TERRITORIAL BEQUEATHAL BY RED SQUIRREL MOTHERS: A DYNAMIC MODEL

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Female red squirrels (Tamiasciurus hudsonicus) sometimes bequeath their territory to their offspring. Late-breeding females are more likely to leave than are early-breeding females. Early-breeding females tend to lose weight during reproduction while late-breeding females do not. Early-born juveniles are more successful at winning territories than are those born late. I use dynamic programming to investigate the trade-offs involved in territorial bequeathal from the female's perspective as a function of breeding date, litter size and female body condition. The model predicts that two classes of females are more likely to bequeath: those in good condition early in the season, and those in poor condition at the season's end. Only versions of the model incorporating a function improving the female's ability to win a territory over the season mimicked the pattern of bequeathal observed in the field. A seasonal effect is likely an important factor in driving the pattern of strategies observed.

Introduction. Female red squirrels (Tamiasciurus hudsonicus) require territories for breeding and overwinter survival. Individuals without a territory at the onset of winter generally perish (Kemp and Keith, 1970; S. Boutin, U. Alta, unpublished data). Thus, a territory is a very valuable commodity to a female red squirrel. Yet, some females bequeath their territories to one of their offspring and search for a new one (Price et al., 1986; Price, 1990). Such territory bequeathal is risky for a female since this search may not be successful. In effect, the female may be sacrificing her prospects for future survival and breeding for those of her offspring. In this paper, I ask two questions: first, why do females bequeath territories to offspring; second, under what conditions is such behaviour favoured?

In an examination of the behaviour of female red squirrels in an unmanipulated field situation, Price (1990) found evidence for a cost of reproduction in the form of a loss of weight and fur condition and a suggestion that this loss increased the probability of losing a territory. Females in poor condition were challenged more frequently and probably were exposed to a higher predation risk. Late-breeding females showed no weight loss and never lost their territories. However, juveniles from late litters were less successful at winning territories than were those from early litters, and late-breeding females were more likely to bequeath their territories to their offspring.
In this paper I use stochastic dynamic programming (Mangel and Clark, 1988) to investigate territory bequeathal in red squirrels. Five basic assumptions underlie the model dynamics (Price, 1990). First, reproduction is energetically costly due to physiological requirements and to increased levels of territorial defence following juvenile emergence; second, decreased body condition increases the probability of death through territory loss (and perhaps from an increased risk of predation through decreased vigilance); third, females that breed early forego access to summer food, and tend to lose body condition; fourth, early litters are worth more to females, due to the increased likelihood that early juveniles obtain territories independently of their mother; and fifth, there are fewer territories available late in the season.

The Model. I model a female squirrel's state and decisions from the time her juveniles emerge until the end of autumn. I use the territorial status of the female and of her juveniles at the end of autumn as a fitness surrogate. In a single season model, with the assumption that territorial ownership, along with body condition, dictates overwinter survival, the number of juveniles with territories in autumn represents reproductive success this season, and the territorial status and body condition of the female represent her residual reproductive value. The season is divided into week long time intervals.

State variables and constraints. Table 1 lists variables and parameter definitions. I use three variables to define a female squirrel's state at any time. \( X(t) \) represents the female's body condition (e.g. fat reserves) at time \( t \) where:

\[
0 \leq X(t) \leq X_{\text{max}}.
\]

\( X(t) = 0 \) implies starvation, and \( X_{\text{max}} \) is an arbitrarily assigned maximum condition. \( R(t) \) is a binary variable representing territory ownership [at time \( t \), if \( R(t) = 0 \), the squirrel is vagrant and owns no territory; if \( R(t) = 1 \), she owns a territory]. \( J_R(t) \) represents the number of a female's juveniles holding independent territories; it is a measure of her reproductive success this year and can take any integer value between 0 and \( N \), where \( N \) equals litter size.

I assume that a squirrel's fat reserves at any time will depend on her status as a territory owner as well as on her prior condition. Hence:

\[
X(t + 1) = X(t) + G(r) - C(r) = X'
\]

where \( G(r) \) and \( C(r) \) represent state-specific \([r = R(t)]\) condition gains and costs. I assume that vagrant squirrels cannot gain condition as readily as can territorial squirrels in any time period, first, because food is more easily available to the territorial squirrel, and second, because energetic costs are higher to the vagrant squirrel due to chasing and contesting activities with territory holders.