trait is expressed in males[12]. Similarly, if male tail length differs among bird populations, females could have a preference for long tails that varies in accordance with the expression of the male trait. But female preferences may not simply be for males with the longest tails; rather, they may be for males with fast-growing ornaments, or for males that can maintain the ornaments over a period of time.

References

1 Darwin, C. (1871) *The Descent of Man, and Selection in Relation to Sex*, John Murray
2 Andersson, M. (1982) *Nature* 299, 818–820
3 Searcy, W.A. (1982) *Annu. Rev. Ecol. Syst.* 13, 57–86
4 Barnard, P. *Biol. J. Linn. Soc.* 40 (in press)
5 Fisher, R.A. (1930) *The Genetical Theory of Natural Selection*, Clarendon Press
6 Lande, R. (1981) *Proc. Natl Acad. Sci. USA* 78, 3712–3725
7 Lande, R. (1982) *Evolution* 30, 253–269
8 Alatalo, R. V., Högland, J. and Lundberg, A. (1988) *Biol. J. Linn. Soc.* 34, 363–374
9 Harvey, P.H. and May, R.M. (1989) *Nature* 337, 508–509
10 Craig, A.J.F.K. (1989) *S. Afr. J. Sci.* 85, 523–524
11 Arnold, S.J (1985) *Experientia* 41, 1296–1310
12 Houde, A.E. and Endler, J.A. (1990) *Science* 231, 1405–1408
13 Verheyen, R. (1956) *Gerfaut* 46, 65–74
14 Smith, L.H. (1965) *Science* 147, 510–513
15 Smith, L.H. (1982) *Aust. J. Wildl. Res.* 9, 311–330
16 Andersson, S. (1989) *Behav. Ecol. Sociobiol.* 25, 403–410
17 Barnard, P. (1989) *Ostrich* 60, 103–117
18 Møller, A.P. (1988) *Nature* 332, 640–642
19 Barnard, P. (1990) *Anim. Behav.* 39, 652–656

The Decline of the Newfoundland Crossbill

Stuart L. Pimm

An endemic subspecies of the red crossbill, *Loxia curvirostra percna*, underwent a dramatic decline on the island of Newfoundland (Canada) in the early 1970s. Its numbers have been reduced to the point where its extinction is quite probable, although it may survive on some nearby smaller islands. In contrast, the white-winged crossbill (*Loxia leucoptera*) appears to have maintained its numbers. Almost certainly, the cause of the red crossbill's decline was the introduction of the red squirrel (*Tamiasciurus hudsonicus*) to Newfoundland.

The introduction of alien species as the cause of the demise of native species is all too familiar (see Refs 1 and 2). What is special about Benkman's work on this decline[3], and on crossbills in general[4–6], is that it provides insight into why island species are so vulnerable to introduced species.

The circumstantial evidence implicating the red squirrel in the decline of the red crossbill is quite strong. First, the timing fits. Red squirrels were introduced to Newfoundland in 1963 and 1964 by the Newfoundland Wildlife Service, to provide prey for the native pine marten (*Martes americana*) which had been trapped to low numbers. The squirrels quickly achieved high densities, and are now perhaps twice as dense in forests on Newfoundland as they are on the mainland. Second, the current distributions are non-overlapping; the squirrels have not reached the small offshore islands, the only places where the crossbills are now known to occur. Third, the mechanism of competition for food seems plausible. Red crossbills once occupied, and red squirrels now occupy, black spruce (*Picea mariana*) forests in Newfoundland. In contrast, the white-winged crossbill feeds more on white spruce (*Picea glauca*) and tamarack (*Larix laricina*). Interestingly, red crossbills in mainland areas typically feed on various pines, rather than spruces, but pines are relatively uncommon in Newfoundland.

While examples of introduced species causing extinctions of native species are common, examples providing convincing evidence for competition (particularly competition between species from such different taxa) are few[1,7]. Certainly, the evidence for competitive replacement that Benkman presents is indirect, as it almost certainly must be for changes on such a large spatial scale. (The evidence does not preclude a mechanism involving a shared predator or parasite; conceivably, the squirrel and the crossbill could share a pathogen to which the squirrels but not the crossbills are relatively immune.)

Island communities are often damaged by introduced species[1]. There are two main reasons for this. First, as is well known, they are typically species poor, and so may be more likely to be invaded than species-rich communities. The more introduced species, the more likely that one of those species will do harm. Second, and more controversially, the chances that any one introduced species will cause marked changes in the abundance of native species is greater on islands than elsewhere[1,8]. Islands often lack generalized herbivores or carnivores, which when introduced without their respective predators and diseases may be expected to wreak the same havoc on lower trophic levels as they would in continental communities if those predators and diseases were removed. Also, island herbivores and carnivores might be more trophically specialized, and so more vulnerable to the loss of their food resources, than trophically more generalized mainland species that can switch to other resources. This is a difficult idea to test, but Benkman's results provide a compelling explanation of how the crossbills might have evolved to be vulnerable.

Benkman argues that the historical absence of red squirrels from Newfoundland has had a direct evolutionary effect on the cones of the black spruce, and a secondary evolutionary effect on the crossbills. The key morphological variable is the thickness of the cone scales, because this correlates with the time required by crossbills to remove seeds from closed cones. Benkman suspected that the black spruce cone scales would be thinner on Newfoundland, because of the absence of the squirrels. If so, seeds in the closed cones would be more accessible to crossbills on Newfoundland than on the mainland.

Stuart Pimm is at the Dept of Zoology and Graduate Program in Ecology, The University of Tennessee, Knoxville, TN 37996, USA, and currently at The Centre for Population Biology, Imperial College at Silwood Park, UK.

Benkman measured the cone scales and found that they are about 15% thinner on Newfoundland than on the mainland. This probably explains why the squirrels are able to attain higher densities on the island than on the mainland: they are more effective competitors on the island because their food is more accessible. In one comparison, red squirrels were able to harvest 64–96% of the cones of black spruce by early October on Newfoundland, but only removed 19% of the cones at a mainland site in Ontario.

What should be the consequences of the different cones for the crossbills? The subspecies of red crossbill on the adjacent mainland, *Loxia curvirostra bendirei*, feeds on the large-coned pines *Pinus strobus* and *P. resinosa*; these cones are very much larger than the spruce cones. Benkman found that on the mainland, the relatively small-billed white-winged crossbill is more efficient at exploiting spruce than pine, and the relatively large-billed red crossbill more efficient at exploiting pine than spruce. Given these arguments, why should the Newfoundland red crossbill have a *larger* bill than the mainland form when it is exploiting much *smaller* cones? The answers have to do with the way cone crops fluctuate.

Cone crops vary greatly from year to year; in some years there are few, if any, seeds available over large areas. For the birds, food availability is also determined by whether the cones are open or closed. Benkman showed that open cones provide the highest rate of energy intake (as one would expect). In North America, closed, large pine cones are inaccessible for all but the red crossbills with the largest bills. Although the smaller-billed white-winged crossbills can extract seeds from open black spruce cones very quickly indeed, closed cones are more accessible to the larger-billed mainland red crossbills. White-winged crossbills gain little energy from closed black spruce cones. Because the Newfoundland red crossbill has an even larger bill, it could probably exploit closed black spruce cones quite efficiently.

These patterns suggest two alternative strategies. Birds could either seek out areas of open cones, which are spatially and temporally very variable, or take both open and closed cones in one area. The former strategy requires mobility, the latter a larger bill. On mainlands, crossbills change from one species of conifer to another as the species open their cones at different times of year. Conifers frequently occur in almost monotypic stands, however, and this often leaves the birds only the option of moving out of one area and seeking others. Moreover, cone crops sometimes fail and, worse, fail over large geographical regions. Crossbills are well known as irruptive species, appearing in large numbers well outside their normal range when cone crops fail, in both North America and Europe. The synchronous failures in cone crops over large geographical areas and the inaccessibility of closed pine cones means that there is no alternative to movement. White-winged crossbills of Newfoundland adopt the same strategy, moving off the island when seeds are inaccessible or in short supply.

In Newfoundland, white spruce and tamarack cone crops fluctuate greatly from year to year, and often fail in the same years, but black spruce cone crops rarely fail and, moreover, the cones hold seeds all year round. This does not help the white-winged crossbill, which cannot open the closed cones and so feeds on black spruce only from winter to early summer. In contrast, the much larger-billed Newfoundland red crossbill was probably able to exploit these seeds throughout the year.

Why was the Newfoundland red crossbill unable to exploit black spruce cones on the mainland? Benkman speculates that it could be due to the thicker cone scales of black spruce there; and, of course, there are squirrels there too.

According to these arguments, island-resident crossbills should have larger bills than comparable mainland crossbills. Interestingly, there are several other examples of this. On the Caribbean island of Hispaniola, there is a very isolated population of white-winged crossbills with larger bills than their more northerly counterparts. This island population feeds on an endemic pine and, indeed, the bill of this subspecies is even larger than that of the subspecies of red crossbill that feeds on the morphologically most similar pine on the mainland. For red crossbills there are unusually large-billed populations on Corsica and Cyprus in the Mediterranean. The pattern of larger bills on islands does not always hold, however. There are unusually small-billed populations on Luzon in the Philippines, and Majorca in the Mediterranean. The endemic Scottish crossbill (*Loxia scotica*) feeds on pine and has a larger bill than the European red crossbill (*L. curvirostra*) (which feeds mainly on spruce), but a smaller bill than the parrot crossbill (*L. pytyopsittacus*), which also feeds on pine. Squirrels are absent from all of these islands except Britain.

How do squirrels and crossbills coexist on mainlands and how do they coexist in Britain? It is always easy to dream up answers to such questions and always hard to answer the questions experimentally. Squirrels are clearly strong competitors, capable of depriving the crossbills when seeds are scarce. Crossbills are much more mobile, however, and are able to move quickly into areas of high seed density, removing seeds before squirrel numbers can increase to levels where they deplete the seeds. Possibly, squirrels and crossbills coexist because the birds take the spatially and temporally rare 'highs' and the squirrels the more common 'lows' in resource abundances. Britain may be much more like a continent than an island in this respect. Scottish crossbills occur across Scotland, which has a very mild west coast but a more continental east coast, so the birds may be taking geographically unpredictable 'highs'. Other islands may lack such spatial and temporal heterogeneity, and so resident, endemic crossbills will only be possible in the absence of squirrels.

Unlike mainland crossbills, the Newfoundland red crossbill did not, and perhaps could not, move when the food supply failed. Rather, it was more trophically specialized; it was adapted to the locally predictable, thin-scaled Newfoundland populations of black spruce. The moral is that the Newfoundland red crossbill was particularly vulnerable because it was critically dependent on one resource.

Acknowledgements

I thank C. Benkman for comments, and J.H. Lawton for hospitality.

References

1 Pimm, S.L. (1987) *Trends Ecol. Evol.* 2, 106–108
2 Pimm, S.L. (1987) *Trends Ecol. Evol.* 2, 293–295
3 Benkman, C.W. (1989) *Evolution* 43, 1324–1330
4 Benkman, C.W. (1987) *Wilson Bull.* 99, 351–368
5 Benkman, C.W. (1987) *Ecol. Monogr.* 57, 251–267
6 Benkman, C.W. (1988) *Auk* 105, 715–719
7 Simberloff, D. (1981) in *Biotic Crises in Ecological and Evolutionary Time* (Nitecki, H., ed.), pp. 53–81, Academic Press
8 Ebenhard, T. (1988) *Swed. Wildl. Res. Viltrevy* 13(4), 1–107