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From Forest Nursery Notes, Winter 2012

**244. © Patterns of exploitation of annually varying *Pinus sylvestris* cone crops by seed-eaters of differing dispersal ability.** Summers, R. W. Ecography 34:723-728. 2011.

Research

**Ecography 34: 723–728, 2011**
doi: 10.1111/j.1600-0587.2010.06498.x
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Subject Editor: Erik Matthysen. Accepted 29 October 2010

# Patterns of exploitation of annually varying *Pinus sylvestris* cone crops by seed-eaters of differing dispersal ability

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Food consumption by animals depends on functional and numerical responses, and particularly the latter for food specialists. Some birds and mammals are conifer seed specialists and are likely to exploit the varying seed production in different ways according to differences in dispersal capabilities. This in turn may determine which species is more likely to affect the evolution of cone morphology. This study examined the inter-annual pattern of foraging on Scots pine *Pinus sylvestris* cones by crossbills *Loxia* spp. (highly dispersive) and red squirrels *Sciurus vulgaris* (weakly dispersive) over 16 yr in three stands of ancient native pines at Abernethy Forest in Highland Scotland. There were synchronous annual variations in cone production across the stands, and an indication of a three-year cycle. The number of cones taken by crossbills was correlated with cone production, indicating a numerical response by the birds, up to a certain limit of cone production. By contrast, the number of cones taken by red squirrels was not correlated with cone production. Rather, the percentage of cones taken by squirrels was high when cone production was low, and low when production was high. There was also a long-term decline in the number of cones taken by squirrels, suggesting a decline in squirrel numbers. Although a high percentage of cones was removed from some cohorts on some trees, either by crossbills (maximum of 94.8%) or red squirrels (100%), the mean percentage of cones taken by crossbills from trees was small, ranging from 3.7 to 17.1% across all cone cohorts. For red squirrels, mean values ranged from 0.1 to 46.1% across all cohorts. However, given that crossbills can track changes in cone production by rapid numerical responses (i.e. through migration), and take a larger percentage of cones from cohorts of high production (10.7%), compared with red squirrels (3.6%), crossbills may be more important in driving the evolution of cone morphology because future trees are more likely to come from cohorts of high cone production.

The impact that animals have on their food supply is dependent on both functional and numerical responses (Holling 1959). For food specialists, the numerical response is likely to be more important. One such group, including insects, birds and mammals, are those that specialise on conifer seeds prior to seed dispersal (Janzen 1971, Smith and Balda 1979). Seeds are extracted and consumed when still held between the scales of the woody cones (pre-dispersal seed consumption) but then taken by many non-specialist feeders on the forest floor after the seeds have been shed from the cones (post-dispersal seed consumption). During the period of seed maturation, the seeds are least accessible because the scales of the cones are closed. In European boreal forests, the main seed-eaters prior to seed dispersal are moth larvae (Lepidoptera), squirrels (Sciuridae), crossbills *Loxia* spp. (Fringillidae) and woodpeckers (Picidae) (Gibb 1958, Cramp and Perrins 1994).

Conifers are one of the many groups of plants that periodically produce large amounts of seed synchronously across wide areas (Koenig and Knops 1998), with varying intervals between the peaks in seed production (Gordon and Faulkner 1992). Although variation in pine seed production has been found to be correlated with the weather (Kelly and Sork 2002, Flade and Schwarz 2004), this is believed to be a proximate factor. Rather, the ultimate cause of peaks in seed production may be to enhance pollination efficiency in wind-pollinated species, or satiate seed-eating animals (Janzen 1971, Kelly and Sork 2002). In such years, the seed-eaters consume a smaller proportion of the seeds, some of which are therefore available to produce future generations of trees. Other potential ultimate causes have been suggested, but the above two have most support (Kelly 1994).

Given the varying seed production by conifers (Herrera et al. 1998, Koenig and Knops 1998, Broome et al. 2007), one might expect highly dispersive groups such as birds and perhaps insects to be good at exploiting such resources by migrating to areas of food abundance. By contrast, animals with weaker dispersal would be able to make only a lesser numerical response, largely through reproduction. In this study, I examined the exploitation of Scots pine cones by crossbills (highly dispersive) and squirrels (weakly dispersive). I expected crossbills to respond numerically to the