The ecology and evolution of crossbills *Loxia* spp: the need for a fresh look and an international research programme

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In this paper, we review how recent studies on crossbills *Loxia* spp. have dramatically changed our understanding of crossbill diversity in Europe. Instead of four separate species, each well-defined by ecology, morphology and distribution, we now can distinguish a larger number of populations that differ in vocalisations, but of which we know very little about their ecology, morphology, and (overlap in) distribution. Genetic differences between subspecies and even species are reported to be absent. We summarise the latest results as they were presented at a workshop at the 4th EOU Conference. Progress is being made to unravel some aspects of the ecology and evolution of crossbills, but new surprises keep arising. For instance, Mediterranean populations of the common crossbill are vocally more like Scottish and parrot crossbills than like common crossbills of northern Europe. We suggest and discuss avenues for further research by professionals and amateurs alike. Most importantly, the vocal identity of each individual or population should be taken into account when testing for geographical, ecological, morphological, physiological or genetic differentiation.
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From relative stability to full blown confusion

Crossbills *Loxia* spp. have always fascinated people, whether they are birdwatchers or not. With their special bill with crossed tips they can remove the seeds from closed cones of conifers as no other bird can. In some years, they appear in large numbers at locations where they normally are not found, such as treeless islands and coasts. Here they can be very tame, and many a person must have wondered what such funny birds were doing in their gardens or fields.

Their unusual feeding habits and irruptive migrations have stimulated many studies, which gradually painted a picture of specialised birds that lived by the rhythm of their food resource. When seeds became available in great numbers, they would breed, even if this was in mid-winter with the forest under full snow cover. Even individuals in juvenile plumage would join the breeding population (Berthold & Gwinner 1972, Jardine 1994). In years that local cone crops failed, all the crossbills would leave the area in search of better feeding sites. If the crop failed over a large area, millions of crossbills would be on the move. Stragglers from the Russian boreal forest have been recorded as far as Greenland, Iceland and the Canary Islands (Cramp & Perrins 1994). The early bird taxonomists realised that three clearly different crossbills could be distinguished in Europe: the two-barred crossbill *Loxia leucoptera* with a rather small bill, the intermediate-billed common crossbill *L. curvirostra*, and the large-billed parrot crossbill *L. pytyopsittacus*. Observations of feeding birds and their general distribution indicated that two-barred crossbills were specialised principally in feeding on the seeds of Siberian larch *Larix sibirica* which are protected by relatively weak cone scales, common crossbills attacked the cones of spruce *Picea* spp., which have fairly strong scales, and parrot crossbills fed mostly on the seeds of Scots pine *Pinus sylvestris*, which are well defended by strong scales (Lack 1944). The common crossbills in the south of Europe were an exception to this pattern, because they fed on pines, not on spruce, and were also characterised by rather large bills (Cramp & Perrins 1994). Some isolated populations were recognised as separate subspecies, albeit sometimes by only slight differences in biometry and colouration (Griscom 1937).

This picture was stable for several decades, and most papers on crossbills would focus on different aspects of their biology (moult, migration, breeding, etc.). A relatively recent change was the acceptance of the Scottish crossbill *L. scotica* as a fourth species, and therefore Great Britain's only endemic bird species, based on the co-occurrence of Scottish and common crossbills apparently without any hybridisation (Knox 1990).

At present, however, these old 'truths' are quickly losing ground. The 'bad news' came from North America. Here a clear, stable classification of crossbill variability had not been attained until recently. Most authors agreed that several types could be distinguished (e.g. Griscom 1937), but they disagreed about their number and distribution. In fact, locations that were visited by different collectors in different years would sometimes yield crossbills that could hardly be more different in biometry. A breakthrough was achieved when the focus shifted from studying the biometry of collected birds towards the vocalisations of live birds. It was realised that eight distinct groups of crossbills could be recognised that differed in their calls (Groth 1993a). Their status as distinct groups was justified by the fact that both the flight calls and the excitement calls clustered together. On top of that, the variation in biometry was highly restricted within these so-called vocal types: some vocal types are composed of only large individuals, other types only of small ones. In addition, many vocal types were found to have widely overlapping distributions, which explained why differently sized individuals had been collected at the same localities in the past.

Such sympatric distributions and size differences among the groups suggested that the vocal types could not be regarded as mere geographic dialects, but should be regarded as full biological species (Groth 1993a). Their specific status is supported by reports on assortative mating between the vocal types in sympatry, although hardly any quantitative data is published yet (Benkman 1993, Groth 1993a,b).

This focus on vocalisations in America was followed up in some European studies, with surprising results. Crossbills in the Pyrenees and the Alps were found to have distinct local vocalisations, despite both being traditionally classified as belonging to the nominate subspecies of the common crossbill *L. c. curvirostra* (Clouet & Joachim 1996). In The Netherlands, the rare parrot crossbill is sometimes difficult to distinguish from some large common crossbills by sight, so an attempt was made to distinguish them on recorded calls. Besides finding a single parrot crossbill, six different vocal types of common crossbills were encountered and described (Robb 2000). In Scotland, the endemic Scottish crossbill was receiving much attention due to its status as a Globally Endangered bird (though it was recognised that data were deficient in this classification) in the IUCN Red List. In one study to determine habitat use by Scottish crossbills, crossbills were caught, measured and colour ringed (Marquiss & Rae 2002). In another (initiated by the Royal Society for the Protection of Birds), crossbills were caught, measured and recorded upon release (Summers et al. 2002). Surprisingly, instead of being rare vagrants, parrot crossbills turned out to be locally common breeders. Even more surprising, three different vocal types of common crossbill were identified and described. These independent studies were in accordance with each other in that at least some of the identified vocal types were the same (see table 1). In the Dutch study, several breeding pairs were found and in each case, both members of the pair were of the same vocal type. Samples sizes were not large enough to draw firm conclusions, but this pattern was suggestive of a species status for the vocal types. If this were true, they would represent the first truly new bird species for science (not raised from lower taxonomic ranks to species) discovered in Europe for almost a century! In this respect, it would mirror the discovery of different species of bats based on their call frequencies.

The Scottish studies provided yet another surprise. An attempt to identify Scottish crossbills by genetic markers not only failed to do that, but also found that

Table 1. Agreement between three studies on the existence and classification of common crossbill vocal types in western Europe. Names for each type differ between the studies and types are distinguished by different criteria, but characteristic sonograms are (virtually) identical (see original papers).

Clouet & Joachim 1996 (flight call)	Robb 2000 (vocal repertoire)	Summers et al. 2002	
		(flight call)	(excitement call)
-	A	2	B
-	B	-	-
French Alps	C	4	E
-	D	-	-
-	E	1	A
-	F	-	-

there was no genetic differentiation between parrot and common crossbills (Piertney et al. 2001). This was despite using rapidly evolving neutral genetic markers (nuclear microsatellites and the mitochondrial control region) that normally have the power to detect such differences (and did show the two-barred crossbill to be highly distinct). Another study, including several European and North American populations of the common crossbill, found a clear genetic difference between North American and European crossbills but that there was neither genetic difference among the North American vocal types nor among the European subspecies of the common crossbill (Questiau et al. 1999).

Thus, the comfortable stability in crossbill systematics has been severely disturbed. Instead of four clear species in Europe, we now have several co-occurring ‘populations’ of common crossbills that do not seem to interbreed. Yet, three of the four formerly recognised crossbill species are genetically indistinguishable, suggesting high levels of hybridisation. Therefore, this situation seems to be similar to that in North American crossbills (Groth 1993a) as well as the ground finches *Geospiza* spp. of the Galapagos (Petren et al. 1999). Resolving this paradox is clearly interesting from an ecological and evolutionary point of view, and is highly relevant for the conservation of the Scottish crossbill and for other crossbill populations that were formerly not recognised as distinctive, but might be threatened. What is going on?

Below, we outline the main results of the workshop organised at the 4th EOU Conference by briefly discussing the presentations given (full abstracts, author affiliations, co-authors and addresses are in Die Vogelwarte 42 (2003): 113–118) and by describing the avenues for future research that were identified in the discussions.

Results

Old problems potentially resolved but new surprises abound

Ian Newton revisited his earlier analysis of recoveries of crossbills ringed in western Europe. Some authors regard the massive invasions of crossbills from Russia and Fennoscandia to western Europe as largely suicidal. Others suggested, based on numbers and directions of migrating crossbills, that birds arriving in western Europe in summer do return but do so within a few months. Ian Newton showed that all recoveries of crossbills within the same year are within western Europe, although sometimes quite far from the place of ringing. In stark contrast, 11 recoveries in subsequent years during the breeding season (January–April) were all in north-western Russia and there was an additional recovery even from southern Russia. This not only shows that (at least some of) the birds of invasions return to Russia to breed, but also that birds wait until the next crop is produced in that region. Indeed, if invasions are triggered by food shortage when the cone crop fails, it makes little sense to return to the same area in the same year since the food situation will not change until the next cohort of cones has been produced. Instead, crossbills flee the scene, and wait somewhere else. If they happen to arrive in western Europe at a site with a good cone production, they will stay and even breed. However, the core distribution of crossbills that occur in western Europe during large invasions seems to be in Russia, west of the Ural Mountains.

Natalia Iovchenko presented results on the annual cycle of the common crossbill. Experimental and field studies show that post-breeding movements are an inherent seasonal event. They generally start in May and function to find sites available for wintering and future breeding. Field observations, captures and some recaptures show that in years with a good new crop, a breeding population is formed by autumn, before the main phase of moult. In years with a poor new cone crop, post-breeding movements are extended in time and acquire the character of invasions. This variation in movements reflects on the moult. Few passerines have such a confusing moult as crossbills, with sometimes up to three generations of feathers present, or feathers of different colours (Noskov & Smirnov 1990a, Jenni & Winkler 1994). The first (spring) stage of post-breeding moult (started in experiments about 4 months after photostimulation and in nature generally in late April–May) is inhibited or interrupted by increasing daylength. The extent and rate of the main phase (August–November) are under photoperiodic control (Noskov & Smirnov 1990a), but can be complicated by the effects of local food availability and the possibility to breed or the need to move. This has the effect that large variation among individuals and among years can be found in moult patterns.

Natalia Iovchenko also demonstrated an example of population variation in moult in the common crossbill. In the subspecies *L. c. tianshanica* from the Tian Shan Mountains in Central Asia, breeding occurs in late summer when the seeds of Schrenk spruce *Picea schrenkiana* ripen (Kovshar 1976). Since this is also the usual time of moult, this creates a dilemma. Examination of study skins showed that many breeding females and males with large testes were in active or suspended primary moult. Others might moult directly after the young fledge and before the onset of winter. Many juveniles did not show a post-fledging moult until the next autumn, and can thus commonly be found to breed in juvenile plumage. These results suggest that, despite a clear flexibility in adjusting features of the annual cycle, ecological specialisation might result in characteristic moult patterns that could be used to distinguish between ecologically differentiated populations occurring in other areas.

Bob Dawson showed the results of a time-lapse video system able to record both day and night at a parrot crossbill nest. It provided unprecedented detailed data on the breeding biology of crossbills, e.g. that feeding visits by parents become increasingly spaced in time, that the female stops incubating the chicks at night at the end of the nestling phase, and that night disturbances by (potential) predators can be a cause for desertion.

Ron Summers presented data on the timing of breeding in a Scottish forest that consists only of Scots pine. This pine species keeps its seeds in closed cones until spring. Parrot and Scottish crossbills with their big bills can already access these seeds early in the year, and can be found to breed in February and March. Common crossbills, with their smaller bills, cannot access the seeds until later in spring, when the sun heats the cones and the scales start to separate, making the seeds readily available. Thus, common crossbills only breed in Scots pine forest in April and May. Differences in bill size thus create ecological differentiation, but it might also create pre-zygotic reproductive isolation between crossbill taxa by causing them to separate their reproduction not in space (allopatry) but in time (allochrony).

Daniel Alonso showed the results of a large comparative study of biometric differences between crossbills from the north, east and south of Spain and the Balearic Islands. The latter population is recognised as the subspecies *L. c. balearica*. Significant differences were observed between several populations in a number of traits. Birds from the east of Spain resembled birds of the Balearic Islands, even though taxonomically all crossbills from mainland Spain are currently assigned to the nominate subspecies. Since Balearic and eastern birds eat seeds of Aleppo pine *P. halepensis* whereas those in the north use other pines, these biometric differences might well reflect ecological differences between the populations involved.

Paul-Christophe Schroder showed that the Balearic birds seem to be genetically differentiated from mainland birds in microsatellite variants and frequencies. This is in agreement with the subspecific status of the Balearic birds, but contrasts with the earlier genetic studies that did not detect genetic differences even at the species level. It is clear that more studies with sufficiently large sample sizes are needed to clarify the genetic relationships among crossbill populations and species.

Pim Edelaar presented results bearing on some of the unknowns of the vocal types recorded in western Europe. Large numbers of crossbills were caught by two different amateur bird ringers at two different locations. Both observers caught individuals of four vocal types (including two types not described before!), and their measures show significant differences in bill depth between the types. These differences are real, since the patterns were almost identical in males and females, and for both observers. This shows that small bill size differences do exist between the vocal types, which indicates that they could be ecologically different too (i.e. utilise seeds of different conifers). However, it is also clear that these average differences are small (about 0.2 mm) whereas the measurement difference between observers is greater! Comparing crossbill biometry between studies conducted by different observers is therefore highly problematic when dealing with such small differences between crossbill populations.

Pim Edelaar also showed that the anecdotal evidence for assortative mating between the vocal types was upheld in a larger study. Within the same small geographical area, 25 breeding pairs of crossbills were found. Despite clear geographic overlap in the breeding of the four vocal types, no mixed pairs were observed. While not all alternative explanations can be refuted at this stage, this pattern is highly similar to the North American situation where several ecologically differentiated vocal types can be found breeding sympatrically without much interbreeding, and which seem to represent incipient species if not full species.

David Jardine presented evidence that while the difference in biometry between crossbill populations and vocal types presented by Alonso and Edelaar suggests ecological specialisation, the importance of ecological specialisation might also be gleaned from the comparison of vocalisations. Currently, the Mediterranean populations and subspecies are classified as common crossbills. One would therefore expect that these populations would have vocalisations that are similar to common crossbills of northern Europe, or perhaps have unique vocalisations if isolation has been strong enough (especially for the subspecies living on islands). In fact, vocalisations of crossbills from North Africa, the Balearic Islands, Cyprus and the Pyrenees were found to be rather similar to the vocalisations of the supposedly less related parrot and Scottish crossbills from northern Europe! Since these two species and the Mediterranean crossbill populations share their utilisation of pine (not spruce such as the northern common crossbills), two explanations are possible. Either feeding on pine selects for bigger bills, and this morphology influences the vocalisations, or the pine crossbills of northern and southern Europe are in fact more closely related to each other than to the northern common crossbill. This latter scenario has been published before based on crossbill fossil evidence and the palaeobiogeography of conifers (Tyrberg 1991), but would call for a remarkable change in crossbill taxonomy. There would also be a need to find the new geographical delineation of the common crossbill (if such a border – or even a single species of common crossbill – indeed exists).

Bob Dawson closed the presentations by showing how one can make sonograms of recordings. Using a crested tit *Parus cristatus* recorded the day before, he showed how a tape recording can be transformed into a picture of the call with a few mouse clicks. All the necessary software can be downloaded free from the Internet, and relatively simple and cheap recording equipment suffices to obtain recordings that can be used for a serious study. When it comes down to crossbills, there is no more need for binoculars or a telescope, just a recorder and a computer.

Discussion

Suggestions for future research by professionals and amateurs in Europe

The results presented at the workshop support the earlier studies reporting previously unrecognised crossbill diversity, and suggested ways of resolving and understanding the ecology and evolution of this diversity. For instance, is the parrot crossbill really a separate species, or is there more hybridisation going on than previously realised? Or, was this taxon perhaps justifiably recognised and described, but there are many more crossbill populations that deserve the same specific status? Given that studies in North America show a strong ecological specialisation of the vocal types (Benkman 1993, 2003), the ecological requirements of the European vocal types clearly also need investigation. This is especially pertinent if the vocal types are found to be widely sympatric yet reproductively isolated, as data suggest they are.

This ecological differentiation might be gleaned from biometric differences between populations, as even tiny differences in bill depth have been shown to have dramatic effects on feeding efficiency and survival (Benkman 2003). However, identical measurement of e.g. bill depth by several observers or by the same observer between years or areas might not be easy. This problem is not specific to the study of crossbills but, given the small degree of differentiation (sometimes less then 2 %), additional sources of variation become acutely important. These sources might not even be just observer effects, but could be changes in the bills themselves by growth and wear, or differential development. A number of experiments could be performed in order to test if, for example, use of a conifer with weak or strong cone scales results in different development or wear of the bill, and which bill measures are most affected by this. These should include breeding experiments that determine the extent of the heritable component of the total variation that we see in the wild.

Some suggestions to cope with the problem of observer bias were brought forward at the workshop: reduction of the number of people that measure plus calibration between observers, calibration of different measuring sessions by a single observer using a number of practise study skins, or photographing bills in a standard way for simultaneous measurement of all bills later. It would be worthwhile to conduct a study where each of these methods is tested simultaneously on the same set of birds, in order to determine whether they yield good results in dealing with the observer effect.

Instead of deriving ecological differentiation from biometric differences between populations, ecological differentiation can be studied directly in the field by observing in which conifer species birds are feeding, as done previously for the four crossbill species in Europe (Lack 1944, Marquiss & Rae 2002). Virtually no data on ecological differentiation between the European vocal types exists, but one member of the audience mentioned that in the same general area he found one vocal type mostly in Scots pine while another used mostly Norway spruce *Picea abies*. Even though this does not mean that these two vocal types are specialised on these two resources, it does indicate that while both resources were equally available at the same time to these birds, they chose to use them differentially.

Recording ecological specialisation by noting which trees are utilised is confounded by the fact that crossbills will prefer trees that have good seed availability. Thus, both parrot and two-barred crossbills might be found feeding on larch if it has a high density of opening cones. When seed availability drops, all crossbills might shift from one conifer species to the next. However, we might observe at least some degree of differentiation of the species/vocal types if they shift at different times or to different conifer species. Such studies could be performed everywhere where crossbills and several conifer species with a cone crop are present at the same time. If the bills differ enough between the crossbills present to have an ecological effect, we should at least sometimes see such different timing of shift or most commonly used conifer species.

It will be more difficult to identify if and to which ecological circumstances the populations have adapted over evolutionary time. This most likely has to be performed in the natural habitat (although specifically designed feeding trials in the laboratory with suspected key resources may also be able to resolve this). Paradoxically, far fewer conifer species are known from the range of the common crossbill than the number of recognised vocal types. Several explanations are possible. Perhaps the vocal types are not specialised at all, but represent cultural differences in vocalisations that arose for reasons unrelated to ecological circumstances, e.g. in stable family groups (the calls are reportedly not genetically inherited but learned from adults, as in many other passerines; e.g. Beecher 1996). Another possibility is that these populations are not specialised on a particular conifer species, but on geographic variants. This has been observed in North America, where two types of crossbill are specialised on local varieties of lodgepole pine *Pinus contorta* that differ in cone structure due to the presence/absence of red squirrels *Tamiasciurus hudsonicus* (Benkman et al. 2001). Perhaps Norway spruce and Scots pine differ enough in relevant cone and seed traits over the range of the common crossbill to favour the evolution of specialised populations. This would predict that the distribution of the different vocal types and species would similarly differ geographically, except in situations of crop failure. Yet another alternative is that each population is not specialised to a particular species or variety of conifer, but to a mix of conifers. This hypothesis is even more difficult to test, although a quantitative description of habitat and resource use over a longer time period would be one way to approach this. A final, perhaps even more speculative but highly intriguing hypothesis is that the vocal types are specialising on the many introduced species of conifer, such as Douglas fir *Pseudotsuga menziesii*, Sitka spruce *Picea sitchensis* and lodgepole pine. This hypothesis has been forwarded to explain the smaller bill of Scottish crossbills relative to parrot crossbills (Marquiss & Rae 2002), but might be applicable in a more general sense. Since these conifers are known to support specialised crossbill populations in North America, it is not inconceivable that large-scale planting of these new resources in Europe will be followed by colonisation and specialisation by European crossbills as well.

Crossbills are highly dispersive (at least in the boreal range) and occur naturally in forests not visited often by ornithologists. So perhaps the application of other techniques such as stable isotopes might be able to show that birds of different vocal type in the same invasion come from different areas or have used different resources. Other clues that would support such a different geographical/ecological background would be a difference in aspects of the yearly cycle, such as moult patterns, temporal patterns of fat storage, migration and breeding, proportions of juveniles, etc. (for examples see Noskov & Smirnov 1990a,b, Marquiss & Rae 2002).

In studying the biometric, ecological and geographic differences of crossbill species and populations, it is highly relevant to give a primary role to vocalisations. While it is not completely clear if and how all the different populations can be identified using vocalisations, it is increasingly clear that ignoring the different kinds of crossbills that can be recognised at a single location could seriously mix up vital data (similar to counting roosting waders or migrating passerines but not differentiate between the many species involved). Differences in biometry or ecology between sites or years might then reflect different proportions of the composite populations. Currently, extensive recording of calls happens far too little but must be done more, as there simply is no alternative.

However, a lot of additional work is needed to determine if and how we can recognise discrete populations of crossbills by distinct vocalisations without (much) overlap. Studying sonograms may seem less enjoyable than studying the behaviour or plumage of birds through binoculars, but the rewards will be great with every step of clarification. It probably takes a professional, computerised, statistical approach to test objectively for discrete classes in crossbill vocalisations, but amateurs could contribute significantly by collecting vocalisations from all the corners of the continent and making them accessible (e.g. through the web). It would also be interesting to find very old (published or unpublished) recordings, in order to test how much these vocalisations have changed over the years.

How exactly these differences in vocalisations have evolved is a complex subject, but existing data sets might shed some light on this. If size differences between and within species and vocal types are correlated to features of the vocalisations (such as mean or maximum frequency), then vocal differentiation might be a by-product of (naturally selected) size differentiation. However, if such a correlation is absent, there might have been direct (sexual) selection on the vocalisations that has led to their differentiation.

One assumption of using the vocalisations as a grouping criterion is that they are stable within an individual's lifetime. Since the calls are presumably not genetically determined but learned from other individuals (Groth 1993a), this might not be true. This assumption of call stability is supported by the finding that there are biometric differences between the vocal types and anecdotal evidence from captive birds and re-recorded colour-ringed birds, but better tests would be welcome. Anybody keeping captive crossbills could test for call stability over the years, e.g. when housed with other crossbill types or when only individuals of a different vocal type or species are available as a breeding partner.

Genetic relationships between populations and even species are badly resolved, and much work needs to be done here. It is clear that, in some cases, no large differences are present, but especially for populations that are more resident it might be possible to achieve a better resolution, especially if sample sizes are sufficiently large. There might also be scope for different markers such as AFLPs, which have given good results in some formerly unresolved species-complexes. Again, it will be necessary not to lump all individuals from a particular location, but to know the vocalisations of each and every individual included in the genetic analyses. Bird ringers are in a good position to collect such data on biometry, moult, breeding and migratory physiology, vocalisations and genetics (blood or feather sample) as well as working on ring recoveries that shed light on movements of the different populations.

Such genetic differences would be expected if the vocal types/species are evolutionarily independent, and interbreeding is rare. So far, this seems supported by the data on assortative mating with respect to vocal type, but many more data on assortative mating (also between other vocal types) are needed for better estimates of interbreeding. Recording both male and female of a pair of crossbills seen mate guarding, courtship feeding, or at a nest, would yield a valuable contributing data point. After fledging, however, unrelated adult crossbills might join feeding families, so a pair bond cannot be reliably assumed between a male and a female in that situation.

Despite the need to resolve the genetic relationships between crossbill populations, genetic differentiation could turn out to be negligible or absent even when hybridisation no longer occurs. Population differentiation of neutral genetic markers depends on mutations and changes in marker frequencies by chance. This process takes a long time, and is slowed down if populations are large and internally well mixed. Crossbill populations are probably large and well mixed, and above all some discrete populations might have evolved rather recently (in the last 15,000 years or less, perhaps even in the last 200 years). Therefore, such differentiation might be most useful in older, smaller and more resident populations.

The Mediterranean crossbills are a clear example where an integrated approach combining ecology, vocalisations and genetics is both needed and expected to be successful. Here, crossbills have been found to be fairly resident. Up to four different conifer species occur in the area that are all known to be able to support a resident crossbill population (mountain pine *P. uncinata*/*mugo*, Scots pine, black pine *P. nigra/laricio* and Aleppo pine). Yet, most research so far has lumped all crossbills from particular geographic localities followed by subsequent comparison of biometry between localities, and this has yielded little insight. Instead, we propose that crossbills are caught and measured in different habitats and their vocalisations recorded upon release. Genetic, biometric and vocal comparison between locations and taking habitat into account, might reveal that several crossbill populations are specialising on these very different resources at any one location. Genetic and vocal population structure could indicate if these populations evolved locally, or if they have large geographic distributions suggesting an allopatric origin. Vocal and biometric differences are already reported for crossbills in different habitats in Spain, and we look forward to seeing the next results.

Despite decades of study, recent findings are uncovering new dimensions in crossbill biology that were unforeseen a few years ago. Any enthusiastic person or group of people can contribute significantly to answering the many questions that remain unanswered. Some of these will be hard to tackle and might be left for professionals with more time and resources available. But several simple projects are possible for the dedicated amateur. Currently, very little is known about crossbills in south-eastern Europe, but it is clear that even in countries such as The Netherlands and Great Britain (perhaps the best studied countries in the world ornithologically) big surprises and achievements lie ahead.

References

Beecher, M. D. 1996. Birdsong learning in the laboratory and field. Pp 61–78 in Kroodsma, D. E. & Miller, E. H. (eds). Ecology and evolution of acoustic communication in birds. Cornell University Press, Ithaca.

Benkman, C. W. 1993. Adaptation to single resources and the evolution of crossbill (*Loxia*) diversity. Ecol. Monogr. 63: 305–325.

Benkman, C. W. 2003. Divergent selection drives the adaptive radiation of crossbills. Evolution 57: 1176–1181.

Benkman, C. W., Holiman, W. C. & Smith, J. W. 2001. The influence of a competitor on the geographic mosaic of coevolution between crossbills and lodgepole pine. Evolution 55: 282–294.

Berthold, P. & Gwinner, E. 1972. Frühe Geschlechtsreife beim Fichtenkreuzschnabel (*Loxia curvirostra*).Vogelwarte 26: 356–357.

Clouet, M. & Joachim, J. 1996. Premiers élements de comparaison de trois populations françaises de beccroisés *Loxia curvirostra*. Alauda 64: 149–155.

Cramp, S. & Perrins, C. M. 1994. The Birds of the Western Palearctic. Vol. 8. Oxford University Press, Oxford.

Dolnik, V. R. 1975. Migratory status in birds. Nauka, Moskow [in Russian].

Griscom, L. 1937. A monographic study of the red crossbill. Proc. Boston Soc. Nat. Hist. 41: 77–210.

Groth, J. G. 1993a. Evolutionary differentiation in morphology, vocalizations, and allozymes among nomadic sibling species in the North American Red Crossbill (*Loxia curvirostra*) complex. University of California, Berkeley and Los Angeles.

Groth, J. G. 1993b. Call matching and positive assortative mating in red crossbills. Auk 110: 398–401.

Jardine, D. C. 1994. Brood patch on a Common Crossbill *Loxia curvirostra* still in juvenile plumage. Bird Study 41: 155–156.

Jenni, L. & Winkler, R. 1994. Moult and ageing of European passerines. Academic Press, London.

Knox, A. G. 1990. The sympatric breeding of Common and Scottish crossbills *Loxia curvirostra* and *L. scotica* and the evolution of crossbills. Ibis 132: 454–466.

Kovshar, A. F. 1976. Summer-autumn breeding of crossbills in Tien Shan as an example of adaptation of a food specialist to the environment. Ecologia 3: 94–97 [in Russian].

Lack, D. 1944. Correlation between beak and food in the crossbill, *Loxia curvirostra* Linnaeus. Ibis 86: 552–553.

Marquiss, M. & Rae, R. 2002. Ecological differentiation in relation to bill size amongst sympatric, genetically undifferentiated crossbills *Loxia* spp. Ibis 144: 494–508.

Noskov, G. A. & Smirnov, Y. N. 1990a. The Common Crossbill *Loxia curvirostra* L. Pp 239–246 in Rymkevich, T. A. (ed.). Moult of passerines of northwestern USSR Izd. Leningradskogo Universiteta, Leningrad [in Russian].

Noskov, G. A. & Smirnov, Y. N. 1990b. The Parrot Crossbill *Loxia pytyopsittacus* L. Pp 246–251 in Rymkevich, T. A. (ed.). Moult of passerines of northwestern USSR. Izd. Leningradskogo Universiteta, Leningrad [in Russian].

Petren, K., Grant, B. R. & Grant, P. 1999. A phylogeny of Darwin's finches based on microsatellite DNA length variation. Proc. R. Soc. London B. 266: 321–329.

Piertney, S. B., Summers, R. W. & Marquiss, M. 2001. Microsatellite and mitochondrial DNA homogeneity among phenotypically diverse crossbill taxa in the UK. Proc. R. Soc. London B. 268:1511–1517.

Questiau, S., Gielly, L., Clouet, M. & Taberlet, P. 1999. Phylogeographical evidence of gene flow among Common Crossbill (*Loxia curvirostra*, Aves, Fringillidae) populations at the continental level. Heredity 83: 196–205.

Robb, M. 2000. Introduction to vocalizations of crossbills in north-western Europe. Dutch Birding 22: 61–107.

Summers, R. W., Jardine, D. C., Marquiss, M. & Rae, R. 2002. The distribution and habitats of crossbills *Loxia* spp. in Britain, with special reference to the Scottish crossbill *Loxia scotica*. Ibis 144: 393–410.

Tyrberg, T. 1991. Crossbill (genus *Loxia*) evolution in the West Palearctic – a look at the fossil evidence. Ornis Svecica 1: 3–10.