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ORIGINAL ARTICLE

Light-level geolocators confirm resident status of a Southern European Common Crossbill population

Daniel Alonso[1] · Juan Arizaga[1] · Christoph M. Meier[2] · Felix Liechti[2]

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Abstract Common Crossbill (*Loxia curvirostra*) populations are dependent on specific key conifer species for their primary food supply, but many of these conifers standardly show irregular cone crop production. Consequently, the species has evolved a nomadic behavior, breeding in areas with a high crop production in given years. Northern European crossbills mostly forage on Norway Spruce (*Picea abies*) and migrate along a northeast–southwest gradient across Europe. In contrast, crossbills from Spain were considered to be resident until recent studies on crossbill populations in the Pyrenees showed that a fraction of the population may also migrate. The type of movements of these Spanish birds, however, remains virtually unknown. The aim of our study was to resolve the question of whether these birds displace on a small local scale or whether they actually move to a distinct non-breeding area for part of the annual cycle. We tracked 14 male Common Crossbills from the Pyrenees with light-level geolocators for an entire year. Our results suggest that these birds were resident; only one bird may have shown a west–east movement of up to 200 km along the Pyrenean axis. We conclude that movement of the Common Crossbill from the Pyrenees may predominantly consist of relocation to nearby mountain ranges in Iberia or vertically in altitude. We expect that such small-scale movements have implications for population dynamics, and we recommend further research with telemetry to resolve the details of this small-scale movement.

Keywords *Loxia* · Movement patterns · Nomadic species · Pyrenees · Spatial ecology · Mountain bird

Zusammenfassung

Geolokatoren bestätigen den Standvogelstatus der Fichtenkreuzschnäbel in Südeuropa

Fichtenkreuzschnäbel (*Loxia curvirostra*) sind spezialisiert auf Nahrung von Nadelgehölz und sind deshalb von den unregelmäßig auftretenden Mastjahren ihrer Futterpflanzen abhängig. Eine evolutive Anpassung daran ist das nomadische Umherziehen zwischen Brutgebieten mit hohem Nahrungsangebot. Besonders nordeuropäische Populationen sind auf Fichtenbestände (*Picea abies*) angewiesen und ziehen innerhalb Europas entlang einer nordöstlich-südwestlichen Achse, während man von spanischen Fichtenkreuzschnäbeln bisher annahm, dass es sich um Standvögel handelte. Dieses Wissen wurde jedoch kürzlich von einer Studie in Frage gestellt, die zeigte, dass in einer gewissen Population in den Pyrenäen ein Teil der Vögel vielleicht auch umherziehen. In dieser Studie wollten wir wissen, ob diese Vögel nur lokal wandern, oder ob es tatsächlich eine saisonale Zugbewegung in ein vom Brutgebiet unterschiedliches Gebiet ist. Hierfür beloggerten wir 14 männliche Fichtenkreuzschnäbel während eines Jahres mit Geolokatoren. Es zeigte sich, dass mit einer Ausnahme alle Vögel ortstreu blieben und dass der eine Vogel

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✉ Juan Arizaga
jarizaga@aranzadi.eus

[1] Department of Ornithology, Aranzadi Sciences Society, Zorroagagaina 11, 20014 Donostia-S. Sebastián, Spain

[2] Swiss Ornithological Institute, Seerose 1, 6204 Sempach, Switzerland

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wahrscheinlich 200 km in Ost-West Richtung entlang der Pyrenäen zog. Daraus schließen wir, dass Wanderungen von Fichtenkreuzschnäbeln in Spanien vor allem zwischen benachbarten Gebirgszügen und innerhalb von Gebirgen in vertikaler Richtung vorkommen. Wir erwarten, dass der lokale Austausch eine wichtige Komponente in der Dynamik lokaler Populationen spielt und wir empfehlen eine Telemetriestudie, um mehr über diese lokalen Bewegungen von Fichtenkreuzschnäbeln zu erfahren.

Introduction

The movement patterns of many nomadic bird species still remain a mystery, predominantly due to the technical challenges encountered in tracking these birds throughout the entire year (Newton 2008). Within species, migratory behavior, including nomadic behavior, can vary across populations (Fraser et al. 2012; Andueza et al. 2013; Finch et al. 2015). In Europe, southern populations of a species commonly migrate shorter distances than their northern counterparts or they become resident in one locality (Alerstam 1993). Data collected through bird ringing have elucidated the movements of various populations of some nomadic species from Northern Europe, such as the Common Crossbill (*Loxia curvirostra*; hereafter referred to as the crossbill) (Newton 2006). However, movement patterns have only become apparent in species and regions where intensive long-term ringing programs have been carried out. The miniaturization of light-level geolocators and their use in small passerine birds has resulted in a rapid increase in our comprehension of bird movement patterns over large geographic areas (Stutchbury et al. 2009; Bächler et al. 2010; Schmaljohann et al. 2012; Tøttrup et al. 2012).

Crossbills are a good example of a nomadic species (Cramp and Perrins 1994) as they are highly dependent on very specific key conifer species as their food source (Benkman 1993; Edelaar et al. 2012). These conifer species are characterized by an irregular cone crop production (Newton 1972) and, accordingly, crossbills have evolved to breed in areas where they can find good crops in a given year (Newton 1972, 2006). Northern European crossbills, which mostly forage on Norway Spruce (*Picea abies*), migrate along a northeast–southwest gradient across Europe (Newton 2006; Marquiss et al. 2012). Irruptions in southwestern European areas occur after a year of seed depletion in northeastern Europe (mostly Russia). These birds reach locations in southwestern Europe in the summer where they may stay to breed, remaining there for as long as the following spring before returning to the north (Newton 2006).

Spain hosts a large crossbill population, assessed to be 140,000–190,000 pairs (Tucker and Heath 2004). This population breeds mainly across the length and breadth of the Pyrenees and in the pine forests of eastern Spain (Borrás and Senar 2003). In contrast to Northern European crossbills, those from Spain are non-nomadic and have a relatively high apparent survival rate from year to year [mean $\pm$ standard error (SE) 0.46 $\pm$ 0.15], which is comparable to apparent survival rates of other local birds with high breeding site fidelity (see, for example, Senar et al. 1993). By contrast, Northern European crossbills have much lower apparent survival rates and show extensive movements, with an absence of a clearly defined population-specific breeding area (Berthold 1996). This non-nomadic status of Spanish crossbills has been attributed to the fact that several Southern European species (*Pinus* spp.) have a more regular between-year cone production than their Northern European counterparts (Senar et al. 1993). However, recent studies on Pyrenean crossbills have produced new evidence which raises doubts about the strict non-nomadic status of this population (Alonso and Arizaga 2013); however, the type of movements of these birds remains virtually unknown. Survival analyses have revealed that the apparent survival rate of Spanish crossbills decreases with increasing wing length. It is therefore possible that long-winged birds have either immigrated from northern European populations or they comprise a fraction of the crossbills from Iberia which show nomadic behavior over longer distances (Alonso and Arizaga 2013). However, subsequent analyses with stable isotopes from Pyrenean crossbills revealed that the population was rather homogeneous, suggesting that most of such possibly nomadic migrant crossbills have an Iberian origin (Arizaga et al. 2014). To describe the type of movements of crossbills from Iberia and resolve the uncertainty associated with indirect measures (survival analyses, biometrics, and stable isotopes), we decided to track crossbills with geolocators (GL) for an entire year.

We expected that birds either would (1) move relatively long distances, from the breeding site where they were marked to non-breeding quarters situated at distances of >200 km or, alternatively, (2) be resident or just only move a short distance and virtually remain stationary for the entire year. GL detect movements beyond an error margin of >200 km (Fudickar et al. 2012; Lisovski et al. 2012). They are more accurate in estimating apparent movements in longitude (with even error margins of <200 km) than in latitude, with inaccuracy also increasing with shadow (such as shadow due to trees or clouds) and around the equinox periods (Lisovski et al. 2012). Crossbills in the Pyrenees are exposed to important environmental variations in light level as they move within trees with dense foliage (pines), in a mountainous area (with

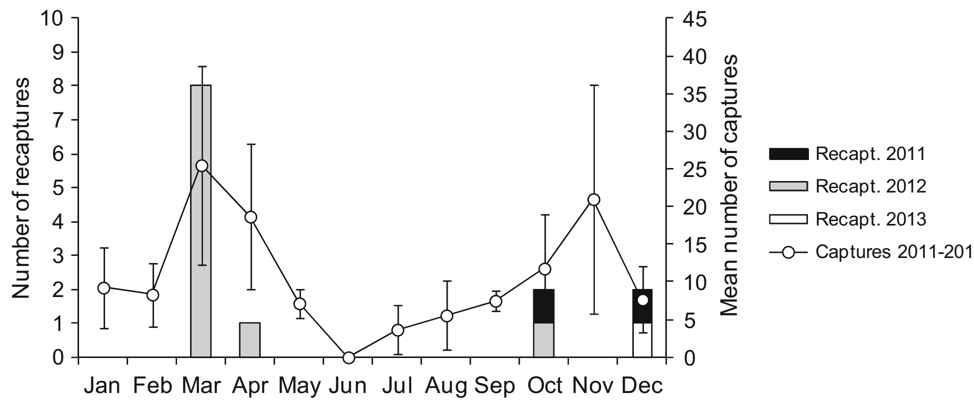

Fig. 1 Monthly pattern of recaptured crossbills with geolocators. Data are presented as the mean number (*bars*) of crossbills captured per day across the annual cycle for the period 2011–2013. *Whiskers* Standard error

great variation among days with clear skies or clouds and in relation to the slope—northern vs. southern slopes). Thus, true medium- to long-distance movement can be identified only if the GL is able to record movement beyond the error margin of the GL (Fudickar et al. 2012; Lisovski et al. 2012) and if the direction of this movement reveals a seasonal pattern (e.g., abandonment of breeding site, flight to one or more non-breeding localities, stay in non-breeding localities, flight back to breeding site—all crossbills were recaptured in the site where they were marked as breeders). The absence of any such pattern would confirm either a true resident status of the population or just small-scale movements of <200 km.

Materials and methods

Study area

During the breeding season of 2011 we tagged 40 male crossbills at Uztarroz, in the west Pyrenees, Northern Spain (42°53′N, 01°00′W, 1340 m a.s.l.). The population of crossbills breeding in this area occupies a region dominated by Scots Pine (*Pinus sylvestris*).

All crossbills were tagged from March to April (Appendix), a period which coincides with the peak of the breeding within the region (Alonso and Arizaga 2011). Only males were tagged because their apparent local survival is greater than that of females (Alonso and Arizaga 2013), thereby increasing our chance to recapture tagged individuals. The wing length of these birds ranged from 94.0 to 104.0 mm [mean ± standard deviation (SD) 98.4 ± 2.5 mm], and the body mass ranged from 33.0 to 42.0 g (mean ± SD 38.0 ± 2.0 g). Wing lengths, accordingly, represent whole range of this variable for the sampling population (Alonso and Arizaga 2005).

To recapture as many crossbills as possible we carried out trapping sessions (i.e., sampling days) every 2 weeks for a period of 32 months from May 2011 up to December 2013. Crossbills were captured with mist nets (mesh size 12 mm) strategically positioned in a zone where the bird go to forage on minerals from the wall of a small refuge for cattle. The mist nets remained open during a period of 4 h, starting at dawn when the birds show higher activity (Alonso and Arizaga 2005). Therefore, one trapping session consisted of one 4-h netting session every 2 weeks, repeated for 32 months. First recaptures were obtained in October of 2011 (Fig. 1).

GL characteristics

An SOI-GDL_V1.0 GL from the Swiss Ornithological Institute (Switzerland) was used in this study. This GL weighs approximately 1.4 g (accounting for 3.2–4.0 % of a crossbill's body mass) and was attached to the birds using a leg-loop harness made of nylon thread (thickness 1.2 mm). The size of the harness was calculated according to Naef-Daenzer (2007) and was adjusted to the size of each bird to be fitted in the field.

The GL started recording on 25 March 2011. Data from recaptured birds fitted with a GL were compiled during a period ranging from 183 to 351 days [mean ± SD 310 ± 46 days; Electronic Supplementary Material (ESM) Fig. 1].

GL analyses

We first detected dawn and dusk times by based on light level within a 5-min interval with Geolocator software (v.14.08.2014) using the threshold method. These data were then processed using the R package GeoLight® version 3.2.2 and GeoLight version 2.0.0; The R Foundation for Statistical Computing, Vienna, Austria) according to Livoski and Hahn (2012). Stationary phases were determined with the function "changeLight" with a $q = 0.97$. The minimum length of a stationary period was set to 5 days. We calculated the sun elevation angle with a habitat calibration assuming that each bird remained stationary in the first phase immediately after logger attachment and in the last phase immediately before the recapture (median observed angle −5.5°; range −6.2° to −4.5°). Using the logger-specific angle and the function "coord" we obtained two positions per day (for midnight and midday, respectively). Succeeding sites in time with a mean position of <200 km were merged since sites with a higher spatial resolution cannot be separated with certainty based on the accuracy of a GL (Lisovski and Hahn 2012). Near equinox, the estimate for latitude, becomes inherently difficult to assess with a GL, and therefore we discarded the latitude for ±12 days around the autumn and spring equinoxes (Ekström 2002).

The movement pattern of crossbills was determined based on the location of stationary sites and the amount of overlap between the interquartile range of positions between sites. If there was a large overlap among stationary sites, the bird was considered to remain in a same position and, hence, to be resident (or to perform just small local movements).

To ensure that we did not overlook any real movement with the assessment of sites, we calculated a running mean for 30 positions at the same time. This mean is very inaccurate in terms of detecting short-scale displacements, but it is a good indicator of consistent bird movement in a particular direction. Tracks produced by this method were also plotted.

Results

Overall, we recaptured 14 crossbills fitted with a GL (recapture rate 35 %), with most birds recaptured in the spring (March–April), but some also outside this period (Fig. 1). All crossbills except one were recaptured at Uztarroz; the exception was recaptured at Bigüezal (bird 2JO), a locality situated 25 km southwest of Uztarroz. The crossbills had a mean body mass of 38.0 (SE 0.6) g when caught, which did not differ from the weight of recaptured birds (38.6 ± 0.6 g; paired t test $t_{12} = 1.342$, $p = 0.204$; $n = 13$; body mass data for 1 bird were missing). GL recorded data during a mean period of 310 days (SD 46 days, range 183–351 days; Appendix).

All crossbills showed a high geographic overlap between stationary periods (ESM Figs. 1, 2), indicating that they probably remained in the same site for the whole annual cycle or, alternatively, did not move long distances. Most (52.5 %) of the stationary points were situated at a distance of <200 km from the point where the crossbills were tagged, and the majority (86.4 %) were situated at a distance of <500 km (Fig. 2). An exception to this general rule was bird 2JS, which was found to perform a west–east movement (Fig. 3; ESM Figs. 1, 2). This bird seemed to remain in or around a mean position at 1.2°E (i.e., near Andorra).

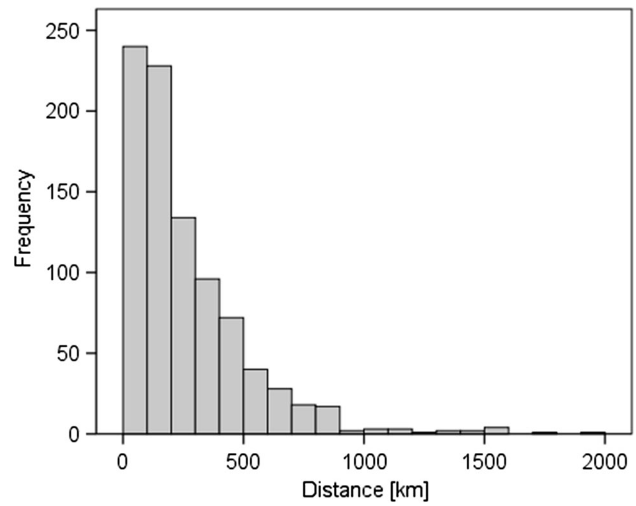

Fig. 2 Frequency distribution of the distance between stationary points and the point where the crossbills were tagged. All data on crossbills have been pooled for the analysis

Estimates of positions based on the GL typically showed a high variance, especially in latitude (ESM Figs. 2, 3). The GL of five crossbills (2IJ, 2IT, 2IZ, 2JC and 2JE) even provided a position (a stationary site per bird) at a latitude far to the south of the study site, in Africa (mean 15°N; range 10°–26°N). Such sites were found at dates close to the September equinox but outside of the ±12-day time window around the equinox.

Running mean maps showed continuous movement across a north–south axis, but without any particular seasonal pattern (see the two examples in Fig. 3). Exception to this rule was again bird 2JS, which seemingly moved from east to west (Fig. 3). The GL of this bird did not record a return movement to the site where this individual was recaptured, although it is also true that the GL stopped logging in March of 2012, but the bird was recaptured in October, hence we might have missed this back-to-home displacement.

Discussion

To our knowledge this is the first study to have used GL to study common crossbills and to assess the movement patterns of a bird population over the whole annual cycle on an individual basis. The data obtained provide direct evidence supporting the resident status of crossbills from the Pyrenees (northern Iberia).

GL fitted on crossbills in one of the main Scots pine patches in the western Pyrenees (northern Iberia) provided scattered data indicating that the birds were situated around

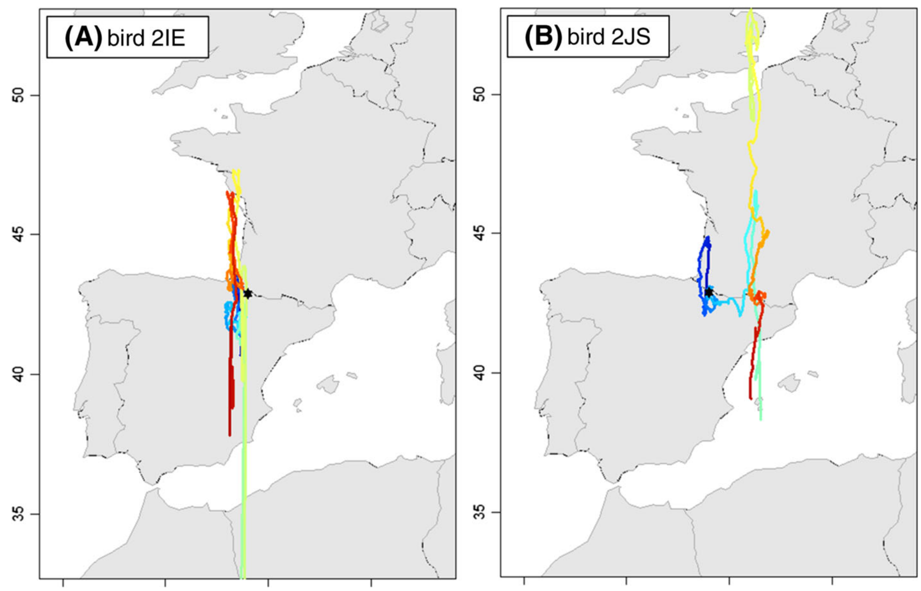

Fig. 3 Two examples of movement patterns of crossbills after application of the running mean approach. **a** Bird 2IE, which was considered to likely have remained stationary for the entire study period, **b** Bird 2JS, which was considered to have performed a west–east movement. Tracks go from *blue* (earliest date) to *red* (latest date). *Star* indicates the location where the birds were caught and tagged (Uztarroz). The majority of the crossbills had a pattern similar to that observed for bird 2IE (color figure online)

the site where they had been captured. The distance between sites falls within the error margin of positioning with a GL (Fudickar et al. 2012; Lisovski et al. 2012), supporting the notion that these birds were sedentary or that they only moved across a small geographic range that may not be detectable with a GL, which is inaccurate with respect to detecting small-range movements. The large variance in our data, in particular across a latitudinal axis, may be due to a number of factors, including (1) increasing inaccuracy around the equinox periods, (2) shadow effects and similar biases associated with crossbills' habitat (coniferous forest in a mountain area), (3) displacements in altitude, or (4) a combination of these three factors (Lisovski et al. 2012).

The decrease in the number of captures around mid-summer (Fig. 1) is unlikely to be associated to long-distance movement, but it is compatible with possible short-distance local displacements. It is also possible that crossbills within the region where the study was carried out may be more difficult to catch during the summer due to, for example, the molting period (Alonso and Arizaga 2011), when birds could be less mobile, or because the birds may visit the catching site (used to forage on minerals) less frequently.

Interestingly, one of the crossbills seemed to have made a detectable movement across a west–east axis, reaching an area located in the central Pyrenees (probably in or near Andorra). However, the GL did not record a return movement to the site where this individual was recaptured, although since the GL stopped logging in March 2012 but the bird was recaptured in October 2012, we may have missed this back-to-home displacement. The west–east movement across the Pyrenean axis has been described previously for the Citril Finch (*Carduelis citrinella*) (Borrás et al. 2011) and the Boreal Owl (*Aegolius funereus*) (Badosa et al. 2007). Although the nature of these displacements could differ between species, to some extent they all may respond to changes in the spatial distribution of feeding sources. Citril Finches also forage on pine seeds (Borrás et al. 2003). In this context, the Pyrenees may act as a corridor along which birds move (Alonso and Arizaga 2004). Movements to other nearby mountain ranges could be also possible. For example, we recaptured a bird ringed in Bigüezal (Pyrenees) just 60 km to the south, which may be a movement towards the Ebro Valley or, even more likely, a mountain range situated to the south of this valley (Iberian System). Similarly, we also recaptured in Uztarroz (Pyrenees) a bird which had been ringed in Zaragoza (Ebro Valley). However, we cannot explain why only one bird out of 14 seemed to perform a long-distance movement. In other bird populations, including the Citril Finch, it is the entire population (and not only some individuals) that moves along this Pyrenean axis.

The data obtained in our study may shed a new light on previous findings. In a previous study in which we used Cormack–Jolly–Seber models with ring-recovery data (Alonso and Arizaga 2013), we observed that long-winged crossbills had lower apparent survival rates than short-winged birds. We interpreted this result as indirect evidence for long-distance movement; for example, birds which came from northern Europe could have bred in the Pyrenees before returning to Northern Europe (Newton 2006). However, additional analyses with stable isotopes (Arizaga et al. 2014) revealed that northern crossbills were likely to be very rare within the population and, therefore, it is possible that these long-winged crossbills could belong to a fraction of birds which might show a higher propensity to move longer distances. We can now confirm that crossbills from the Pyrenees are indeed mostly resident and that long-winged birds are more likely to be a subset of this population. Interestingly, the only bird which had a possible true detectable movement (2JS) showed a wing length of 100.5 mm, which is at the upper range of wing length for the Pyrenean population (Alonso and Arizaga 2013). One could speculate that those birds belonging to the long-winged subset of the population may be less restricted in their diet on Scots pine crop than the resident population and may therefore also forage in other nearby areas where other pines species might contribute to their diet (e.g., Mountain Pine *Pinus uncinata*) (Edelaar et al. 2012; Björklund et al. 2013). Thus, these crossbills might exploit other conifer patches if they find sufficient food in given years or seasons, even though their bills would not be as well adapted as those from the local, strictly resident populations (Benkman 1993). The bird moving to the east was observed to reach an area in the Pyrenees where mountain pines together with Silver Fir (*Abies alba*) are the dominant conifers.

In conclusion, data derived from GL-tagged Pyrenean crossbills show that these birds were resident, with the exception of one bird which might have moved, at the most, approximately 200 km along the Pyrenean axis—provided this was not an artifact of a GL malfunction. Alternative movements to nearby mountain ranges in Iberia, or in latitude, cannot be excluded, although the data provided by the GL did not support this possibility. Future research on these possible local movements is needed, and it would be interesting to know how crossbills use pine forests locally, given that the latter show large variations in local productivity.

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Appendix

See Table 1.

Table 1 Crossbills caught and tagged with geolocators at Uztarroz (Pyrenees, northern Iberia) during the spring of 2011 and thereafter recaptured

Geolocator ID	Wing length (mm)	Age[a]	Capture date	Body mass at capture (g)	Recapture date[b]	Body mass at recapture (g)	Last record date	Number of survey days
2IT	97.0	Second-year	20/03/2011	37.6	24/03/2012	40.4	21/02/2012	338
2JE	97.0	Adult	26/03/2011	41.9	04/03/2012	40.0	03/03/2012	343
2IJ	97.0	Second-year	26/03/2011	39.4	24/03/2012	40.5	08/03/2012	348
2IE	96.0	Second-year	26/03/2011	35.7	29/12/2013	35.4	11/03/2012	351
2II	97.0	Second-year	02/04/2011	39.4	02/10/2011	40.6	02/10/2011	183
2IV	97.0	Adult	09/04/2011	35.2	24/03/2012	35.7	28/02/2012	325
2JR	96.0	Adult	09/04/2011	36.3	21/04/2012	35.6	07/03/2012	333
2JO	97.5	Second-year	09/04/2011	37.4	10/03/2012	41.3	08/03/2012	334
2IZ	97.0	Second-year	09/04/2011	36.6	26/12/2011	38.2	26/12/2011	261
2JN	97.5	Second-year	16/04/2011	42.0	04/03/2012	41.6	03/03/2012	322
2JC	97.0	Adult	16/04/2011	37.7	17/03/2012	–	16/02/2012	306
2JS	100.5	Adult	16/04/2011	38.2	28/10/2012	37.7	02/03/2012	321
2IR	101.0	Adult	21/04/2011	38.1	15/01/2012	38.3	14/01/2012	268
2IU	97.5	Adult	26/04/2011	37.1	29/03/2012	37.1	27/02/2012	307

[a] Crossbills which hatched in 2010 were considered to be second-year birds, while those wich hatched in 2009 or earlier were considered to be adult (older) birds

[b] All crossbills were recaptured at Uztarroz, with the exception of bird 2JO which was recaptured at Bigüezal

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