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Seed availability and timing of breeding of Common Crossbills *Loxia curvirostra* at Sitka Spruce *Picea sitchensis* dominated forestry plantations

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In Britain the Common Crossbill *Loxia curvirostra* population has increased markedly in abundance and range with the maturing of the post-war forestry plantations. However, little published information exists on the breeding ecology of the species in these plantations. Crossbills were more abundant in years of high Sitka Spruce *Picea sitchensis* cone production in the upland forestry plantations of South Wales. The breeding season began early in the year with a median laying date of 13 February and declined after this peak with few nests initiated after April, when the availability of Sitka Spruce seeds declined. The modal clutch size was 3 eggs and an estimated 35% of nests produced fledged young. Most nest failures were associated with adverse weather. Our observations indicate ephemeral occupancy of Sitka Spruce forests as a consequence of variable seed availability, a peak in breeding activity determined by photoperiod and food supply and a low level of breeding productivity.

Key words: Crossbill, *Loxia curvirostra*, nesting success, forestry, Sitka Spruce

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Crossbills *Loxia curvirostra* were formerly rare, sporadic breeders in Wales but became established as regular breeders with the maturing of the post-war conifer plantations (Lovegrove *et al.* 1994). The second UK National Atlas Survey 1988–91 (Gibbons *et al.* 1993) documented a major increase in breeding Crossbills in Wales compared with the previous 1968–72 survey (Sharrock 1976). The coniferous forestry plantations of Wales are dominated by Sitka Spruce *Picea sitchensis* (56%), the species most suited to producing softwood timber in the Welsh topography and climate; the other main species in Welsh forestry plantations are Japanese/hybrid Larch *Larix kaempferi/hyb.* (15%), Norway Spruce *Picea abies* (7%) and Douglas Fir *Pseudotsuga menziesii* (7%), whilst Scots Pine *Pinus sylvestris* comprises just 3% of Welsh coniferous forestry (West & Thomas 2005).

Spruce, larch and Douglas Fir cones develop in the summer and start shedding seeds from autumn through to spring of the following year, whilst Scots Pine cones containing seed can remain on trees for several years (Philipson 1997). Spruces produce cone crops sporadically, typically with a 4-year period between mast crops, during which cone production is very low or absent (Broome *et al.* 2007). However, reports of spruce mast years in Britain over the period 1974–2001 suggest more frequent coning every 1 to 3 years (data from Shaw 1990, Petty *et al.* 1995, Bryce *et al.* 2005, Broome *et al.* 2007, McKenzie *et al.* 2007) and seven years of data (1993–1999) in Clocaenog Forest, Wales showed that Sitka Spruce produced some cones every year and good cone crops in two out of three years (Bryce *et al.* 2005). Scots Pine and larch also exhibit a variable pattern of coning, although their cone production tends to be more consistent than spruces (Summers & Procter 2005, Broome *et al.* 2007, Poncet *et al.* 2009 but see also Bryce *et al.* 2005). In the Sitka Spruce dominated plantations of Wales, Crossbills face large fluctuations in seed availability both seasonally and across years.

Immigration and cone production are major factors influencing the number of Crossbills breeding in Welsh forests. Crossbills are 'irruptive' migrants and periodically large numbers seeking areas of seed abundance

arrive in the UK, mainly in June and July, from the boreal regions of the continent (Newton 2006a,b, Marquiss *et al.* 2012). If they find sufficient cones in the forests many will remain and breed the following spring (Marquiss & Rae 1994). In years when the Sitka Spruce cone crop is large, the scale of any Crossbill population increase will depend on the number of immigrants, and when the Sitka Spruce cone crop is low, Crossbills leave to seek conifer seeds elsewhere (Summers 1999). As Spruce coning is synchronous across the whole of Britain (Broome *et al.* 2007), most Crossbills will leave Wales in the years when cones are scarce and any that remain must exploit different, less abundant conifer species such as larch and pine.

Across their Eurasian breeding range, populations of Crossbills can breed in every month of year to coincide with seed production in the local conifers (Newton 1972, Nethersole-Thompson 1975). However, there is little information on the breeding season of Crossbills in the post-war conifer plantations in the uplands of northern and western Britain where spruce trees predominate. There are few published studies on the breeding success of Crossbills in plantation forests in Britain, though Marquiss and Rae (1994) reported high failure rates and low productivity in mixed forestry. In this study of Crossbills in Welsh forestry plantations, we report on changes in breeding abundance in relation to Sitka Spruce coning, examine the timing of breeding in relation to Sitka Spruce seed availability and present data on breeding success of Crossbills breeding in Sitka Spruce dominated plantations.

METHODS

We studied breeding Crossbills during five years (2008–12) at Sitka Spruce dominated plantations in South Wales. Most of our survey work and nest searches were conducted in three forest areas: Carno, a 27 ha study site within a 77 ha single-age plantation of Sitka Spruce, with some Scots Pine and larch, altitude 415 m asl; Ystrad, a 119 ha site within a 339 ha mixed-age plantation of Sitka Spruce, with some Scots Pine, larch and Norway Spruce, altitude 335 m asl; Beili, a 109 ha site within a 805 ha mixed-age plantation of Sitka Spruce with some larch and Scots Pine, altitude 475 m asl.

We undertook fieldwork mainly during November–June, with fewer visits to the forests in July–October. We used the number of Crossbill nests found each year as an Index of Crossbill abundance in the forests, as the time we spent searching for nests during the peak nesting period in January–March was broadly similar across years, i.e. most weekends. The Sitka Spruce cone crop was assessed in January using an Index Scale of 0–10 (following Petty *et al.* 1995), and in 2011/12 the cone crop was assessed monthly from October–May. In addition, in 2011/12 a sample of 10 cones were collected each month (except December) from a single tree from November–May and seeds were extracted and counted after drying each cone in an oven to open the scales.

We made observations on the behaviour of Crossbills, especially noting signs of breeding activity and searching for nests. On finding nests, we noted clutch or brood size, recorded chick development stage by photography and monitored breeding success where it was practical to do so. We monitored 31 nests making an average of 2.8 visits per nest (range 2–6 visits). We used photographs of chicks to estimate their age in days and hence the clutch hatching date. We estimated laying dates (first-egg date) either by finding nests during egg-laying (one egg laid each day) or by back-dating from hatching dates (assuming hatching 13 days after the last egg was laid). We also encountered fledged broods during our field work, which enabled us to estimate approximate laying dates for additional pairs whose nests we did not find. However, these were not included in our analysis but have been reported in the results to show that some nests were initiated earlier and later than those that we found.

Observed breeding success was recorded for nests of known outcome, and we used the nest survival model in MARK 5.1 to estimate daily survival rate (DSR) of nests (White & Burnham 1999, Dinsmore *et al.* 2002). We estimated the cumulative probability of a nest surviving the 40-day egg and nestling stages (3 days to lay a modal clutch of three eggs, 14 days incubation and 23 days fledging period) by raising the DSR to the power 40.

RESULTS

Sitka Spruce trees held large numbers of cones in January in 2008, 2011 and 2012, with low to very low numbers of cones in 2009 and 2010. Crossbill abundance closely reflected Sitka Spruce cone production, with more nests found in years of high cone availability (Figure 1). Seed availability also varied within a season because the number of cones diminished through windfall and removal by foraging animals; in November 2011–January 2012 we judged Sitka Spruce blocks in the study plantations to have a cone crop index of 8, but by early February this had declined to 7 and by late

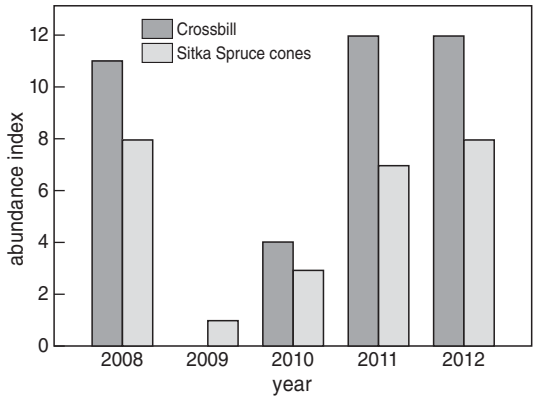

Figure 1. Abundance indices for Crossbill numbers and Sitka Spruce cones in 2008–12; an index value of 1–2 = very low cone production, 3–4 = low, 5–6 = medium, 7–8 = high and 9–10 = very high (based on Petty *et al.* 1995).

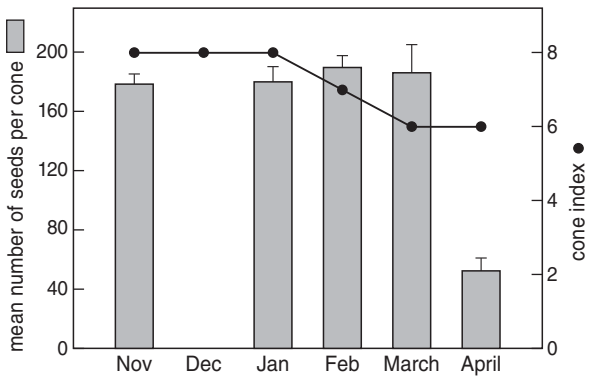

Figure 2. Mean number of seeds per cone (+SE bars) from ten cones sampled each month (November 2011–April 2012) from the same tree. No cones were collected in December. Cone availability (cone index) over the same period is indicated by the solid line.

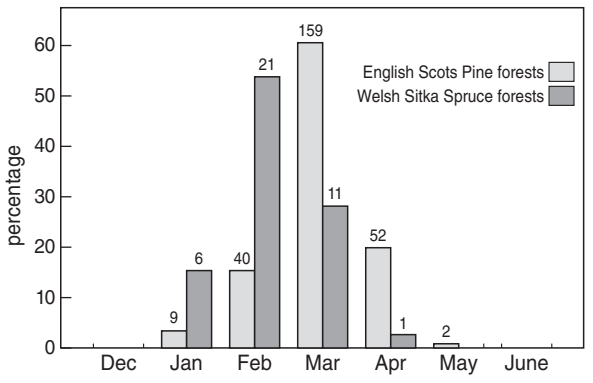

Figure 3. Egg-laying dates for Crossbill nests found in Welsh Sitka Spruce forests and English Scots Pine forests). Value above columns is the number of clutches laid in each month (data from Wales, this study: England: Nethersole-Thompson 1975).

March had further declined to 6 (Figure 2). In addition to a decline in the number of cones, seeds are shed from autumn onwards, though we only found a considerable drop in the number of seeds per cone in April, when the average number of seeds per cone declined from 186 (SE 18) in March to 53 (SE 8; Figure 2).

Our nest records indicated that Crossbills in Sitka Spruce forests lay from January to April with egg-laying peaking in February and a decline in nesting activity after March (Figure 3). The median egg-laying date was 13 February (n = 39 nests; range 11 January to 1 April). Additional sightings of recently-fledged broods indicated an extended breeding season, with early clutches laid in December and late clutches in July. Furthermore, we found evidence of possible autumnal breeding, based on a sighting of an independent juvenile in early February.

The modal clutch size was 3 eggs (n = 32 clutches; mean 3.2; range 2 to 4 eggs). Observed nesting success was low, with only 31.3% of nests producing fledged young (n = 16 nests), with a mean fledged brood size of 2.4 chicks (n = 5 nests). However, using daily survival rates at monitored nests, our calculated nest survival over a 40-day nesting period was 0.35 (SE = 0.11, 95% confidence limits = 0.15–0.56, n = 31 nests; Table 1), indicating that each breeding pair produced an average of 0.8 fledglings (95% confidence limits = 0.4–1.3 fledglings). In the 11 cases of known nest failures, chicks were found dead at four nests, all with seeds in their crop, suggesting chilling rather than starvation as the cause of death, one clutch was destroyed by wind, two clutches were deserted after egg reduction probably as a result of strong wind, two other clutches were deserted without any egg reduction and eggs/chicks disappeared at two other nests possibly as a result of predation.

Table 1. Estimated daily survival rate of nests, survival over a 40-day nesting period (SE) and 95% confidence limits of nest survival estimates for the years 2008, 2010–12 and the whole study period combined.

Year	Daily survival rates	Nest survival (SE)	95% CL	Number of nests
2008	0.96063	0.20 (0.16)	0.01–0.55	8
2010	0.96142	0.21 (0.33)	0.00–0.81	2
2011	0.98333	0.51 (0.20)	0.13–0.81	11
2012	0.97404	0.35 (0.21)	0.04–0.71	10
Overall	0.97399	0.35 (0.11)	0.15–0.56	31

DISCUSSION

Variation in Crossbill abundance in relation to the size of the Sitka Spruce cone crop supports previous analyses (Nethersole-Thompson 1975, Watson *et al.* 2009) and indicates high levels of immigration and emigration, even outside 'irruption years'. The geographical origin of the immigrant Crossbills is not known; though it is likely immigrants from the continent arrive in Britain in most years, possibly from the same boreal forest regions as in irruption years (see Newton 2006a,b, Marquiss *et al.* 2008, 2012). In the poor cone year of 2009 most Crossbills left the Welsh forests. In 2010, Sitka Spruce cone production was also low but larches produced a bumper crop of cones, which enabled some Crossbills to breed in mixed plantations. Sitka Spruce produced large numbers of cones in two consecutive years in 2010/11 and 2011/12, and it is likely that many Crossbills remained in the forests between these two years.

In Britain, published information on the breeding season of Common Crossbills comes mainly from populations occupying pine plantations in eastern and southern England that were established following major invasions in the early 20th century. In these forests the breeding season can extend from December to June, with the main season between February and April and egg-laying peaking in March (Figure 3; Newton 1972, Nethersole-Thompson 1975). Crossbills in Welsh Sitka Spruce forests bred earlier than those in pine plantations in England. Peak egg-laying periods correspond to differences in the accessibility of seeds for Common Crossbills in Sitka Spruce and Scots Pine forests; seeds are more easily obtained from Sitka Spruce cones in February than closed pine cones, which do not open until March (Marquiss & Rae 1994, Summers & Broome 2012).

The apparent sharp decline in nest initiation from April onwards partly reflects the fact that we made fewer nest searches after March, though breeding activity steadily declined after the peak in February and there was a marked reduction in the number of Crossbills seen in the forests in April, suggesting seasonal emigration. Breeding activity declined in tandem with seed availability resulting from a combination of reduced cone and seed availability. The number of cones on Sitka Spruce trees declines from the time of their maturation in September as they are removed by foraging animals and birds, especially Grey Squirrels *Sciurus carolinensis*, Great-spotted Woodpeckers *Dendrocopos major* and Crossbills in our study plantations. Furthermore, the availability of seeds in the remaining cone crop also diminishes through shedding and removal by foraging birds, especially Coal Tits *Periparus ater*, Siskins *Carduelis spinus* and Crossbills.

In Sitka Spruce plantations seed availability reaches its nadir in June to August, and this is the period when adult Crossbills typically begin their post-breeding moult and young birds their juvenile moult; moult is normally completed by October in both age classes but can be protracted or suspended (Svensson 1992, Jenni & Winkler 1994). However, some late-hatched Crossbills from summer nests may not complete their juvenile moult and still exhibit juvenile plumage in winter. The complex moult pattern of Crossbills means that some sexually mature, breeding birds can retain juvenile plumage (Jardine 1994). Thus, the bird we saw in juvenile plumage in February could have been from a late summer nest and autumnal nesting by Crossbills in Wales has yet to be proved conclusively. A study in Deeside, Scotland, in an area of mixed species conifer plantation, also found no evidence of autumn breeding, with the peak egg-laying period in March (Marquiss & Rae 1994).

It is believed that Crossbills can breed opportunistically in response to food supply (Newton 1972, Cramp & Perrins 1994), although evidence for this is limited and relates mainly to geographical differences in the timing of cone production in conifers. Sitka Spruce seed availability was highest from November to March, yet we found no proof of nesting prior to December and the main peak of breeding was in February; suggesting that something other than food availability influences the onset of breeding. It seems likely that photoperiod also plays an important role, as testes development and the production of reproductive hormones is linked to increasing daylength with a regular seasonal pattern like other temperate zone birds (Tordoff & Dawson 1965, Hahn 1998), with some opportunistic capability for breeding at times of high food production overlain on this basic pattern (Benkman 1990, Hahn 1998). Crossbills in Sitka Spruce plantations usually begin nesting after the winter solstice during a period of increasing daylength and cease breeding when seed availability declines in spring, whilst breeding does not normally occur in autumn and early winter, even in the presence of abundant food (Deviche & Sharp 2001).

Breeding success was low at 35%, but within the typical range for finches, as a previous study has shown a nesting success rate of 24–38% for four finch species, Greenfinch *Carduelis chloris*, Linnet *C. cannabina*, Bullfinch *Pyrrhula pyrrhula* and Chaffinch *Fringilla coelebs* (Mayer-Gross *et al.* 1997). Low breeding success was also reported for Crossbills breeding in mixed forestry

in north-east Scotland, where only one of six egg-laying pairs were successful in fledging chicks (17%) and estimated productivity was less than 0.5 young per pair (95% confidence limits = 0.2–1.1 young; Marquiss & Rae 1994). Nest failure was associated with adverse weather particularly cold, damp conditions, which were probably responsible for the death of four broods, and strong winds which resulted in the failure of three clutches.

Crossbills are now considered to be a 'resident' species in Wales and there are consistent annual sightings of the species in many large forests (Green 2002). Cone production is highest in older, larger Sitka Spruce trees (Holimon *et al.* 1998), thus spruce-dominated forestry plantations require stands of mature trees to retain a resident population in years of low seed availability.

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SAMENVATTING

De Kruisbek *Loxia curvirostra* heeft zich in Groot-Brittannië sterk uitgebreid met het ouder worden van de bossen die na de Tweede Wereldoorlog hier zijn aangeplant. De soort is sindsdien ook fors in aantal toegenomen. Toch is er weinig bekend over de broedbiologie van Kruisbekken in dergelijke bossen. In dit artikel wordt de broedbiologie van de soort in bosaanplantingen in Zuid-Wales onderzocht. De soort was het talrijkst in jaren met een hoge productie aan kegels van de Sitkaspar *Picea sitchensis*. De mediane datum waarop het eerste ei werd gelegd, was 13 februari. In april, met het afnemen van de hoeveelheid zaden in de kegels, waren er nog amper vogels die gingen broeden. De meest voorkomende legselgrootte was drie eieren. In 35% van de nesten vloog ten minste één jong uit. Het mislukken van nesten viel vaak samen met slecht weer. Het onregelmatig voorkomen van de Kruisbek in de aanplant van Sitkaspar had te maken met de grote variatie in zaadproductie, een korte broedperiode onder invloed van daglengte en voedselaanbod, en een gering broedsucces. (JP)

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