Ringing & Migration (2011) **26**, 64–70

Seasonal patterns of breeding, moulting, and body mass variation in Pyrenean Common Crossbills *Loxia curvirostra curvirostra*

DANIEL ALONSO and JUAN ARIZAGA*
Aranzadi Ringing Scheme, Aranzadi Sciences SocietyZorroagagaina 11, E-20014 Donostia, Spain

The aim of this study was to investigate the relationship between breeding, moulting and fuel load of Common Crossbills *Loxia curvirostra curvirostra* inhabiting a Scots pine Pyrenean forest. Data were collected from two locations (Sierra de Uztarroz and Bigüezal) in northern Iberia by systematic mist netting between 2000 and 2008. Breeding females were detected in most months of the year except June, October and November, and with two main peaks, one in late winter (March), and another in the summer (August). Between years, reproduction was more variable in some months than in others, particularly in summer months. This suggests that breeding during the summer was more likely to be influenced by external factors and relatively opportunistic compared to winter breeding. Moulting adults of both sexes were captured during almost every month with a unimodal pattern peaking in June, similar to the pattern described for Mediterranean Crossbills. Moulting did not overlap with breeding, and our data do not support suspended moult patterns. Mean fat scores overall were low and, as was the case for body mass, showed little month-to-month variation.

The Common Crossbill *Loxia curvirostra* is a widespread passerine of Holarctic conifer forests (Newton 1972). As a paradigm of high specialisation, Crossbills feed almost exclusively on coniferous seeds. Therefore, their lives are governed by the time when conifers crop, including breeding (Benkman 1990, Clouet 2000), moulting (Hahn 1998), dispersion (Senar *et al* 1993, Newton 2006) and morphology (Marquiss & Rae 2002, Alonso *et al* 2006). Our aim in this study was to describe the seasonal patterns of breeding, moulting and fuelling of a Pyrenean population of Common Crossbills *L. c. curvirostra* living in a Scots pine *Pinus sylvestris* forest.

To rear broods successfully, birds normally breed when food availability peaks, which at high and temperate latitudes is commonly during spring (reviewed by Podulka *et al* 2004). Although, within their entire distribution range, Crossbills breed during the whole annual cycle (Newton 1972), the period for breeding in particular areas is geared to the availability of seeds when the conifer cones open or, to a lesser extent, become ripe (Benkman 1990). Northern European Crossbills depend mostly on spruce *Picea* species and the exploitation of other conifers tends to be marginal (normally Scots or mountain pine *Pinus uncinata*; Cramp & Perrins 1994). In contrast, southern European Crossbills feed on several pine species. Pine-eating Crossbills have been shown to breed during the winter, mainly from December until March/April, when cones open (Cramp & Perrins 1994), with additional second broods during the autumn (Clouet 2000, P. Edelaar pers comm). Crossbills inhabiting the Pyrenees are documented to occupy both mountain and Scots pine forests equally (Génard & Lescourret 1987), but data relative to breeding patterns of Scots-pine-associated Crossbills are scarce. Scots and mountain pines share some similarities with respect to cone size and crop period, so Crossbills in areas of Scots pine should be expected to show similar breeding periods to Crossbills in mountain-pine areas. At least two peaks might be expected (Clouet 2000): a main peak when cones open, in winter (DA pers obs) and another one when cones are ripe in summer or autumn. Alternatively, Scots-pine Crossbills may breed once a year, with a peak when cones open (*ie* during winter), as reported in regions further north (Cramp & Perrins 1994).

Although Crossbills are one of the few birds that moult even while breeding (reviewed by Newton 1972; for more recent data see also Cramp & Perrins 1994), normally most adults seem to start their moult once fledglings have left the nest (Cramp & Perrins 1994). Most data on the moult of European Crossbills come mainly from British, central and northern European populations, including Russia (reviewed by Cramp & Perrins 1994; for more recent publications see also Noskov *et al* 2003,

* Correspondence author
Email: jarizaga@aranzadi-zientziak.org

Iovchenko 2003). In these areas, Crossbills start to moult by June/August, and finish by September/November. Conversely, relatively few data are reported for the southern European populations. Massa (1987) observed that these populations moult regularly from May to September. Pyrenean Crossbills have been reported to behave more like Mediterranean (southern European) than northern European Crossbills (Senar *et al* 1993, Clouet 2000), so the timing of their moult may be more similar to Mediterranean than to northern European populations.

Adult Crossbills start to moult after the winter breeding period. Moulting is then suspended during spring/summer (when second broods are reared), to be resumed from August onwards (Cramp & Perrins 1994). This phenomenon has not been analysed in detail in southern Europe (Massa 1987). If it is common, we should expect two chief moulting peaks in a year, one before and another one after the second main breeding period. In contrast, if this type of moult is rare, we should expect a single moulting peak, after the main breeding period in winter.

Seasonally associated variation in body mass and fat reserves can be indicative of how birds manage their fuel loads and energy stores, and can be used to gain insights into the costs of different life processes. Breeding birds must face extra energy costs to rear their broods; therefore, fuel load may be predicted to be lower during this period. A similar pattern may be predicted for moulting birds, since a proportion of their energy budget would go to growing new plumage (Jenni & Winkler 1994, Schaub & Jenni 2000). However, moulting birds have been shown to be heavier than non-moulting ones, mainly since growing feathers contain blood (hence being heavier than older ones), and because the amount of body water is higher (Newton 1968). In this case, a peak of body mass should not be linked to one of fuel load (fats).

METHODS

Sampling area and protocol

Crossbills were captured at two locations 25 km apart in the west Pyrenees, northern Iberia: Bigüezal (42°40'N 1°07'W; 1,096 m above sea level [asl]), and Uztárroz (42°52'N 1°00'W; 1,383 m asl). Vegetation in these sites is dominated by large forest areas of Scots pine, the dominant tree species from 1,000 to 1,600–1,700 m asl in southern-facing slopes of the west Pyrenees (Loidi & Báscones 1995). Other conifers near this area are the mountain pine (restricted to a relatively small patch of *c* 25 km^2 to the northeast of Uztárroz) and the European silver fir *Abies alba*, which appears mixed with beech *Fagus sylvatica* in humid areas of valley bottoms.

Crossbills were mist netted periodically in both localities (one sampling day per week), for 4 h starting at dawn, with the same number of mist nets within each site. Mist nets were placed around sites at which birds gathered to ingest minerals (salt deposits in Bigüezal, a cattle-rail composed of stones in Uztárroz). Data used here were collected between June 2000 and May 2008.

Once captured, each bird was ringed and its sex (Svensson 1998) and EURING age code were assigned: fledglings or juvenile birds with entire plumage comprising juvenile feathers, code 3J; first-year birds, code 3 (birds in their first calendar year of life after having performed a partial, or exceptionally a complete, post-juvenile moult: *ie* 3J become 3 after the post-juvenile moult); adults, code 4 or higher. Though Crossbills with juvenile feathers can show sexual dimorphism in colour and pattern of contour plumage (Edelaar *et al* 2005), we were unable to determine the sex of a proportion of juvenile-feathered Crossbills, so sex was not considered in biometric analyses pertaining to juvenile birds (code 3J or 3). We measured tarsus length ($\pm$ 0.1 mm), body mass (Tanita digital balance, $\pm$ 0.1 g), fat scores (scaled from 0 to 8, following Kaiser 1993; $\pm$ 0.5), presence or absence of active moult in adult birds, and the presence of brood patch in females (scored from 0 to 5, following Pinilla 2000: 0, no brood patch; 1,incipient developing brood patch; 2, almost-grown brood patch; 3, completely developed brood patch; 4, regressing brood patch; 5, refeathering brood patch; scores 2 and 3 are indicative of incubating period). All measurements were recorded by a single author (DA).

Data analysis

Overall, 2,046 captures were made (Table 1), comprising 1,791 different Crossbills and 255 (12.5%) recaptures. We used months as the unit of time for the analysis. To avoid repeat measurements on the same individuals within a time unit, data on recaptures within the same month of that year were removed from the data set.

We calculated the proportion of incubating adult female birds (birds with brood patch scores 2 or 3) during the whole annual cycle. Birds in their first calendar year of life (code 3J or 3) were removed from the data set because, depending on their hatching dates, they may or may not breed in their first calendar year of life (Cramp & Perrins 1994; see Results for further details). Moreover, we calculated the proportion of moulting Crossbills (only for adults). For this analysis, sexes were considered separately. Frequencies were compared with chi-square contingency tables.

Table 1. Number of captures of Common Crossbills (each bird considered only once per month within the same year). Birds aged as 3J were not distinguished from those aged as 3 in 2000 and 2001.

Year	Age (EURING code) 3J	3	4 or higher	Total
2000	0	51	36	87
2001	0	20	55	75
2002	11	56	164	231
2003	9	9	168	186
2004	26	13	166	205
2005	10	12	85	107
2006	28	133	243	404
2007	66	87	268	421
2008	30	23	277	330

Finally, we analysed how size-corrected body mass and fat scores varied among months for each sex. In both cases only adults were considered. We used tarsus length to correct for body size (Pascual & Senar 1996, Senar & Pascual 1997) by calculating an index of body mass/tarsus length. Data on body mass/tarsus length fitted a normal distribution (Kolmogorov–Smirnov [K–S] test, $P > 0.05$ for each sex), so parametric procedures were used (a two-way ANOVA on body mass/tarsus length, with sex and time – months – as factors). In contrast, fat scores did not fit a normal distribution (K–S test, $P < 0.001$ for each sex), so for these data a Kruskal–Wallis [K–W] test for designs of factors was used (we performed a two-way ANOVA on ranks of fat scores and calculated a chi-square for each variable, taking the sum of squares into account; Sokal & Rohlf 1995). Student's t-tests or Mann–Whitney U tests were used for two-way comparisons. SPSS v.15.0 for Windows was used for statistical analyses; means are given ± standard error (SE).

RESULTS

Breeding

Breeding Crossbills (female adults with an almost or fully grown brood patch) were detected during practically the whole annual cycle, except in June and October–November (Fig 1). The proportion of breeding birds varied between months, whether compared by averaging years for a given month (K–W test: $\chi^2_{11} = 33.630$, $P < 0.001$), or by pooling years into a single sample for each month (contingency test: $\chi^2_{11} = 31.152$, $P = 0.001$). Seasonally associated variation in the proportion of breeding females followed a similar pattern for both data sets, with a main peak in March (when, for the averaged analysis, more than 80% of captures were breeding), and a smaller peak (nearly 50% breeding) in August. In the months with no breeding females (June, October and November) there were fewer captures overall, despite the fact that the sampling effort remained constant for the whole annual cycle (Fig 2). This suggests that population size during these months must be very low in the study area.

The proportion of years in which breeding birds were found varied between months ($\chi^2_{11} = 45.636$, $P < 0.001$; Fig 3), and the likelihood for breeding was more

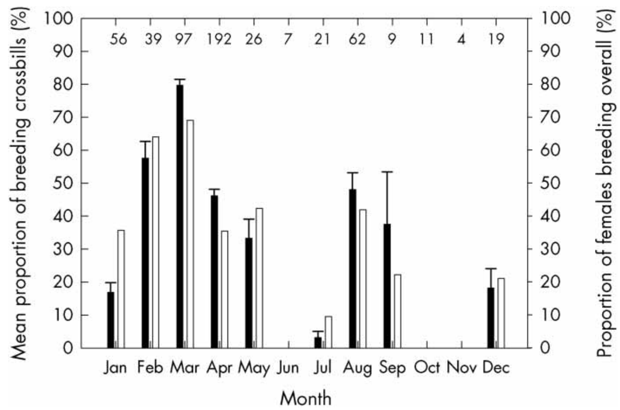

Figure 1. Percentage (± SE) of adult female Crossbills with a developing or fully formed brood patch (scores 2 or 3) and classified as breeding females. Black bars, mean percentage of breeding birds in each month; white bars, percentage of breeding birds pooled across years. Total sample sizes of adult females are shown below the top axis.

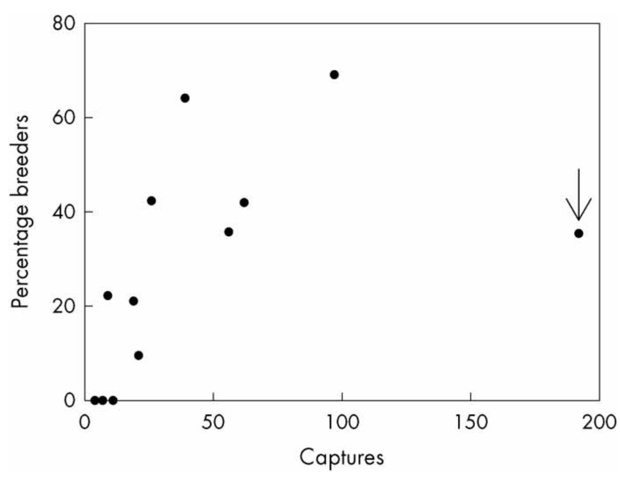

Figure 2. Relationship between the monthly number of captures and the percentage of breeding females overall (Pearson's correlation: $r = 0.498$, $P = 0.099$). By excluding April (arrow), the relationship becomes significant ($r = 0.819$, $P = 0.002$).

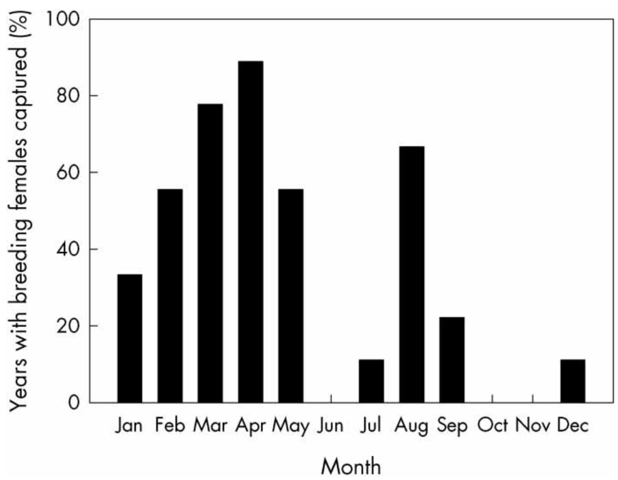

Figure 3. Percentage of years by month in which breeding activity was detected. Data are from 2000–08.

variable during some months than during others. In particular, breeding females were present in more than 60% of the study years for the months of August, March and April, whilst in July, September and December this proportion was very low (<20%).

A small fraction of fledged Crossbills (code 3J) were captured with a well-developed brood patch (0.02%), while for Crossbills identified as age code 3 (*ie* in first calendar year, with both juvenile and post-juvenile feathers), this proportion rose to 5.6% (Table 2). Breeding Crossbills aged as 3J or 3 were first captured as early as March. In both cases, sexes were pooled.

Moulting

Moulting adult birds (with growing flight feathers, including wing and tail feathers) were captured during most months of the year, with the only exceptions being February and December (Fig 4). Both sexes had a similar moult pattern with respect to the monthly distribution of birds in moult ($\chi^2_9 = 11.307$, $P = 0.240$), with a single peak in June, when more than 90% of adult birds were moulting. This peak is situated between breeding periods and, as shown in Fig 5, the small overlap between moult and breeding was due to Crossbills that were either starting or finishing their moult.

Body mass and fat scores

Overall, body mass in relation to body size varied with time, but not with sex (sex: $F_{1,\ 1,217} = 1.631$, $P = 0.202$; month: $F_{11,\ 1,217} = 5.118$, $P < 0.001$; month × sex: $F_{11,\ 1,217} = 1.682$, $P = 0.072$). Nevertheless, a *post hoc* analysis (pairwise comparisons, Tamhane's test, graph not shown) indicated that month-to-month variation was small. Crossbills did not have much fat (mean fat score 0.7 ± 0.1 in a scale from 0 to 8), and fat scores varied only among months and not in relation to sex (sex: $\chi^2_1 = 2.137$, ns; month: $\chi^2_{11} = 63.810$, $P < 0.05$; month × sex: $\chi^2_{11} = 18.092$, ns). However, there were no significant differences between months in *post hoc* analyses.

In months when the breeding activity was at a maximum (March and August), there was no significant difference between breeders and non-breeders in body mass relative to body size (Table 3); however, breeding birds in August had significantly lower fat scores than non-breeders (Mann–Whitney U = 251.0, $P = 0.002$; Table 3).

Moulting Crossbills had a similar mean body mass relative to body size than non-moulting Crossbills (data from May to July), but lower fat scores (Mann–Whitney U = 1188.5, $P = 0.030$; Table 4).

DISCUSSION

Breeding

Crossbills bred during almost the whole annual cycle, except in June and October–November, with two main breeding attempts a year: the first in late-winter/spring, with a peak in March, and the second one during late-summer/autumn, mainly in August. The sampling method was not likely to affect the result because sampling effort was kept constant throughout the year; furthermore,

Table 2. First-year female Crossbills with a fully developed brood patch (breeders) as a percentage of all first-year females captured within each month of the annual cycle, before and after the post-juvenile moult. Total sample sizes are given in brackets.

Age code	Jan	Feb	Mar	Apr	May	Jun	Jul	Aug	Sep	Oct	Nov	Dec
3J (before moult)	–	–	3.7	1.0	0.0	50.0	0.0	0.0	0.0	0.0	0.0	0.0
			(27)	(105)	(8)	(2)	(11)	(14)	(6)	(4)	(1)	(2)
3 (after moult)	–	–	8.3	0.0	33.3	20.0	2.2	2.5	6.1	10.8	5.2	7.5
			(12)	(51)	(6)	(10)	(46)	(80)	(33)	(37)	(39)	(94)

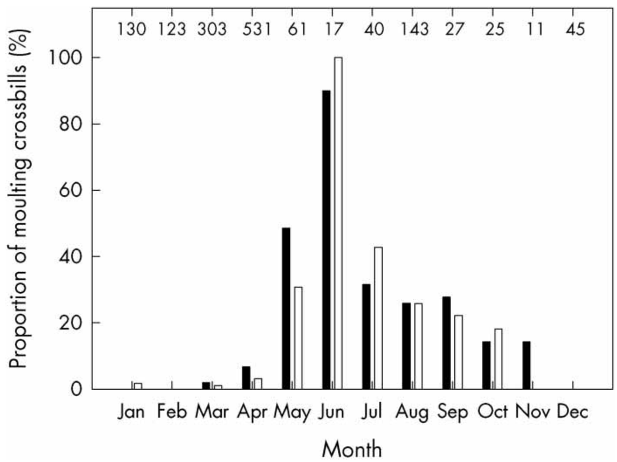

Figure 4. Percentage of adult Crossbills moulting in each month of the annual cycle. Sample sizes are shown for each month below the top axis. Males, black bars; females, white bars.

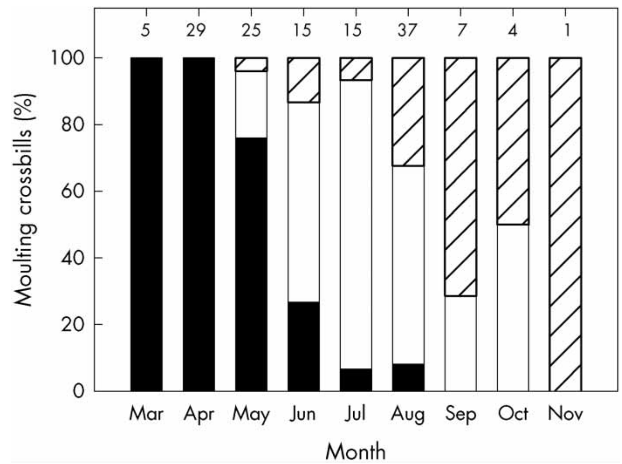

Figure 5. Percentage of moulting adult Crossbills in each month that were starting moult (growing primary feather P1–3; P1 is the innermost one; black bar), in the middle stage (growing P4–6; open bar) or finishing moult (growing P7–9; vestigial P10 not considered; hatched bar). Sample sizes for each month are shown below the top axis.

Crossbills were much less abundant (no visual contacts, calls not heard) during months with few captures (DA pers obs). This breeding pattern is similar to that observed by Clouet (2000) in mountain-pine-associated Pyrenean Crossbills, as well as in some other pine-associated Mediterranean populations (Clouet 2000). Conversely, northern European Crossbills, even pine-seed eaters, typically lack a breeding peak in late summer (reviewed by Cramp & Perrins 1994). This difference between northern and southern European pine-associated Crossbills could be due to the fact that northern European Crossbills will experience a more marked decrease of photoperiod in late summer, which may hinder a second breeding attempt in autumn (Hahn 1998). Differences between northern and southern Europe in the timing of seed ripening could also be an important factor.

Reproduction was less likely to occur in some months than others, as indicated by annual variation in breeding in particular months. This phenomenon was particularly evident for the summer/autumn breeding period, suggesting that breeding at this time may be more influenced by external factors and therefore more opportunistic than the winter breeding period (Hahn 1995, 1998). In years with low food availability, only a small fraction of the total adult population may be able to breed (Svärdson 1957). Furthermore, it is likely that a significant proportion of the population may be absent from the area for a long time in years in which seeds may be scarce (Génard & Lescourret 1987). Although southern European pine forests generate more stable cone crops than northern European forests (Senar *et al* 1993, Clouet 2000), yearly fluctuations in crop size may occur with Scots pine (Summers & Proctor 2005). Such fluctuations would give rise to invasions into other areas with higher food supplies. In support of such a hypothesis, a bird ringed in July 2002 in Bigüezal (Pyrenees) was recaptured in September 2006 in a small patch of Aleppo pine *Pinus halepensis* at Falces (Ebro Valley) 60 km away, and a bird

Table 3. Variation in body mass and fat score between breeding and non-breeding female Pyrenean Crossbills. Sample sizes are given in brackets.

		Body mass/tarsus length		Fat	
Period	Status	Values	Statistics	Values	Statistics
March	Breeding	1.857 ± 0.017 (58)	$t_{84} = 1.065$	0.8 ± 0.1 (56)	$U = 693.5$
	Non-breeding	1.823 ± 0.025 (28)	$P = 0.290$	0.7 ± 0.1 (28)	$P = 0.307$
August	Breeding	1.793 ± 0.020 (23)	$t_{53} = 0.854$	0.4 ± 0.1 (26)	$U = 251.0$
	Non-breeding	1.771 ± 0.017 (32)	$P = 0.397$	0.8 ± 0.1 (34)	$P = 0.002$

Table 4. Variation in body mass and fat score between moulting and non-moulting adult Pyrenean Crossbills. Data are from May–July. Sample sizes are given in brackets.

	Body mass/tarsus length		Fat	
	Values	Statistics	Values	Statistics
Moulting	1.825 ± 0.019 (48)	$t_{98} = 0.833$,	0.6 ± 0.0 (53)	$U = 1188.5$,
Non-moulting	1.800 ± 0.022 (52)	$P = 0.407$	0.8 ± 0.0 (58)	$P = 0.030$

ringed in June 2001 also in an Aleppo pine forest in Tauste (Ebro Valley) was recaptured in Bigüezal (Pyrenees) in March 2004 (96 km). Movement over such relatively short distances may explain why Crossbills in our study population did not accumulate large fat loads before moving elsewhere.

Our results support the idea that some juvenile Crossbills will be able to breed only a few weeks after reaching independence (45 days after hatching; Cramp & Perrins 1994). This precocious breeding behaviour is also reported in some other seed eaters (Gibbs *et al* 1984), and *Loxia* species in particular (*eg* Benkman 1992, Jardine 1994, Edelaar *et al* 2005), though it had not been reported in detail for the west Pyrenees.

Moulting

Moulting adults were caught during most of the year, but mainly from May to November, with a peak in June, when more than 90% of adults were moulting. This phenological pattern was similar to that observed in Mediterranean Crossbills (Massa 1987), and was about a month earlier than in northern European populations, which moult between June–August and September–November (Cramp & Perrins 1994). Pyrenean birds seem to be more similar in their breeding and moulting patterns to Mediterranean than to northern European Crossbills. The phenological patterns of ripening and opening of Mediterranean pine cones may be the cause of these differences (Benkman 1990).

Although it has been reported that Crossbills may be able to breed and moult at the same time (Newton 1972), this does not seem to be the case for west Pyrenean Crossbills breeding in Scots pine. Indeed, the peak of birds in moult was two months later than the main breeding peak, in March, and two months before the second yearly breeding peak, in August, suggesting that most Crossbills avoided the overlap between these processes, as do most bird species (Ginn & Melville 1983). A detailed analysis of our data set revealed only three active breeding females that were also in the process of a complete moult. Authors have frequently documented that Crossbills start moult by midwinter, thereafter suspending it when breeding in late winter or spring and resuming moult from midsummer (Cramp & Perrins 1994). Although birds with suspended moult have been observed in our study sites (DA pers obs), this does not seem to be a common strategy within this population, since this implies that a major proportion of Crossbills would be in moult after breeding in summer. Conversely, it is possible that, rather than suspending, Crossbills may interrupt their moult when they start to breed.

Another conclusion is that Scots-pine-associated Pyrenean Crossbills only moult once a year, as documented for the species overall (Svensson 1998), and that sex-associated variations in moult pattern were absent or were too weak to be detected. This uniformity in moult timing of males and females could be due to the fact that parental care is divided equally between the sexes (Cramp & Perrins 1994).

Body mass and fat scores

Although month of capture made a significant contribution to variation in body mass relative to body size and fat load, *a posteriori* comparisons were unable to reveal significant differences between particular months, probably as a result of relatively small sample sizes for some months and the high overdispersion of data. In addition, the mean fat score was quite low (in most months, less than 1), which could be due to the resident nature of Pyrenean Crossbills (Senar *et al* 1993) in contrast to the more migratory behaviour of northern European Crossbills (Marquiss & Rae 1994, Summers *et al* 2002).

Nevertheless, breeding and non-breeding Crossbills had significantly different fat loads in August (summer breeding peak), but not in March (winter breeding peak), with summer breeders having lower fuel loads than summer non-breeders whereas breeding Crossbills during winter had a similar fat content to non-breeding ones. This suggests that, during winter, breeding birds can find enough food to rear broods and keep fat reserves as high as non-breeders, and also supports the idea that breeding in late-summer/autumn is more constrained by external factors, such as food supply. The lower fat load of moulting Crossbills compared to non-moulting birds, is consistent with the fact that moulting is an energy-demanding process (Jenni & Winkler 1994).

ACKNOWLEDGEMENTS

We are indebted to the people who collaborated with us during the field work, particularly to A. Mendiburu, A. Crespo, D. Mazuelas and M. Andueza, as well as to I. Ainzua, for her help during all these years. The Government of Navarra authorised the ringing activities. JA was supported by a postgraduate fellowship from the Basque Government. P. Edelaar, C. Redfern and two anonymous reviewers provided valuable comments that helped improve an earlier version of the manuscript. The English was checked by an expert (M. Díez-León).

REFERENCES

Alonso, D., Arizaga, J., Miranda, R. & Hernández, M.A. (2006) Morphological diversification of Common Crossbill (*Loxia curvirostra*) populations within Iberia and the Balearics. *Ardea* **94**, 99–107.

Benkman, C.W. (1990) Intake rates and the timing of Crossbill reproduction. *Auk* **107**, 376–386.

Benkman, C.W. (1992) White-winged Crossbills. In *The Birds of North America*, (eds Poole, A., Stettenheim, P., & Gill, F.B.) (Vol. 27, pp. 11–12. The Academy of Natural Sciences of Philadelphia, Philadelphia.

Clouet, M. (2000) The breeding biology of the Common Crossbill *Loxia curvirostra* in the Central Pyrenees. *Bird Study* **47**, 186–194.

Cramp, S. & Perrins, C.M. (eds) (1994) *Handbook of the Birds of Europe, the Middle East and North Africa*. Volume VIII: Crows to Finches. Oxford University Press, Oxford.

Edelaar, P., Phillips, R.E. & Knops, P. (2005) Sexually dimorphic body plumage in juvenile Crossbills. *Wilson Bulletin* **117**, 390–393.

Génard, M. & Lescourret, F. (1987) The Common Crossbill *Loxia curvirostra* in the Pyrenees: some observations on its habitats and on its relations with conifer seeds. *Bird Study* **34**, 52–63.

Gibbs, H.L., Grant, P.R. & Weiland, J. (1984) Breeding of Darwin's finches at an unusually early age in an El Niño year. *Auk* **101**, 872–874.

Ginn, H.B. & Melville, D.S. (1983) *Moult in birds*. Guide 19. BTO, Tring.

Hahn, T.P. (1995) Integration of photoperiodic and food cues to time changes in reproductive physiology by an opportunistic breeder, the Red Crossbill, *Loxia curvirostra* (Aves: Carduelinae). *Journal of Experimental Zoology* **272**, 213–226.

Hahn, T.P. (1998) Reproductive seasonality in an opportunistic breeder, the Red Crossbill *Loxia curvirostra*. *Ecology* **79**, 2365–2375.

Iovchenko, N.P. (2003) Relationship of moult and breeding in the Tien Shan subspecies of the Common Crossbill *Loxia curvirostra tianshanica*. *Vogelwarte* **42**, 117.

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.

Kaiser, A. (1993) A new multicategory classification of subcutaneous fat deposits of songbirds. *Journal of Field Ornithology* **64**, 246–255.

Loidi, J. & Báscones, J.C. (1995) *Mapa de series de vegetación de Navarra*. Gobierno de Navarra, Pamplona.

Marquiss, M. & Rae, R. (1994) Seasonal trends in abundance, diet and breeding of common crossbills *Loxia curvirostra* in an area of mixed species conifer plantation following the 1990 crossbill 'irruption'. *Forestry* **67**, 31–47.

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

Massa, B. (1987) Variations in Mediterranean Crossbills *Loxia curvirostra*. *Bulletin of the British Ornithologists' Club* **107**, 118–129.

Newton, I. (1968) The moult seasons of some finches and buntings. *Bird Study* **15**, 84–92.

Newton, I. (1972) *Finches*. Collins, London.

Newton, I. (2006) Movement patterns of Common Crossbills *Loxia curvirostra* in Europe. *Ibis* **148**, 782–788.

Noskov, G.A., Iovchenko, N.P. & Smirnov, N. (2003) Sexual activity, moult and movements in the annual cycle in the Common Crossbill *Loxia curvirostra*. *Vogelwarte* **42**, 114–115.

Pascual, J. & Senar, J.C. (1996) What are different biometric measures of avian body size measuring? *Butlletí del Grup Catalá d'Anellament* **13**, 1–8.

Pinilla, J. (ed.) (2000) *Manual para el anillamiento científico de aves*. SEO/BirdLife–DGCN–MIMAM, Madrid.

Podulka, S.R., Rohrbaugh, W. & Bonney, R. (2004) *Handbook of bird biology*. Cornell Laboratory of Ornithology, New Jersey.

Schaub, M. & Jenni, L. (2000) Body mass of six long-distance migrant passerine species along the autumn migration route. *Journal of Ornithology* **141**, 441–460.

Senar, J.C. & Pascual, J. (1997) Keel and tarsus length may provide a good predictor of avian body size. *Ardea* **85**, 269–274.

Senar, J.C., Borrás, A., Cabrera, T. & Cabrera, J. (1993) Testing for the relationship between coniferous crop stability and Common Crossbill residence. *Journal of Field Ornithology* **64**, 464–469.

Sokal, R.R. & Rohlf, F. (1995) *Biometry: the principles and practice of statistics in biological research*. Freeman, New York.

Summers, R.W. & Proctor, R. (2005) Timing of shedding seeds and cones, and production in different stands of Scots pines at Abernethy Forest, Scotland. *Forestry* **78**, 541–549.

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.

Svärdson, G. (1957) The invasion type of bird migration. *British Birds* **50**, 314–343.

Svensson, L. (1998) *Guía para la identificación de los paseriformes de Europa*. SEO/Bird Life, Madrid.

(MS received 10 June 2010; accepted 19 February 2011)