

# INTAKE RATES AND THE TIMING OF CROSSBILL REPRODUCTION

CRAIG W. BENKMAN<sup>1</sup>

*Department of Biological Sciences, State University of New York at Albany,  
1400 Washington Avenue, Albany, New York 12222 USA,*

*and*

*Department of Biology, Princeton University, Princeton, New Jersey 08544 USA*

**ABSTRACT.**—I measured the foraging rates of breeding and nonbreeding populations of White-winged Crossbills (*Loxia leucoptera*) and Red Crossbills (*L. curvirostra*) throughout the year in the northeastern United States and adjacent Canada. I compared actual food intake rates (80 samples from 26 populations) to those predicted for five hypotheses that pertain to the timing of reproduction. To form eggs, crossbills required greater intake rates to meet energy demands than to meet protein requirements. Intake rates predicted to be necessary for the nestling stage (first five days after eggs hatch) were greater than those required for egg formation. Nearly all breeding and nonbreeding populations had intake rates adequate for egg formation. Thus, the ability to form eggs may only infrequently limit nesting. Crossbills nested when intake was sufficient for the nestling stage, but ceased nesting if intake rates were declining so that they would be inadequate for the nestling stage. When intake rates were less than those required for the nestling stage, crossbills nested if intake rates were increasing and would be sufficient for the nestling stage. The timing of crossbill reproduction was most consistent with the hypothesis that crossbills bred whenever intake was sufficient for egg formation and would be sufficient three weeks later during the nestling stage. That is, crossbills bred as if they were sensitive to both net intake and rates of change in intake. Intake rates may provide a proximate cue for crossbills to nest, but other factors such as maturing cone crops and changing day length probably affect breeding readiness. Received 19 August 1988, accepted 12 December 1989.

IN SEASONAL environments the timing of breeding profoundly affects reproductive success (Perrins 1970, Murton and Westwood 1977, Sedinger and Raveling 1986), and early breeding in relation to food availability often results in higher juvenile survivorship (e.g. Nilsson and Smith 1988). For many bird species breeding should begin as soon as females can accumulate enough energy and nutrients to form eggs (Perrins 1970), provided food will be sufficient during later stages of the breeding cycle. Correlations between initiation of reproduction and increases in food abundance are well documented (e.g. Payne 1969, Bryant 1975, Turner 1982). Food provisioning experiments also generally advance breeding (see Arcese and Smith 1988 for a recent summary).

The extensive literature on the energy and nutrient demands of reproduction (King 1973;

Ricklefs 1974; Robbins 1981, 1983; Walsberg 1983) has not yet determined how closely the timing of reproduction corresponds to the energy and nutrient demands of egg formation or any other food requirements. This is due, in part, to the difficulty in measuring actual *food intake rates* (energy or nutrients consumed per unit time) in the field (see Wiens 1984).

Crossbills (*Loxia*) are seed-eating birds that are ideal for testing hypotheses concerning the possible dependence of the timing of reproduction on rate of food intake. The diet of adult and nestling crossbills consists almost entirely of seeds extracted from conifer cones (Bailey et al. 1953; Austin 1968; Newton 1972; Benkman 1987a, pers. obs.), and crossbills nest when abundant seed supplies are located (e.g. Bailey et al. 1953, Newton 1972, Nethersole-Thompson 1975). Moreover, the food intake rates of crossbills can be measured readily (Benkman 1987a, b).

I considered two sets of hypotheses concerning the timing of crossbill reproduction (Table 1). First, breeding may commence as soon as the

<sup>1</sup> Present address: Department of Zoology, University of British Columbia, 6270 University Boulevard, Vancouver, British Columbia V6T 2A9, Canada.

TABLE 1. Summary of the five hypotheses for the timing of crossbill reproduction.

Hypotheses	Statement
<b>Egg formation hypotheses</b>	
Egg Energy Hypothesis	Breeding begins when females can meet energy requirements for maintenance and egg production.
Egg Protein Hypothesis	Breeding begins when females can meet protein requirements for maintenance and egg production.
<b>Nestling-stage hypotheses</b>	
Nestling Energy Hypothesis	Breeding begins when males can gather enough energy for themselves, their mates, and their nestlings.
Future Nestling Energy Hypothesis	Breeding begins when intake rates are sufficient for egg formation and will be adequate three weeks later during the nestling stage.
Null Hypothesis	Breeding is unrelated to intake rates.

female can form eggs (Perrins 1970). If energy requirements limit egg formation, then breeding should begin when females can simultaneously satisfy energy requirements for maintenance and egg production. This is the *Egg Energy Hypothesis*. During winter months short days reduce foraging time and cold elevates thermostatic requirements. Consequently, higher energy intake rates are required than during summer months. Protein, however, may limit reproduction instead of total energy (Jones and Ward 1976, 1979; Fogden and Fogden 1979; Raveling 1979; Krapu 1981), and the ability to procure enough protein before and during egg production may determine the timing of breeding (Jones and Ward 1976, Ankney and MacInnes 1978, Krapu 1981). The *Egg Protein Hypothesis* posits that breeding is delayed until sufficient dietary protein is available for the female to produce eggs.

Second, the timing of breeding may be more limited by demands during the nestling stage. Lack (1954) hypothesized that nesting is timed so that the period of greatest nestling food demand coincides with the period of greatest food availability. Caring for nestlings is the most energy-demanding nesting stage for most passerines, which produce relatively small eggs and altricial young (Walsberg 1983; but see Smith 1978, Martin 1987). In crossbills, energy demands on adults peak during the first five days after hatching, when females brood almost constantly, and males must forage for themselves, females, and nestlings (Bailey et al. 1953, Newton 1972, Nethersole-Thompson 1975). In other nestling stages, lower intake rates suffice because both parents feed nestlings (see Ricklefs 1983). Breeding may begin when energy intake

rates equal or exceed that necessary for the most energy-demanding nestling stage. This, the *Nestling Energy Hypothesis*, is reasonable if intake rates do not change much or if they are unpredictable.

Alternatively, if intake rates and daily energy demand change in regular patterns, it might be advantageous to time breeding to account for temporal changes in intake rates and energy requirements. For instance, when intake increases over time, crossbills could initiate breeding when intake rates are lower than that necessary during the nestling stage. When intake decreases over time, higher intake rates than that necessary to care for nestlings should be required for nesting to begin. The *Future Nestling Energy Hypothesis* predicts that the necessary intake rate for breeding must be sufficient for the female to form eggs (egg formation hypotheses), but should also depend on the rate at which intake rates change so that young can be raised successfully (Nestling Energy Hypothesis). Finally, a *Null Hypothesis* is that the probability of breeding is unrelated to intake rates.

I examined patterns of energy and protein intake of breeding and nonbreeding crossbill populations throughout the year to evaluate the extent to which the timing of crossbill reproduction is determined by the demands of egg laying and nestling care. *Breeding* includes all stages of nesting from nest building to feeding fledglings. Even though species vary in the extent to which accumulated protein and fat stores provide the necessary nutrients for egg formation and nesting (Jones and Ward 1976, 1979; Ankney and Scott 1980; Drent and Daan 1980), females of smaller species may replenish pro-

tein and fat reserves daily to produce eggs (Jones and Ward 1979). Therefore, the ability of most small passerines, such as crossbills, to obtain sufficient nutrients and energy for egg formation and nesting likely depends on current net intake rates (Murton and Westwood 1977). Because White-winged Crossbills (*L. leucoptera*) and Red Crossbills (*L. curvirostra*) breed in every month of the year (Godfrey 1966, Newton 1972) and in a variety of climatic conditions, hypotheses based solely on day length or other factors such as rainfall are not considered. Day length and temperature, however, do affect the necessary intake rates for all but the Null Hypothesis.

#### METHODS

*Study areas.*—I studied crossbills from April 1982 to February 1985, from June to September 1987, and from September 1988 to April 1989 in coniferous forests of the northeastern United States and adjacent Canada. I gathered data on White-winged Crossbills at Wonderland-Ship Harbor and Otter Point-Blackwoods in Acadia National Park, Maine; near Wenlock Crossing, Vermont; near Good Luck Lake in the southern Adirondacks, New York; near Mare du Sault in Laurentides Reserve and at four areas in La Verendrye Reserve, Quebec; near Achray and along the Highway 60 Corridor in Algonquin Provincial Park, Ontario; at two areas near Foleyet, Ontario; 40 km northeast of St. Leonard, 60 km east of Plaster Rock, and near Point Wolfe in Fundy National Park, New Brunswick. I obtained data on Red Crossbills at Otter Point-Blackwoods, Good Luck Lake, and both areas in Algonquin Provincial Park, on the Tongue Mountain Range, and in Albany, New York. I visited study areas year-round from 1982 to 1985 for 1–6 days for a total of 186 days. In 1987, I remained at the two areas near Foleyet almost continuously. During 1988 and 1989, I visited the area east of Plaster Rock for 1–3 weeks every 1–2 months. I refer to the crossbills at an area as a population and to data gathered during a visit as a sample.

*Intake rates.*—Intake rate was defined as mass (dry weight) of seed kernel consumed per second. I measured intake rates of foraging crossbills by recording the number of kernels individual crossbills consumed during timed intervals. Crossbills remove and discard the seed coat from each seed before swallowing the kernel (female gametophyte and embryo). Crossbills were timed from when they began to forage on a cone, or had finished handling a seed, until that cone or a subsequent cone was discarded. These intervals included time spent handling seeds, extracting seeds from cones, and travel time between cones within trees. I excluded intervals when crossbills did not forage actively, such as when scanning for more than brief moments. Travel time between trees was ex-

cluded because it represented little of the total foraging time (Benkman 1987a). To account for travel time between cones within trees, I measured intake rates while crossbills foraged on more than one cone, and included travel time in the total foraging time. Alternatively, I measured both intercone travel time and the average amount of time spent foraging per cone. In the first case, intake rate was the number of kernels consumed ( $n$ ) multiplied by dry mass of kernel ( $k$ ) divided by time foraging ( $T$ ). In the second case, intake rate was the average dry mass of kernel consumed per unit time ( $\bar{X}$ ), multiplied by the mean total time per cone ( $\bar{T}_c$ ) divided by the sum of the mean time per cone ( $\bar{T}_c$ ) and mean travel time ( $\bar{T}_s$ ):

$$\text{Intake rate} = n(k)/T = (\bar{X} \cdot \bar{T}_c) / (\bar{T}_c + \bar{T}_s).$$

I used a 15–60× or a 40× telescope to observe crossbills. Events were timed to the nearest 1.0 s with a stopwatch. Foraging data for White-winged Crossbills are based on 4,559 foraging bouts and 44,315 seeds consumed. Those for Red Crossbills are based on 566 foraging bouts and 4,135 seeds consumed.

Crossbills may forage on more than one conifer species on a given day, and I present the average intake rate on all conifers weighted by the proportion of time spent foraging on each conifer (Benkman 1987a). I excluded balsam fir (*Abies balsamea*) because crossbills foraged on fir <10% of the time (Benkman 1987a). The estimated mass of fir kernel consumed is not a good estimate of caloric value because resin in the seed coat deters many seed predators (e.g. Smith 1970) and may reduce digestibility, especially of protein (Bryant and Kuropat 1980).

Once, White-winged Crossbills in early July foraged for spruce budworms (*Choristoneura fumiferana*) (Benkman 1987a), which were very abundant. The kernel intake rate data for this sample does not accurately portray actual intake rates and was excluded. For all other samples, conifer kernels made up most of the diet (see Martin et al. 1951, Newton 1972).

I gathered conifer cones to obtain samples for kernel mass. The cones were brought to Albany, New York, or Princeton, New Jersey, and stored for up to four months at 0–2°C before the kernels were removed from the cones. Kernels were separated from seed coats and dried (60–70°C) for 3–8 days. The kernels were weighed to the nearest 0.1–0.01 mg. Sample sizes were usually 10 kernels from each of 3–5 trees per site. If kernel mass was not obtained from a given site, I substituted mass of the appropriate species from the nearest site, or the average of the two closest sites.

Specific caloric and nutritive value of kernels varied little during the period when most of the data were gathered. However, between June and mid-August, specific caloric and nutritive kernel values increase (e.g. Dickmann and Kozlowski 1969), thus kernel value (see Appendix 1) was overestimated. This affected only three samples (6A, 16A, and 17A in Fig. 1).

**Breeding status of crossbill populations.**—Crossbills at a site were considered breeding if I found nests or young being fed. Populations were “marginal” if breeding was about to begin (males singing, birds paired, but no nests found) or had just ended (one or a few pairs feeding fledglings, and no sign of new nest starts). I classified populations as nonbreeding if I observed no breeding activities.

**Energy estimates.**—Estimates of the necessary intake rates, at monthly intervals, for the Egg Energy, Egg Protein, Nestling Energy, and Future Nestling Energy hypotheses are based mainly on formulas given by Robbins (1981, 1983) and Walsberg (1983). Each hypothesis has a minimum necessary intake rate called its respective threshold (see Appendix 1). The different thresholds are presented in terms of intake rate (mg of kernel [dry weight] consumed per second), but energy or protein intake is implicit. The methods and assumptions used to estimate the thresholds, and a sensitivity analysis are in Appendix 1.

RESULTS

**White-winged Crossbill.**—I found a positive relationship between the intake rates and the probability of breeding for White-winged Crossbills (Kendall’s rank correlation,  $P < 0.001$ , based on the proportion of samples breeding for the different intake-rate intervals  $\geq 0.1$  mg/s with  $\geq 3$  samples,  $n = 10$  intake-rate intervals; see Fig. 1), therefore the Null Hypothesis, that there was no such relationship, was rejected.

I evaluated the remaining hypotheses by how well their estimated thresholds separate breeding from nonbreeding populations. Breeding should have occurred when intake rates were above the predicted intake-rate threshold, but not when they were below. The Future Nestling Energy Threshold (FNET) provides nearly complete separation of breeding from nonbreeding populations (Fig. 1). Only 1 of 33 (3%) breeding samples was below FNET, and 0 of the 19 nonbreeding samples were above. The thresholds for the other hypotheses provide less complete separation (Fig. 1). Three (9%) breeding samples were below and three (16%) nonbreeding samples were above the Nestling Energy Threshold (NET). All breeding and nonbreeding samples were above both the Egg Energy Threshold (EET) and the Egg Protein Threshold (EPT).

Of the 8 “marginal” populations, 7 were near or on FNET. Only 2 were near NET and EET. Of the 8 “marginal,” 3 represent populations with increasing intake rates (1E, 16A, 17A) and nesting had just begun. The remaining 5 represent populations with declining intake rates,

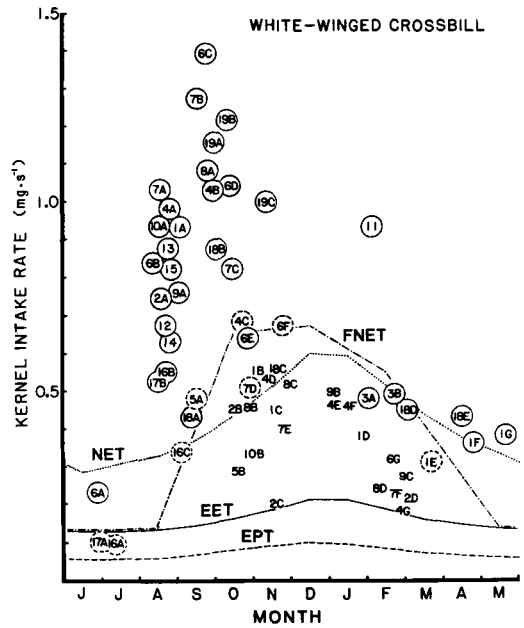


Fig. 1. The mean kernel intake rates of White-winged Crossbills throughout the year. Numbers in solid circles represent different breeding populations. Numbers in dashed circles represent populations just before nesting or at the end of caring for fledglings (i.e. “marginal” populations). Uncircled numbers represent different nonbreeding populations. Letters signify different dates. The lines represent the estimated thresholds, or minimum necessary intake rates, for breeding for each hypothesis: solid line = Egg Energy Threshold (EET); dashed line = Egg Protein Threshold (EPT); dotted line = Nestling Energy Threshold (NET); and dot-dash line = Future Nestling Energy Threshold (FNET).

and these populations were ceasing to nest. Thus, not only does FNET separate nearly all breeding from nonbreeding populations, but those that were either just beginning to nest or were ceasing to nest usually had intake rates near FNET.

**Red Crossbill.**—The patterns of breeding and intake rates for Red Crossbills were similar to those for White-winged Crossbills (Fig. 2). Data were insufficient, however, to estimate the Future Nestling Energy Threshold, so the two nestling-stage hypotheses cannot be compared.

DISCUSSION

It has long been known that crossbills breed when conifer seed is abundant (e.g. Newton

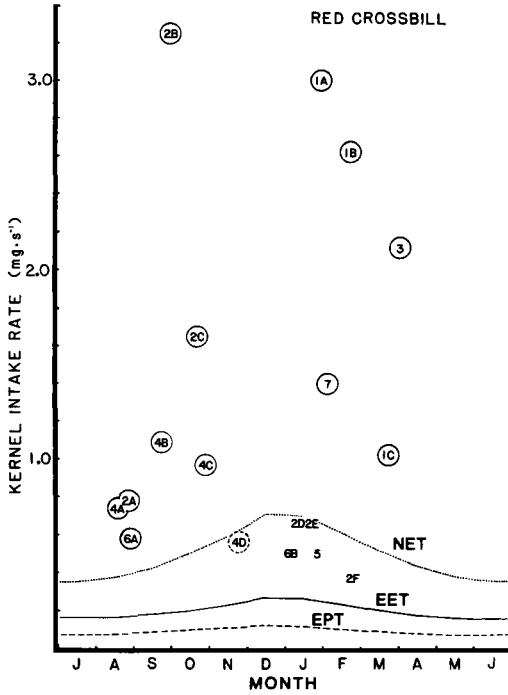


Fig. 2. The mean kernel intake rates of Red Crossbills throughout the year. The circles and lines as in Figure 1.

1972). It was not known, however, the extent to which crossbills, or any other avian species, breed when food is just adequate for successful nesting. The close correspondence between the predicted energy requirements for crossbills to breed successfully and their breeding behavior indicates that they are highly adapted for breeding whenever conifer seed availability is adequate for nesting. One caveat is that many assumptions were made to estimate the thresholds (Appendix 1). Consequently, how close nesting corresponds to meeting actual energy requirements must await more detailed measurements on individuals. Nevertheless, the thresholds are rather robust to the assumptions (Appendix 1) and the patterns are distinct enough to warrant general conclusions.

Crossbills timed nesting so that intake rates would be sufficient for the most energy-demanding nestling stage. At times crossbills initiated nesting as soon as the energy demands of nesting could be met, or ceased nesting when future nesting requirements would not be met. For example, when intake rates were increasing, nesting began before they were sufficient

for the nestling stage, possibly as soon as females could form eggs. Nesting was not attempted if intake rates were declining so that they would be insufficient for crossbills to raise nestlings. This implies that sufficient food for the nestling stage is the ultimate factor limiting crossbill reproduction.

I have emphasized the importance of conifer seeds to crossbill breeding behavior. During most of the year this is reasonable because conifer seeds make up most if not all of the crossbill's diet (Martin et al. 1951, Bailey et al. 1953, Austin 1968, Newton 1972, Benkman 1987a). In late June and early July, however, insect larvae may make up a major part of the diet (Benkman 1987a; Patuxent Stomach Card Files, pers. obs.). When insects are plentiful, crossbills could begin to nest in June or July before kernel intake rates are sufficient for egg formation. Nevertheless, because insects are consumed less frequently in August, nesting may be delayed until kernel intake rates would be sufficient for the nestling period. Thus, insect availability has only a minor and limited effect on the timing of crossbill breeding.

*Cause and effect.*—Crossbills may breed because they have high intake rates or, alternatively, the relatively high intake rates of breeding crossbills as compared with nonbreeding crossbills may arise because breeding individuals forage faster (e.g. Robinson 1986; but see Sullivan 1988). For instance, breeding individuals may reduce the amount of time spent on other behaviors such as scanning for predators. This effect was minimized by excluding long periods of scanning and by confining measurements to individuals that were considered, based on extensive observations in the laboratory, to be actively foraging. Moreover, several patterns indicate that intake rates were more influenced by cone-ripening phenology and cone structure than by crossbill breeding status.

First, intake rates of breeding and nonbreeding White-winged Crossbills that foraged on tamarack (*Larix laricina*) were related to the number of seeds in the cones (Fig. 3). When the two variables were ln-transformed, a significant linear correlation was found ( $r = 0.91$ ,  $n = 10$ ,  $P < 0.0005$ ). Furthermore, the patterns of intake rates of both species of crossbills in relation to cone-ripening phenology in the laboratory (nonbreeding crossbills; data in Benkman 1987b) were similar to those in the field (breeding and nonbreeding crossbills; data in Benkman 1987a,

this study). Second, even if it is to be argued that the differences between the intake rates of breeders and nonbreeders were due to different efforts, one must explain the variation between and within populations of breeders (e.g. White-winged Crossbills were feeding fledglings at 6C, 6D, 6E, and 6F [Fig. 1], yet intake rates varied tremendously). This variation in intake rates influenced the amount of time crossbills foraged. For example, when intake rates were twice that of NET, crossbills needed to forage <50% of the day even when feeding nestlings. In fact, adults in populations with high intake rates did not forage constantly. Only when eggs were laid and intake rates were near EET, or during the first five days after the eggs hatched and intake rates were near NET, did crossbills need to forage most of the day. Indeed, individuals feeding fledglings in populations with intake rates near NET (e.g. 4C and 6F in Fig. 1) appeared to forage nearly continuously during the day. I conclude that most of the differences in intake rates between breeding and nonbreeding crossbills were due to differences in seed availability, not breeding status.

*Resource predictability.*—Only one hypothesis tested (Future Nestling Energy Hypothesis) considered changes in intake rates, but it assumed that rates of change were constant during the different stages of cone ripening. Rates of change may at times be unpredictable (Benkman 1987a). This might influence the timing of nesting. For example, decreased predictability might restrict nesting to periods of more abundant food (see Turner 1982). Between June and September, intake rates increased consistently (Fig. 1, Appendix 2) because of seed and cone maturation (Benkman 1987a, b). During this time, intake rates and short-term estimates of rates of increase generally provide reliable information for intake rates several weeks into the future. Occasional insect (e.g. *Hylemya laricicola*) outbreaks can severely decimate developing seed crops and cause crossbills to cease nesting and to emigrate (pers. obs.). Between November and March, changes in profitability are more variable (Appendix 2, Benkman 1987a), and intake rates can decline unpredictably. At this time breeding was initiated usually when intake rates were well above that necessary for the nestling stage (i.e. Nestling Energy Threshold). White-winged Crossbills, however, began to nest in late January when their intake rates were below NET (3A in Fig. 1). In fact, these

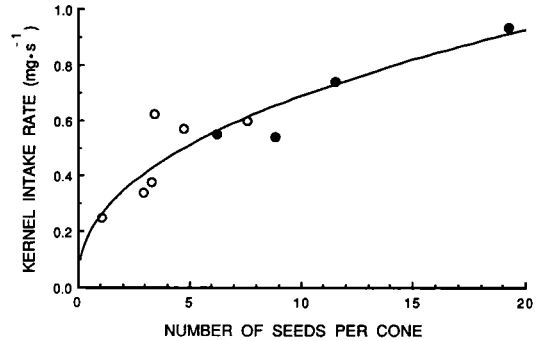


Fig. 3. The mean intake rates of White-winged Crossbills in relation to the mean number of seeds per tamarack cone. The mean number of seeds per cone is usually based on samples of 10–40 cones from each of 5–10 trees. The solid and open circles represent breeding and nonbreeding populations, respectively; the curve is the best fit logarithmic equation.

crossbills subsequently deserted their nests after a warm spell in March that caused white spruce (*Picea glauca*) cones to open and release most of their seeds. The average number of seeds per cone declined from 9.4 to 0.5. Crossbills nest frequently in late winter (Newton 1972, Benkman 1985), when food availability can decline unpredictably, causing nest failure. This indicates that resource unpredictability has little effect on the timing of crossbill reproduction.

*Proximate factors.*—There is presumably a complex of proximate factors that influence the timing of crossbill breeding. Proximate factors that might influence breeding behavior include large developing cone crops and day length. These two factors predict future intake rates and energy requirements, respectively. This combination of factors could provide a mechanism for cessation of nesting.

Tordoff and Dawson (1965) suggested that conifer cone crops provide a proximate stimulus for crossbill reproduction. Such a mechanism has been demonstrated for Pinyon Jays (*Gymnorhinus cyanocephalus*) (Ligon 1974, 1978). Crossbills search for large developing cone crops during summer (Benkman 1987a) and breed most frequently from late summer to early autumn when cone crops are maturing. As cone crops mature, intake rates increase (Benkman 1987a, b) and crossbills may then nest as soon as they are able to produce eggs. On the other hand, during most of the year cone crops are not maturing and crossbills do not breed unless

intake rates are much greater than that necessary for egg formation. Thus, maturing cone crops may be essential for early nesting when intake rates are low.

Increasing day length causes Red Crossbill testes to enlarge (Tordoff and Dawson 1965), and crossbills breed often in late winter and early spring (Newton 1972). Indeed, I have induced captive male Red Crossbills to sing daily in late winter and spring by providing them with conifer cones containing sufficient seed for weight gain. Such behavior was not induced during other times of the year even though similar quantities and types of cones were available. Nevertheless, the effect of increasing day length on reproductive condition is not as great for crossbills as in other species resident in the north-temperate zone (Tordoff and Dawson 1965, Immelmann 1971). This is expected because conditions favorable for nesting are not strictly correlated with day length. For example, temporal and geographic variation—both within and between conifer species in seed abundances, and in the ripening and shedding of seeds—reduce correlations between intake rates and day length (Benkman 1987a, b; see Benkman 1985 for a detailed discussion of the patterns of breeding in relation to conifer seed phenology).

Decreasing autumnal day length and declining intake rates may cause crossbills to terminate breeding when intake rates are above those necessary for the nestling stage. Indeed, termination of nesting when food is still plentiful is not unusual among north-temperate nesting passerines (e.g. Bryant 1975). At least two factors may select against breeding in late autumn. First, young fledged late in autumn may have lower survivorship than those fledged earlier (see Murton and Westwood 1977, Drent and Daan 1980, Daan and Dijkstra 1982). Crossbills fledged late may have reduced survivorship because they are less experienced foragers. For example, White-winged Crossbills fledged between August and October had intake rates in late November and December that were significantly less than, and only 76% of, those for adults (LSD multiple range test,  $P < 0.05$ ; unpubl. data). Second, although molting and nesting are not mutually exclusive for crossbills (Bailey et al. 1953, Kemper 1959, Newton 1972, pers. obs.), their combined energy demands restrict nesting to periods of even higher intake rates (Murton and Westwood 1977). Comple-

tion of the autumn molt before winter is probably critical in providing maximum insulation during cold winter months (see Dawson and Carey 1976). White-winged Crossbills usually molt between late August and December (Sealy et al. 1980, pers. obs.; see also Todd 1963). Molt is apparently less regular for Red Crossbills (Jollie 1953), although molting commonly occurs in autumn (Bailey et al. 1953, Newton 1972).

Rates of food intake may be a proximate cue for breeding. Although the mechanism by which intake rates might directly influence breeding behavior is unknown, crossbills behave as if they are very sensitive to variation in intake rates (Benkman 1987a, 1989). In fact, populations of White-winged Crossbills responded differently to nearly identical intake rates at the same time of the year. One (18A in Fig. 1), when intake rates increased, was just beginning to nest (females were caught with brood patches). In contrast, another (5A) with decreasing intake rates and nearly independent fledglings gave no indication of new nesting attempts. This suggests that crossbills are sensitive to both net intake and rates of change in intake.

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#### LITERATURE CITED

- ANKNEY, C. D., & D. D. MACINNES. 1978. Nutrient reserves and reproductive performance of female Lesser Snow Geese. *Auk* 95: 459-471.
- , & D. M. SCOTT. 1980. Changes in nutrient

- reserves and diet of breeding Brown-headed Cowbirds. *Auk* 97: 684-696.
- ARCESE, P., & J. N. M. SMITH. 1988. Effects of population density and supplemental food on reproduction in Song Sparrows. *J. Anim. Ecol.* 57: 119-136.
- AUSTIN, O. L. 1968. Life histories of North American cardinals, grosbeaks, buntings, towhees, finches, sparrows and allies, part 1. U.S. Nat. Mus. Bull. 237, Washington, D.C.
- BAILEY, A. M., R. J. NIEDRACH, & A. L. BAILY. 1953. The Red Crossbills of Colorado. *Publ. Denv. Mus. Nat. Hist.* 9: 1-64.
- BENKMAN, C. W. 1985. The foraging ecology of crossbills in eastern North America. Ph.D. dissertation, Albany, State University of New York.
- . 1987a. Food profitability and the foraging ecology of crossbills. *Ecol. Monogr.* 57: 251-267.
- . 1987b. Crossbill foraging behavior, bill structure, and patterns of food profitability. *Wilson Bull.* 99: 351-368.
- . 1989. Intake rate maximization and the foraging behaviour of crossbills. *Ornis Scandinavica* 20: 65-68.
- BRYANT, D. M. 1975. Breeding biology of House Martins *Delichon urbica* in relation to aerial insect abundance. *Ibis* 117: 180-216.
- , C. J. HAILS, & R. PRYS-JONES. 1985. Energy expenditure by free-living Dippers (*Cinclus cinclus*) in winter. *Condor* 87: 177-186.
- BRYANT, J. P., & P. J. KUROPAT. 1980. Selection of winter forage by subarctic browsing vertebrates: the role of plant chemistry. *Annu. Rev. Ecol. Syst.* 11: 261-285.
- DAAN, S., & C. DIJKSTRA. 1982. Annual cycles of breeding in the Kestrel: individual tuning to vole availability. *Ibis* 124: 389-390.
- DAWSON, W. R., & C. CAREY. 1976. Seasonal acclimatization to temperature in cardueline finches I. Insulative and metabolic adjustments. *J. Comp. Physiol.* 112: 317-333.
- , & H. B. TORDOFF. 1964. Relation of oxygen consumption to temperature in the Red and White-winged crossbills. *Auk* 81: 26-35.
- DICKMANN, D. I., & T. T. KOZLOWSKI. 1969. Seasonal changes in the macro- and micro-nutrient composition of ovulate strobili and seeds of *Pinus resinosa*. *Can. J. Bot.* 47: 1547-1554.
- DRENT, R. H., & S. DAAN. 1980. The prudent parent: energetic adjustments in avian breeding. *Ardea* 68: 225-252.
- ETTINGER, A. O., & J. R. KING. 1980. Time and energy budgets of the Willow Flycatcher (*Empidonax traillii*) during the breeding season. *Auk* 97: 533-546.
- FOGDEN, M. P. L., & P. M. FOGDEN. 1979. The role of fat and protein reserves in the annual cycle of the Grey-backed Camaroptera in Uganda (Aves: Sylviidae). *J. Zool.* 189: 233-258.
- GODFREY, W. E. 1966. The birds of Canada. Nat. Mus. Can. Bull. 203, Ottawa, Canada.
- GRISCOM, L. 1937. A monographic study of the Red Crossbill. *Proc. Boston Soc. Nat. Hist.* 41: 77-210.
- GRODZINSKI, W., & K. SAWICKA-KAPUSTA. 1970. Energy values of tree-seeds eaten by small mammals. *Oikos* 21: 52-58.
- GROTH, J. G. 1984. Vocalizations and morphology of the Red Crossbill (*Loxia curvirostra* L.) in the southern Appalachians. M.S. thesis, Blacksburg, Virginia Polytechnic Inst. State Univ.
- HOLMES, R. T., C. P. BLACK, & T. W. SHERRY. 1979. Comparative population bioenergetics of three insectivorous passerines in a deciduous forest. *Condor* 81: 9-20.
- IMMELMANN, K. 1971. Ecological aspects of periodic reproduction. Pp. 341-389 in *Avian biology*, vol. 1 (D. S. Farner and J. R. King, Eds.). New York, Academic Press.
- JOLLIE, M. 1953. Plumages, molt, and racial status of Red Crossbills in northern Idaho. *Condor* 55: 193-197.
- JONES, P. J. 1976. The utilization of calcareous grit by laying *Quelea quelea*. *Ibis* 118: 575-576.
- , & P. WARD. 1976. The level of reserve protein as the proximate factor controlling the timing of breeding and clutch-size in the Red-billed *Quelea quelea quelea*. *Ibis* 118: 547-574.
- , & ———. 1979. A physiological basis for colony desertion by Red-billed *Queleas (Quelea quelea)*. *J. Zool.* 189: 1-19.
- JONES, Q., & F. R. EARLE. 1966. Chemical analysis of seeds II: oil and protein content of 759 species. *Econ. Bot.* 20: 127-155.
- KEMPER, T. 1959. Notes on the breeding cycle of the Red Crossbill (*Loxia curvirostra*) in Montana. *Auk* 76: 181-189.
- KING, J. R. 1973. Energetics of reproduction. Pp. 78-107 in *Breeding biology of birds* (D. S. Farner, Ed.). Washington, D.C., Natl. Acad. Sci.
- KIRKWOOD, J. K. 1983. A limit to metabolizable energy intake in mammals and birds. *Comp. Biochem. Physiol.* 75A: 1-3.
- KRAPU, G. L. 1981. The role of nutrient reserves in Mallard reproduction. *Auk* 98: 29-38.
- KREMENTZ, D. G., & C. D. ANKNEY. 1986. Bioenergetics of egg production by female House Sparrows. *Auk* 103: 299-305.
- LACK, D. 1954. The natural regulation of animal numbers. London, Oxford Univ. Press.
- LIGON, J. D. 1974. Green cones of the piñon pine stimulate late summer breeding in the Piñon Jay. *Nature* 250: 80-82.
- . 1978. Reproductive interdependence of Piñon Jays and piñon pines. *Ecol. Monogr.* 48: 111-126.
- MARTIN, A. C., H. S. ZIM, & A. L. NELSON. 1951. American wildlife and plants. New York, Dover Publ.



- MARTIN, T. E. 1987. Food as a limit on breeding birds: a life-history perspective. *Annu. Rev. Ecol. Syst.* 18: 453-487.
- MASMAN, D., S. DAAN, & C. DIJKSTRA. 1988. Time allocation in the Kestrel (*Falco tinnunculus*), and the principle of energy minimization. *J. Anim. Ecol.* 57: 411-432.
- MCKEEVER, S. 1964. Food habits of the pine squirrel in northeastern California. *J. Wildl. Manage.* 28: 402-404.
- MONSON, G., & A. R. PHILLIPS. 1981. Annotated checklist of birds of Arizona, 2nd ed. Tucson, Univ. Arizona Press.
- MURTON, R. K., & N. J. WESTWOOD. 1977. Avian breeding cycles. Oxford, Clarendon Press.
- NETHERSOLE-THOMPSON, D. 1975. Pine Crossbills: a Scottish contribution. Berkhamsted, T. & A. D. Poyser.
- NEWTON, I. 1972. Finches. London, Collins.
- NILSSON, J., & H. G. SMITH. 1988. Effects of dispersal date on winter flock establishment and social dominance in Marsh Tits *Parus palustris*. *J. Anim. Ecol.* 57: 917-928.
- PALADINO, F. V., & J. R. KING. 1984. Thermoregulation and oxygen consumption during terrestrial locomotion by White-crowned Sparrows *Zonotrichia leucophrys gambelii*. *Physiol. Zool.* 57: 226-236.
- PAYNE, R. B. 1969. Breeding seasons and reproductive physiology of Tricolor and Red-winged blackbirds. *Univ. Calif. Publ. Zool.* 90: 1-115.
- PERRINS, C. 1970. The timing of birds' breeding seasons. *Ibis* 112: 242-255.
- RAVELING, D. 1979. The annual cycle of body composition of Canada Geese with special reference to control of reproduction. *Auk* 96: 234-252.
- RICKLEFS, R. E. 1974. Energetics of reproduction in birds. Pp. 152-292 in *Avian energetics* (R. A. Paynter, Ed.). Cambridge, Massachusetts, Publ. Nuttall Ornithol. Club 15.
- . 1983. Some considerations on the reproductive energetics of pelagic seabirds. *Stud. Avian Biol.* 8: 84-94.
- ROBBINS, C. T. 1981. Estimation of the relative protein cost of reproduction in birds. *Condor* 83: 177-179.
- . 1983. *Wildlife feeding and nutrition*. New York, Academic Press.
- ROBINSON, S. K. 1986. Three-speed foraging during the breeding cycle of Yellow-rumped Caciques (*Icterinae: Cacicus cela*). *Ecology* 67: 394-405.
- SEALY, S. G., D. A. SEXTON, & K. M. COLLINS. 1980. Observations of a White-winged Crossbill invasion of southeastern Manitoba. *Wilson Bull.* 92: 114-116.
- SEDINGER, J. S., & D. G. RAVELING. 1986. Timing of nesting by Canada Geese in relation to the phenology and availability of their food plants. *J. Anim. Ecol.* 55: 1083-1102.
- SIMKISS, K. 1975. Calcium and avian reproduction. *Symp. Zool. Soc. London* 35: 307-337.
- SMITH, C. C. 1970. The coevolution of pine squirrels (*Tamiasciurus*) and conifers. *Ecol. Monogr.* 40: 349-371.
- SMITH, J. N. M. 1978. Division of labour by Song Sparrows feeding fledged young. *Can. J. Zool.* 56: 187-191.
- SMITH, K. G. 1979. Common Redpolls using spruce seeds in northern Utah. *Wilson Bull.* 91: 621-623.
- SULLIVAN, K. A. 1988. Ontogeny of time budgets in Yellow-eyed Juncos: adaptation to ecological constraints. *Ecology* 69: 118-124.
- TODD, W. E. C. 1963. *Birds of the Labrador Peninsula and adjacent areas*. Toronto, Univ. Toronto Press.
- TORDOFF, H. B., & W. R. DAWSON. 1965. The influence of daylength on reproductive timing in the Red Crossbill. *Condor* 67: 416-422.
- TURCEK, F. J. 1959. Some observations on the gross-metabolism of the Coal Tit and Hawfinch on seed-diet under laboratory conditions. *Aquila* 46: 20-23.
- TURNER, A. K. 1982. Timing of laying by swallows (*Hirundo rustica*) and Sand Martins (*Riparia riparia*). *J. Anim. Ecol.* 51: 29-46.
- WALSBERG, G. E. 1983. Avian ecological energetics. Pp. 161-220 in *Avian biology*, vol. 7 (D. S. Farner, J. R. King, and K. C. Parkes, Eds.). New York, Academic Press.
- WIENS, J. A. 1984. Resource systems, populations, and communities. Pp. 397-436 in *A new ecology: novel approaches to interactive systems* (P. W. Price, C. N. Slobodchikoff, and W. S. Gaud, Eds.). New York, John Wiley & Sons, Inc.
- WILLSON, M. F., & J. C. HARMESON. 1973. Seed preferences and digestive efficiency of Cardinals and Song Sparrows. *Condor* 75: 225-234.
- YOM-TOV, Y., & R. HILBORN. 1981. Energetic constraints on clutch size and time of breeding in temperate zone birds. *Oecologia* 48: 234-243.

## APPENDIX 1. Estimation of thresholds for hypotheses for timing of reproduction and a sensitivity analysis.

The daily energy cost for the Egg Energy Threshold (EET) is:

$$((\text{BMR}_{\text{m}})[\text{TR}]N) + ((0.06)[7.3][\text{BMR}_{\text{d}}]D) + ((0.94)[3.5][\text{BMR}_{\text{d}}]D) + ((0.52)[\text{BMR}_{\text{d}}]24),$$

where  $\text{BMR}_{\text{m}}$  is basal metabolic rate of a sleeping female crossbill in kJ per hour ( $19.99X^{0.726}$ ;  $X$  is mass of the crossbill in kg [0.025 kg for White-winged and 0.033 kg for Red Crossbills (Sealy et al. 1980; pers. obs.)]), TR is thermostatic requirements ( $\text{TR} = 1.532 - 0.0423[\text{°C}]$ ), estimated from Dawson and Tordoff [1964] for average daily minimum temperature of each month, and  $N$  is number of non-daylight hours. 0.06 is the proportion of the day spent flying, estimated using an allometric equation given in Walsberg (eq. 11, 1983), 7.3 is the conversion factor used for the energetic cost of flying (Ettinger and King 1980),  $\text{BMR}_{\text{d}}$  is the hourly cost in kJ for a resting bird during the day ( $24.54X^{0.704}$ , where  $X$  was mass of a female crossbill in kg [Robbins 1983]), and  $D$  the number of daylight hours. 0.94 is the proportion of the day spent foraging, and 3.5 is the conversion factor for cost of foraging (between values for hopping [5; Holmes et al. 1979] and perching [2.1; Ettinger and King 1980; also see Yom-Tov and Hilborn 1981]). 0.52 is the conversion factor for the energetic cost when energetic demands for egg synthesis are maximal (Walsberg 1983), and this is multiplied by 24 because  $\text{BMR}_{\text{d}}$  is an hourly rate. All BMRs, except for cost of egg production itself, are multiplied by factors of 1.07 for White-winged and 1.19 for Red Crossbills (Dawson and Carey 1976), because crossbills have elevated BMRs relative to allometric predictions.

To estimate nightly thermostatic requirements, I used average daily minimum temperature for each month because it represents the most severe temperature likely to be experienced during a several-day period, such as that of egg formation. For White-winged Crossbills, I used average minimum monthly temperatures for the period 1950–1981 from weather stations near study areas in Laurentides Reserve (Mont Apica Weather Station) and Algonquin Provincial Park (Petawawa National Forestry Weather Station) and averaged monthly means for the two areas. Because all data on Red Crossbills were gathered in Algonquin Provincial Park or south, I used temperature data only from the Petawawa weather station. Monthly temperatures available for the study period did not differ much from long-term averages (pers. obs.). Average day length ( $D$ ; where  $24\text{ h} - D = N$ ) during a month is the time between sunrise and sunset for approximately the 15th of each month for  $46^{\circ}\text{N}$ . I assumed complete substitution of the heat increment of locomotion for thermostatic requirements (see Paladino and King 1984; but see Walsberg 1983, Bryant et al. 1985).

The necessary intake rate while foraging is solved by dividing daily energy cost by the number of hours available for foraging each day (i.e.  $0.94[D] - 0.33\text{ h}$ , where 0.33 h represents time foraging for grit). During egg (shell) formation crossbills must forage for calcium daily (Simkiss 1975) because conifer seeds are low in calcium (Dickmann and Kozłowski 1969, Robbins 1983). The females of many species modify their foraging behavior during the egg-laying period to include calcium (Jones 1976, Fogden and Fogden 1979, Turner 1982), and in one study it was estimated that <30 min was spent gathering grit (their presumed calcium source) while nesting (Turner 1982). Crossbills frequently consume grit (pers. obs.), and I assumed crossbills spent 20 min/day foraging for grit.

The daily energy cost for the Nestling Energy Threshold (NET) is:

$$((\text{BMR}_{\text{m}})[\text{TR}]N) + ((0.94)[3.5][\text{BMR}_{\text{m}}]D) + ((0.06)[7.3][\text{BMR}_{\text{m}}]D) + ((\text{BMR}_{\text{d}})[\text{TR}]N) + ((\text{BMR}_{\text{d}})[\text{TR}]D) + ((14.05M_{\text{g}}^{0.440})3),$$

where  $\text{BMR}_{\text{m}}$  is the basal metabolic rate, as before, but for the male (0.027 kg for White-winged Crossbills [Sealy et al. 1980] and 0.033 kg for Red Crossbills).  $14.05M_{\text{g}}^{0.440}$  is the average daily energy requirement in kJ/nestling (Walsberg 1983, eq. 6), with  $M_{\text{g}}$  being the mass (g) of the adult, and is multiplied by 3 because the clutch of crossbills is usually 3 eggs (e.g. Bailey et al. 1953, Newton 1972). I found the necessary energy intake rate to meet NET by dividing the above sum by the number of hours available for foraging per day.

I assumed that the brooding female had thermostatic requirements during the day as well as at night because she is relatively inactive on the nest. The nest provides insulation, but this is assumed to be countered by the extra energy required to keep the nestlings warm. I used the average daily temperature for each month to compute TR during daylight hours and the average daily minimum temperature, as before, to compute TR for nighttime. I used the average, rather than peak, energy expenditure per nestling because peak energy expenditures per nestling usually occur during mid- to late stages of the nestling period (cf. Drent and Daan 1980).

The Future Nestling Energy Threshold (FNET) is:

$$\text{FNET} = \text{NET} - (\text{IR}' - \text{NET}')/21\text{ days; where FNET} \geq \text{EET}.$$

NET is the Nestling Energy Threshold in mg of kernel per second,  $\text{IR}'$  is the change in intake rate in mg of kernel per second per day, and  $\text{NET}'$  is the change in NET per day (see Appendix 2). Twenty-one days was assumed to be the interval between the beginning of egg formation (7 days are needed to form and lay a three-egg clutch [e.g. Kremetz and Ankney 1986]) and hatching (a 14-day incubation period [incubation period is unknown for White-winged Crossbills but the range for Red Crossbills is 13–16 days; Newton 1972]).

I determined both the average increase in intake rates for White-winged Crossbills and the average rate of change in NET for three-to-four-month intervals (Appendix 2). The intervals I chose represent periods with consistent changes in intake rates and they correspond to different stages of cone ripening and seed shedding (Benkman 1987a, b).

Estimating necessary intake rates for the above thresholds requires two assumptions. First, based on values for other seed-eating birds (Turcek 1959, Willson and Harneson 1973), crossbills are assumed to assimilate 80% of the energy in a kernel. Second, caloric value for kernels is estimated to be 27 kJ/g dry weight, which is the average for kernels of several spruce (*Picea*) and larch (*Larix*) species (Grodzinski and Sawicka-Kapusta 1970, Smith 1979). In general, caloric values of conifer kernels differ little among species.

The threshold for the Egg Protein Hypothesis is determined by estimating the necessary amount of kernel that must be consumed to meet protein requirements for maintenance and egg production divided by time available for foraging. Daily protein maintenance requirements for birds are estimated to be 2.68 g protein ( $X^{0.725}$ ) $^{-1}\text{ day}^{-1}$ , and protein requirements for egg production by passerines are estimated to be 3.0 times maintenance requirements, assuming 55% production efficiency of eggs (Robbins 1981).  $X$  is mass (in kg) of female crossbill. Conifer kernels are assumed to consist of 23% protein (range 20.7–25.0, 3 conifers: 2 *Pinus*, 1 *Picea* [McKeever 1964, Jones and Earle 1966]) and number of hours spent foraging is as given for the energy estimates.

Foraging data were gathered on at least three size classes of Red Crossbill, with average body weights ranging from 26–35.5 g (Monson and Phillips 1981). Most of the data, however, were gathered from the largest size class (see Benkman 1987a) and the thresholds were estimated for the largest size class. One data point of a non-large-size class was near the estimated thresholds, but accounting for reduced energy demands would not alter the relation of this point to the thresholds.

*Sensitivity analyses.*—Assumptions of the thresholds thought most likely in error were subjected to sensitivity analyses. The thresholds were not very sensitive to variation in proportion of day spent flying. For example, a doubling of flight time to 12% of the day increased NET 8% in January and 9% in July for White-winged Crossbills, whereas halving flight time to 3% of the day reduced NET 5% in January and 6% in July. Similar modifications in the assumptions resulted in slightly larger changes in the Egg Energy and Egg Protein thresholds. For example, the Egg Energy Threshold was increased by 14% in January if flight time was increased to 12% of the day.

The assumption that 94% of the day was spent foraging assumes that all non-flight time was spent foraging. This is an extreme value, but it seems reasonable to assume that crossbills could maintain foraging most of the 1–5 days concerned for each of the thresholds when food intake

## APPENDIX 1. Continued.

rates are most limiting. Moreover, the energetic cost for crossbills to forage is probably around 3.5 (BMR) which is less than both the maximum sustained working level of approximately 4 (BMR) found for many bird species caring for nestlings (Drent and Daan 1980) and the maximal intake rates estimated for birds (4-5 [BMR]; Kirkwood 1983). Consequently, foraging time may be limited most by day length (see Masman et al. 1988). Nonetheless, if instead we assume that 4 or 9% of the day was spent loafing (resting, preening), then the NET would be increased 4% and 9%, respectively, in January, and 4% and 8%, respectively, in July.

If we assumed that the heat increment from locomotion did not substitute for thermostatic requirements, then the estimated intake rate for the NET in January was increased 4%. The thresholds were not affected in summer because daily temperatures were in the thermoneutral zone.

It was assumed that females continuously brood nestlings. This may not be true during the warmer months (pers. obs.). If, for example, in July the female is absent from the nest for 1 h/day and spends 94% of that time foraging, the NET would be lowered 5%. A 2-h absence would lower the threshold 9%. If the female did not brood the nestlings, such as late in the nestling stage, and assuming thermostatic requirements for the nestlings (as for resting adults) and peak, rather than average, expenditure per nestling, then NET would be reduced by 8% in January and 30% in July.

The NET is most sensitive to the number of nestlings. For example, if the number of nestlings is reduced from 3 to 2, then the threshold is reduced 15% in January and 17% in July. Nevertheless, relatively major changes in the variables most likely to be in error have a relatively slight impact on the estimated thresholds; possible errors suggest a tendency for underestimation of the thresholds in winter and overestimation of the thresholds in summer.

APPENDIX 2. The slopes of the regression equations for changes in both intake rates and Nestling Energy Threshold (NET) of White-winged Crossbills during different periods of the year (data in Fig. 1). \* =  $P < 0.05$ , \*\* =  $P < 0.01$ , \*\*\* =  $P < 0.0001$ .

	Slope* ( $\times 10^{-3}$ )	<i>n</i>	<i>r</i> <sup>2</sup>
June to Sept.			
Intake rate	10.07***	24	0.52
NET	0.93*	4	0.97
Sept. to Nov.			
Intake rate	-7.87**	28	0.33
NET	2.30*	3	1.00
Nov. to Jan.			
Intake rate	-1.93	13	0.09
NET	1.30	3	0.66
Jan. to Mar.			
Intake rate	-3.94	14	0.17
NET	-2.58**	3	1.00
Mar. to May			
Intake rate	0.96	4	0.26
NET	-1.76	3	0.98

\*  $\text{mg} \cdot \text{s}^{-1} \cdot \text{day}^{-1}$ .