Problem 2a

For competitive models we need to start first with making clear to ourselves what "competition" means in a two-species model. Commonly, one says that competition refers to the fact that each species does worse the larger the number of individuals of the other species -- for example because there is a finite resource both species need to survive. The resource could, for example, be grass for herbivores, light or soil nutrients for plants, prey for carnivores, or abandoned water snail shells for hermit crabs. So let's assume that we have two species P,Q whose population at time t is given by $p(t), q(t)$. Then we want to model their growth as

$diff(p(t), t) = g_p(p(t), q(t)) \cdot p(t);$

$$\frac{\mathrm{d}}{\mathrm{d}t} p(t) = g_p(p(t), q(t))\, p(t) \tag{1}$$

$diff(q(t), t) = g_q(p(t), q(t)) \cdot q(t);$

$$\frac{\mathrm{d}}{\mathrm{d}t} q(t) = g_q(p(t), q(t))\, q(t) \tag{2}$$

Note that we write the population growth of both species as the product of a net rate times the number of individual, keeping with the principle that both births and deaths should be proportional to the number of individuals of that species. Here, $g_p(p, q)$ and $g_q(p, q)$ are the net growth rates of the two species, which we expect to depend on the populations of the two species. Let's talk about these two functions:
- If the the number of individuals of both species is very small, we want the growth rates to be positive.
- The larger the population of species P, the smaller $g_p(p, q)$ should be, under the assumption that all those Ps will compete among themselves for the limited resource
- Similarly, the larger the population of Q the smaller $g_p(p, q)$ should be, under the assumption that the Ps will also compete with the Qs for the limited resource
- Similar considerations should hold for the net growth rate of the Qs, $g_q(p, q)$
- If the joint population of Ps and Qs is large enough to completely eat up the resource, then the net growth rates of both species should become zero. Beyond this point their growth rates should become negative, indicating that the resource is overexploited and that populations will shrink because they can't sustain themselves.

So in essence, we need functions g_p, g_q that start positive and will decrease with p, q until they eventually become negative. Now, there are many such functions and most functions that satisfy these criteria are going to lead to models that are probably equally valid qualitatively and equally wrong quantitatively. Below are two possible approaches:

Approach 1

We want that the growth rates decrease with both p and q. Let's say that we measure time in years (and growth rates in births per individual per year) and let c_p, c_q be the amounts of the resource each individual needs at the very least per year. Let K be the amount of resource that is available per year. Then we could model the growth functions as

$$g_p(p, q) = a_p \cdot \left(1 - \frac{c_p \cdot p + c_q \cdot q}{K}\right)$$

$$g_q(p, q) = a_q \cdot \left(1 - \frac{c_p \cdot p + c_q \cdot q}{K}\right)$$

Essentially, what this says is that $c_p p + c_q q$ is the amount of the resources the two populations consume,

$\frac{c_p p + c_q q}{K}$ is the fraction of the total resource that is consumed, and $1 - \frac{c_p p + c_q q}{K}$ is the fraction that is left. As this fraction becomes smaller the growth rates decrease and the growth rate becomes negative if the two populations consume more than there is. The coefficients a_p, a_q are the growth rates of the two species if the population is zero or very small, i.e. if there is no competition for food. The resulting two-species model is then this:

$$diff(p(t), t) = a_p \cdot \left(1 - \frac{c_p \cdot p(t) + c_q \cdot q(t)}{K}\right) \cdot p(t);$$

$$\frac{d}{dt} p(t) = a_p \left(1 - \frac{c_p p(t) + c_q q(t)}{K}\right) p(t) \tag{3}$$

$$diff(q(t), t) = a_q \cdot \left(1 - \frac{c_p \cdot p(t) + c_q \cdot q(t)}{K}\right) \cdot q(t);$$

$$\frac{d}{dt} q(t) = a_q \left(1 - \frac{c_p p(t) + c_q q(t)}{K}\right) q(t) \tag{4}$$

Approach 2

A second approach is this: We still want that the growth rates decrease with both p and q. With the same symbols we have above, we could say that the amount of resource that's left for species P is $K - c_q q$ and the amount of resource available to Q is $K - c_p p$. Then we could model the growth functions as

$$g_p(p, q) = a_p \cdot \left(1 - \frac{c_p \cdot p}{K - c_q \cdot q}\right)$$

$$g_q(p, q) = a_q \cdot \left(1 - \frac{c_q \cdot q}{K - c_p \cdot p}\right)$$

Again, both of these functions decrease as a function of both arguments, as can easily be verified. The resulting two-species model is then this:

$$diff(p(t), t) = a_p \cdot \left(1 - \frac{c_p \cdot p(t)}{K - c_q \cdot q(t)}\right) \cdot p(t);$$

$$\frac{d}{dt} p(t) = a_p \left(1 - \frac{c_p p(t)}{K - c_q q(t)}\right) p(t) \tag{5}$$

$$diff(q(t), t) = a_q \cdot \left(1 - \frac{c_q \cdot q(t)}{K - c_p \cdot p(t)}\right) \cdot q(t);$$

$$\frac{d}{dt} q(t) = a_q \left(1 - \frac{c_q q(t)}{K - c_p p(t)}\right) q(t) \tag{6}$$

An example

There are many examples of competitive systems: buffalo and prairie dogs competing for grass; trees of different species competing for light; Aggies and Longhorns competing for stadium seats for the Thanksgiving game. Let's consider buffalo and prairie dogs and assume that they both require grass. There are $K = 100$ square kilometers of grass available. A buffalo requires the grass of $c_p = 0.01$ square kilometers (i.e. an area of 100 by 100 meters). Prairie dogs are about 1000th of a buffalo's size, so let's say they require $c_q = 0.00001$ square kilometers of grass. Per couple, buffalos have 1 calf per year whereas prairie dogs have 10 offspring. On the other hand, buffalos live for 20 years if there is enough food and prairie dogs for 1 year. So if we define a_p, q_q as those rates that happen when sufficient food is available, then $a_p = \frac{1}{2} - \frac{1}{20} = 0.45$ and $a_q = \frac{10}{2} - \frac{1}{1} = 3.5$. Let's assume there are initially 500 buffalos and 50000 prairie dogs in our 100 square miles. We then have to solve the following system:

$$ode1 := \left\{diff(p(t),t) = a_p \cdot \left(1 - \frac{c_p \cdot p(t) + c_q \cdot q(t)}{K}\right) \cdot p(t), diff(q(t),t) = a_q \cdot \left(1 - \frac{c_q \cdot q(t) + c_p \cdot p(t)}{K}\right) \cdot q(t), p(0) = p_0, q(0) = q_0\right\};$$

$$\left\{p(0) = p_0, q(0) = q_0, \frac{\mathrm{d}}{\mathrm{d}t} p(t) = a_p \left(1 - \frac{c_p p(t) + c_q q(t)}{K}\right) p(t), \frac{\mathrm{d}}{\mathrm{d}t} q(t) = a_q \left(1 - \frac{c_p p(t) + c_q q(t)}{K}\right) q(t)\right\} \tag{7}$$

$$coefficients1 := \{K = 100, c_p = 0.01, c_q = 0.00001, a_p = 0.45, a_q = 3.5, p_0 = 500, q_0 = 50000\};$$

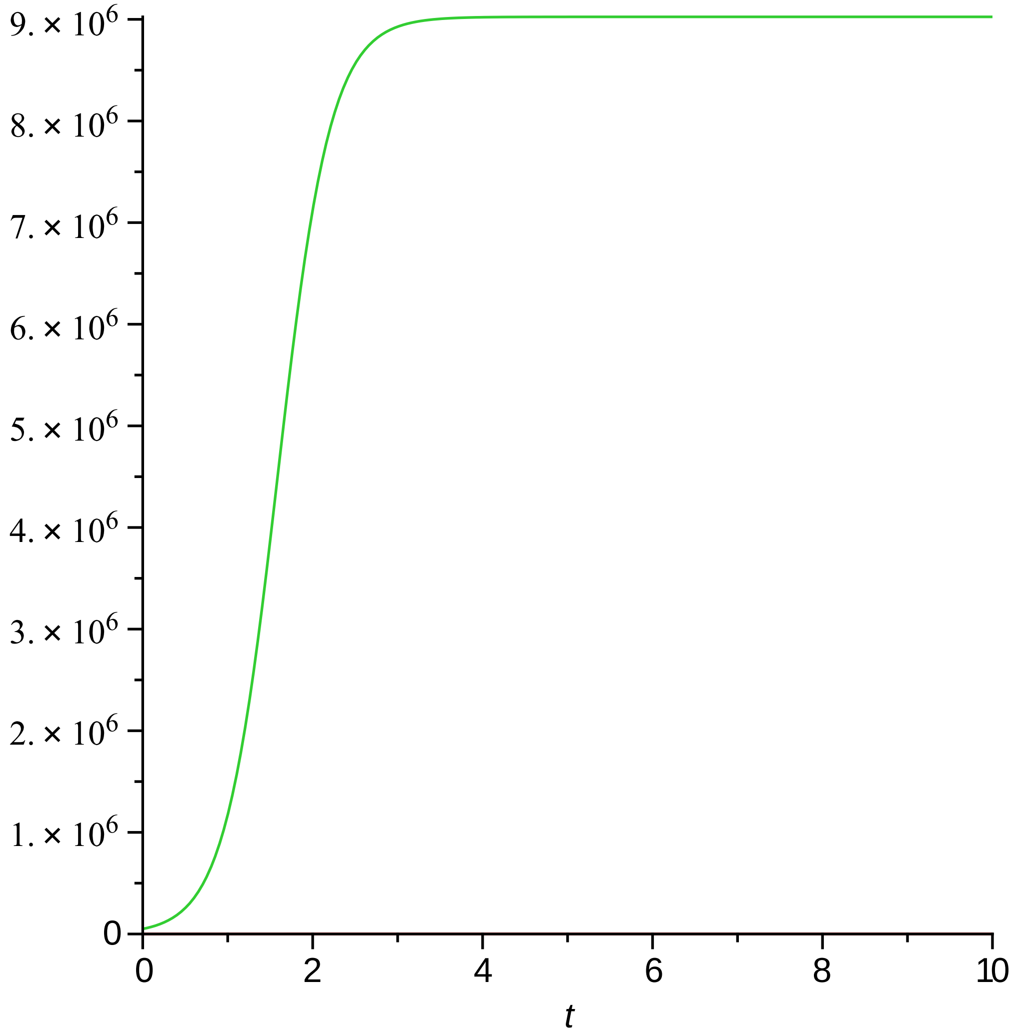
$$\{K = 100, a_p = 0.45, a_q = 3.5, c_p = 0.01, c_q = 0.00001, p_0 = 500, q_0 = 50000\} \tag{8}$$

We can plot the solution of this system for the first 10 years as follows:

$$solution1 := dsolve(subs(coefficients1, ode1), numeric, output = listprocedure);$$

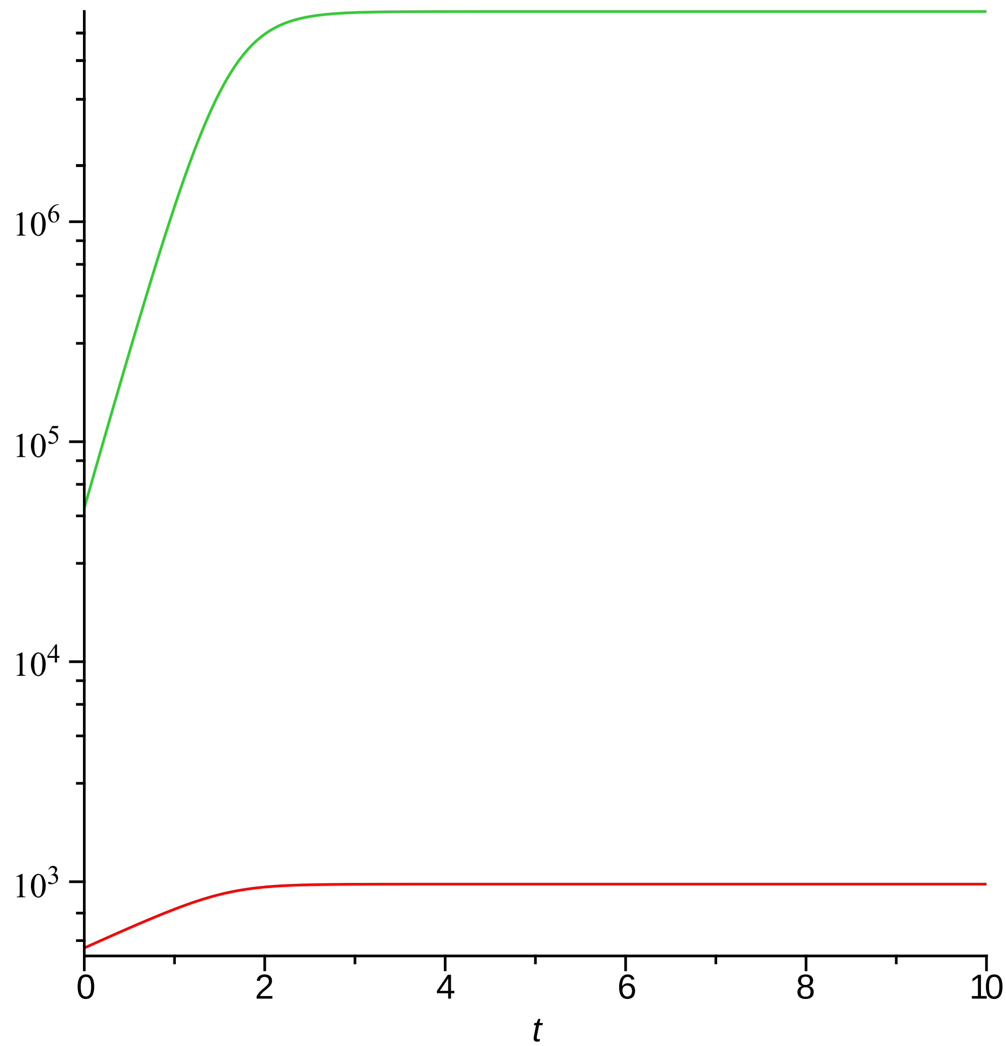
$$[t = \mathbf{proc}(t) \ \ldots \ \mathbf{end\ proc}, p(t) = \mathbf{proc}(t) \ \ldots \ \mathbf{end\ proc}, q(t) = \mathbf{proc}(t) \ \ldots \ \mathbf{end\ proc}] \tag{9}$$

$$plot(\{rhs(solution1[2])(t), rhs(solution1[3])(t)\}, t = 0..10);$$



That's only moderately enlightening because we can only see one line -- the other one is presumably so small that it lies right on the time axis. Let's try this again with a logarithmic axis:

$plots[logplot](\{rhs(solution1[2])(t), rhs(solution1[3])(t)\}, t = 0..10);$



That makes more sense: so the number of prairie dogs and buffalos increases until they both hit the resource limitation. Note that without the prairie dogs, the number of buffalos would have reached $\frac{K}{c_p} = \frac{100}{0.01} = 10^4$, i.e. significantly more than it actually reaches here.

We can also plot the solution we would have gotten from the same system using the second model:

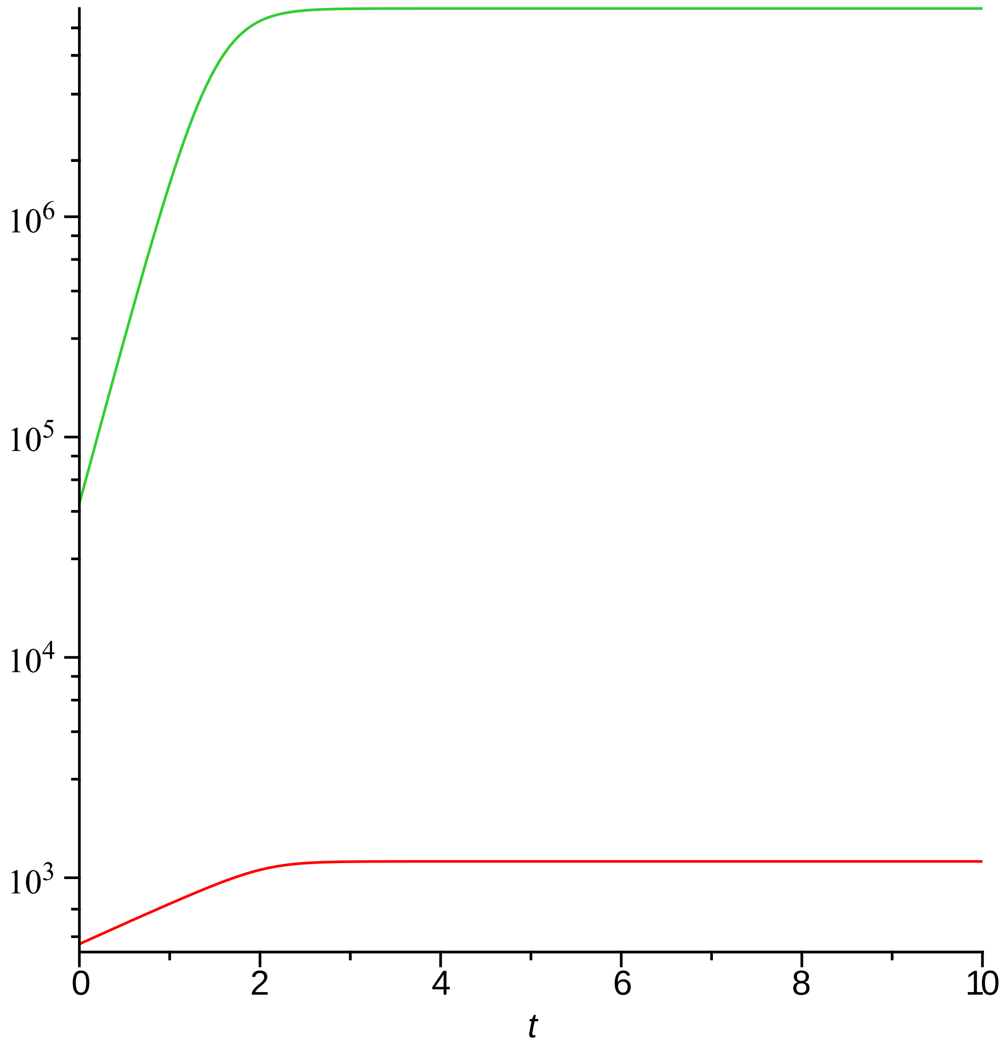
$$ode2 := \left\{ diff(p(t), t) = a_p \cdot \left(1 - \frac{c_p \cdot p(t)}{K - c_q \cdot q(t)}\right) \cdot p(t), diff(q(t), t) = a_q \cdot \left(1 - \frac{c_q \cdot q(t)}{K - c_p \cdot p(t)}\right) \cdot q(t), p(0) = p_0, q(0) = q_0 \right\};$$

$$\left\{ p(0) = p_0, q(0) = q_0, \frac{\mathrm{d}}{\mathrm{d}t} p(t) = a_p \left(1 - \frac{c_p p(t)}{K - c_q q(t)}\right) p(t), \frac{\mathrm{d}}{\mathrm{d}t} q(t) = a_q \left(1 - \frac{c_q q(t)}{K - c_p p(t)}\right) q(t) \right\} \quad \textbf{(10)}$$

$$solution2 := dsolve(subs(coefficients1, ode2), numeric, output = listprocedure);$$

$$[t = \mathbf{proc}(t)\ \ldots\ \mathbf{end\ proc}, p(t) = \mathbf{proc}(t)\ \ldots\ \mathbf{end\ proc}, q(t) = \mathbf{proc}(t)\ \ldots\ \mathbf{end\ proc}] \quad \textbf{(11)}$$

$plots[logplot](\{rhs(solution2[2])(t), rhs(solution2[3])(t)\}, t = 0..10);$



Qualitatively, both models produce very similar results. We can compare them quantitatively and find that the actual numerical results are slightly different. The fact that we have gotten qualitatively the same result from both approaches validates that they both must have incorporated the same kind of information roughly correctly.

Problem 2b

The problem with symbiosis can be modeled very similarly, i.e. with an ansatz of the kind

$diff(p(t), t) = g_p(p(t), q(t)) \cdot p(t);$

$$\frac{d}{dt} p(t) = g_p(p(t), q(t))\, p(t) \tag{12}$$

$diff(q(t), t) = g_q(p(t), q(t)) \cdot q(t);$

$$\frac{d}{dt} q(t) = g_q(p(t), q(t))\, q(t) \tag{13}$$

The difference is that now we expect the growth functions g_p, g_q to decrease with the number of the species which it models (because the individuals of this species compete for the same amount of the resource) but to *increase* with the number of individuals of the other species. There are again different ways to model this behavior. For example, we could use these functions:

$$g_p(p,q) = a_p \cdot \left(1 - \frac{c_{p1} \cdot p}{K_p}\right)\left(1 - \frac{c_{p2} \cdot p}{d_{p2} \cdot q}\right):$$

$$g_q(p,q) = a_q \cdot \left(1 - \frac{c_{q1} \cdot q}{K_q}\right)\left(1 - \frac{c_{q2} \cdot q}{d_{q2} \cdot p}\right):$$

It is easy to verify that g_p decreases with p but increases with q, and the other way around with g_q. These formulas can be interpreted in the following way: There is a resource (e.g. food) of quantity K_p that species P needs. Each individual needs c_{p1} of this resource, so whenever the population $p(t)$ is so that $c_{p1} \cdot p(t)$ comes close to K_p then the growth rate must go to zero. There is also a second resource that species Q provides to species P. Each individual of species P needs c_{p2} units of this resource, and each individual of species Q produces d_{p2} units of it. So the demand is $c_{p2} \cdot p$ and the supply is $d_{p2} \cdot p$. Again, if supply comes close to demand, then the growth rate of species P should go to zero. A similar interpretation can then be given to the growth rate $g_q(p,q)$ of species Q.

Note that these formulas do not explicitly require that the populations of the two species are in a particular ratio. In fact, neither species really minds if there are too many of the other kind -- that would just mean a plentiful supply of the second resource. All they care is if there are too few of the other species. Of course, in the end, a particular ratio will probably happen: if there are a lot of Ps in the beginning and few Qs, then P can't grow initially because it is lacking the resource that Q produces. But Q can grow rapidly because there is plenty of the resource around that P produces. After some time, the populations will be in a ratio that allows both of them to grow until the first resource becomes the limiting factor. So this ratio will happen, but we don't have to explicitly specify it in the model.

There are of course other ways to model the situation we want, again likely leading to qualitatively the same answers even if they quantitatively differ. For example, one could have chosen these functions, which also have the required behavior in terms of growth and decrease as a function of p, q:

$$g_p(p,q) = a_p \cdot \left(1 - \frac{c_{p1} \cdot p - c_{p2} \cdot q}{K_p}\right):$$

$$g_q(p,q) = a_q \cdot \left(1 - \frac{c_{q1} \cdot q - c_{q2} \cdot p}{K_q}\right):$$

This could model the situation where there is only one limiting resource for each species. For example, species P needs resource 1 of which there is K_p available in nature and species Q can produce this resource in quantity c_{p2} per individual, making the demand the difference between what P needs and Q produces. The second formula can be interpreted similarly. A different way to present this would be these formulas:

$$g_p(p,q) = a_p \cdot \left(1 - \frac{c_{p1} \cdot p}{K_p + c_{p2} \cdot q}\right):$$

$$g_q(p,q) = a_q \cdot \left(1 - \frac{c_{q1} \cdot q}{K_q + c_{q2} \cdot p}\right):$$

Note that each of these two sets of formulas are exactly equivalent to formulas we had for the competition model, just with different signs. This is, in effect, true for all the models we've discussed: the difference between predator-prey, competitive, and symbiotic models is essentially only in the signs of some of the terms in the model.