

Intake rate maximization and the foraging behaviour of crossbills

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Foraging Two-barred Crossbills *Loxia leucoptera* remove seeds first from the basal scales of tamarack cones, then proceed to the distal end. Seeds, however, are often left in the distal-most scales. To determine if crossbill cone-leaving behaviour maximized intake rates, seed kernels were weighed from the different cone scales and the foraging behaviour of crossbills was quantified. Crossbills usually removed seeds from one scale more than that which would have maximized intake rates. Nevertheless, this behaviour provided an intake rate that nearly equaled the maximum. Crossbills appear to use a cone-leaving rule of "leave when kernel mass declines".

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Introduction

The length of time an animal forages in a patch influences its intake rate (Charnov 1976, Pyke et al. 1977, Stephens and Krebs 1987). A solution to maximizing intake rate is to leave a patch when the intake rate in the patch declines to the overall average intake rate among patches (marginal value theorem; Charnov 1976). Although such behaviour is best for an omniscient forager, animals in nature are not omniscient. Consequently, there is a growing interest in plausible patch leaving rules (e.g., Green 1980, 1984). I will show that even though Two-barred Crossbills *Loxia leucoptera* do not leave patches (conifer cones) when intake rates (mg seed kernel eaten s^{-1}) are maximized, the rule they use provides an intake rate that is close to the maximum. Crossbills appear to use the simple rule "leave when kernel mass declines". Because of variation among cones, this rule provides a higher intake rate than any other envisioned rule.

The extent to which crossbills maximize intake rates when foraging depends, in part, on when they depart from cones. Elsewhere (Benkman 1987a) I show that crossbills most often forage on the conifer species yielding the highest intake rates. Two-barred Crossbills often

remove closed (i.e., before cone is ripe and open) tamarack *Larix laricina* cones from the branch, extract seeds from the cone, husk the seeds and swallow the kernels, and then discard the cone. Tamarack cones usually have 13 to 15 scales, with two seeds at the base of all but most basal and distal scales. Crossbills first remove seeds from the basal cone scales, then systematically proceed toward the distal cone scales removing seeds. They then move to another cone and repeat the whole process. Crossbills forage on hundreds of cones a day throughout the year.

Determining whether crossbill foraging behaviour on individual tamarack cones maximizes overall intake rate requires information on the cumulative intake rate within a cone (i.e., the gain function), the point at which cones are discarded, and travel time between cones. Travel time can be measured directly and cone or patch residence time is related to the last scale from which seeds are removed. The gain function was determined indirectly, as described below. Unfortunately, the gain function could only be estimated for the average cone. As a result, variation in patch residence time can only be indirectly addressed and estimates for how close patch residence times come to maximizing intake are less precise.

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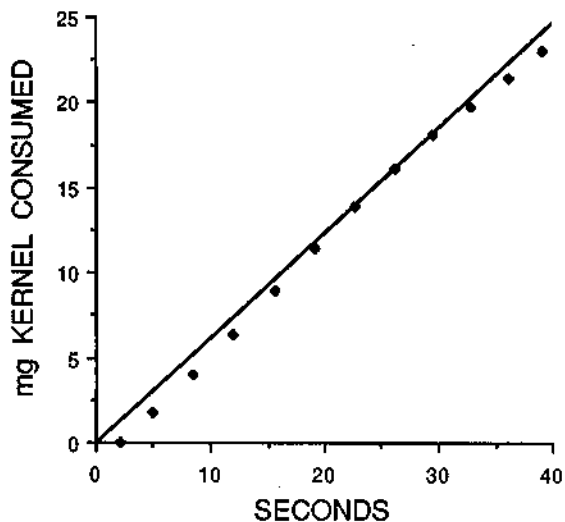


Fig. 1. The gain function for crossbills foraging on a tamarack cone. The first data point on the abscissa represents travel time (2.12 s) and each successive dot represents the cumulative intake and time after eating seeds from consecutive scales (i.e. the first dot with a positive gain represents scale 1, the second represents scale 2, and so on). The line from the origin is tangent to scale 7 and represents the maximum intake rate.

Methods

Travel time between closed tamarack cones was measured for crossbills foraging at a study site in northern Ontario, Canada. All data were gathered at this site and all foraging observations were made on 4 and 6 July 1987 with the aid of a Questar telescope (40X). I used a digital stopwatch to record events to the nearest 0.1 s. Foraging crossbills can, at times, be observed easily. In earlier studies I had recorded crossbills consuming >60,000 seeds (Benkman 1987a, b).

The mass of kernel consumed and time spent at each cone scale were estimated to determine the gain function. Mass of kernel (E_i) consumed for scale i was the product of the average mass of the kernel (\bar{M}_i) for scale i times the mean number of seeds (\bar{S}_i) from scale i :

$$E_i = \bar{M}_i \cdot \bar{S}_i$$

To determine \bar{M}_i , I gathered cones from 10 tamarack trees on 25 August 1987. Kernels (female gametophyte and embryo) were separated from their surrounding seeds coats, dried at 70°C for 3 d and weighed to the nearest 0.01 mg. For nearly all cone scales, I weighed one kernel from each of the 10 trees. Note that the foraging data were gathered in early July when seeds were developing and of small size, whereas kernel mass was determined for mature seeds. It is assumed, however, that the relative sizes of kernels among the scales did not differ between dates. This is a critical, but reasonable assumption.

I gathered 10 cones, that had recently been discarded by foraging crossbills, from the base of each of 10 tamarack trees on 1 July 1987. For each cone the most basal scale with a seed removed by a crossbill or with a full seed (i.e. containing a kernel) was designated scale one. Seeds removed by crossbills could be determined because "seed scars" remained on the scales. Scales were then successively numbered to the distal end and I recorded the last scale from which a seed had been removed by a crossbill. To determine \bar{S}_i , I recorded for each scale both the number of seeds that had been removed by crossbills and the number of seeds remaining with kernels. This number accurately reflects the number of seeds because seeds did not fall out after cones were discarded by the crossbills and other vertebrates were not harvesting tamarack seeds at this time. Cones damaged by insects were discarded.

The average time spent per scale i (\bar{T}_i) was the product of the mean time per seed (\bar{T}_h) times the mean number of seeds from scale i , \bar{S}_i , as above:

$$\bar{T}_i = \bar{T}_h \cdot \bar{S}_i$$

\bar{T}_h was 1.81 s (SE = 0.05, N = 24 cones). Note that \bar{T}_h includes both time to extract and handle a seed, and that it was assumed not to differ among scales or cones. This assumption is reasonable. Tamarack has thin cone scales, and slight variation in size or thickness should not affect time to separate them (Benkman 1987b). Neither should seed handling time vary measurably among the seed sizes within the tamarack cones sampled (see Benkman 1987b, Benkman and Pulliam 1988).

Results

Fig. 1 shows the mass of kernel consumed in relation to time foraging on a cone, in addition to the initial travel

Tab. 1. Tamarack seed kernel masses (mg dry weight) under different cone scales*. Sample sizes (N) are the number of kernels.

Scale	\bar{X}	Kernel mass SE	N
1	1.11	0.07	9
2	1.20	0.07	10
3	1.18	0.06	9
4	1.31	0.08	10
5	1.32	0.07	10
6	1.20	0.07	10
7	1.20	0.07	10
8	1.04	0.08	10
9	0.93	0.07	10
10	0.93	0.06	10
11	0.96	0.11	3

* The only significant difference between the masses of kernels under adjacent scales was between scales 7 and 8 ($P < 0.05$, Multiple Range test).

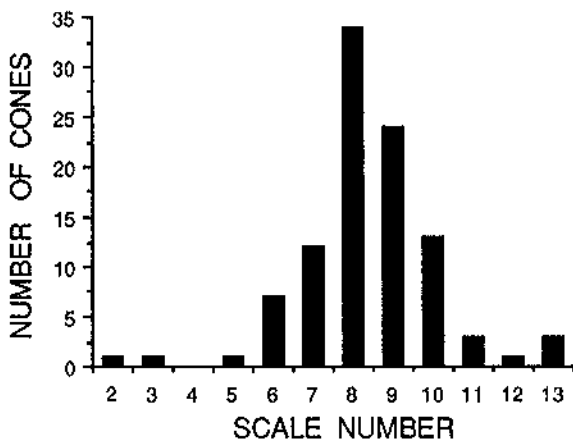


Fig. 2. The distribution of the last scales from which seeds were removed by crossbills. Sample size is 100 cones. The predicted optimum is scale 7.

time, for each successive scale. The mean travel time between cones was 2.12 s (SE = 0.28, N = 48). The line from the origin represents the maximum marginal intake rate and is tangent to the point representing scale 7. Crossbills, therefore, should leave the cone after removing seeds from scale 7. The reason the marginal intake rate declined between scale 7 and 8 was a significant reduction in mean kernel mass (Tab. 1). Prior to scale 8 there were no other significant declines in kernel mass between successive scales (Tab. 1, $P > 0.05$, Multiple Range tests). After scale 8 there was a further decline, although not significant, in kernel mass.

The last scale from which seeds were removed was most often scale 8 ($\bar{x} = 8.4$, SE = 0.16, N = 100 cones; Fig. 2). This indicates that crossbills did not always attain the highest intake rate possible, but instead often removed seeds from at least one scale too many. There was considerable variation, however, in the number of the last scale from which seeds were removed (Fig. 2). This variation may have resulted, in part, because there were differences among cones in both size and the number of scales with seeds. Consequently, kernel mass and overall intake rate may often first decline between scales other than 7 and 8. For instance, on larger cones, with more seed-bearing scales, the decline should occur at larger scale numbers than on smaller cones. Indeed, there was a significant correlation between the last scale foraged on and the number of seed-bearing scales per cone ($r_s = 0.70$, N = 10 trees, $P < 0.05$).

These data imply that crossbills left cones after encountering scales with smaller seeds. Crossbills almost instantaneously dropped empty seeds (i.e. without kernels) after removing them from the cone (pers. obs.) suggesting that crossbills were sensitive to variation in seed mass. In fact, there was a significant correlation between the probability that a seed was removed from scale i and the mean kernel mass for scale i ($r_s = 0.88$, N = 10 scales, $P < 0.01$).

Assuming crossbills left after scale 8, then their average intake rate was 99.1% of the rate they would have had if they had left after scale 7 (the maximum). Based on the actual cone-leaving behaviour (Fig. 2), the intake rate was 97.8% of the maximum. If instead crossbills had left after scale 11 (the end) or had left with an equal probability after each scale then their intake rate would have been 95.3 and 90.6% of the maximum, respectively. These estimates are based on the assumption that all cones are identical, which they are not as shown above. These estimates, therefore, are only approximate.

Crossbills could have used other cone-leaving rules. Intake rates should decline when the number of full seeds (i.e. with kernels) per scale decreased and crossbills might then leave cones. This is because crossbills apparently must pick up a seed to assess whether it has a kernel, and as the proportion of empty seeds increases more time is spent picking up empty kernels. The number of seeds per scale (the remaining number seeds with kernels plus the number of seeds removed by crossbills), however, did not decline much between scales 7 and 8 (1.93 and 1.89 seeds per scale, respectively) or between other adjacent scales. Alternatively, crossbills might use a decline in scale size to recognize declines in kernel mass. Scale size is correlated with kernel mass in lodgepole pine *Pinus contorta* (McGinley et al., unpubl.) and other conifers (pers. obs.). If scale size could be recognized before seeds were extracted, then crossbills should have terminated foraging one scale earlier than observed. Such a result was not found, but nevertheless, crossbills may use scale size as a cue to recognize kernel mass declines.

Discussion

The behaviour of Two-barred Crossbills foraging on individual tamarack cones comes close to maximizing overall intake rates. The strategy that crossbills appear to use is to leave a cone as soon as kernel mass declines. This is a simple strategy that is consistent with data on kernel mass and modal cone leaving behaviour. Such a strategy is also consonant with the positive correlation between the number of scales with seeds removed and the number of scales with seeds. Moreover, it provides an intake rate that approaches the maximum and is possibly the best strategy that can be assumed to evolve. To obtain the maximum intake rate crossbills would be required to anticipate somehow when seed mass will decline. Variation among cones, however, makes it difficult to anticipate declines in kernel mass precisely.

Crossbills may often use declines in kernel mass to assess when to leave closed conifer cones. Seed mass declines near the distal end of many conifer cones (McGinley et al., unpubl., pers. obs.) and crossbills often leave closed cones before foraging on the last several cone scales (pers. obs.). Variation among cones in both the number of full seeds and kernel mass should

also influence cone leaving behaviour. This type of variation is greatest among trees and does appear to influence which trees crossbills forage on (pers. obs.). After conifer cones open and seeds are shed, variation in the number of seeds per cone within a tree may increase. As variation increases, the effect of cone assessment on intake rates will increase (e.g., Green 1980) and the timing of cone leaving should be influenced more by such variables as the number of seeds encountered per scale.

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