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How important are different non-native conifers in Britain to Common Crossbills *Loxia c. curvirostra*?

Eilidh McNab[a], Ron Summers[b], Gavin Harrison[c, d] and Kirsty Park[a]

[a]Biological and Environmental Sciences, University of Stirling, Stirling, FK9 4LA, Scotland, UK; [b]RSPB Centre for Conservation Science, North Scotland Regional Office, Etive House, Beechwood Park, Inverness, IV2 3BW, Scotland, UK; [c]The Royal Zoological Society of Scotland, Costorphine Road, Edinburgh, EH12 6TS, Scotland, UK; [d]National Trust, Waddesdon Manor, Aylesbury, HP18 0JH, England.

Corresponding author: Ron Summers (ron.summers@rspb.org.uk)

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[a]Biological and Environmental Sciences, University of Stirling, Stirling, FK9 4LA, Scotland, UK; [b]RSPB Centre for Conservation Science, North Scotland Regional Office, Etive House, Beechwood Park, Inverness, IV2 3BW, Scotland, UK; [c]The Royal Zoological Society of Scotland, Costorphine Road, Edinburgh, EH12 6TS, Scotland, UK; [d]National Trust, Waddesdon Manor, Aylesbury, HP18 0JH, England.

ABSTRACT

Capsule: Pines physically defend their seeds against seed-eating birds and mammals more than spruces or larches. Cone characteristics reflect the rate at which Common Crossbills *Loxia c. curvirostra* extract seeds from different non-native conifers in Britain.

Aims: To assess the profitability of different non-native conifers in Britain for Common Crossbills in winter.

Methods: We measured cone and seed parameters of conifers (Norway Spruce *Picea abies*, Sitka Spruce *Picea sitchensis*, Lodgepole Pine *Pinus contorta* and Japanese Larch *Larix kaempferi*) introduced into Britain and compared these with the native Scots Pine *Pinus sylvestris*. Feeding trials with captive crossbills assessed intake rates.

Results: The pines had thick and long scales, Japanese Larch had thin, short scales but thick seed coats and Sitka Spruce had thin, papery and short scales, and the thinnest seed coat. The two spruce species had more seeds per cone and the kernels had a higher energy content than the pines and larch. Feeding trials, simulating cones in winter, found that crossbills failed to access seeds in closed Scots Pine cones. They also had difficulty in prising the scales of closed Lodgepole Pine cones but were able to forage on partially-open cones. They took longer to extract seeds from large, open Lodgepole Pine cones than small ones, reflecting the effect of increasing scale thickness in larger pine cones. They also took longer to extract Lodgepole Pine seeds than Sitka Spruce and larch seeds. Although crossbills could extract seeds quickly from open Sitka Spruce cones, the small seed size made the energy intake rate similar to Japanese Larch, if all seeds contained a kernel. However, after accounting for the proportion of seeds with a kernel, Sitka Spruce was the more profitable.

Conclusion: The conifer food resource for crossbills in Britain has changed through the planting of non-native conifers. The physical properties of the cones and seeding phenology influence the rate at which Common Crossbills can extract seeds.

Western Europe has experienced a long-term decline in natural habitats (European Environment Agency 2015). One major habitat change was the loss of natural forests and the establishment of conifer plantations for timber production. Whilst some wildlife has benefited from the provision of plantation woodland, other woodland species have declined (Väisänen *et al*. 1986, Virkkala 1987, Avery & Leslie 1990, Staines *et al*. 1987). Within Britain, most of the conifer plantations are composed of non-native species, particularly from North America, such that about 70% of the woodland area of Scotland is now comprised of non-native conifers (Forestry Commission 2009).

In northern Europe, the Common Crossbill *Loxia c. curvirostra* is generally associated with Norway Spruce *Picea abies*, the Two-barred Crossbill *L. leucoptera* with larch *Larix* spp. and the Parrot Crossbill *L. pytyopsittacus* with Scots Pine *Pinus sylvestris* (Lack 1944, Cramp & Perrins 1994). Originally, the only conifer available to crossbills in Britain was the Scots Pine (Birks 1989), creating a habitat in which the Scottish Crossbill *Loxia scotica* is thought to have evolved. Nethersole-Thompson (1975) and Newton (in Nethersole-Thompson 1975) have slightly different views on the possible evolutionary route for the Scottish Crossbill. Unable to exploit Scot Pine, the Common Crossbill would have occurred temporarily in Britain during irruptions from continental Europe and western Asia in years when Norway Spruce failed to produce cones across large parts of the continent (Svärdson 1967, Newton 1970).

Over the past 300 years, and particularly in the 20th century, the area and number of non-native conifer species has increased though planting (Anderson 1967, Warren 2002), providing the possibility for irrupting Common Crossbills to exploit a range of conifers (Knox 1990, Marquiss & Rae 2002). The Common Crossbill is now a widespread breeding species (Balmer *et al.* 2013), but numbers are particularly large when irrupting birds from the continent arrive (Davies 1964, Jardine 1992), after which many stay to breed before returning to the continent in a subsequent season (Marquis & Rae 1994, Newton 2006).

Even though each crossbill taxon may be adapted to and has co-evolved to feed on a particular conifer species (Benkman 1993, Benkman *et al*. 2010), multiple conifer species can be utilized (Benkman 1987a, Marquiss & Rae 2002). The introduced conifers on which Common

Crossbills forage on in Britain include the Sitka Spruce *Picea sitchensis*, Norway Spruce *Picea abies*, Lodgepole Pine *Pinus contorta*, Japanese *Larix kaempferi*, European *L. decidua* and Hybrid Larches *L.* x *eurolepis* (Marquiss & Rae 1994, 2002, Summers *et al*. 2002, Summers 2018). The latter is a hybrid of European and Japanese Larches, and has cones similar to those of Japanese Larch in that the tips of the scales turn outwards. Common Crossbills also forage on the native Scots Pine after the scales open in the spring (Marquiss & Rae 1994, 2002; Summers *et al*. 2010). However, it is not known which conifer is most profitable for Common Crossbills.

To obtain a kernel from a cone, a crossbill may, or may not, remove the cone from a tree by cutting through the peduncle (the cone-bearing stalk), then prise apart the cone scales with its mandibles, extract a seed from the base of a scale with its tongue, and remove the seed's wing and seed coat to eat the kernel (Newton 1972, Benkman 1987b). Cones defend the seeds with overlapping scales that vary in thickness and length, whilst the kernel is defended by a seed coat. Therefore, we first described the physical cone characteristics to measure how well the seeds of different conifers are defended against seed-eating birds and mammals. Further, we assessed which cones were the most profitable (energy intake per unit time of foraging) to crossbills by measuring the energy content of the seeds and feeding rates. We focussed on conditions that crossbills encounter in winter, when intake rates are near the estimated minimum rate to survive (Benkman 1987a), and when crossbills tend to forage on a single (key) conifer species to which they are adapted (Benkman 1993). During winter, Scots Pine, Norway Spruce and larch cones are closed, but Sitka Spruce is shedding seed and Lodgepole Pine cones are opening (Summers & Proctor 2005, Summers 2018, this study). This information may thereby indicate which conifer is likely to have the greatest impact on Common Crossbill populations in Britain.

Methods

Cone characteristics

To determine the degree of physical defence of seeds against seed-eaters in different conifer species, we measured peduncle thickness, scale thickness and scale length of cones, and the percentage of the mass of a seed that was seed coat. Single cones were collected in autumn or winter from each of 15 or 25 arbitrarily chosen live or recently felled trees for different conifer species in Highland Scotland, prior to shedding seed in 2003/04. Scots Pine cones came from Morangie Forest (UK grid reference NH7480), Norway Spruce from Strath Dearn (NH7524), Sitka Spruce from Morinish (NJ2230), Japanese Larch cones from Glen Ferness (NH9846) and Lodgepole Pine cones from Moray (NJ2245).

There are four subspecies of Lodgepole Pine in North America: *P.c. contorta, P.c. bolanderi, P.c. murrayana* and *P.c. latifolia*. The first two are coastal in their distribution, whereas *P.c. murrayana* occurs in the Sierra Nevada, Klamath Mountains and Cascade Range, and *P.c. latifolia* in the Rocky Mountains (Critchfield 1957). A key characteristic of the cones from the different subspecies is the degree of serotiny. If serotinous, the cone relies on the heat from forest fires to open the cones (Anderson 2003). Coastal stands tend not to be serotinous, but the habit varies for the inland populations (Lines 1996). The Lodgepole Pine seeds that were imported to Britain originated from both coastal (South Coastal USA, Lower Fraser River and SE Vancouver Island seed zones) and inland regions (Central Interior British Columbia and South Interior British Columbia seed zones), so belonged to the *contorta* and *latifolia* subspecies, respectively (Lines 1996). Therefore, it is possible that serotinous populations occur in Britain. However, serotiny has not been observed here, likely because it develops with age, and as Lodgepole Pines rarely exceed 60 years before felling, its apparent absence in Britain could be due to the immaturity of trees, as well as provenance and our maritime climate (Lines 1996). In the current study, we were unable to obtain information on the subspecies of samples, because such data are not available on forestry stock maps.

Cone length and breadth (two measurements of breadth were averaged) and peduncle width were measured using digital callipers. The cones were dried in an oven at 60^{o}C for three days to open the scales and allow seeds to be removed. The thickness of a scale in the mid part of the tip of larch cones was measured to 0.01 mm using digital callipers by applying the tines of the callipers perpendicular to the outer 4 mm of three scales in the mid part of cones. Mean scale thickness was then calculated for each cone. This was done for only larch because values for other species were already available (Summers & Broome 2012). The length of a seed plus its wing was used as a measure of scale length because the seed and wing lie along most of the length of a scale. Seeds (empty and full) were removed from the cones and counted. Tiny seeds from the base and apex of cones were ignored. The number of seeds with a kernel was measured by placing seeds (with their wings removed) in 90% ethanol. Seeds with a kernel sank whilst empty seeds floated for most conifer species. However, most larch seeds floated regardless of having a kernel, so these seeds were cut open with a scalpel to check for a kernel. Five seeds per cone were arbitrarily selected and their length measured using digital callipers under a binocular microscope. Seeds were weighed whole to 0.01 mg, and again with the seed coat removed. Values were averaged for each cone.

Energy content

Kernels were removed from seed coats using a scalpel. To make pellets for measuring energy content, kernels were compressed into the bottom of a crucible with a metal spatula. Two of the Lodgepole Pine samples were small, so benozoic acid was used as a 'spiking agent' to ensure combustion. Samples were made with approximately 50% benzoic acid and 50% kernel, and the energy value for the seeds calculated by removing the energy from the benzoic acid from the final result. A Parr 6100 calorimeter was used to obtain the energy values of the seeds. To calibrate the machine, a 1 g pellet of benzoic acid was run in standardisation mode, after which the seed samples were run in determination mode.

The timing of opening of Lodgepole Pine cones

Whilst there is information on the maturation and seeding phenology of Scots Pines and spruces in Britain (Summers & Proctor 2005, Summers 2018), there is none available for Lodgepole Pine. Therefore, in Strath Rory (NH6679), 20 Lodgepole Pine cones, each on a different tree, were marked with a label on the shoots they grew upon, and visited at the start of each month through the autumn, winter and spring to describe the time of opening of the scales prior to shedding seed. The scales were described as closed, slightly open, half open and fully open.

Feeding trials

Eight crossbills (four females and four males) were captured in East Ross-shire in spring 2010 (under licence from Scottish Natural Heritage). One female died from aspergillosis, which, based on its advanced state, was assumed to be a pre-existing condition (Royal Zoological Society of Scotland vet). The four males had a mean bill depth of 10.45 mm (SD = 0.43 mm), wing length of 99.8 mm (2.2) and mass of 40 g (1.7), whilst the four females had a mean bill depth of 10.28 mm (SD = 0.10), wing length of 96.5 mm (1.3) and mass of 41 g (0.6). These measurements are typical for Common Crossbills (Knox 1976). They were kept together in an indoor aviary at the Royal Zoological Society of Scotland in Edinburgh and provided with water, fresh cones of various species, and commercial Greenfinch *Chloris chloris* Seed Mix. They were released at the trapping area after the trials had been completed, seven months after capture.

Cones for the feeding trials were collected in winter 2009/10, prior to the trials in summer 2010. Scots Pine cones were collected in Abernethy Forest (NH9618), Lodgepole Pine cones from Easter Ross (NH7180) and Sitka Spruce and Japanese Larch cones from Glen Ferness (NH9846). The Sitka Spruce cones (collected in January) would have shed about 30% of their seeds by then (Summers 2018), whilst the other species had their full complement of seeds in closed cones. Cones were collected from either live trees or those that had been recently felled. Cones were kept frozen to prevent scales opening or shedding further seeds, and thawed out at room temperature before the trials. The mean cone lengths used in the trials were 69.6 mm (SD = 7.3, range 57.4-85.5 mm) for Sitka Spruce, 40.1 mm (SD = 6.9, range 29.0-50.4 mm) for Lodgepole Pine, and 23.3 mm (SD = 2.9, range 18.2-30.3 mm) for Japanese Larch.

Feeding trials were carried out on single birds in a wire cage (1 x 1 x 0.5 m) with a one-way viewing window, following the protocol of Benkman (1993). A short perch was placed in the trial cage, and a bowl set alongside the perch where cones were placed. Water was always available. Trials were filmed on a Flip Ultra camcorder attached to the side of the cage. Cones of the different species were given one at a time, either with closed or opened scales, depending on their state in winter. In winter, Scots Pine and Japanese Larch cones are closed, though Japanese Larch cones have a partially open structure due to the outward bending scales, so both open and closed cones were tested, Lodgepole Pine cones are opening (this paper), and Sitka Spruce cones are open, though may partially close in wet weather (Summers 2018). Opening was forced in a drying oven at 70^{o}C for 5-15 minutes and then cones were soaked for *c.*10 minutes in water to partially re-close the scales (Benkman 1993). The length of each cone (with scales closed) was measured with digital callipers before being given to a bird. The bird was left with the cone until at least 11 seeds were removed and eaten, after which the cone was removed and replaced with a fresh one. The time for handling and consuming 10 seeds was measured after the first seed had been consumed because the time for each bird to start feeding on a cone after it had been picked up varied. A trial was terminated if a bird failed to extract any seeds within 10 minutes.

Statistical analysis

Detailed cone measurements were made from only a small number of cones. Therefore, it was possible that these cones were not representative of the sizes selected by crossbills or the average size available, making it difficult to make direct comparisons among conifer species. Therefore, to make these comparisons, values were adjusted to mean cone lengths available, as derived from extensive sampling programmes (Summers 2002, Summers & Broome 2012, unpublished data). Linear regression analyses were used to examine relationships among cone and seed variables, and thereby adjust values. The percentage of the seed that was seed coat was arc-sine transformed before analysis. One-way ANOVAs and *t*-tests were carried out to test for differences among conifer species.

Regression analyses were used to determine variables and factors that were related to the time for crossbills to remove 10 seeds from each cone. The data for feeding rates for each conifer were analysed separately, and because multiple records came from several birds, BIRD (*i.e.* an individual bird) was included as a random effect. The effect of open *versus* closed cones was a fixed factor, where this applied, and cone length was a covariate. Interactions between open *versus* closed and cone length were tested. The times for feeding on larch were positively skewed, so a log transformation was carried out before analysis. The times for the other species were normally distributed. Regression analyses were carried out in SAS (SAS Inst. 2000).

Results

The timing of opening of Lodgepole Pine cones

The scales on Lodgepole Pine cones were closed until the start of November, when the first one was noted as being slightly open (Fig. 1). Thereafter, larger numbers were classed as slightly or half open through the winter, making the seeds accessible to crossbills. The observations at the start of May coincided with wet weather, resulting in the scales closing partially and temporarily (Fig. 1). By the start of June, almost all were fully open. There was no evidence of serotiny.

Cone characteristics

The number of seeds in a cone was positively related to cone length for all conifer species (Table 1). For cones of an average length based on an extensive survey, the spruces had more seeds than the pines or larch (Table 2). Seed length and seed plus wing length (a measure of scale length) increased with cone length for pine and larch cones (Table 1). For average cone lengths from the extensive survey, Norway Spruce had the longest seed plus wing, and Sitka Spruce and Japanese Larch had the shortest (Table 2). The pines had the thickest scales and the Sitka Spruce the thinnest (Table 2).

The percentage of the seed mass comprising seed coat varied significantly among the conifers ($F_{4,77} = 96.7$, $P < 0.001$), with larch having the greatest percentage (Table 1). This was followed by Norway Spruce, Lodgepole Pine and Scots Pine (the latter two were not significantly different). Sitka Spruce had the lowest percentage of seed coat.

The energy content of the kernels varied significantly among the conifers ($F_{4,10}$ = 5.79, P = 0.011). There was no difference between the two spruce species (t = 1.6, df = 4, P = 0.18), nor between the two pine species (t = 0.9, df = 4, P = 0.43), but the kernels of spruce had a significantly greater energy content (mean = 29.8 kJ/dry g, SD = 1.60) than those of pines (mean = 25.6 kJ/dry g, SD = 1.92) (t = 4.1, df = 10, P = 0.002) (Table 1).

Feeding trials

The crossbills were unable to prise open the scales of closed Scots Pine cones in any of the 14 trials conducted for this species and cone condition, and managed to obtain seeds from only two closed Lodgepole Pine cones out of 19 trials. Excluding the data for closed Lodgepole Pine cones, cone length had a significant negative effect on the speed of seed extraction for open cones ($F_{1,11}$ = 15.6, P = 0.002) (Fig. 2). The mean time to extract 10 seeds was 87.0 s (SD = 28.3, n = 15). The mean cone length used in the trials (40.1 mm) was similar to the mean value from an extensive survey (Table 2).

There was no effect of cone length ($F_{1,142}$ = 1.47, P = 0.23) on the log time to extract Japanese Larch seeds, nor was there a difference between open and closed cones ($F_{1,142}$ = 0.49, P = 0.48). There was no significant interaction ($F_{1,141}$ = 3.09, P = 0.08). The mean time to extract 10 seeds was 43.5 s (SD = 23.3, n = 152) from all cones, but given the skewed nature of the times, the median was also calculated, at 35.8 s (inter-quartile range 26.8-53.0 s). The mean cone length for the feeding trials (23.3 mm) was slightly smaller than the mean cone length from the extensive survey (Table 2).

For Sitka Spruce cones, there was a significant interaction between the open/closed status and cone length ($F_{1,24}$ = 7.87, P = 0.01); there was no effect of cone length on feeding times of seeds from closed cones but it took longer to extract seeds from longer cones if they were open (Fig 2). The mean time to extract ten seeds from closed cones was 41.1 s (SD = 8.5, n = 10), and 28.7 s (SD = 8.1, n = 20) for open cones. The mean cone length used in the trials (69.6 mm) was similar to the mean cone length from the extensive survey (Table 2).

Using the feeding rates, kernel mass and kernel energy content, the intake rate was calculated, assuming firstly that all seeds contained a kernel and secondly, if the proportion containing a kernel was as measured (Tables 1 and 3). The most profitable cones in terms of energy intake were open Sitka Spruce and Japanese Larch cones, if all seeds had a kernel. Lodgepole Pine cones were least profitable. If only a certain proportion of seeds had kernels, as per those cones where this was measured, open or closed Sitka Spruce cones were the most profitable, by a factor of 1.1-1.8 over Japanese Larch and by a factor of 2.5-3.6 over Lodgepole Pine.

Discussion

For North American Red Crossbills (also *Loxia curvirostra*), the scale thickness of cones is a key determinant of intake rate (Benkman 2010). Intake rate is faster when crossbills forage on cones with thinner scales. Our study concurs with results presented by Benkman (2010); Common Crossbills took longer to extract seeds from long Lodgepole Pine cones with thick scales than short pine cones with thin scales. For those species where scale thickness did not vary with cone length (Sitka Spruce and Japanese Larch) there was either no relationship between seed extraction time and cone length (larch), or a minor effect of length (Sitka Spruce). The slower extraction rate for longer Sitka Spruce cones is perhaps because it is more difficult to manipulate larger cones. Finally, the mean seed extraction time for 10 seeds from the three conifers ranked according to scale thickness: 28.7, 43.5, and 87.0 s for Sitka Spruce, Japanese Larch and Lodgepole Pine, respectively.

In terms of kernel intake rates, the values presented in this study (Table 3) are similar to intake rates recorded for Red Crossbills (*L.c. bendirei*) in North America, where the kernel intake ranged from about 0.2 mg/s for closed White Spruce *Picea glauca*, Red Spruce *Picea rubens* and Black Spruce *P. mariana* cones to 0.4 mg/s for open cones of these species. By contrast, intake rates on Jack Pine *Pinus banksiana*, Pitch Pine *P. rigida* and White Pine *P. strobus* varied from 0.4 mg/s for closed cones to 1-2 mg/s for open pine cones (Benkman 1987b), showing the range of intakes according different circumstances (Common Crossbill subspecies, cone species, and open *versus* closed cone scales).

Whether cones are open or closed is a key determinant of intake rate (Benkman 1987b), with the latter state slowing or even preventing intake. This may explain why Common Crossbills failed to extract seeds from closed Scots Pine cones in our trials, and why Common Crossbills nesting in stands of Scots Pine do so only when the cones start to open in spring (Summers *et al.* 2010). Despite Lodgepole Pines having thinner scales than Scots Pines, they too presented difficulties for Common Crossbills when closed. However, because Lodgepole Pine cones open earlier than Scots Pine cones (Summers & Proctor 2005, Fig. 1), Common Crossbills can forage on Lodgepole Pines in winter and are known to associate with this species at this season (Summers & Broome 2012).

The scales of Norway and Sitka Spruce cones are thinner than those of the pines and their seed energy content was higher (Tables 1 and 2; Summers & Broome 2012). In addition, the scales of Sitka Spruce are short and not tightly fitting, making seeds more accessible than in the longer-scaled Norway Spruce cones (Table 2). The thin papery scales of Sitka Spruce probably accounted for the fast rate of seed extraction, despite the fact that Sitka Spruce has already shed many seeds by winter. No feeding trials were carried out on Norway Spruce, but it would prove interesting to determine its profitability for crossbills, given its large and many seeds.

Sitka Spruce seeds were the least defended in terms of its seed coat. Their only attributes that would make foraging less profitable are the small seed size (Table 2) and the declining number of seeds from autumn to spring (Summers 2018). Sitka Spruce has peaks in shedding of seed during autumn and spring when cone scales are open, but they partly re-close in wet weather in winter, slowing down the rate of shedding seed (Summers 2018), and perhaps the extraction rate by crossbills.

Field studies in eastern Scotland have shown that Common Crossbills forage on Sitka Spruce from autumn to spring (Marquiss & Rae 1994, Summers 2018). Interestingly, when foraging on Sitka Spruce in one winter (1990/91), Common Crossbills did not attempt to breed and did so only when they switched to foraging on opening Scots Pines in spring (Marquiss & Rae 1994). Perhaps intake rates were not high enough on Sitka Spruce to attempt breeding

(Benkman 1990), and this may have been a consequence of small seed size or a limited number of remaining seeds.

Japanese Larch and Hybrid Larch have scales that turn outwards at the tip, providing an open appearance to the scales. We found neither a difference in the seed extraction rate of open *versus* closed Japanese Larch cones, nor an effect of cone length. The scale length of larch is short, making the seeds relatively easy to access. Compared to the other conifers, the prime defence of larch is the thick seed coat (Table 1).

A wide-ranging study in Highland Scotland during late winter revealed that Common Crossbills were strongly associated with coning Sitka Spruce, Lodgepole Pine and to a lesser extent with larches (Summers & Broome 2012). There was no significant association with Scots Pine or Norway Spruce, even although both species were coning in the year of the survey (Summers & Broome 2012). The non-association with Scots Pine is understandable because of the difficulty with which Common Crossbills have in prying the scales to access seeds from closed Scots Pines. Common Crossbills are, however, able to readily remove seeds from open Scots Pine cones, and breed when utilising this food source (Marquis & Rae 1994, Summers *et al*. 2010). Further, when irrupting Common Crossbills are present in southern Europe, they are able to utilise Scots Pines, along with other subspecies of Common Crossbill (some with larger bills than the nominate subspecies of northern Europe; Knox 1976) resident in southern Europe (Newton 2006, Alonso *et al*. 2006, Edelaar *et al*. 2012). However, it is not clear if they are taking seeds from closed or open cones. Understanding the lack of an association with Norway Spruce is less clear, given the importance of Norway Spruce to Common Crossbills on the European continent, and the fact that it is used in Scotland (Summers 2018). Perhaps this was due to the small area of Norway Spruce in Scotland relative to other conifers (Summers & Broome 2012). The positive association that Common Crossbills had with Sitka Spruce and larch can be explained by their profitability (this study), though the association with Lodgepole Pine is less clear unless they select the smaller cones.

An important variable that determines intake rate is the proportion of seeds that contain a kernel (Tables 1 and 3). Kernels do not develop if the seeds have not been cross-fertilised

(Kramer & Kozlowski 1979, Gordon & Faulkner 1992), and this may be influenced by the crop of male cones and weather conditions during pollination (Summers & Waddell 2004). Dry, windy conditions ensure a greater spread of pollen than wet weather. Therefore, in addition to annual variations in the size of the cone crop (Broome *et al*. 2007) the proportion of seeds with kernels will impose further variation on food availability and abundance.

Although cone removal from the trees by crossbills was not studied, it is worthwhile speculating on the difficulty of removing cones. Crossbills do this by biting through the peduncle and taking the cone to a stout branch. This allows the crossbill to manipulate the detached cone with its feet and bill and perhaps exert more leverage on the cone scales with the bill than on cones that are still attached to the tree. Lodgepole Pine cones are probably the most difficult; even North American Red Squirrels *Tamiasciurus hudsonicus* and Douglas Squirrels *T. douglasii* have difficulty in removing Lodgepole Pine cones from branches (Smith 1970). This is partly because they are sessile, and when groups of cones occur, the bases of cones grow beside one another, thereby protecting points of attachment of neighbouring cones. Further, there are spines on the apophyses of Lodgepole Pine cones (Smith 1970), which reduce the rate at which crossbills extract seeds from open Ponderosa Pine *Pinus ponderosa* and Table Mountain Pine *P. pungens* cones (Coffey *et al*. 1999). Of the conifer species used by crossbills in our study, larch had the thickest peduncles, so may be more difficult to remove than those with thinner peduncles. As well as considering the difficulty in removing a cone, crossbills have to consider the mass of the cone. Norway Spruce cones can weigh more than the mass of a crossbill, so would be difficult to handle if removed (Summers 2018). For the other conifers with smaller cones, cone removal is common when foraging (Newton 1972, RS pers. obs.).

The planting of non-native conifers has transformed the food base for seed-eating birds and mammals in Britain. In Highland Scotland, Sitka Spruce and Lodgepole Pine comprise over half of the area of conifer woodland. Scots Pine comprises approximately 30% and larches about 5% (Summers & Broome 2012). Although Sitka Spruce is the most profitable for crossbills, annual cone production is variable (Broome *et al*. 2007), which is an alternative form of defence against seed-eaters. By contrast, it is likely that Lodgepole Pine is a more regular producer of cones, though the production of male and female cones, plus pollination, will be determined by the weather at key times of the annual cycle.

Common Crossbills are sympatric with Scottish and Parrot Crossbills in Britain (Knox 1990, Summers *et al*. 2002). Similar studies on feeding rates of these latter two species are required to establish the relative importance on non-native conifers to these crossbills species, given their higher conservation importance relative to Common Crossbills (Eaton *et al*. 2015). The strong association that Scottish Crossbills have with Lodgepole Pine is particularly important; an association that is analogous to the association that Common Crossbills have with Sitka Spruces (Summers & Broome 2012). Given that Lodgepole Pine is currently being affected by Red Band Needle Blight *Dothistroma septosporum* (Brown & Webber 2008) and remedial action involves clear-felling infected stands, it is likely that there will be continuing change in the composition of the conifer seed resource for crossbills in Britain.

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Table 1. Mean values for samples of cones from different conifers. Standard deviations are in brackets. Lengths are in mm and energy content of kernels in kJ/dry g. The sample size for energy content was three for each species.

	Scots Pine	Lodgepole Pine	Norway Spruce	Sitka Spruce	Japanese Larch
Sample size	25	15	15	15	15
Cone dry mass (g)	5.7 (2.4)	3.6 (1.2)	22.7 (4.5)	7.7 (1.6)	3.1 (1.0)
Peduncle thickness	4.9 (0.7)	-	4.3 (0.7)	5.0 (1.3)	7.0 (0.9)
Cone length	44.7 (7.9)	36.9 (4.8)	114.9 (16.0)	79.1 (9.6)	32.1 (5.9)
Cone breadth	23.1 (3.2)	19.8 (3.0)	28.4 (1.4)	21.5 (2.5)	22.2 (2.5)
Number of seeds	27 (11)	26 (15)	184 (60)	267 (35)	73 (17)
Percent with kernel	50.8 (26.5)	37.4 (23.6)	39.9 (21.0)	76.3 (22.5)	33.1 (16.6)
Length of seed plus wing	17.8 (2.5)	11.7 (2.0)	16.2 (1.6)	10.5 (0.7)	11.3 (1.2)
Length of seed	4.56 (0.42)	3.50 (0.48)	4.58 (0.35)	3.08 (0.18)	4.40 (0.29)
Breadth of seed	2.45 (0.22)	1.78 (0.24)	2.40 (0.12)	1.70 (0.08)	2.59 (0.25)
Dry mass of seed (mg)	6.1 (1.5)	2.5 (0.1)	8.4 (1.9)	2.7 (0.3)	6.0 (1.1)
Dry mass of kernel (mg)	4.2 (1.1)	1.9 (0.6)	5.7 (0.7)	2.0 (0.2)	2.8 (0.6)
Percent seed coat	33.5 (3.2)	33.9 (3.1)	41.5 (2.9)	27.0 (1.4)	55.2 (8.1)
Energy content of kernel	26.4 (1.9)	24.9 (2.1)	30.7 (2.0)	28.9 (0.1)	29.4 (1.7)

Relationships between peduncle thickness (y) and cone length (x)

Scots Pine $y = 2.90 + 0.044\,x$ ($r^2 = 0.26$, $P = 0.004$)

Larch $y = 4.36 + 0.0825\,x$ ($r^2 = 0.30$, $P = 0.03$)

Relationships between number of seeds (y) and cone length (x)

Scots Pine $y = -18.9 + 1.03\,x$ ($r^2 = 0.58$, $P < 0.001$)

Lodgepole Pine $y = -16.3 + 1.64\,x$ ($r^2 = 0.34$, $P < 0.001$)

Norway Spruce $y = -208.1 + 3.41\,x$ ($r^2 = 0.83$, $P < 0.001$)

Sitka Spruce $y = 36.20 + 2.92\,x$ ($r^2 = 0.64$, $P < 0.001$)

Larch $y = 11.36 + 1.93\ x$ ($r^2 = 0.46$, $P = 0.006$)

Relationships between seed plus wing length (*y*) and cone length (*x*)

Scots Pine $y = 2.14 + 0.333\ x$ ($r^2 = 0.67$, $P < 0.001$)

Lodgepole Pine $y = -0.734 + 0.335\ x$ ($r^2 = 0.67$, $P < 0.001$)

Larch $y = 7.33 + 0.123\ x$ ($r^2 = 0.37$, $P = 0.015$)

Relationships between seed length (*y*) and cone length (*x*)

Scots Pine $y = 2.43 + 0.046\ x$ ($r^2 = 0.64$, $P < 0.001$)

Lodgepole Pine $y = 0.35 + 0.086\ x$ ($r^2 = 0.72$, $P < 0.001$)

Relationships between seed mass (*y*) and seed length (*x*)

Scots Pine $y = -0.00649 + 0.00277\ x$ ($r^2 = 0.64$, $P < 0.001$)

Lodgepole Pine $y = -0.00474 + 0.00206\ x$ ($r^2 = 0.67$, $P < 0.001$)

Norway Spruce $y = -0.00387 + 0.00269\ x$ ($r^2 = 0.24$, $P = 0.064$)

Sitka Spruce $y = -0.00297 + 0.00185\ x$ ($r^2 = 0.92$, $P < 0.001$)

Larch $y = -0.00574 + 0.00266\ x$ ($r^2 = 0.49$, $P = 0.0036$)

Table 2. Mean attributes of cones and seeds sampled in Scotland. Mean cone lengths, with standard deviations in brackets, were based on extensive sampling and are shown on the first line (from Summers 2002, Summers & Broome 2012 and unpublished data). Mean values were estimated from regression equations for cones from different conifers where these vary according to cone length (Table 1). No peduncle measurement was made for Lodgepole Pine, which is sessile. Scale thicknesses (apart from larch) were taken from Summers & Broome (2012). Masses are in dry mg, and lengths in mm.

	Scots Pine	Lodgepole Pine	Norway Spruce	Sitka Spruce	Japanese Larch
Cone length	40.9 (6.7)	41.3 (8.0)	115.7 (17.1)	69.2 (10.7)	25.7 (4.8)
Cone length in feeding trials	-	40.1	-	69.6	23.3
Peduncle thickness	4.7	Sessile	4.3	5.0	6.5
Scale thickness	2.12	1.81	0.32	0.11	0.27
Number of seeds	23	51	186	238	61
Length of seed plus wing	15.8	13.1	16.2	10.5	10.5
Length of seed	4.31	3.90	4.58	3.08	4.40
Mass of seed	5.45	3.29	8.45	2.73	5.96
Proportion kernel	0.665	0.661	0.585	0.730	0.448
Mass of kernel	3.62	2.18	4.94	1.99	2.67

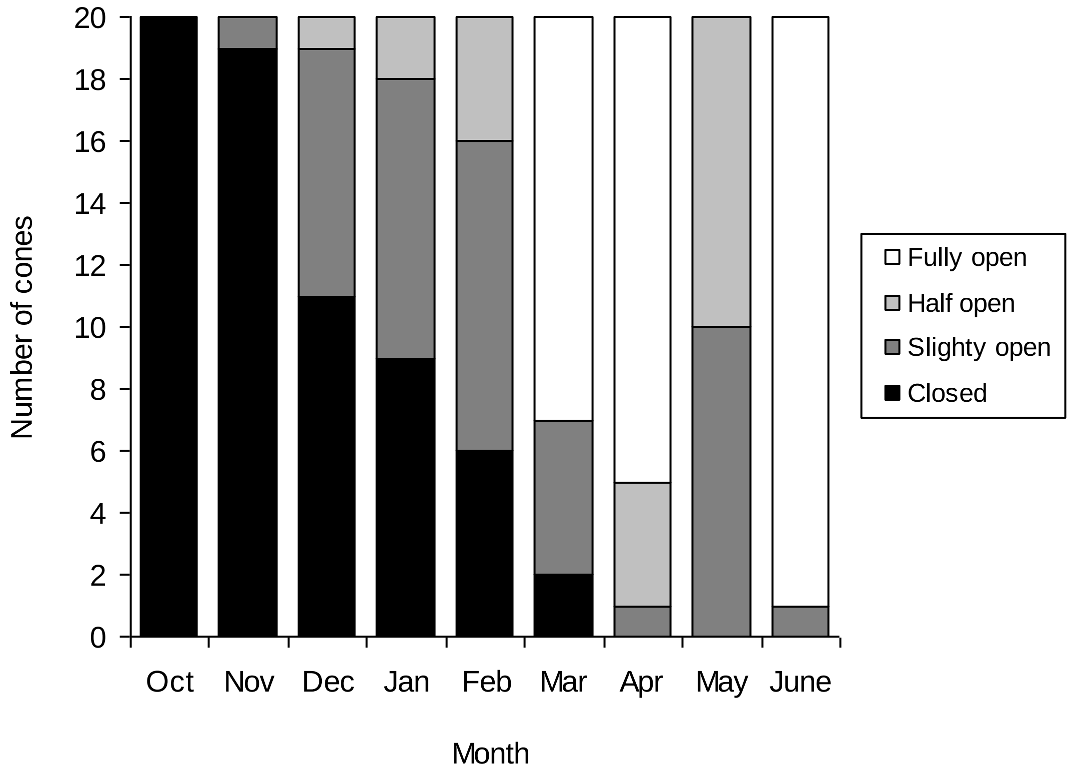
Table 3. Mean feeding and intake rates of Common Crossbills feeding on different conifers. Intake rates assume that each seed had a kernel, and if the proportion with kernels was as measured (Table 1). Median times are also given for larch, in brackets.

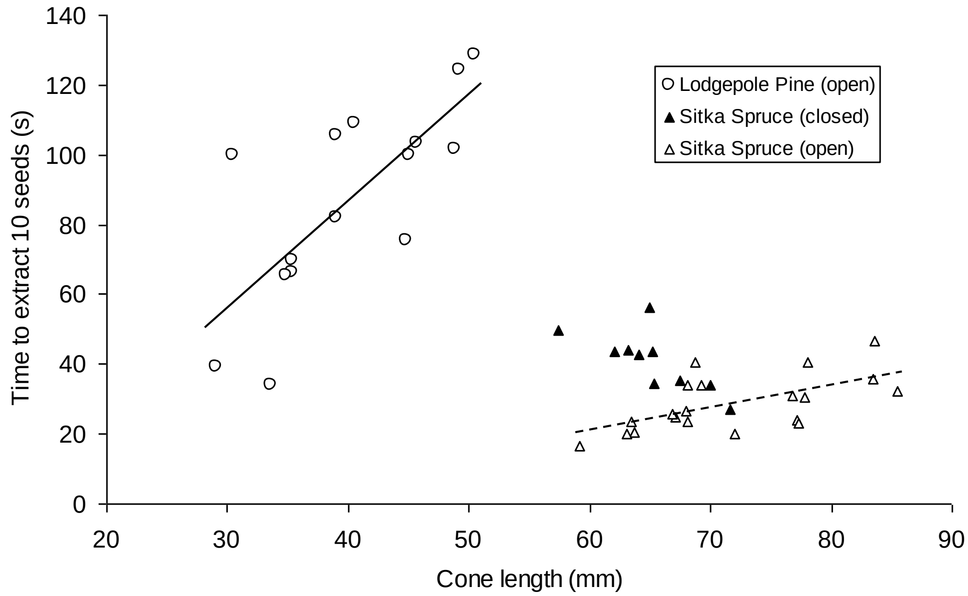
Conifer	Scales	Time to remove 10 seeds (s)	Intake rate – kernels in all seeds (mg/s)	Intake rate (kJ/s)	Intake rate – seeds with proportion with kernels as measured (mg/s)	Intake rate (kJ/s)
Japanese Larch	Open and closed	43.5 (35.8)	0.614 (0.746)	0.0180 (0.0219)	0.275 (0.334)	0.0081 (0.0098)
Sitka Spruce	Closed	41.1	0.484	0.0140	0.353	0.0102
Sitka Spruce	Open	28.7	0.693	0.0200	0.506	0.0146
Lodgepole Pine	Open	87.0	0.251	0.0062	0.166	0.0041

Legends for the figures.

Figure 1. The stage of opening of Lodgepole Pine cone scales at the start of each month, from autumn to summer.

Figure 2. The relationship between the time for Common Crossbills to remove 10 seeds and cone length for open Lodgepole Pines cones, and open and closed Sitka Spruce cones. The marginal and conditional r^2 values were the same for Lodgepole Pine (0.53). The marginal and conditional r^2 values for Sitka Spruce were 0.41 and 0.63 respectively. The regression equations are; y = -33.8 (se = 31.0) + 3.01 (0.76) x, (r^2 = 0.55, P = 0.0017) for Lodgepole Pine and y = -17.7 (se = 14.5) + 0.65 (0.20) x, (r^2 = 0.36, P = 0.005) for open Sitka Spruce cones.


Number of cones
20
18
16
14
12
10
8
6
4
2
0
Oct
Nov
Dec
Jan
Feb
Mar
Apr
May
June
Month
Fully open
Half open
Slighty open
Closed


140
120
100
80
60
40
20
0
20
30
40
50
60
70
80
90
Time to extract 10 seeds (s)
Cone length (mm)
Lodgepole Pine (open)
Sitka Spruce (closed)
Sitka Spruce (open)

620