Ecological Archives E089-098-A1.

Peter A. Abrams. 2008. Measuring the impact of dynamic antipredator traits on predator-prey-resource interactions. *Ecology* 89:1640-1649.

Appendix A: Analysis of the model with predator avoidance via lower activity rate for zero handling times.

Equilibrium densities in the presence of adaptive behavior and the predator

The following densities are obtained by solving Eqs. 1a,b after setting handling times to zero, and substituting expression (2) for C.

$$\hat{R} = (1/B)\left(d_1 + s_1 P + 2\sqrt{(d_0 + s_0 P)(d_2 + s_2 P)}\right) \qquad \text{(A.1a)}$$

$$\hat{N} = \frac{r\left((KB - d_1 - s_1 P)\sqrt{\dfrac{d_2 + s_2 P}{d_0 + s_0 P}} - 2(d_2 + s_2 P)\right)}{KB} \qquad \text{(A.1b)}$$

$$\hat{C} = \sqrt{\frac{d_0 + s_0 P}{d_2 + s_2 P}} \qquad \text{(A.1c)}$$

Taking derivatives with respect to P shows that R always increases with P: C always increases with P if $d_2/s_2 > d_0/s_0$, and always decreases with P if this inequality is reversed; and N may either decrease with P for all values of P (true when the equilibrium C increases with P), or may increase with P at low values and decrease with P at higher values of P. The latter (unimodal) outcome can only occur when $d_2/s_2 < d_0/s_0$ (implying that the equililbrium C declines with P) and when K is sufficiently large. The critical value of K may be shown to be:

$$K_{crit} = \frac{2d_0 d_2 s_1 + d_0 d_1 s_2 + 4d_0 s_2 \sqrt{d_0 d_2} - d_1 d_2 s_0}{B\left(d_0 s_2 - d_2 s_0\right)}$$

The above equations also provide the equilibrium in the absence of the predator, simply by substituting P = 0; in this case,

$$\hat{R} = \frac{d_1 + 2\sqrt{d_0 d_2}}{B};\ \hat{C} = \sqrt{\frac{d_0}{d_2}};\ \ \hat{N} = \frac{r\left[(KB - d_1)\sqrt{\frac{d_2}{d_0}} - 2d_2\right]}{KB} \qquad \text{(A.2a,b,c)}$$

2. *Equilibrium densities in the presence of adaptive defense but the absence of actual predation* (Here P denotes the number of predators to which the cue corresponds).

$$\hat{R} = \frac{d_1 d_2 + 2d_1 s_2 P + s_1 s_2 P^2 + (d_2 + s_2 P)\sqrt{s_1{}^2 P^2 + 4d_0(d_2 + 2s_2 P)}}{B(d_2 + 2s_2 P)} \qquad \text{(A.3a)}$$

$$\hat{C} = \frac{-s_1 P + \sqrt{4d_0 d_2 + s_1{}^2 P^2 + 8d_0 s_2 P}}{2(d_2 + 2s_2 P)} \qquad \text{(A.3b)}$$

$$\hat{N} = \frac{2r\left[KB(d_2 + 2s_2 P) - \left(d_1 d_2 + 2d_1 s_2 P + s_1 s_2 P^2 + (d_2 + s_2 P)\sqrt{s_1{}^2 P^2 + 4d_0(d_2 + 2s_2 P)}\right)\right]}{KB\left[-s_1 P + \sqrt{s_1{}^2 P^2 + 4d_0(d_2 + 2s_2 P)}\right]} \qquad \text{(A.3c)}$$

These formulas are rather complicated, but it is possible to determine how they change with P in some circumstances. Taking derivatives of the above formulas shows that the equilibrium C must decrease with P when P is close to zero. The short term response of C to increased P is also a decrease, regardless of the initial value of P. This decrease leads to the possibility that greater predator density increases the equilibrium prey density by forcing the prey to exploit the resource more prudently. The derivative of the equilibrium N with respect to P is positive when

$$P < \frac{d_1{}^2 - 4d_0 d_2 - 2KBd_1 + (KB)^2}{2(-d_1 s_1 + KBs_1 + 4d_0 s_2)},$$

and $\hat{N}$ decreases with P when this threshold value is exceeded. This means that there is some range of P for which the equilibrium N increases with P provided $d_2 < (BK - d_1)^2/(4d_0)$, but this latter inequality is implied if N is able to achieve a positive population density in the absence of P.

3. *Equilibrium in a case with predation, but no anti-predator behavior*

Here C takes on the optimum it would have in the absence of predators; $C = (BR - d_1)/(2d_2)$. By substituting this in the equation for dN/dt, we obtain an expression of the equilibrium R in the absence of behavior and the presence of the predator. This can in turn be used to get an equilibrium C and R under the same conditions:

$$\hat{R} = \frac{d_1 d_2 + (s_1 d_2 - s_2 d_1)P + d_2\sqrt{s_1^2 P^2 - 4s_0 s_2 P^2 + 4(d_2 s_0 - d_0 s_2)P + 4d_0 d_2}}{B(d_2 - s_2 P)}$$

$$\hat{N} = \frac{-4rd_2(d_0 + s_0 P) + r\left(KB - d_1\right)\left(-s_1 P + \sqrt{s_1^2 P^2 - 4s_0 s_2 P^2 + 4(d_2 s_0 - d_0 s_2)P + 4d_0 d_2}\right)}{2KB(d_0 + s_0 P)}$$

$$\hat{C} = \frac{s_1 P + \sqrt{s_1^2 P^2 - 4s_0 s_2 P^2 + 4(d_2 s_0 - d_0 s_2)P + 4d_0 d_2}}{2(d_2 - s_2 P)} \qquad \text{(A.4a,b,c)}$$

Taking derivatives of these formulas shows that C increases with P, R increases with P, and N decreases with P in this case.

The only additional treatment discussed in the text is a system in which predators are absent; equilibrium densities are obtained from Eqs. A.1 by substituting P = 0.