achieved by producing a large number of low-quality offspring) is often called an "*r*-strategy". In contrast, a strategy that is based on producing of offspring of high competitive ability (which may be achieved by producing fewer but larger offspring) is called a "*K*-strategy". Accordingly, Sinervo classifies orange-throated females as *r*-strategists, and yellow-throated females as *K*-strategists. He assumes that the *r*-strategy of O-females provides a selective advantage at low population densities (where competition among offspring is weak) while the *K*-strategy of Y-females is favourable under high-density conditions (where competition is intense and only high-quality offspring survive).

The terms *r*- and *K*-strategists derive from the parameters of the so-called "logistic equation," perhaps *the* most important dynamic model in population biology. The logistic equation is a differential equation of the form [see http://www.eoearth.org/article/Logistic_growth]:

$$\frac{dN(t)}{dt} = r \cdot N(t) \cdot \left(1 - N(t)/K\right) = r \cdot N(t) \cdot \frac{K - N(t)}{K}\,. \qquad (2)$$

Here $N(t)$ is the density of a population at time *t*, *r* is the maximal "*per capita* growth rate" of the population, and *K* is the "carrying capacity" of the population. Equation (2) describes how the change of population density [dN/dt] in time depends on the population density *N*.

At low densities (the conditions for "r-selection"), the term $(1-N/K)$ is negligible and the population will grow at an exponential rate with growth rate r. The bigger r is, the faster the population will grow. The term $(1-N/K)$ describes how the growth rate dN/dt of the population growth decreases with population density, presumably because of more and more intense intraspecific competition for limiting resources. When the population density is equal to the carrying capacity [i.e., if $N = K$], the growth rate of the population is zero, that is, the population will neither grow nor decline. The higher the value of K, the better the population is able to cope with intraspecific competition. This explains the term "K-selection" for selection under high-density conditions.

A differential equation like (2) cannot easily be implemented in Excel. Fortunately, Sinervo uses a discrete-time version of the logistic equation, most probably (he is not very explicit about this):

$$N(t+1) = r \cdot N(t) \cdot \frac{K - N(t)}{K}. \tag{3}$$

With the help of this equation, you should be able to simulate how population densities change in the course of time.

(a) Before going on, you should first read the article by Sinervo et al. (2000).

We will now try to reconstruct the model that Sinervo and coworkers described in the later part of their article. The differential equations (2) in the article corresponds to two logistic growth equations [like eqn (2) above], one for the orange morph [$i = O$] and one for the yellow morph [$i = Y$]. The only difference is that the maximal *per capita* growth rate r_i of morph is given by:

$$r_i = F_i \cdot \frac{W_i(t)}{\bar{W}}. \tag{4}$$

Here W_i represents the fitness of morph i [$i = O$ or Y] while $\bar{W}$ is the average fitness of the population. Fitness is frequency dependent and assumed to be given by equations of the form:

$$W_i(t) = W_{i,isol} + \sum_j G_{ij} \cdot N_{ij}(t) \tag{5}$$

[see eqn (1) in the article]. The terms G_{ij} indicates how the fitness of morph i is affected by neighbours of type j. For example, the fact that the term G_{oy} is positive [where do you find this information in the article??] indicates that orange females benefit from the presence of yellow neighbour females.

(b) Make sure that you understand the details of these two equations. The parameters were estimated by the authors and can be found in the text (end of page 986) and in the text explaining table 1. First identify all these [Hint 1: there is one small typo, which may be confusing, and there is one "mystery" parameter. Hint 2: the fitness is partitioned into fitness due to clutch size and survival of clutch 1 and fitness due clutch size and survival of clutches 2-5.]

(c) Now simulate this "discrete logistic ESS model" in Excel. Use the parameters given in the text and try out different values of the "mystery" parameter. You also need to calculate total fitness of the female morphs (that had been partitioned into fitness of clutch1 and fitness of clutches 2-5).

(d) Can you reconstruct the dynamics observed in figure 4 (top)? For which values of the parameter F_i do you find stable oscillations of both morphs? Which other outcomes do you observe?

In the 2000 article, Sinervo and colleagues implicitly assume that O-females produce orange-throated offspring while Y-females produce yellow-throated offspring. In other words, they assume that the females reproduce asexually.

(e) Extend now your model to also account for Mendelian females. Start with two alleles (where either the *y* or the *o* is dominant) and then move on to the more realistic case with three alleles. For the latter case, use the assumption described in Alonzo & Sinervo (2001) that the *o* allele is dominant [*i.e.*, *oo*, *ob*, *oy* are orange], and females lacking the *o* allele [*i.e.*, *by*, *bb*, *yy*] are yellow. It may be a good idea to compare your outcome with Sinervo (2001).

We are content if you have come this far. But if you have time left, you should definitely tackle the final exercise, where everything is brought together into an integrative model. You can earn some bonus points with this…

Exercise Liz 4: (Males and females combined: the RSP-*rK* lizard game)

Previously, Sinervo and co-workers had demonstrated cycles in the frequency of male morphs underlying the same genetic system [*o*, *y*, *b* alleles]. Cycles in the male genotypes can of course not be independent of the cycles in the female genotypes.

(a) Try to incorporate both systems into one combined analysis. Start with the easier asexual system and then move on to analyse the more realistic case with Mendelian lizards. For this purpose it might be a good idea to again consult Sinervo (2001). For the males you have to assume one of the genetic models that you used previously. Good luck!

Somewhat later Sinervo and co-workers had the clever idea that females might benefit by changing their mating behaviour depending on whether there is a female crash or boom year. If next year will be a boom year it will beneficial to have orange daughters and if next year will be a crash year yellow daughters are more worth. Similarly males have an advantage when rare. Therefore it should be advantageous to select male mates in a way that sons and/or daughters are of the right morph.

(b) Read the article by Alonzo & Sinervo et al. (2001) and if you have time try to incorporate some of these ideas to your previous analyses. If you do not have time to make an actual simulation, you could start by trying to figure out which additional steps will be necessary to incorporate in order to do this – you could for instance use a sketch to illustrate this.