Sowls for helpful comments on earlier drafts of this manuscript. Funding was provided in part by National Science Foundation grant BNS-8606548 and by smaller grants from the Nongame Branch of the Arizona Game and Fish Department, Raptor Education Foundation, Arizona Wildlife Foundation, Tucson Audubon Society, Southwest Hawk Watch, Arizona Falconers Association, and a James R. Silliman Memorial Grant. The Arizona Cooperative Fish and Wildlife Research Unit generously allowed the use of its facilities and equipment. We especially thank M. McKenzie for logistic support during the study.

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# Breeding Opportunities, Foraging Rates, and Parental Care in White-winged Crossbills

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There has been much research on factors that promote interspecific differences in the relative contribution of the sexes to parental care (Trivers 1972, Maynard Smith 1977, Ridley 1978, Wells 1981), but there has been less work on intraspecific variation in

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parental care (e.g. Keenleyside 1983, Beissinger and Snyder 1987). I demonstrate that (1) when White-winged Crossbills (Loxia leucoptera) have immediate breeding opportunities and energy intake rates are sufficient to permit one parent to care for the fledglings, only the male feeds them (presumably because the female deserts and renests), but (2) when crossbills have no immediate breeding opportunities and lower intake rates, both parents care for the fledglings.

TABLE 1. Number of individuals observed to regurgitate food boluses to fledglings.

| Nesting attempts ($n$) | Individuals regurgitating | |
| --- | --- | --- |
| | Male ($n$) | Female ($n$) |
| 1 | 30 | 22 |
| >1, early[a] | 21 | 1 |
| >1, late | 8 | 7 |

[a] Early refers to the first group of fledglings observed at the site, and late refers to those observed on visits 18–61 days later.

I studied White-winged Crossbills from September 1982 to September 1987 in coniferous forests in Vermont and Maine, USA, and in Manitoba, Ontario, Quebec, and New Brunswick, Canada. I observed adults feeding fledglings for periods of >2 months at four study sites and for periods of <1 month at four study sites. Because there is about a 40-day interval between the start of egg laying and fledging of young in crossbills (Newton 1972), I considered populations where adults fed fledglings for >2 months to consist of individuals *possibly* raising two or more broods. For populations where adults fed fledglings for periods of <1 month, I assumed that no individuals bred successfully more than once.

Crossbills feed almost exclusively on conifer seeds and regurgitate boluses of seed kernels to their young (Bailey et al. 1953, Newton 1972). To determine the relative amounts of parental care given by each sex, I recorded observations of crossbills regurgitating food boluses to fledglings. Most of my observations were of young that followed adults from tree to tree. Crossbills are sexually dimorphic (Newton 1972) and at one site many of the adults were color-banded. I distinguished unbanded individuals by plumage differences, offspring age, and by location. I did not follow individual crossbills for extended periods and I usually observed only one regurgitation from a given adult. I compared the number of males and females that regurgitated boluses to fledglings, and treated all regurgitations by an individual as a single observation.

*Intake rate* was defined as the mass of dry kernel consumed per unit time foraging. I measured intake rates as the number of seeds eaten during timed intervals that included both time spent foraging on cones and traveling between cones. I determined the mean dry mass of the seed kernels to the nearest 0.01 mg (see Benkman 1987, 1989 for more details on methods).

The *net intake rate* is the gross intake rate of adult crossbills minus the necessary intake rate to meet the daily energy demands of four adults (see Benkman 1985). This value was chosen because it provides a measure of the ability of one individual to provide enough energy for itself and three fledglings. Crossbills generally lay three eggs per nest (Newton 1972)
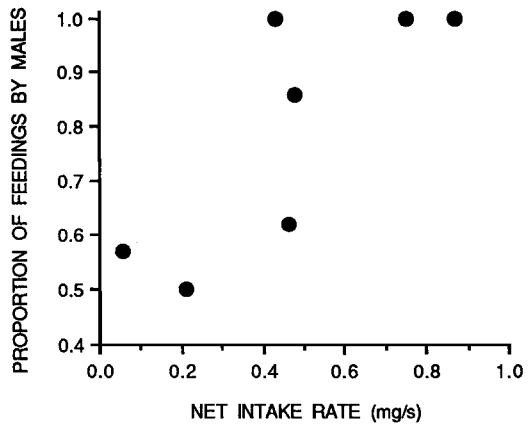


Fig. 1. The proportion of regurgitations by males in relation to net intake rate. Each point represents data from 1 visit to 1 site (6 total sites) and regurgitations from a minimum of 5 individuals ($\bar{x} = 11$ birds, SD = 10.9). Foraging data represent a range from 56 foraging bouts (797 seeds) to 452 bouts (2,933 seeds).

and often have three fledglings (pers. obs.). I assumed fledglings have daily energy demands equal to adults, because crossbill fledglings, although growing, have only ca. 90% of the mass of adults (pers. obs.). To estimate the necessary kernel intake rates to meet the daily energy demands of one adult crossbill and three fledglings, I used standard allometric equations (Walsberg 1983). Assumptions concerning time budget, conversion factors for different activities, thermostatic requirements, specific energy values of seed kernels, and assimilation efficiencies are given in Benkman (1985).

Females were as likely as males to feed fledglings when nesting occurred only once, or during the late nesting attempts when nesting occurred more than once (Table 1; $P > 0.5$, $\chi^2 = 0.07$, df = 1; in neither case did the ratio of male to female regurgitations differ from 1:1 [Chi-square tests, $P > 0.1$]), but females rarely fed fledglings during the first nesting attempt when further nesting attempts were possible (Table 1). The relative number of males to females that fed fledglings differed between early nesting attempts and late nesting attempts, when nesting more than once ($P < 0.005$, $\chi^2 = 8.4$, df = 1) and between early nesting attempts and when nesting only once ($P < 0.01$, $\chi^2 = 7.4$, df = 1).

There was a significant positive correlation between the proportion of feedings of fledglings by males and net intake rate (Fig. 1, $r = 0.80$, $P = 0.03$, df = 5). When the net intake rate was less than ca. 0.4 mg/s, both males and females fed the fledglings. Only males fed the fledglings when net intake rates were >0.5 mg/s. When net intake rates were between 0.4 and 0.5 mg/s, females fed fledglings at two of three sites.

Overall, when (gross) intake rates were high (mean intake rate = 1.14 mg/s, SE = 0.11, $n$ = 4 populations) females rarely fed fledglings and crossbills continued to nest. When intake rates were lower, such as near the end of extended nesting periods (mean intake rate = 0.84 mg/s, SE = 0.09, $n$ = 5 populations) or when individual crossbills nested successfully once (mean intake rate = 0.88 mg/s, SE = 0.08, $n$ = 3 populations), both males and females fed fledglings. This pattern of parental care where females desert fledglings from early nests (but not late nests) occurs in other passerine species (Oring 1982), including other cardueline species (Newton 1972).

These data are consistent with the hypothesis that female crossbills desert their fledglings to renest, but direct evidence of females renesting was not obtained. Desertion to renest has been reported in other species (e.g. Grant and Grant 1987). Nevertheless, if female crossbills did not attempt to renest, there is no compelling reason why females rather than males should consistently desert. On the other hand, if there is renesting, then the female instead of the male should desert. This follows because only females build nests, females alone are capable of incubating eggs in crossbills (Newton 1972), and deserting females should be able to find another mate, because males generally outnumber females (Newton 1972, pers. obs.). For the same reason, males are unlikely to find another mate.

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# An Effective Anti-estrogen for Feral Birds

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Estrogens in the plasma of both sexes of birds correlate with a variety of reproductive and behavioral functions (e.g. Lehrman and Brody 1957, Hinde 1965, Wingfield and Farner 1978, Moore 1983, Pröve 1983, Hutchison et al. 1984, Marler et al. 1988). To elucidate the functional role of estrogens (in particular, 17$\beta$-estradiol), endogenous levels in both sexes can be supplemented through estradiol-filled silastic implants. Conversely, estradiol titers can be reduced by gonadectomy, although this procedure does not completely suppress estradiol levels in males (Marler et al. 1988).

Anti-estrogenic drugs are an alternative method to eliminate the effects of estradiol in both sexes. I suppressed estradiol-induced oviduct growth in non-

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