

Some aspects of Chaffinch *Fringilla coelebs* biology, based on an analysis of individuals ringed during 1991 to 2003 in Norfolk, England

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From 1991 to 2003, 2,954 Chaffinches *Fringilla coelebs* were caught and ringed, year-round, at Hilborough, Norfolk, England. The age and sex composition of Chaffinches varied between winters, but no systematic pattern was apparent. The age and sex composition of Chaffinches caught during winter did not vary significantly from that of Chaffinches caught during the breeding season. Chaffinch wing lengths and body weights did not vary significantly between seasons. Male Chaffinches had wings that were on average 6 mm longer than females and adult wings were on average 2-3 mm longer than immatures and juveniles. Male Chaffinches were on average 2 g heavier than females. Approximately 40% of juvenile Chaffinches retained unmoulted greater coverts after their post-juvenile moult, retaining 1.47 ± 0.04 and 1.67 ± 0.09 for males and females respectively. Compared to immature females, twice as many immature males retained juvenile greater coverts. Over the period of study, Chaffinches showed relatively consistent annual productivity, with captures of between 1.5 and 2 times as many juveniles or immatures as adults during the months following the breeding season. The higher productivity in some years was not explained by variations in average monthly temperature during the breeding season. The mean duration between initial and final capture on the study site was between 1.6 and 2.3 years, and the longest period between initial capture and last recapture was over ten years. Only 0.14% of Chaffinches were recorded moving distances greater than 5 km from the site of capture, confirming the sedentary nature of the species. This study shows that few, if any, continental immigrants supplement the local Chaffinch population at the study site in Norfolk.

The Chaffinch *Fringilla coelebs* is one of the most abundant and widespread bird species breeding in Europe (Newton & Väisänen 1997, Newton 1993). In Europe, the breeding population is estimated at 83 - 240 million pairs (Heath *et al* 2000) and in Britain & Ireland it is estimated that 7.5 millions pairs breed (Newton 1993). Chaffinches use a range of habitats, and while they are thought of as a woodland species in continental Europe (Cramp & Perrins 1994), a much higher proportion of pairs are found on farmland in Britain & Ireland, particularly in winter, when an estimated 10 - 20 million birds immigrate from northern Europe (Newton 1993, Norman 1986, 2002). The ecology of Chaffinches is similar to a range of other farmland birds, which consume a diet of seeds, and feed their young on invertebrates (Cramp & Perrins 1994), however, unlike many of these species that have undergone severe population declines in recent years, the Chaffinch breeding population in Britain & Ireland has increased (Fuller *et al* 1995,

Siriwardena *et al* 1998). It is thought that the species reliance on foraging in trees, rather than arable fields, for food for their young, and its willingness to use supplementary food provided in gardens during the winter, have prevented the species' decline (Whittington *et al* 2001, Macleod *et al* 2004).

Given that the Chaffinch is a very common bird in Britain & Ireland, it is surprising how relatively understudied it has been, particularly in recent years. During the 1950s and 1960s a number of studies were undertaken by Marler (1956) and Newton (1964, 1967 & 1972) that provided a range of information on the species' biology. More recently, Whittingham *et al* (2001) undertook a study of Chaffinch biology in lowland farmland and established the reasons for the continued success of the species in England, and Macleod *et al* (2004) undertook a similar study in Scotland. In this paper, I use the data collected from 2,954 captures of Chaffinches at a site in Norfolk, to provide additional

information on various aspects of the species' biology. Additionally, I investigate the theory put forward by Newton (1967) that continental Chaffinches that come to Britain & Ireland in winter are larger than resident birds, dominated by one sex and would therefore alter the sex composition and mean wing length of birds caught in winter, compared to those caught in summer.

METHODS

Study site

The study was carried out in an area of approximately 2,000 ha surrounding the village of Hilborough (52° 34' N 0° 4' E) in Norfolk, England, during the period March 1991 to February 2003. The study site comprised typical Breckland farmland, with a range of arable crops being interspersed with hedges, heathland, scrub and small woodlands. Breeding Chaffinches were numerous and widespread throughout the study site, where they were thought to occur at densities that were representative of lowland farmland in southern England. During the winter, Chaffinches were regularly encountered in flocks of between ten to 400 individuals, utilising supplementary food, set-aside strips and stubbles. Chaffinches used supplementary food provided in gardens throughout the year.

Ringling

Ringling took place throughout the year, with about 40% of birds being caught during winter. Most birds (77%) were caught within a large (2 ha) semi-wooded rural garden, where annually approximately three tonnes of supplementary food was provided throughout the year. The supplementary food was a commercially available seed mix that comprised mainly black sunflowers, millet and a range of other seed, with the addition of chopped peanuts. The remaining birds were caught around arable fields, at two smaller rural gardens, patches of scrub and woodland sites. During the winter 73% of the Chaffinches were caught in gardens, with the others being caught in farmland (26%) and woodland (1%). During other times of the year, 84% of Chaffinches were caught in gardens, 11% in farmland and 5% in woodland. Ringling effort during different times of year and in different habitats did not vary between years.

Birds were predominantly caught in mist nets set through breeding habitats in the spring and summer or adjacent to supplementary food in the winter. Ringling was undertaken most weekends, weather permitting. All birds were fitted with an individually numbered, metal British Trust for Ornithology (BTO) ring and the wing length (maximum chord), body weight and the number

of old (unmoulted, juvenile) greater coverts was recorded for most birds (Redfern & Clark 2001). Each bird was aged and sexed using the criteria in Svensson (1992) and in summary the following were used. Juvenile birds had characteristic loose and sparse feathering, and in most cases, white feathering on the back of the head. Immature birds retained a number of unmoulted feathers within various tracts and the presence of one or a combination of duller and shorter greater coverts, duller and more pointed alula and primary coverts and differently coloured and more pointed tail feathers. In addition, for females, tertial colour, shape and wear were also used as criteria. Over the course of the study a number of ringers were involved and, although attempts were made by the author to check the measurements and ages of the Chaffinches, it was not possible to check all of them. Birds were caught and ringed in accordance with the rules of the BTO ringling scheme (Redfern & Clark 2001) and under permit from the BTO. The numbers of Chaffinches caught during the study are summarised in Table 1.

Statistical analysis

The terms 'new birds' and 'retraps' are used throughout. New birds are those caught and ringed for the first time on the study site. Retraps are trapped birds that have been previously ringed on the study site. Captures of all birds were assigned to four seasons (winter, spring, breeding, autumn), based on their reported migration and breeding behaviour. Winter comprised November, December of one year and January, February of the

Table 1. The number of Chaffinches caught each year in Hilborough, Norfolk during March 1991 to February 2003. Years run from March to February (see text). Retraps may include repeat handlings of the same individual.

Year	New birds	Retraps	Total
1991	92	11	103
1992	28	3	31
1993	117	33	150
1994	374	121	495
1995	335	132	467
1996	220	39	259
1997	197	49	246
1998	280	90	370
1999	152	68	220
2000	203	87	290
2001	155	37	192
2002	101	30	131
Total	2,254	700	2,954

following calendar year, and the breeding season comprised May to July. Accordingly, a 'year' was defined as the period from 1 March of one year to the last day of February in the following calendar year.

Chaffinches were grouped into three age groups based on plumage characteristics. Juveniles included birds that had fledged the nest, but had not completed their post-juvenile moult (EURING age code 3J). Immatures were birds that had completed their post-juvenile moult but had retained some unmoulted (juvenile-type) feathers (EURING age codes 3 & 5). Adults were all birds that had moulted into full adult plumage with a post-nuptial moult (EURING code 4 & 6). Some of the adult birds (<1%) were not sexed at ringing and were excluded from some of the analyses. Immediately after fledging, but before the start of post-juvenile moult, the sexes are indistinguishable, so it was possible to assign a sex to only 68% of the juveniles.

Contingency table analysis (loglinear modelling using a generalised linear model with Poisson error and logarithmic link function) was used to compare the proportions of Chaffinches, in each combination of age and sex categories, which were caught as new birds during each year in winter. Juveniles were excluded as some were unsexed.

Compositional analysis (Aitchison 1986) was used to compare the age and sex composition in winter with that in the breeding season. Three ratios were produced by dividing the number of adult females, adult males and immature females by the number of immature males. The resulting ratios were log-transformed for further analysis. These logratios were analysed using multivariate analysis of variance (MANOVA), with the logratios being the dependent variables and season (breeding & winter) as the factor. Differences in wing lengths and body weights with respect to age, sex, year, habitat and season were assessed using an analysis of variance (ANOVA).

The proportions of individuals classified by plumage type (juvenile, immature and adult) were analysed using compositional analysis. The proportion of birds in each plumage category was converted to logratios, using the proportion of adult plumaged birds as the denominator. The logratios (dependant variables) were analysed using a MANOVA with month and year as factors.

Differences in the number of immature Chaffinches with or without one or more old greater covert were assessed in relation to year, sex and the interaction with logistic regression. Differences in the number of old greater coverts retained by new immature male and female Chaffinches each year were compared using ANOVA, with sex and year as factors.

In order to investigate whether breeding success of Chaffinches on the study site had fluctuated annually, an index of breeding success was calculated as the ratio of the proportion of new individuals that were juveniles (and later immatures) and the proportion of new individuals that were adults caught during the months following the breeding season (ie August to April). In years of poorer overall breeding success it was assumed that the index would be lower, whereas in better years it would be higher. This ratio was log-transformed and analysed using linear regression with the log-ratios being the dependent variable and year as the independent. To investigate the effect of weather on the breeding success of Chaffinches the index of breeding success was related to mean temperature during the breeding season using linear regression. Temperature data for 1991 to 2003 were extracted from Manley's Central England monthly air temperature database (www.met-office.gov.uk/research/hadleycentre/CR_data/Monthly/HadCET_act.txt).

The length of time (in days) between initial and final capture was used to provide a measure of longevity for individual birds. Although this is not a true representation of longevity, the lack of a suitable number of dead, recovered ringed birds within the sample means that this is the best measure currently available. The length of time (in days) between initial and final capture (log transformed) was analysed using an ANOVA with age and sex as factors. In order to remove the potential effect of migrant birds lowering this value, the analysis was repeated using birds with a length of time between initial and final capture that was greater than 120 days.

All interactions were tested in the ANOVAs and MANOVAs, and the main factors were tested only if the interactions were not significant. The analyses were carried out using the statistical package SYSTAT 10 (SPSS Inc, Chicago). Average values are given as means \pm 1 SE.

RESULTS

Age and sex composition

The age and sex composition of new birds caught during winter at the study site are summarised in Table 2. The interaction between age, sex and year was not significant ($\chi^2_{11} = 4.17$, NS). The interaction between sex and year ($\chi^2_{11} = 13.90$, NS) was not significant, however, the interactions between age and sex ($\chi^2_1 = 5.15$, $P = 0.019$) and age and year ($\chi^2_{11} = 38.55$, $P < 0.001$) were significant, showing that there were significant variations in age and sex composition between winters. It is therefore not possible to produce a meaningful comment

Table 2. Age and sex composition of Chaffinches caught during Winter 1991/92 to 2002/03 at Hilborough, Norfolk. Values are expressed as percentages of the total numbers of aged and sexed Chaffinches caught each winter.

Year	Adult		Immature	
	females	males	females	males
1991	23.5	17.6	26.5	32.4
1992	22.2	7.4	33.3	37.0
1993	7.7	15.4	25.6	51.3
1994	20.8	20.8	28.0	30.4
1995	12.0	12.0	30.4	45.7
1996	21.7	23.6	24.5	30.2
1997	16.7	23.3	23.3	36.7
1998	13.7	8.8	32.4	45.1
1999	27.8	31.5	18.5	22.2
2000	16.7	10.0	30.0	43.3
2001	21.6	16.2	29.7	32.4
2002	11.1	20.4	14.8	53.7
Overall	18.0	17.2	26.4	38.4

on an average annual age and sex composition of Chaffinches caught during winter at the study site. However, overall more females were adult (41%) compared to males (31%). The age and sex composition of Chaffinches caught during winter did not vary significantly from that of Chaffinches caught during the breeding season ($\chi^2 = 0.836$, $F_{3,18} = 1.17$, NS).

Biometrics

Wing length

Wing lengths were recorded for 1,681 individual Chaffinches. The interactions between age, sex, season, habitat and year on Chaffinch wing length were not significant (all $P > 0.05$). Chaffinch wing length varied significantly with age ($F_{2,1662} = 119.89$, $P < 0.001$), sex ($F_{1,1662} = 2152.46$, $P < 0.001$) and year ($F_{11,1662} = 2.65$, $P = 0.002$), but not season ($F_{3,1662} = 1.75$, NS) or habitat ($F_{2,1662} = 3.35$, NS). The wing lengths of males were on average about 6 mm longer than those of females (Fig 1). The wing lengths of adult males were, on average, 2.6 mm (2.9%) longer than those of immature males, whereas for females, wing lengths of adults were 1.2 mm (1.4%) longer than those of immatures. The wing lengths of immatures were similar to those of juveniles (Fig 1). Although there was significant variation in wing length between years, no systematic pattern was apparent (Fig 2).

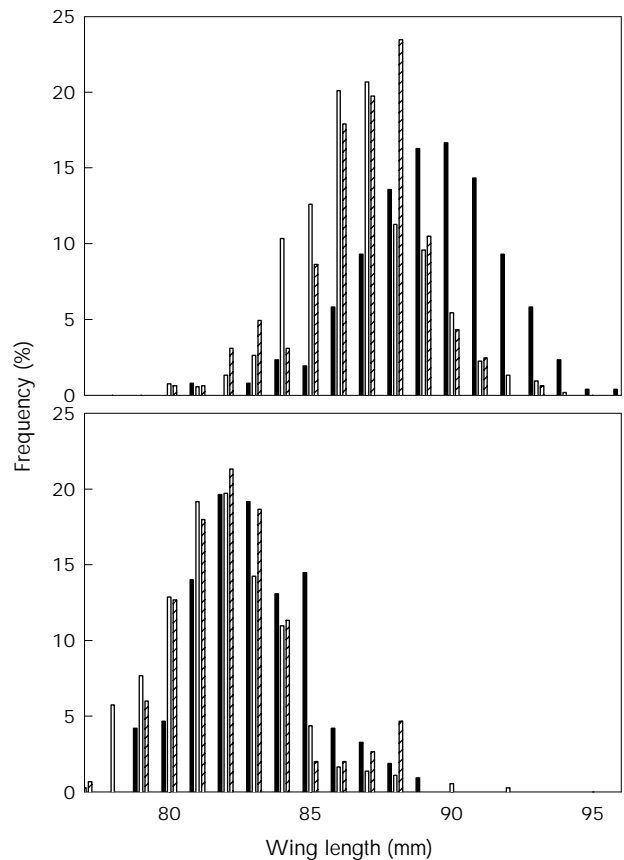


Figure 1. Distribution of wing lengths of a) male ($n = 952$) and b) female ($n = 729$) Chaffinches caught during 1991 to 2003 at Hilborough, Norfolk. Adults (black bars), immatures (open bars) and juveniles (hatched bars) are shown separately.

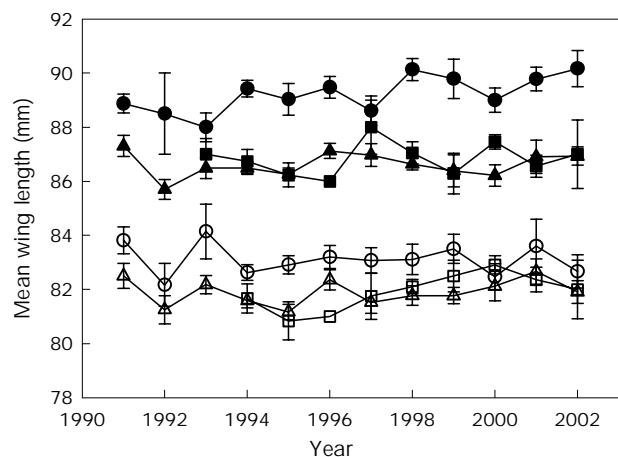


Figure 2. Mean wing length (\pm se) of male ($n = 952$; filled symbols) and female ($n = 729$; open symbols) Chaffinches caught between 1991 and 2003 at Hilborough, Norfolk. Adults (\bullet), immatures (\blacktriangle) and juveniles (\blacksquare) are shown separately.

Body weight

Body weight was recorded for 1,300 individual Chaffinch. The interactions between age, sex, season and year on Chaffinch body weight were not significant (all $P > 0.05$). Chaffinch body weight varied significantly with sex ($F_{1, 1281} = 408.15$, $P < 0.001$), season ($F_{3, 1281} = 19.29$, $P < 0.001$), year ($F_{11, 1281} = 4.94$, $P < 0.001$), but not age ($F_{2, 1281} = 2.37$, NS) or habitat ($F_{2, 1281} = 0.05$, NS). The body weight of males was, on average, about 2 g heavier than females (Fig 3). Although there was significant variation in Chaffinch body weight with respect to season and year, no systematic patterns were apparent.

Moult

Chaffinches were caught with three types of plumage; juvenile, immature or adult. As expected, the proportion of individuals that were in either juvenile, immature or adult plumage varied with month ($\Lambda = 0.293$, $F_{22, 164} = 6.29$, $P < 0.001$) as the yearly cycle of moult progressed,

however, the proportion of individuals in the three plumage types in each month did not vary with year ($\Lambda = 0.888$, $F_{22, 164} = 0.45$, NS). Accordingly, the annual progression of the moult, whereby juveniles moult into immature and then adult plumage is shown in Fig 4.

After fledging, Chaffinches have juvenile plumage, but from June to September undergo a partial moult into immature plumage, which is essentially the same as adult plumage, but with a number of unmoulted juvenile-type feathers being retained. In the following year these birds undertake a post-nuptial full moult into full adult plumage during June to September, by which time juveniles from the following breeding season will have started to assume immature plumage (Fig 4)

Three hundred and sixty-eight immature Chaffinches had retained one or more unmoulted greater coverts, representing 37% of all immature Chaffinches caught. The interaction between year and sex on the presence, or not, of at least one old greater covert was not significant ($\chi^2_1 = 0.42$, NS). The presence of old greater coverts did not vary significantly in relation to year ($\chi^2_1 = 1.77$, NS), but did vary significantly between sexes ($\chi^2_1 = 60.92$, $P < 0.001$). A higher proportion of immature males had old greater coverts (44%) compared to immature females (22%). The interaction of year and sex on the number of old greater coverts was not significant ($F_{11, 344} = 1.65$, NS). The number of old greater coverts retained by immature Chaffinches did not vary significantly with year ($F_{11, 355} = 0.882$, NS), but did vary significantly with sex ($F_{1, 355} = 5.53$, $P = 0.019$). The number of old greater coverts retained varied from one to five, with males on average retaining 1.47 ± 0.04 old coverts and females 1.67 ± 0.09 .

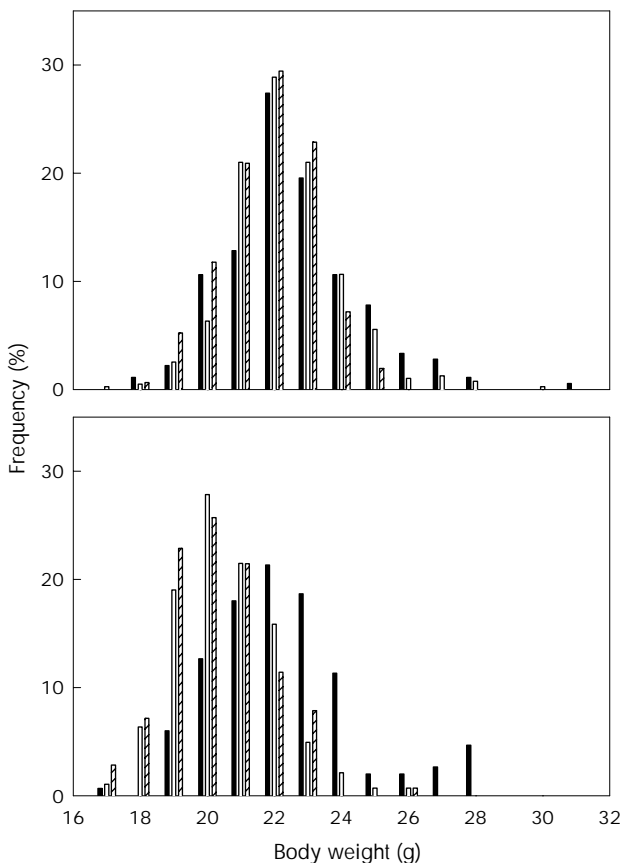


Figure 3. Distribution of body weights of a) male ($n = 727$) and b) female ($n = 573$) Chaffinches caught during 1991 to 2003 at Hilborough, Norfolk. Adults (black bars), immatures (open bars) and juveniles (hatched bars) are shown separately.

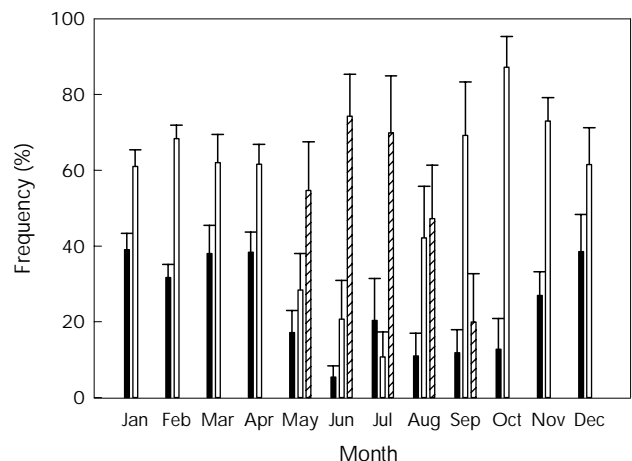


Figure 4. Mean proportion (\pm se) of Chaffinches with adult ($n = 575$; black bars), immature ($n = 1047$; open bars) and juvenile ($n = 503$; hatched bars) plumages during each month in the period 1991 to 2003 at Hilborough, Norfolk.

Breeding success

Breeding success, measured as the ratio of new adults and young birds caught during the months following the breeding season, varied significantly between years ($\chi^2_{11} = 97.33$, $P < 0.001$) but there was no significant linear trend to the pattern ($r_{10} = 0.014$, NS, Fig 5). Averaged over all years, in the months following the breeding season there were 1.82 (± 0.24) times as many juvenile and immature Chaffinches as there were adults. In 1993, breeding success was higher than in the other years, and in 1999 and 2000 breeding success was lowest (Fig 5). Mean temperature during the breeding season did not explain the variation in breeding success ($r_{10} = -0.24$, NS).

Longevity

Four hundred and thirty-five individual Chaffinches were caught and subsequently retrapped. When considering all individuals, the interaction between age and sex on the length of time between initial and final capture was not significant ($F_{2, 429} = 0.74$, NS). This did not vary significantly with age ($F_{2, 431} = 1.67$, NS) or sex ($F_{1, 431} = 0.47$, NS). For about 55% of the Chaffinches that were caught and retrapped, the length of time between initial and final capture was less than one year, with the majority (80%) being caught for the final time less than three years after initial capture (Fig 6). The maximum length of time between initial and final capture was 3695 days; just over ten years. Overall, the average length of time between initial and final capture for all ages combined, and throughout the entire study period, was 592.26 ± 30.2 days.

If birds that were caught for the final time less than 120 days after initial capture were removed from the analysis, the interaction between age and sex remained

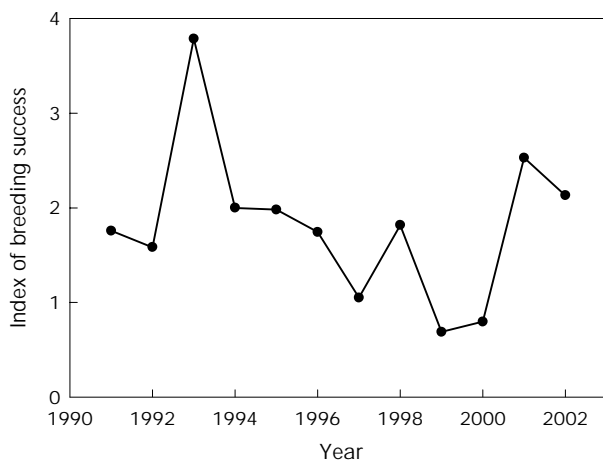


Figure 5. Index of breeding success (see text) for Chaffinches caught during 1991 to 2003 at Hilborough, Norfolk.

non-significant ($F_{2, 327} = 0.94$, NS). The length of time between initial and final capture did not vary significantly with sex ($F_{1, 329} = 0.27$, NS) but varied significantly with age ($F_{2, 329} = 4.58$, $P = 0.011$). The mean capture interval for birds initially ringed as juveniles was 624.8 ± 50.0 days, for immatures it was 815.7 ± 55.5 days and for adults the capture interval was 849.5 ± 77.9 days.

Movements

Only 20 (<1%) Chaffinches caught at the study site have been recovered elsewhere. The longest distance between ringing and recovery site was 44 km by one individual, three other birds had moved about 15 km, and the rest had moved less than 5 km.

DISCUSSION

Although Chaffinches were caught in a range of habitats during this study, the majority were caught in gardens, whilst attracted to supplementary food and consequently the information presented may not be truly representative of all Chaffinches that inhabited the area surrounding the study site.

Whilst it is known that continental Chaffinches over-winter in Britain & Ireland, and combine with resident birds to form flocks, their influence in altering the age and sex composition of the resident population studied here was not apparent. Additionally, although these immigrant Chaffinches are widely believed to be larger and longer-winged than British residents, no significant increase in average wing length was detected during winter, either for all birds or those caught specifically on farmland. These findings are at odds with those

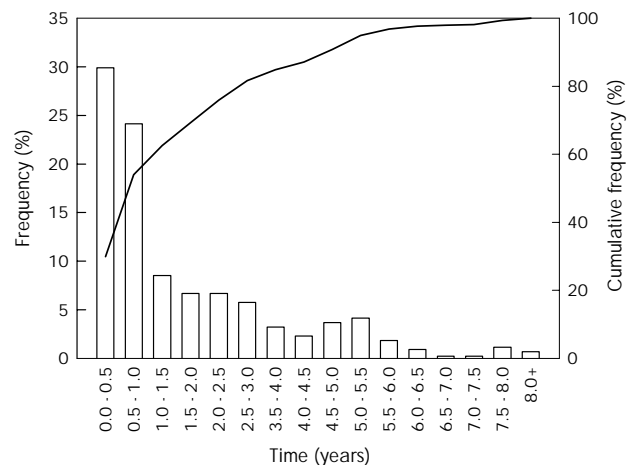


Figure 6. Distribution of longevity for all Chaffinches caught and subsequently retrapped ($n = 435$) during 1991 to 2003 at Hilborough, Norfolk.

reported by Newton (1972), who shows that in Britain, during winter, males predominate and wing lengths should, on average, be longer. Newton (1972) found these differences in the sex composition and wing length of the population he studied in Oxfordshire, whereas Swann (1988) found that such differences were not apparent amongst Chaffinches in northern Scotland. Therefore, as concluded by Swann (1988), it is likely that there are regional differences within Britain & Ireland in the extent to which continental immigrants augment the resident population in winter. It is possible that although large numbers of Chaffinches do migrate into Norfolk (Browne 1999) most continue their migration west into central and southern England (Norman 2002). In support of this theory, only very few of the Chaffinches ringed in Norfolk have been recovered abroad (Browne 1999).

In common with Bramblings (Browne & Mead 2003), Chaffinches are sexually dimorphic with respect to wing length and body weight, and wing-length also varied in relation to age. Males are longer-winged and heavier than females, and adults are longer-winged than juveniles. However, unlike other studies that have shown that the difference between adults and immatures was similar for females and males (Norman 1995), the differences between the sexes reported here were not the same. This may be a consequence of some females being incorrectly aged, so that a number of immature birds were assigned as adults (see below).

Chaffinches undertake a partial post-juvenile moult in their first year, retaining a number of unmoulted juvenile-type feathers, and one full moult each year after breeding (Ginn & Melville 1983). All Chaffinches leave the nest in juvenile plumage and within 20-30 days of completing the growth of their juvenile feathers they undertake a post juvenile moult into immature plumage. The post juvenile moult is only partial, with some (1-5) greater coverts, tail feathers, tertials and primary coverts being retained. After breeding, adults undertake a complete post nuptial moult, when first-year birds replace all feathers, including retained juvenile feathers, and assume full adult plumage (Jenni & Winkler 1994). The birds studied here were only caught with juvenile plumage during May to September. Of those that moulted into immature plumage, 37% retained between one to five unmoulted greater coverts, which is much lower than the 86% recorded by Jenni & Winkler (1994). This is possibly because Jenni & Winkler (1994) were studying birds on passage, which may be more likely to arrest moult and retain unmoulted coverts compared to a more resident population. However, of those that had the number of retained greater coverts recorded, the average number retained by males was 1.47 and by

females 1.67, which is similar to the average of 1.5 reported by Jenni and Winkler (1994) for 9,404 Chaffinches caught in Switzerland. A higher proportion of immature males retained old greater coverts compared to females. However, this may be because old greater coverts are easier to see on males and were consequently under-recorded on females. This may also have resulted in the apparently higher proportion of females that were recorded as adults and the smaller difference between immature and adult female wing lengths, compared to males.

Although it was only possible to calculate a rather crude index of annual breeding success for Chaffinches on the study site, in general it appears that Chaffinches have similar breeding success each year. Chaffinches are very persistent in their approach to breeding, for although they only undertake one successful breeding attempt per year, they will undertake numerous nesting attempts, up to six have been recorded, until they fledge young (Newton 1964, 1972, Cramp & Perrins 1994). Newton (1964) states that the main cause of breeding failure was losses due to predation of nest contents, with the other nests being lost to desertion, a mixture of adult predation, weather and disturbance, or directly to bad weather. The study site was managed for shooting, as were many estates in the surrounding area, and a number of gamekeepers were employed to control predator numbers, so while predation was likely to have some effect on Chaffinch breeding success on the study site, probably of more importance was bad weather. However, breeding success on the study site was not significantly related to mean temperature during the breeding season. Whilst it is likely that temperature does give some indication of good and bad weather, it does not accurately reflect periods of wet and windy weather, which are more likely to affect adult foraging and consequently breeding success.

Newton (1972) provides information that shows for two studies (one in Sweden and one in Finland), the mean expectation of life is at least 2.5 and 2.7 years. For Chaffinches in this study, the average length of time between initial and final capture (which might be taken to represent an underestimate of longevity) for all birds was 592 days, about 1.6 years. However, if the possible effect of immigrants lowering this value was removed, it rose to 623 to 850 days, about 1.7 to 2.3 years, with the maximum length of time (in days) between initial and final capture being over ten years. These values are likely to underestimate longevity, as they do not allow for the effect of juvenile dispersal, which probably accounts for the differences in the length of time between initial and final capture in relation to age at ringing.

In common with the conclusions drawn by Newton (1972) and Norman (2002), very few of the total number of Chaffinches caught on the study site moved distances greater than 5 km, and none were caught or originated from other countries. This confirms the very sedentary nature of the Chaffinches studied in this population and probably supports the theory that very few immigrant Chaffinches over-winter in the Breckland area of Norfolk.

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Although much of the data used here was collected by the author, it all formed part of the dataset of ringing information collected by the late Chris Mead. Chris dedicated his life to the ringing and study of birds and the publication of this paper is in some small way a testament and memorial to him. I thank the numerous ringers who have helped catch the Chaffinches. Dr Nicholas Aebischer provided statistical advice and comments that helped improve the paper. Professor David Norman and Dr Ian Hartley provided helpful comments, for which I am grateful.

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