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ORIGINAL ARTICLE

The impact of vagrants on apparent survival estimation in a population of Common Crossbills (*Loxia curvirostra*)

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Abstract The impact of nomadism on animal population dynamics (e.g. survival) is poorly understood. This factor is not inconsequential because our current view on animal survival rates could suffer from biases if it is ignored. The degree of nomadism in Common Crossbills (*Loxia curvirostra*) is reported to differ population-specifically, and thus they constitute a good model for the study of survival in nomadic species. Southern Europe hosts resident birds, probably also local vagrant birds and non-local, vagrant, northern European Crossbills. The impact of vagrants on the estimation of apparent survival rates has never been determined in areas where Crossbills have been reported as resident. We hypothesise that transients (birds for which survival from year t to year $t + 1$ is zero) will be detectable if a majority of vagrants remain at a particular site for just a few months. Alternatively, if vagrants remain for longer, transients will be absent by definition, so apparent survival estimation will be lower than would be if transients did not exist. As wing length in vagrants is commonly longer than in residents, we can expect a negative effect of wing length on survival, as long-winged (vagrant) Crossbills emigrate from the area after a few years, thus demonstrating lower apparent survival rates than resident, local birds on a local scale. Alternatively, if vagrants have a negligible impact on the estimation of local apparent survival rates (i.e. if residents clearly outnumber vagrants), we should not detect transients nor find any effect of wing length on survival. To test this hypothesis, we used data collected over a period of 16 years at a site located in a Scots pine (*Pinus sylvestris*) forest in northern Iberia. Capture–recapture data were analysed with Cormack–Jolly–Seber (CJS) models. Although transients were not detected, the CJS models showed that survival was negatively affected by wing length. Our results support the hypothesis that vagrants occurred in the area for more than 1 year before subsequently disappearing, and that their presence has a strong impact on local survival estimation. Accordingly, if the presence of vagrants is not considered, this can lead to the underestimation of local survival rates of resident Crossbill populations.

Keywords Conifers · Iberia · Population dynamics · Pyrenees · Vagrancy

Zusammenfassung

Der Einfluss vagabundierender Vögel auf Schätzungen der Überlebensrate bei einer Population des Fichtenkreuzschnabels (*Loxia curvirostra*)

Vom Einfluss des Nomadisierens auf die Populationsdynamik von Tieren (z.B. auf ihre Überlebensraten) weiß man bislang nur wenig. Dieser Faktor ist aber nicht unwesentlich, weil unsere derzeitige Einschätzung der Überlebensraten darunter leiden könnte, ließe man ihn ganz unberücksichtigt. Von Fichtenkreuzschnäbeln (*Loxia curvirostra*) ist bekannt, dass ihr Ausmaß an Nomadentum von Population zu Population unterschiedlich ist; daher bieten sie sich als guter Modellorganismus für die Untersuchungen von Überlebensraten bei einer nomadisierenden Vogelart an. In Südeuropa kommen sie als Standvögel, vermutlich auch als lokale Wanderer, vor; es gibt aber auch nordeuropäische umherziehende Fichtenkreuzschnäbel.

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Der Einfluss des Umherwanderns auf die Einschätzungen der Überlebensraten wurde für Gegenden untersucht, in denen die Fichtenkreuzschnäbel Standvögel sind. Wir stellen die Hypothese auf, dass umherwandernde Vögel (für die das Überleben von Jahr t zu Jahr t + 1 Null ist) erfasst werden können, wenn ein größerer Teil der Wanderer nur ein paar Monate an einem Ort bleibt. Bleiben die Wanderer länger, gibt es andererseits per definitionem keine Umherzieher, und die übliche Einschätzung der Überlebensrate wird niedriger ausfallen als wenn die Wanderer nicht existierten. Da die Flügellänge bei Wanderern normalerweise größer als bei Standvögeln ist, könnte man einen negativen Zusammenhang zwischen Flügellänge und Überlebensrate erwarten, weil die flügellängeren (wandernden) Fichtenkreuzschnäbel nach ein paar Jahren aus einem Gebiet abwandern und damit eine scheinbar niedrigere Überlebensrate als die Standvögel zeigen. Wäre andererseits aber der Einfluss der Umherzieher auf die geschätzte lokale Überlebensrate vernachlässigbar (wenn es also viel mehr Standvögel als Wandernde gibt), sollten wir keine Durchreisenden feststellen und auch keinen Zusammenhang zwischen Überleben und Flügellänge. Zur Überprüfung dieser Hypothese benutzten wir Daten, die über einen Zeitraum von 16 Jahren an einem Standort in einem Kiefernwald (*Pinus sylvestris*) im Norden der Iberischen Halbinsel gesammelt worden waren. Die Fang- und Wiederfang-Daten wurden anhand des Cormack-Jolly-Seber (CJS)-Modells analysiert. Obwohl keine Durchzieher festgestellt werden konnten, zeigte das CJS-Modell einen negativen Zusammenhang zwischen Überleben und Flügellänge. Damit unterstützen unsere Ergebnisse die Hypothese, dass sich Umherzieher länger als ein Jahr an diesem Standort aufhielten, bevor sie abwanderten, und dass ihr Vorkommen einen starken Einfluss auf die Einschätzung der lokalen Überlebensraten hatte. Dementsprechend kann das Nicht-Berücksichtigen von Umherziehern dazu führen, dass die Überlebensraten lokaler Standvogel-Populationen von Fichtenkreuzschnäbeln zu niedrig eingeschätzt werden.

Introduction

Survival analyses are fundamental to the understanding of population dynamics and the identification of parameters affecting population growth (Dobson 1990; Baillie and Peach 1992; Newton 1998; Siriwardena et al. 1998). Studying survival in nomadic species is not straightforward due to the difficulty in achieving consistent recaptures; thus further studies dealing with this issue are still necessary. Populations of these species often overlap, since members from one population irrupt in areas where another is already present (Edelaar and Terpstra 2004; Newton 2006). The role of nomadism on animal population dynamics (e.g. survival) and its impact at a local level are still poorly understood. This is important because our current view on the survival of nomadic species could suffer from biases if such factors are omitted.

Crossbills (*Loxia* spp.) are seed-eating closely-related finch species specialised in feeding on conifer seeds prior to seed dispersal (Cramp and Perrins 1994). Normally, Crossbills forage on a single conifer tree species population-specifically (Benkman 1987; Summers et al. 2002). This high rate of foraging specialisation, together with the fact that many conifers show major year-to-year oscillations in crop production, forces Crossbills to be nomadic (Newton 2006). Thus, Crossbills are not only a paradigmatic model for the study of evolution through natural selection (Benkman 1993; Smith and Benkman 2007) but also for the analysis of the survival of nomadic species.

The Common Crossbill (*L. curvirostra*) is spread from Iberia in Europe across to Canada and the United States of America, and from the tundra border to northern Africa and the Middle East, the Himalayas and Central America (Collar et al. 2010). Its degree of nomadism is reported to decrease from north to south in Europe, although not linearly but in relation to the distribution of key conifer species (Newton 2006). Southern populations (e.g. those breeding in the Mediterranean) feed on conifers with a relatively stable cone production, allowing southern Crossbills to be resident or to show high site-fidelity to a particular breeding site/area from year to year (Génard and Lescourret 1987; Senar et al. 1993). Thus, in theory, southern Crossbills are resident, but exceptions to this rule cannot be excluded, as Crossbills in southern Europe could also move over wide areas in order to feed on specific conifers, especially when cones open (Förschler and Kalko 2009). In conclusion, southern Europe is likely to host both local resident birds and "southern" vagrants, that are also local but do not behave as strictly resident. Southern Europe is also a target region for northern European Crossbills that reach the south (even arriving in southern Iberia; Schloss 1984), generally during irruptive years (Newton 2006). Consequently, apparent survival in southern Europe is expected to be affected by both (1) possible local vagrant birds (hereafter, southern vagrants), and (2) the occurrence of northern Crossbills (hereafter, northern vagrants). However, earlier studies carried out in the south of Europe have failed to detect vagrants (Génard and Lescourret 1987; Senar et al. 1993), and therefore the impact of these birds on the estimation of apparent survival at a local scale remains virtually unknown.

When evaluating the possible impact of vagrants on apparent survival at a local level, two hypotheses can be considered: (1) vagrants have or (2) do not have any detectable impact on apparent survival estimation in southern Europe. If they do, two strategies are possible: vagrants remain at a site in southern Europe for only a very short time period (i.e. some months), and thereafter the site is left definitively, or alternatively, they stay in the site for longer (possibly for more than 1 year) before departing.

If vagrants remain at the site for only some months (Newton 2006), they should be detected as transients (i.e. birds for which survival from year t to year $t + 1$ is zero by definition) (Pradel et al. 1997), and the apparent survival rate of local resident birds can then be easily calculated once transients are considered apart (Pradel et al. 1997; Belda et al. 2007). However, vagrants may remain for longer than a year at a particular site (Newton 2006), so in this case apparent survival for vagrants from year t to year $t + 1$ is >0 and hence these birds cannot be detected as "pure" transients. A solution to this problem is to include individual covariates associated to vagrancy degree in survival models. As wing length is positively correlated with migration distances and also vagrancy versus resident strategy at both an intra- and inter-population level (Senar et al. 1994; Copete et al. 1999; Calmaestra and Moreno 2001; Förschler and Bairlein 2010), it can be stated that vagrants will be long-winged rather than short-winged birds (Cramp and Perrins 1994). Assuming this rule, we expect to obtain a negative effect of wing length on apparent survival, as long-winged Crossbills, being vagrants, will definitely emigrate from the site after breeding.

Alternatively, if vagrants have a negligible impact on the estimation of apparent survival in southern Europe (e.g. if southern Crossbills clearly outnumber foreign ones), we should not detect either transients or any effect of wing length on apparent survival.

Using data collected over a period of 16 years at a ringing station located in a Scots pine forest in the Pyrenees, in northern Iberia, we aimed to test if vagrants, either of northern or southern origin, affect apparent survival estimation in southern Europe. There is strong evidence indicating that long-winged Crossbills in the Pyrenees are vagrants (for details, see "Results").

Methods

Sampling area and protocol

Data were collected over a period of 16 years (1995–2010) at a ringing station at Uztarroz, in the Navarran Pyrenees (42°53′N, 01°00′W; 1,340 m above sea level). This station was located in a mature Scots pine (*Pinus sylvestris*) forest. Crossbills in this area mainly breed during the winter and spring (Alonso and Arizaga 2011). Thereafter, they become much less abundant (Alonso and Arizaga, unpublished data), indicating that a number of them leave this area during the summer and autumn. This latter period is when Crossbills from abroad normally arrive in southern Europe (Newton 2006) and therefore mix with local, possibly resident (Senar et al. 1993), birds. For our analyses, we selected only the data obtained from January to June because by doing so (1) we focused on a period when Crossbills were more abundant and stationary in the area and (2) the occurrence of non-local birds was minimised.

Crossbills were captured with mist nets (normally 12 linear m) that remained open during a period of 4 h starting at dawn, 2–4 times per month. Nets were placed near a small refuge where Crossbills went to eat salt and minerals as a complement to diet (Alonso and Arizaga 2005). Once captured, Crossbills were ringed, aged as first-year birds (born in year t when captured in year t, EURING code = 3), second-calendar year (born in year $t - 1$ when captured in year t, EURING code = 5) or adult birds (born in year $t - 2$ when captured in year t, EURING code = 6) (Jenni and Winkler 1994). Their sex was determined (Svensson 1996), and we also recorded wing length (±0.5 mm, method III from Svensson 1996). All measurements were recorded by a single observer (D. Alonso).

Wing length analyses

We conducted a number of tests in order to ensure that long-winged Crossbills in the Pyrenees are likely to be vagrants. It has been well reported that Crossbills originating from mainland northern Europe, which are known to be nomadic (Newton 2006), have longer wings than those native to southern Europe (Cramp and Perrins 1994). We used a t test (the original data provided by Cramp and Perrins 1994 were not available to us) in order to compare whether mean wing lengths from several regions in Europe (Table 1) differed from the mean values obtained in the Pyrenees.

Two main irruptions have been documented in our sampling locality during the period 1995–2010: the first one in 2005 (also detected in other areas in Iberia; Borrás et al. 2011), and another one in 2009 (when we recaptured a bird ringed in Switzerland and another one from The Netherlands). Additionally, 1997 was considered to be a year of irruption in Iberia (Borras and Senar 2003), but this was not detected in our sampling locality (D. Alonso, personal observations). Therefore, we did not consider it as a year of irruption for the purposes of our analyses. We tested if wing length of Crossbills caught during the irruptions of 2005 and 2009 differed from that of Crossbills caught in the previous and subsequent years of these irruptions. For that, we used ANOVAs on wing length with sex and year (irruptive and non-irruptive) as factors. We used a Duncan a posteriori test.

Table 1 Geographic variation in wing length (mean ± SD, sample size) of adult Common Crossbills (*Loxia curvirostra*) captured in different locations in Europe

Location	Male	*t* test	Female	*t* test	Source
Pyrenees	98.5 ± 2.2, 461		95.2 ± 1.9, 247		This work
N Europe[a]	99.5 ± 1.4, 20	9.982 (<0.001)	96.0 ± 1.6, 17	6.641 (<0.001)	Cramp and Perrins (1994)
Belgium[b]	99.9 ± 2.4, 50	13.928 (<0.001)	97.4 ± 2.8, 43	18.240 (<0.001)	Cramp and Perrins (1994)
E Iberia	94.9 ± 2.8, 79	35.395 (<0.001)	92.1 ± 2.7, 61	25.669 (<0.001)	Alonso et al. (2006)
S Iberia	95.3 ± 2.0, 33	31.449 (<0.001)	93.4 ± 2.0, 23	14.899 (<0.001)	Alonso et al. (2006)
Balearics	93.7 ± 2.3, 6	47.233 (<0.001)	89.1 ± 4.2, 8	50.523 (<0.001)	Alonso et al. (2006)

We used a *t* test (*p* values in parentheses; original data provided by Cramp and Perrins (1994) were not available to us) in order to compare whether mean wing lengths from several regions in Europe differed from the mean values obtained in the Pyrenees. Other references relative to wing length at other sites have been omitted due to pooling of both adult and first-year birds

[a] Crossbills from northern, central and western continental Europe

[b] Crossbills caught during an invasion in 1983–1984

Crossbills from northern Europe have been reported to show brighter coloration than their southern counterparts (Massa 1987; Cramp and Perrins 1994). We should therefore expect a higher proportion of brightly coloured Crossbills in long-winged than in short-winged birds. To test this, the proportion of brightly coloured Crossbills was plotted against wing length. Colour was assessed visually within the sample of adult males ($n = 461$), which were classified as either pale- or brightly-coloured. Pale-coloured Crossbills were those with either yellow or pale-reddish plumage, whilst brightly-coloured were those showing bright reddish plumage. This visual scoring system is valid since it corresponds with quantitative data obtained by colorimetry (Del Val et al. 2009). SPSS 18.0. was used for the statistical procedures.

Survival models

We used Cormack–Jolly–Seber (CJS) models to estimate apparent survival. Such models estimate both apparent survival (ϕ, probability that a bird captured in t is still alive in $t + 1$) and recapture probability (p, probability that a bird captured in t and still alive in $t + 1$ is recaptured in $t + 1$) separately.

The number of captures/recaptures was relatively small for first-year Crossbills (Table 2). Since survival of first-year birds is normally lower than for adults (Newton 1998), we did not lump the first-year birds in with adults. First-year birds were omitted from our analyses due to low sample size. Moreover, we did not consider second-calendar year Crossbills either, as this fraction of is the population was formed by both newly hatched birds (some Crossbills hatched at the end of the year, if captured at the beginning of the next year, are aged as EURING 5, although in biological terms they could be considered as first-year birds), and older birds which are more than 1 year old. We thus used a matrix of 14 × 708 adult birds (for details see Table 3).

Before starting to select models, we explored the fit of the data to CJS assumptions using a goodness-of-fit (GOF) test. CJS models assume that all marked individuals have the same probability of recapture and survival from time i to time $i + 1$. To test this, a GOF test on a CJS model where both ϕ and p varied from year (y) to year [ϕ (y) p (y)] was run with U-CARE software (Choquet et al. 2001), allowing us to identify a basic starting model with which to begin model selection. A global GOF test revealed that the data set fitted the CJS assumptions well ($\chi^2 = 14.394$, $df = 20$, $p = 0.810$). The specific Test 3SR, used to detect transience, was non-significant ($Z = 1.366$, $p = 0.172$), as was the specific test for trap-dependence ($Z = 0.795$, $p = 0.427$). Therefore, theoretically, we did not have transients in our dataset and the data fitted the CJS assumptions well.

Apart from year, we also considered sex (s) as a factor, so ϕ (y × s) p (y × s) was the most complex model from which to start model selection. We also conducted models which included biometry-associated covariates (wing length). In models that included sex as a factor, we tested for both an additive effect, i.e. ϕ (wing + s), and an interacting one, i.e. ϕ (wing × s), with wing length. This same type of models was also run to test for a quadratic effect of wing length on apparent survival. We also conducted models accounting for the presence of transients. With this in mind, we considered two possible age groups for each dataset: t_1, which equalled the survival prospect from year 1 (year of first capture event) to the next year and t_2, which equalled the annual survival from Year 2 to Year 3 and so on. The proportion of transients in such models is equal to $1 - [\phi\ (t_1)/\phi\ (t_2)]$ (Pradel et al. 1997). Additionally, we tested whether apparent survival differed between years without and with irruptions. We considered

Table 2 Number of captures + recaptures from previous years of Crossbills ringed in 1995 or later, at a ringing station located in the Pyrenees

Years	First-year birds		Adults	
	Male	Female	Male	Female
1995	11	5	56	28
1997	–	–	30	9
1998	0	1	88	68
1999	3	1	20	10
2000	15	4	50	30
2002	2	4	27	16
2003	1	1	26	11
2004	3	3	16	3
2005	3	2	14	9
2006	5	1	44	26
2007	34	26	25	7
2008	13	10	44	19
2009	25	10	44	16
2010	5	0	17	6

Data were collected from January to June. Years with less than 20 captures in total were removed from the analyses in order to obtain more robust statistical models (1996, 2001). Each bird is considered only once per year

2005 and 2009 as years of irruption with the rest being non-irruptive years. We tested 28 models in total.

Small sample size-adjusted Akaike values (AICc) were used to rank the fit of models to the data (Burnham and Anderson 1998). Models with an AICc difference <2 were considered to have no significant differences between them, and those for which the difference was >2 were considered to differ significantly. Models with an AICc difference <2 from the first model were averaged based on their AICc weight. We used the software MARK 5.1 (White and Burnham 1999) to run the CJS models.

Results

Wing length analyses

Wing length distribution was unimodal for both sexes and males were found to have longer wings than females ($t_{565.1} = 20.870$, $p < 0.001$; Fig. 1). Wing length in the Pyrenees was longer than in more southern regions but shorter than that of Crossbills captured in northern Europe (Table 1). Interestingly, the longest wings were found in a sample of Crossbills caught in Belgium during irruptions (Table 1), thus supporting the non-resident nature of long-winged Crossbills.

Wings tended to be longer in years of known irruptions (2005 and 2009) than in the previous and subsequent years (Fig. 2), although the difference was not significant (almost in 2009; see Table 4). During the invasion of 2005, the variance was higher than in the previous and subsequent years ($F_{\text{Levene}} = 4.221$; $p = 0.007$), but this effect was not observed during the invasion of 2009 ($F_{\text{Levene}} = 1.489$; $p = 0.225$).

The proportion of brightly-coloured Crossbills was much higher in long-winged than in short-winged birds (Fig. 3; logistic regression: $\chi^2 = 217.25$, $df = 1$, $p < 0.001$; B parameters (±SE): constant, -100.4 ± 9.7, Wald = 107.358, $p < 0.001$; wing length, $+1.0 \pm 0.1$, Wald = 108.233, $p < 0.001$).

Survival models

The longest interval between the first and last capture year was 4 years for adult birds. Models that best fitted the data were those with both a sex and a negative effect of wing length on apparent survival (Table 5). Models supporting a quadratic effect of wing length on survival fitted the data as well as did those models which considered a linear effect of wing length on survival (Table 5). Models supporting an effect of transients or known irruption years on survival were far from having a high ranking position. Thus, males showed higher rates of apparent survival than females overall, and long-winged Crossbills had lower apparent survival rates (Fig. 4).

The best models supported year-associated variations in p, which ranged from 0.02 to 0.42 (Table 5).

Discussion

Using data obtained at a ringing station with a constant sampling effort, operating over a period of 16 years (from 1995 to 2010), we analysed if apparent survival estimation in Common Crossbills was affected by the presence of vagrants.

The proportion of recaptures of Common Crossbills from 1 year to the next was relatively low (9.2 % for males and 7.6 % for females), thus giving rise to quite relatively small sample sizes of recaptures. This scarce number of recaptures bears out the findings of previous studies carried out in the Pyrenees (Senar et al. 1993). This fact did not, however, prevent us from obtaining a consistent matrix to run the CJS models. The software U-CARE did not have problems in running the tests with which we checked whether the data fit the CJS assumptions as well as those used to detect transients or trap-dependence.

The apparent survival of a population of Common Crossbills breeding in a Scots pine forest in southern Iberia depended on sex and wing length. In particular, long-winged birds had lower survival rates than short-winged ones. This result is in accordance with our prediction

Table 3 Detailed m-array tables for both sexes of adult Crossbills captured/recaptured at a ringing station located in the Pyrenees

	R_i	1997	1998	1999	2000	2002	2003	2004	2005	2006	2007	2008	2009	2010	Total
Males															
1995	56	3	3	0	0	0	0	0	0	0	0	0	0	0	6
1998	30		5	1	0	0	0	0	0	0	0	0	0	0	6
1999	88			5	1	0	0	0	0	0	0	0	0	0	6
2000	20				0	0	0	0	0	0	0	0	0	0	0
2002	50					0	0	0	0	0	0	0	0	0	0
2003	27						0	1	0	0	0	0	0	0	1
2004	26							0	0	0	1	0	0	0	1
2005	16								2	1	0	0	0	0	3
2006	14									0	2	0	0	0	2
2007	44										3	3	1	0	7
2008	25											1	0	0	1
2009	44												1	4	5
2010	44													2	2
Females															
1995	28	0	0	0	0	0	0	0	0	0	0	0	0	0	0
1998	9		1	0	0	0	0	0	0	0	0	0	0	0	1
1999	68			3	0	0	0	0	0	0	0	0	0	0	3
2000	10				0	0	0	0	0	0	0	0	0	0	0
2002	30					0	0	0	0	0	0	0	0	0	0
2003	16						0	0	0	0	0	0	0	0	0
2004	11							0	0	0	0	0	0	0	0
2005	3								0	0	0	0	0	0	0
2006	9									0	0	0	0	0	0
2007	26										5	1	0	0	6
2008	7											1	0	0	1
2009	19												0	0	0
2010	16													0	0

Years with less than 20 captures in total (1996, 2001) were removed from the analyses. R_i = number of Crossbills released (marked + unmarked) at year j_i

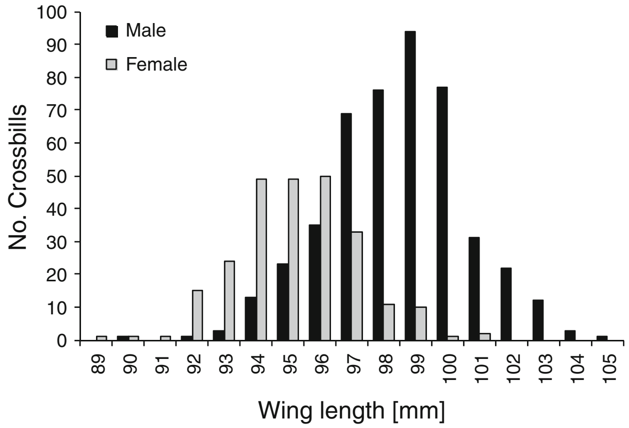

Fig. 1 Wing length distribution in Common Crossbills (*Loxia curvirostra*) (adult birds) captured in a Scots pine forest in the Pyrenees

supporting the presence of long-winged vagrants, which had an impact on the estimation of apparent survival on a local scale. The origin of these vagrant birds is, however, still unknown. Thus, they could come from northern Europe, i.e. be northern vagrants, because in general Crossbills from northern Europe have longer wings than those from southern Europe (Table 1) (although Crossbills' wing length patterns across Europe are more or less mosaic; Cramp and Perrins 1994). We registered two recaptures from abroad: (1) a bird ringed in The Netherlands (date remains unknown) and recaptured at Bigüezal (25 km in a straight line from Uztárroz) in January 2009; and (2) a bird ringed in Switzerland (in August 2008) and recaptured at Uztárroz in April 2009. This supports the theory that northern vagrants visit our study region. Moreover, recovery data of Crossbills ringed in several regions across

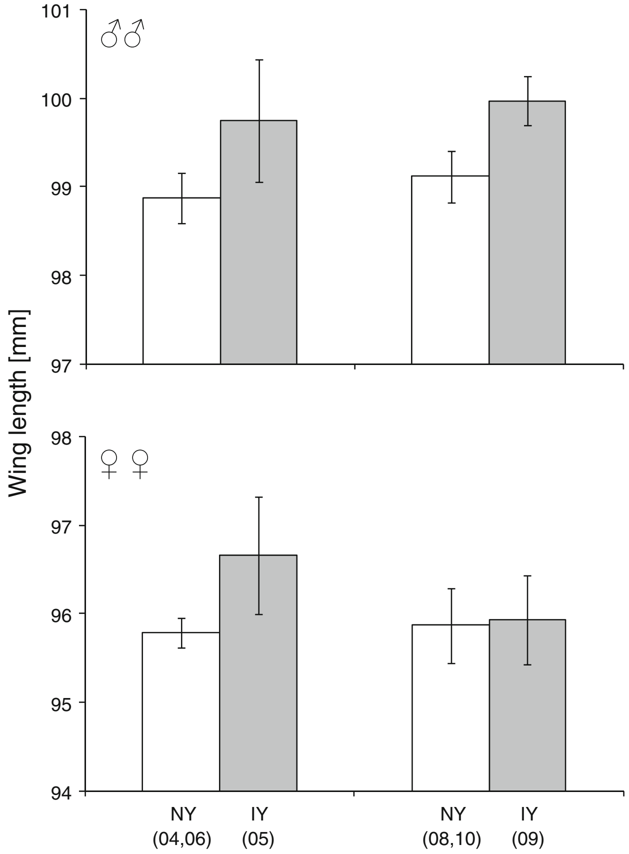

Fig. 2 Wing length (mean ± SD) variation between irruptive years (*IY*, 2005 and 2009; *shaded bars*) and the previous and subsequent non-irruptive years (*NY*, *unshaded bars*; years 2004 and 2006, and 2008 and 2010, have been pooled for the irruptions of 2005 and 2009 respectively) in adult Crossbills

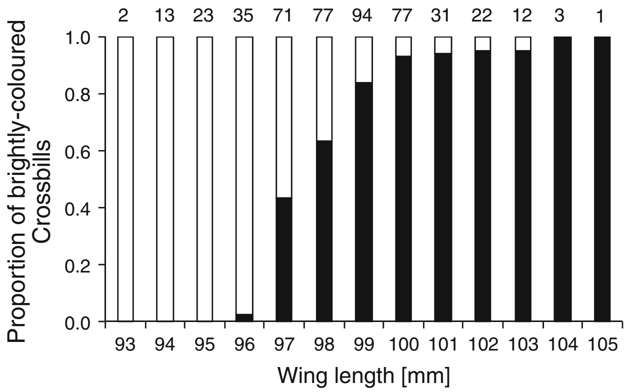

Fig. 3 Proportion of Crossbills (adult males) with pale- (*white bars*) and brightly-coloured (intense reddish plumage; *black bars*) body feathers. Sample size is shown above

Europe have also demonstrated that northern vagrants irrupt periodically in Iberia (Newton 2006). We can thus be sure that a fraction of the long-winged Crossbills at our site was composed of northern vagrants. Additionally, we cannot reject the idea that some long-winged Crossbills might be local vagrants, i.e. belonging to a fraction of local birds that, compared to resident ones (or high site-fidelity birds), move over wider areas (Förschler and Kalko 2009). Notably, Crossbills associated with mountain pine (*P. uncinata*), which grows close to the Scots pine forested area within the Pyrenees, have longer wings than those associated with other pine species (Borrás et al. 2008). The lower survival rates of long-winged Crossbills, either from northern or southern Europe, were probably due to the fact that these birds were vagrants and therefore had a higher emigration rate (emigration = 1 − survival) than residents.

Table 4 ANOVAs on wing length, with sex (*Sx*) and year (*Yr*; irruptions: 2005 and 2009; non-irruptions: the previous and subsequent years to years of irruption) as factors, used to test whether wing length differed between irruptive and non-irruptive years

Variables	SS	*df*	*F*	*p*
2005 irruption				
Sx	154.623	1	44.280	<0.001
Yr	12.359	1	3.539	0.063
Sx × Yr	<0.001	1	<0.001	0.998
Error	363.164	104		
2009 irruption				
Sx	355.412	1	92.125	<0.001
Yr	5.746	1	1.489	0.225
Sx × Yr	4.184	1	1.085	0.300
Error	493.817	128		

Wing length distribution did not show a bimodal frequency pattern, indicating that vagrants (most of which would be long-winged Crossbills) were likely to constitute only a marginal population when compared with the number of local, probably resident, birds.

The fact that the apparent survival rate in long-winged Crossbills was higher than zero suggests that they stayed in the area for a period in excess of 1 year. Although the CJS models did not detect transients (for which the survival rate from 1 year to the next is zero by definition), our results support the existence of long-winged Crossbills, probably vagrants, breeding in the area for one or even a few seasons before leaving permanently. Although our results are not against the idea that southern European Crossbills show a sedentary behaviour (Génard and Lescourret 1987; Senar et al. 1993), we show for the first time that local apparent survival is, or can be, severely affected by vagrants, thus modifying the structure and dynamics estimation at a local level. This highlights that survival estimation in nomadic species must be interpreted cautiously. If wing length is excluded from models, we obtain only an effect of sex on apparent survival (Table 5), which gives a rate of 0.51 ± 0.06 for males and 0.30 ± 0.08 for females (mean for both sexes: 0.47 ± 0.06; Model 5 from Table 5).

Table 5 The top ten CJS models estimating survival (ϕ) and recapture probability (p) (birds captured first as adults) of Crossbills in relation to year (y), sex (s) and time of capture (t_1: survival from Year 1 to Year 2, Year 1 was the year of the first capture event; t_2: annual survival in subsequent years in which year is ≥2), wing length (wing)

Models	AICc	ΔAICc	AICc weight	Parameters	Deviance
1. ϕ (wing^2 × s), p (y)	417.746	0.000	0.331	15	387.079
2. ϕ (wing^2 + s), p (y)	418.469	0.722	0.231	15	387.802
3. ϕ (wing × s), p (y)	418.558	0.812	0.220	15	387.892
4. ϕ (wing + s), p (y)	418.584	0.834	0.218	15	387.917
5. ϕ (s), p (y)	432.087	14.341	0.000	15	401.421
6. ϕ (wing^2), p (y)	434.914	17.168	0.000	15	404.247
7. ϕ (wing), p (y)	434.931	17.185	0.000	15	404.265
8. ϕ (t_1, t_2 × s), p (y)	435.680	17.934	0.000	16	402.924
9. ϕ (t_1 × s, t_2), p (y)	435.921	18.175	0.000	16	403.165
10. ϕ (t_1 × s, t_2 × s), p (y)	436.120	18.374	0.000	17	401.267

Only the 10 best models are shown. We considered both additive (+) as well as interactive (×) models to evaluate the effect of both wing length and sex on survival

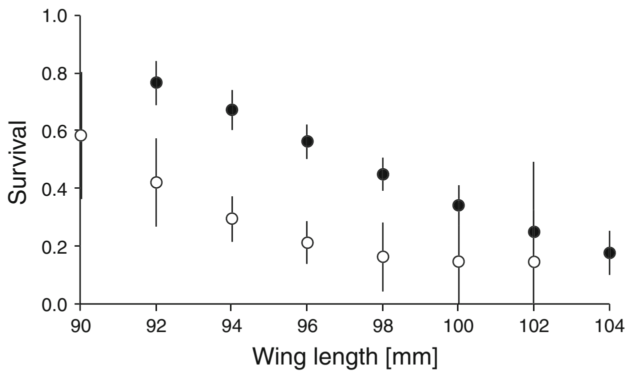

Fig. 4 Annual mean ± SE apparent survival rates of adult Crossbills in relation to wing length. Survival values obtained after model averaging (Mmodels 1–4). Sexes: male, *black dots*; female, *white dots*

A previous study reported a survival rate of 0.46 ± 0.15 (mean for both sexes) for a population from the eastern Pyrenees (Senar et al. 1993), a similar value to that which we obtained on omitting both the effects of sex and wing length. Such values, however, are below the ones reported for Crossbills with short wings when we included wing length into the CJS models. Accordingly, not considering the occurrence of non-local irruptive birds can lead to an underestimation of the local apparent survival rates of native Crossbills in southern Europe.

Alternative hypotheses explaining a negative effect of wing length on apparent survival are not supported by our models and thus must be rejected. One of these hypotheses is that, if we assume that wing length represents body size (Gosler et al. 1998), then our results may indicate that apparent survival tended to be higher in small birds. This interpretation does not fit the rule that survival rate is normally higher among larger birds because they have a higher social position, leading to priority access to food (Garnett 1981; Lindström et al. 1990) and/or they endure the low winter temperatures better. Another hypothesis is that large birds have a larger bill, thus leading to reduced efficiency in opening cones of local Scots pines (Benkman 1987, 2003), since the Scots pines have cones with smaller scales than those found in other Mediterranean pine species (Alonso et al. 2006; Borrás et al. 2008). Within Iberia, larger bills are found in Mediterranean Crossbills that feed on Aleppo pine (Alonso et al. 2006), a species that has much larger cones than those of the Scots pine. However, Mediterranean Crossbills have shorter wings than Pyrenean Crossbills (Alonso et al. 2006), and hence the lower survival rates observed for the long-winged Crossbills were not due to the fact that these Crossbills might have a Mediterranean origin.

Sex had a significant effect on apparent survival, which was higher overall in males than in females. Mechanisms explaining this sex-associated effect were not the goal of our study and they may be due to different selection pressures acting over sex classes (for a general review, see Krebs and Davis 1993). Sex-specific dispersal patterns might also give a reasonable explanation for the difference in apparent survival between sex classes observed in this study, since dispersal is usually greater in females.

In conclusion, although true transients were undetected in the Pyrenees, the negative effect of wing length on apparent survival rates supports the occurrence of vagrants in the area, since they had lower apparent survival rates than short-winged, local birds. Our results suggest that vagrants remain in the area for more than 1 year and therefore they are not "true" or strict transients.

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