AN OPTIMAL FORAGING MODEL FOR THE RED-COCKADED WOODPECKER

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ABSTRACT.—Various means have been used to estimate the territorial needs of the red-cockaded woodpecker. In this work we propose a model derived using optimal foraging techniques and avian energetics as a means to assess the viability of even-age stands of pines as red-cockaded woodpecker foraging territories.

The red-cockaded woodpecker (rcw), once abundant in the southeastern United States, has suffered severe reduction in numbers as the mature pine forests which are its preferred habitat have been reduced by clearing, logging and fire suppression. In 1970 the species was officially declared endangered; since that time the rcw been studied intensively, at least partly with a view to estimating territorial requirements and population sizes required for survival (U.S. Fish and Wildlife Service 1985; Ligon, et al. 1986; Walters 1990, 1991 and references therein).

We have not seen in the literature any attempts to relate directly the viability of a territory as rcw habitat to the vital processes of the bird; this may be due at least partly to the difficulty of quantifying the presence of arthropods in a forest environment (Dahlsten et al. 1990). Recently, however, R. G. Hooper (1996) has given empirical equations in terms of tree and stand parameters for pine boles and for arthropod densities on southern pines. Using Hooper's equations and parameters derived from avian energetics, we offer here a way to compare suitability of even-age stands of pines as rcw foraging territories.

THE OPTIMAL FORAGING MODEL

We consider an even-age stand of pines to be a patchy foraging area, each pine being a patch, and apply optimal foraging theory to maximize the net metabolic energy an rcw is able to achieve within the constraint of a fixed amount of foraging time within a 24-hour period. We assume that the pines are evenly spaced, of equal height and diameter, and bearing equal densities of arthropods as prey, and that the understory is of uniform height, but we see no reason why the analysis cannot be extended to stands not of even age and also with variable prey densities.

Following Repasky (1984), we idealize the bird's foraging pattern as follows: the rcw flies in a direct line from the top of a pine to alight on a next pine at understory height, hitches directly to ground level without seeking prey, and then hitches, meanwhile seeking and capturing prey, to the top of the pine. The cycle is then repeated until the allotted foraging time is exhausted (Fig. 1). This may on the face of it seem like a strange way to forage a pine, particularly in an optimality model, but is close enough for our purposes to the actual foraging behavior of the woodpecker and in addition has striking similarities to an optimal pattern discussed by Norberg (1983).

Let T denote the total time allotted for foraging, n the number of trees foraged, t_o the fixed time (the flight time plus the downhitching time) in the cycle for one tree, and t the variable time spent uphitching while seeking prey. Then

$$T = n(t_o + t).$$

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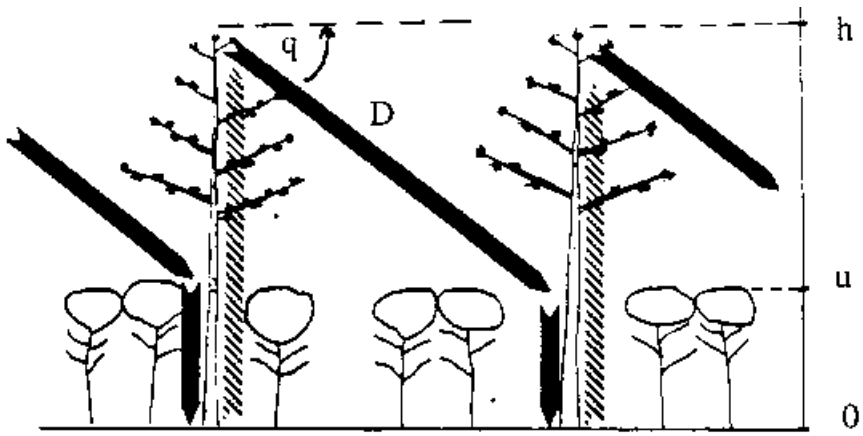

Figure 1.—Foraging pattern of the red cockaded woodpecker.

The Cost Per Tree

The cost per tree C(t) is given as the sum of the fixed cost C_F and the variable cost $C_V(t)$. For the rcw we derive the hitching metabolic rate of 1.88 joules per second from the allometric equation

$$FMR = 18.2M^{0.749} \text{ (units are W. and kg.)}$$

given by Nagy (1987) for the field metabolic rate for passerine birds, with the result that

$$C_V(t) = 1.88\ t.$$

The fixed cost C_F is the sum of the flight cost C_{FL}, the downhitching cost C_H, and the cost C_{PE} of the potential energy gained by climbing to the top of the pine. Taking the weight of the rcw to be 0.47 Newtons (Repasky) and converting mechanical power to metabolic power by the factor 4.35 (Pennycuick 1975) gives

$$C_{PE} = 2.06\ h,$$

where h is the pine height. The flight cost is obtained by converting Repasky's expression for the mechanical power of flight for the rcw to a metabolic rate and adding a standard metabolic rate calculated from the allometric equation

$$SMR = 6.83\ M^{0.704}$$

of Aschoff and Pohl (see Norberg, U.M. 1990, p. 43). This gives

$$C_{FL} = (D/12)(0.81 + 4.35\{0.1\cos^2 q + \max[0, 0.9 - 5.6\sin q]\}),$$

where D is the slant flight distance from the top of a pine to the next pine at understory height, q is the angle below the horizontal of the flight path, and the factor D/12 is the time the rcw takes to cover the distance D at 12 m. per sec., its most economical flight speed (calculated by Repasky from formulas in Pennycuick).

Estimates of Fedak et al. (1973) and Tucker (1970) imply that running cost per meter for birds is 9 times the most economical flight cost, which estimate Repasky takes for the hitching cost for the rcw. This estimate, together with our assumption of the FMR of 1.88 j. per sec. as the metabolic cost of hitching, imply that the hitching velocity of the rcw is 0.328 m. (12.9 in.) per sec. We are not aware of any data-based estimate of the downhitching velocity of the rcw, but this value seems high to us, and since Repasky himself remarks that hitching, being a jerky movement that involves changes in kinetic energy, is no doubt more expensive than running, we take our hitching cost estimate to be 11 (rather than 9) times the economical flight cost. This produces an estimate of 0.268 m., or 10.6

in., per sec. for the hitching velocity, and the incremental metabolic cost of downhitching a distance u, the height of the understory, turns out to be 3.98 u. The standard metabolic rate of 0.81, divided by the rate of hitching(0.268 m. per sec.) gives the rate of energy per meter and so contributes 3.02 u, and the total downhitching cost is

$$C_H = 7u.$$

Finally, then, the total cost function per tree is given by

$$C(t) = C_F + C_V(t) = 2.06h + 7u + (D/12)(0.81 + 4.35\{0.1\cos^2 q + \max[0, 0.9 - 5.6\sin q]\}) + 1.88t.$$

The Gross Gain Per Tree

We assume that the rate of increase of the gross gain function G(t) decreases exponentially as time increases, that is, for some constant k,

$$G'(t) = ke^{-rt} \quad (\ )' = d(\ )/dt\ ),$$

that G(0) = 0, and that G(t) approaches the total amount M of prey (expressed in joules of metabolic energy) as t grows large. With these assumptions, integration of the equation for G'(t) yields

$$G(t) = M(1 - e^{-rt}).$$

The parameter r is the relative rate with respect to time of capture of prey; to see this explicitly, notice that M - G(t) is the amount of prey remaining after elapsed time t and that

$$G'(t) = rMe^{-rt} = r(M - G(t)).$$

Now let B, p, and c denote, respectively, the pine bole in square meters, the prey density in grams dry weight per square meter, and the factor which converts grams (dry weight) of prey to joules of metabolic energy for the rcw. Then M = cpB and so

$$G(t) = cpB(1 - e^{-rt}),\ t \geq 0.$$

The conversion factor c is taken to be 17.22 (Bell, 1990). Hooper's empirical equations estimating B and p are

$$B = -17.1528 + 1.0899Dbh - 0.3596h,$$

where the diameter at breast height is in cm. and the pine height h is in meters, and

$$p = 10^{-3}(211.88 - .006687A^2 - 6.4433R),$$

where A is the age in years of the pine and R is the radial increment in mm. from 10 years prior time to 5 years prior time.

Optimization Of The Total Net Energy Gain

The net energy gain per tree is N(t) = G(t) - C(t), and the total net energy gain is

$$E(t) = nN(t) = TN(t)/(t + t_o).$$

The value t* of t which maximizes E(t) must satisfy E'(t) = 0, or equivalently,

$$(t + t_o)N'(t) = N(t).$$

For our expressions for G(t) and C(t) this simplifies to

$$Mrt + M + Mrt_o = (M + 1.88t_o - C_F)e^{rt},$$

whose unique positive solution t* must be found numerically.

To show that there indeed is a unique positive t* unless the rcw cannot even make expenses in the stand, we define the functions f(t) and g(t) by

$$f(t) = Mrt + M + Mrt_o,\ g(t) = (M + 1.88t_0 - C_F)e^{rt}$$

(the left- and right-had sides, respectively, of the equation defining t*). Since Mr is the maximal rate of accumulating and 1.88 is the rate of energy expended while foraging, we must have

$$Mr > 1.88$$

for the stand to be viable, so that

$$f(0) = M + Mrt_o > M + 1.88t_o > M + 1.88t_o - C_F = g(0)\ ;$$

that is, at t = 0 the graph of y = f(t) starts out above the graph of y = g(t).

Further, since the total amount M of prey available must be greater than the fixed cost C_F of foraging for the bird to have a chance of making a living, we must have

$$g(0) = M + 1.88t_o - C_F > 1.88t_o > 0.$$

Since y = f(t) is a straight line and y = g(t) is an exponential curve with positive coefficient and positive exponent, and since by the above analysis the graph of y = f(t) starts out above the graph of y = g(t), the graphs have a unique point of intersection for t > 0, so the value t* that maximizes the total net energy E(t) is positive and unique (Fig. 2).

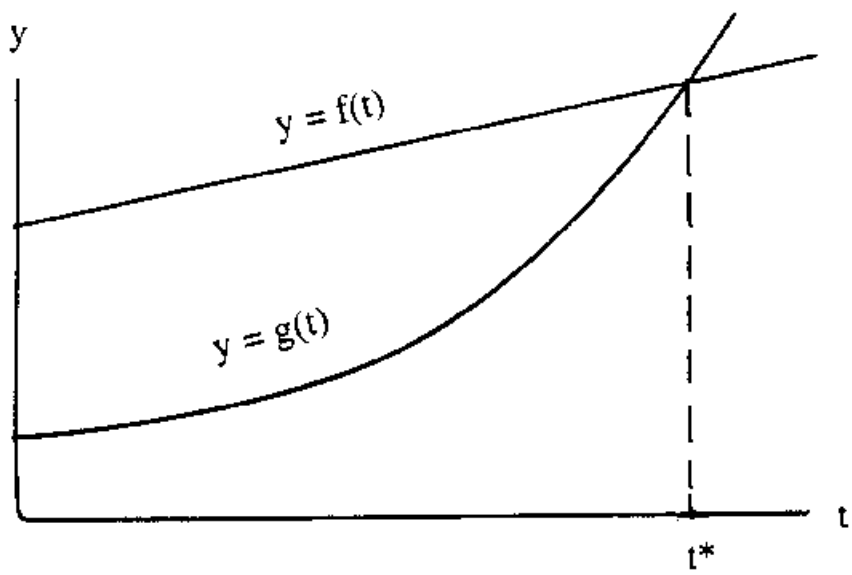

Figure 2.

Finally, using the equation defining t* to get the next-to-last of the following equalities, we have

$$E(t^*) = nN(t^*) = TN(t^*)/(t^* + t_o) = TN'(t^*) = T(Mre^{-rt^*} - 1.88).$$

DISCUSSION

The model needs to be validated against existing data. This is particularly true of the relative rate of predation r. Just as quantification of arthropods has proved to be difficult, so, it seems, has estimation of r in general and in particular. Feasible parameter ranges might be obtained by measurements of prey consumed relative to prey present as given by Hooper's empirical equations giving boles and prey densities.

We are fully aware that application of optimal foraging theory, both in general and to in particular to foraging behavior in birds, has both its adherents and its detractors (Maurer 1990, 1996; Stephens 1990). We emphasize here that we make no claims that the rcw makes any decisions, either consciously or unconsciously, to forage using the strategy we have described (we do suggest, however, that whether the bird indeed does forage in a way that to some degree approximates this strategy could be tested in the field). Likewise, we make no assertions regarding population demographics, since the model includes no birth or death processes or incremental energetic requirements because of seasonal variations or breeding requirements for the bird, or any population dynamics for the prey. What we do suggest is that the maximal energy $E^* = E(t^*)$ available to a single rcw foraging an even-age stand during a fixed time T, using this optimal foraging strategy, might be useful as an index of viability for such a stand as a foraging area.

We have already pointed out that if $Mr \leq 0$ the stand might be thought inadequate as a foraging area; the same conclusion might be drawn if we find that if $E^* \leq 0$, that is, even using a strategy defined as optimal under our assumptions the basic costs of foraging outweigh the benefits to be gained.

Even if the E^* which our analysis yields is negative, since the bird might not forage optimally the stand might not qualify as a foraging area. In addition, we have not included fixed costs F such as travel, defense, and so on. They would depend on the particular stand in ways that do not enter into our analysis; they are independent of t and so do not affect the value of t^*, but should be incorporated by using $E^* - F$ rather than E^* as the true viability index, so that a necessary (but not sufficient) condition for viability is

$$E^* - F \geq 0.$$

Of course, if n^* is the number of trees corresponding to t^*, a further necessary condition would be that the stand contain n^* pines, or kn^* pines to support communal foraging by a group of k birds.

In the above senses, then, $E^* - F$ provides a quantitative estimate of viability. However, even if the above necessary conditions are not met, $E^* - F$ would provide a qualitative estimate for comparing the value of different stands as possible foraging areas for a single rcw.

Finally, our model estimates the desirability of even-age stands as foraging area in a way that involves avian energetics but whose use requires knowledge only of stand parameters that can be both measured in the present and estimated for the future. We hope that the index derived by its use, together with other methods to assess territorial suitability, will prove useful in making the management decisions necessary to provide for not only an adequate harvest of timber but also the continued existence of the red-cockaded woodpecker.

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