Introduction to Mathematical Biology
Exercises 3.1-3.5

3.1 *Allee effect from predator saturation.* Consider a logistic population of prey which is harvested by a fixed number P of predators with Holling type II functional response:

$$\frac{dN}{dt} = r_0 N\left(1 - \frac{N}{K}\right) - \frac{\beta N}{1 + \beta T N} P$$

Find all biologically meaningful equilibria and establish their stability. Draw bifurcation diagrams using P as bifurcation parameter (there are several qualitatively different bifurcation diagrams depending on T!). In particular, determine at which value of P the prey population goes extinct, and whether extinction happens through a transcritical or a fold bifurcation.

3.2 *The functional response of predators with handling time both before and after capturing the prey.* Suppose a searching predator encounters prey at a rate β. Upon each encounter, the predator pursues the prey for a constant time T_1, after which it either captures the prey (with probability p) or the prey escapes (with probability $1 - p$). If the prey is captured, the predator needs T_2 time to consume and digest the prey. Derive the functional response of the predator, i.e., the number of prey individuals a predator consumes per unit of time, $\phi(N)$, as a function of prey density, N.

3.3 *Arbitrary distribution of handling times.* Assume that the handling time of a predator, τ, has an arbitrary distribution with finite support $[0, \tau_{max}]$ (i.e., if $F(\tau)$ is the probability that handling is finished by τ time after capturing the prey, then $F(\tau) = 1$ for all $\tau \geq \tau_{max}$; see a note on the function F below). Show that at equilibrium, the number of searching predators is $\hat{S} = \frac{P}{1+\beta T N}$, where P and N are respectively the (constant) numbers of predators and prey, β is the capture rate of searching predators, and $T = \int_0^{\tau_{max}} \tau F'(\tau) d\tau$ is the mean handling time. *Hint:* start with formulating a conservation law stating that the number of searching and handling predators always adds up to P, and proceed roughly along the lines the lecture followed when we derived the same result for $\tau = T = const$.

In probability theory, $F(x) = Prob$(the random variable takes a value less than x) is known as the *probability distribution function* of the random variable. In the present context, $F(\tau)$ is the probability that the random handling time is shorter than τ, and $1 - F(\tau)$ is the probability that handling is longer than τ, i.e., that a predator who caught a prey τ time ago is still handling it. The probability that handling ends between τ and $\tau + d\tau$ is

$F(\tau+d\tau)-F(\tau) = F'(\tau)d\tau$. The mean handling time is therefore $T = \int_0^{\tau_{max}} \tau \cdot Prob$(handling ends between τ and $\tau+d\tau) = \int_0^{\tau_{max}} \tau F'(\tau)d\tau$ as stated above. $f(\tau) = F'(\tau)$ is called the *probability density function* of handling time. Using the probability density function, the probability that handling ends between τ and $\tau+d\tau$ is $f(\tau)d\tau$, and the mean handling time is $\int_0^{\tau_{max}} \tau f(\tau)d\tau$; this is the most common way of writing the average of a continuously distributed random variable.

THE NEXT TWO EXERCISES ARE OPTIONAL (but give extra credit)

3.4 *The fold bifurcation.* Consider a one-dimensional dynamical system $\frac{dx}{dt} = f(x,\mu)$ near a fold bifurcation point $(\hat{x}_0, \mu_0)$. There are four possible configurations of equilibria near $(\hat{x}_0, \mu_0)$; a pair of equilibria may exist either for $\mu < \mu_0$ or for $\mu > \mu_0$, and either the upper branch or the lower branch of equilibria is asymptotically stable. Determine which configuration occurs in terms of the derivatives of f.

Note that these configurations can be transformed into each other by changing the variable (use $-x$ instead of x) and/or the parameter (use $-\mu$ instead of μ), so they are mathematically equivalent. For practical purposes, however, we need to know which configuration is at hand in a particular model.

3.5 *The transcritical bifurcation.* Consider a one-dimensional dynamical system $\frac{dx}{dt} = xg(x,\mu)$ near a transcritical bifurcation point of its trivial equilibrium $(0, \mu_0)$. There are four possible configurations of equilibria near $(0, \mu_0)$; the nontrivial branch of equilibria is positive either for $\mu < \mu_0$ or for $\mu > \mu_0$, and the positive equilibria are either asymptotically stable or unstable. Determine which configuration occurs in terms of the derivatives of f.

Once again, these configurations are mathematically equivalent. However, since only non-negative equilibria are interpretable biologically, these configurations do differ from a biological point of view.