

A population study of the Dipper *Cinclus cinclus* in the Italian Prealps

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Abstract - The Dipper population breeding in a 12.5 km stretch of the River Posina (Vicenza Prealps, north-eastern Italy) was studied during 1991-1996 and results were compared with those from other researches throughout Europe. The breeding density (mean = 1.46 ± 0.04 pairs/km) was relatively constant through years, but it was highly variable along the stream. A total of 127 nests were located, most of them (81.1%) built in artificial sites. The median laying date was 9 March for first breeding attempts and 23 April for second ones. Laying dates of first clutches were influenced by pair age and habitat features of the different stream stretches. The overall mean clutch size was 5.11 ± 0.54 , comparable with values observed in northern populations of continental Europe. Clutch size did not vary during the season, apart from a sharp decrease in May. Of 54 successful first nestings, 25 (46.3%) were followed by a genuine second brood. The overall percentage of nests producing at least one young was 80.8%, second clutches being more successful than first and replacement ones. Young from clutches laid in different periods showed different recapture rates, nestlings hatched around mid-May showing the highest recapture rate. The annual adult survival rate, estimated from between-year recaptures, was 56.8%. Posina Dippers exhibited a strong territory fidelity both during the breeding season and in the following years.

Introduction

The Dipper *Cinclus cinclus* is one of the most specialized passerine of European avifauna, living in close association with fast-flowing upland water-courses. The ecological peculiarities of this species have since long stimulated many studies upon several aspects of the breeding biology, such as feeding habits, breeding performances and habitat requirements (reviewed in Creutz 1986 and in Tyler and Ormerod 1994). Most recent studies have highlighted the role of the Dipper as an indicator of water quality in polluted or acidified rivers (e. g. Lachenmayer *et al.* 1985; Ormerod and Tyler 1987). Despite the literature richness, southern populations have been poorly investigated. In particular, researches on breeding ecology in the Alps were carried out only by Wagner (1984) and Breitenmoser-Würsten (1988, 1997).

The aim of this study was to gather information on breeding performances and population dynamics of a Prealps population of *Cinclus c. aquaticus*. Data on density, laying date, clutch and brood size and second brood rate were compared with the results of studies from other parts of Europe.

Study area

The research was carried out along the River Posina, a small stream flowing from Passo della Borcola (1050 m above sea level) into the River Astico, south of the town of Arsiero (255 m a. s. l., $45^{\circ} 48' N$, $11^{\circ} 21' E$, Vicenza province, NE Italy; for further details see Tasinazzo *et al.* 2000). Fieldwork was conducted in the part of the stream most suitable to Dippers, from Contrada Beber (600 m above sea level) 12.5 km downstream to Stancari (400 m), including the terminal tracts of tributaries. Downstream the main study area, where the habitat is increasingly unsuitable to Dippers because of hydroelectric drawing off, we only counted few scattered breeding pairs. The study area was divided into sixtytwo 200-m segments, upstream grouped into four stretches (A-D) according to homogeneous environmental features (Table 1), and which all data collected were referred to.

Methods

Breeding

The fieldwork was conducted on the River Posina from January 1991 to July 1996.

Table 1. Features of the four stretches of the River Posina (Maio G., Marconato E. & Salviati S. pers. comm.).

Stretch	A	B	C	D
length (km)	2.10	3.65	4.10	2.65
wet river bed (mean width, m)	13.00	9.00	7.00	5.00
gradient (m/km)	<15	15-19	20-24	≥25
banks	n	a	n-a	n
water permanence	c	d	c	c
EBI	10	9-11	10-11	12
nesting site abundance	h	l	h	h

n=mainly natural; a=mainly artificial; c=continuous; d=discontinuous; h=high; l=low. EBI=Extended Biotic Index (Ghetti 1986).

Breeding parameters were recorded during weekly visits carried out from 1 February to 30 June 1992-95. The 1991 and 1996 breeding seasons were only partially covered, since the nest checks were interrupted before the end of the laying period.

All territories were located and census accuracy was confirmed by repeated observations of territory owners involved in doubling back flights or in antagonistic interactions with neighbouring birds at the boundaries of each defended area.

A wooden board, suitable as nest support, was placed inside each established territory, under every concrete bridge crossing the stream, to prevent nest falling from unsuitable ledges and to facilitate nest checking. Indeed, most pairs took advantage of these simple structures for nesting. In order to minimize disturbance, nest inspections were limited to recording laying and hatching dates and to ringing nestlings at 7-17 days. When unknown, the first-egg laying date was calculated back from the nestling age as estimated by the growth curve. The incubation period of 16 days, from the last egg laying to the first chick hatching (Glutz and Bauer 1985, Cramp 1988, Smiddy *et al.* 1995), was confirmed by our observations in two cases where nests were accurately followed.

The identity of parents involved in most breeding attempts could be assessed by checking ringed birds at the nest. Thus, we were able to estimate the age of paired adults and recognize genuine second broods.

Survival

Survival estimates are based on capture-recapture data collected during 1992-1995 breeding seasons. Birds were mist-netted in the breeding territories or close to their nest-sites during the nesting season from early January to the end of June. Breeding birds, hereafter called 'adults', included also first-years. The analysis was carried out applying the program SURGE (Lebreton *et al.* 1992) which uses a modification of

the Cormack-Jolly-Seber model to estimate survival rates (S) and recapture probabilities (P) from mark-recapture data. For our data set, models with time-dependent or constant parameters were fitted iteratively using the maximum likelihood method, among which the simplest one was selected by likelihood ratio tests.

Dispersion

To measure movements of birds within the study area, all captures were mapped on topographic 1:10000 scale maps. In the following analyses, the annual cycle of the population was subdivided into two main periods: breeding season (1 January to 30 June) and non-breeding season (1 September to 31 December). In the analysis of dispersion movements we excluded July and August, when birds were moulting or finishing breeding. Moreover, we did not consider January captures because our observations suggested that Dippers are, then, engaged in pair formation and territory establishment or defense.

The statistical analysis was performed with the STATISTICA package (StatSoft 1995).

It was not possible to gather enough data on all variables and this accounts for differences of sample sizes between analyses.

Results

Density

In January the Dipper population of River Posina was settled, apart from very rare 'floaters', which were not considered in density computation.

During 1992-1995 years, 23 different territories (annual mean = 18.3 ± 0.5 sd) were occupied in the main study area, 52.2% of them being held every year, 13% in only one season. The observed annual density ranged between 1.44 and 1.52 pairs/km, but territories were not homogeneously spaced along the stream (Table 2). Mean densities (pairs/km, \pm sd) for the whole study period were: 1.79 ± 0.46 (stretch A), 0.68 ± 0.16 (B), 2.07 ± 0.24 (C) and 1.32 ± 0.22 (D).

Table 2. Number of Dipper territories annually recorded in different stretches of River Posina.

Stretch	length (km)	1992	1993	1994	1995
A	2.10	5	4	3	3
B	3.65	2	3	3	2
C	4.10	8	8	8	10
D	2.65	3	3	4	4
Tot	12.50	18	18	18	19

Breeding season

The laying dates of the first-egg ranged between 2 February and 25 May with an overall median date of 24 March (Fig. 1). The median first-egg date was 9 March ($n = 72$) for first clutches and 23 April ($n = 27$) for the second ones without any significant difference among years 1991-1996 (Kruskal-Wallis $H = 4.21$, $df = 5$, $p = 0.5$).

Dippers started laying a second clutch soon after the successful rearing of the first brood. The mean interval between the first-egg laying dates of subsequent breeding attempts by the same pair was $54.8 \text{ days} \pm 5.19 \text{ sd}$ (range 45-67, $n = 20$).

For first clutches, the start of breeding was strongly correlated with the age of pair members, being earlier the older the pair (Fig. 2). The regression line was: $\text{date} = 93.4 - 5.6 \text{ pair age}$ ($F_{1,34} = 13.9$, $p < 0.001$, $r^2 = 0.29$, $n = 36$).

Laying date did not show a one-way relation with

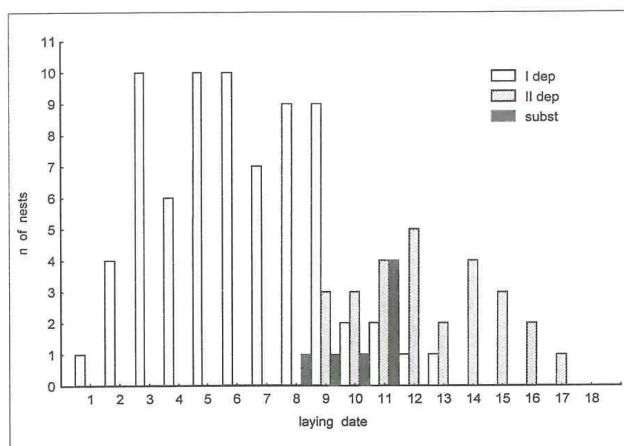


Figure 1. Frequency distribution of first-egg laying dates in 106 Dipper clutches, recorded along River Posina during 1991-96. Dates were grouped by 7-day periods (1=1-7 February).

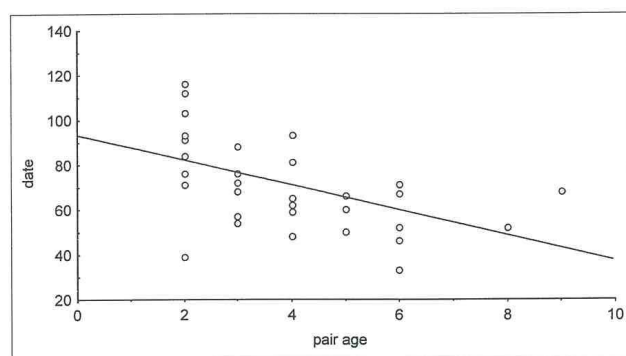


Figure 2. Relation between pair age and starting date of laying in first clutches of Posina Dippers. A minimum age was assigned to the few birds first time captured as adults. Pair age was obtained summing up the age of both members.

altitude along the stream course. Below 500 m, the mean altitude of our study area, the onset of breeding was slightly correlated with altitude ($b = -0.16$, $t_{37} = -1.99$, $p = 0.05$, $r^2 = 0.10$), whereas above this limit the start of laying was clearly delayed by increasing altitudes ($b = 0.43$, $t_{31} = 4.98$, $p = 0.00002$, $r^2 = 0.44$). Considering that other stream characteristics probably affected the laying date, we related this breeding parameter with 200 m-segments. The fittest model found to describe the variation in reproduction timing was a third-order polynomial which reached a minimum in correspondence of the stretch C, where Dippers initiated laying unexpectedly early (Fig. 3).

Clutch size

Data were available for 64 nests, of which 50 were first, 10 second and 4 were replacement clutches. Nests contained 4 (9.4%), 5 (70.3%) and 6 (20.3%) eggs, with an overall mean clutch size for all years of $5.11 \pm 0.54 \text{ sd}$ (Fig. 4).

First (mean = $5.06 \pm 0.44 \text{ sd}$) and second clutches (mean = $5.10 \pm 0.88 \text{ sd}$) did not differ significantly in size (Mann-Whitney median test $p = 0.80$), whereas replacement clutches (mean = $5.75 \pm 0.50 \text{ sd}$) were significantly larger than first ones (Mann-Whitney $p = 0.03$). This difference should be taken with care because of small sample size. Mean clutch size was not homogeneous along River Posina (Kruskal-Wallis $H = 11.63$, $df = 3$, $p = 0.009$), the highest value occurring in stretch C.

Considering the first attempts only, there was no significant difference in clutch size across years (Kruskal-Wallis $H = 2.85$, $df = 5$, $p = 0.72$).

Clutch size kept approximately constant throughout the breeding season, except for a sharp decrease in the latest laying period (Fig. 5).

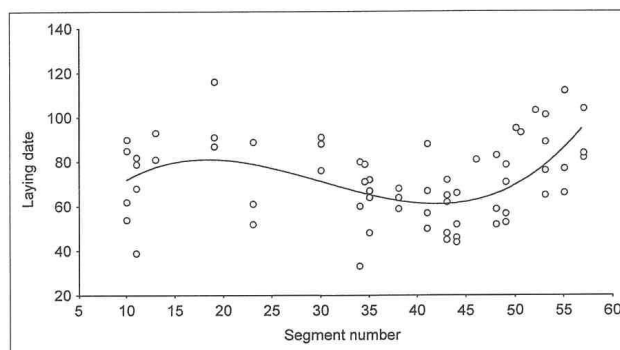


Figure 3. Relationship between first clutch laying date ($n=72$) of Dippers and River Posina segment. The fitted polynomial was: $y = 26.54 + 6.981x - 0.274x^2 + 0.003x^3$ ($F_{3,68} = 8.59$, $p = 0.00007$, $r^2 = 0.27$). 1=1 January; Segment 10 to 15=stretch A, 16 to 31=B, 32 to 49=C and 50 to 60=D.

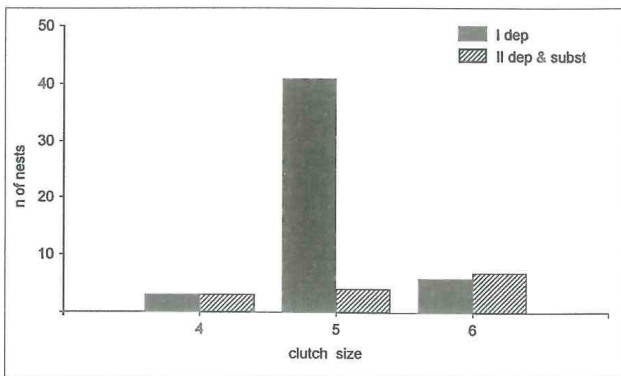


Figure 4. Frequency distribution of Dipper clutch size on River Posina.

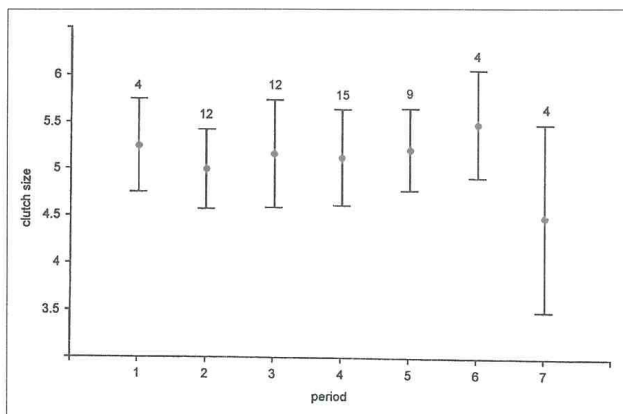


Figure 5. Mean clutch size variation of Posina Dippers in relation to laying date, subdivided into 6 15-day periods (period 1=2-16 February); period 7 includes two latest periods (3 May-1 June). Standard deviation (bars) and sample sizes are shown.

Brood size

Brood size was recorded at ringing when nestlings were 7-17 days old.

Mean brood size were 4.64 ± 0.58 sd ($n = 59$) and 4.50 ± 1.07 sd ($n = 26$) for first and second attempts respectively; including two replacement nests, the overall mean brood size was 4.64 ± 0.79 sd ($n = 87$). Mean brood size resulted slightly, but not significantly, higher in stretch C than in the remaining tracts of the water course (Kruskal-Wallis $H = 3.48$, $df = 3$, $p = 0.32$). There were not significant differences between either years (first broods: Kruskal-Wallis $H = 2.90$, $df_{1991-96} = 5$, $p = 0.72$; second broods: Kruskal-Wallis $H = 1.77$, $df_{1992-96} = 4$, $p = 0.78$) or subsequent nesting attempts (Mann-Whitney $p = 0.75$).

Second broods

We computed as second broods only those following

a successful outcome to a previous nesting. Of 54 breeding pairs which fledged young in their first reproductive attempt, 25 laid a genuine second clutch, i. e. 46.3% (1992: 35.7%, 1993: 61.5%, 1994: 46.2%, 1995: 42.9%). In these years, when nests were most intensively searched, there was no difference among years in the number of second broods ($\chi^2 = 1.91$, $df = 3$, $p > 0.1$). The percentage of second attempts tended to increase with the age of pair members: 22% of 9 first year-first year pairs, 56% of 9 first year-adult pairs and 71% of 14 adult-adult pairs ($\chi^2 = 5.36$, $df = 2$, $p = 0.07$). Marked fluctuations in the proportion of second broods were observed along the river course reaching the maximum in section C (83.3%, $n = 18$) and the minimum (0%, $n = 9$) in the upper stretch D, where the laying dates fell later in the season (Fig. 3). Females involved in a genuine second attempt laid earlier in the season (median date = 26 February, $n = 27$) than those which did not initiate a second clutch (median date = 23 March, $n = 33$; Mann-Whitney $p = 0.0002$).

Nest site characteristics

In our study area, Dippers built nests in a great variety of natural and artificial places. Of 127 nesting attempts 81.1% were on man-made sites, mostly on wooden boards purposely placed between girders under bridges; other artificial sites used were sluice-gates, weirs, crevices in stone bridges and tunnels. Natural sites (18.9%) chosen for nest building were on rock ledges and, more rarely, concealed among tree roots or on mossy rocks in mid-stream. Along the four stretches of river, the selection of natural versus artificial nest sites was not homogeneous ($\chi^2 = 11.93$, $df = 3$, $p = 0.008$), because of a greater frequency of nests built on natural sites in the upper stretch D (individual component of $\chi^2 = 6.12$), due to a higher degree of naturalness of the water course.

For subsequent nesting in the same season or in successive seasons, female Dippers usually re-used the same nest or built a new one bound with or very close to the previous nest.

Breeding success

To avoid premature departure, nest checking was interrupted in the last days of brood rearing. As a consequence, the number of fledged young was not accurately recorded and we could only estimate the proportion of eggs surviving as nestlings at ringing age (7-17 days old). Of 322 eggs laid in 63 nests, we ringed 254 young, giving a survival rate of 78.9%. Egg or nestling losses was mostly due to total nest failures, the causes of which are reported in Table 3.

The overall percentage of nests which produced at least one young was 80.8% ($n = 120$; years 1991-96).

Table 3. Causes of failure in Dipper nests on River Posina.

Cause of failure	Number	%
Predation	4	17.4
Starvation	3	13.0
Human interference	5	21.7
Infanticide	3	13.0
Desertion	4	17.4
Unknown	4	17.4
Total	23	100

The rates of successful nests in first (75.9%, n = 79), second (96.6%, n = 29) and replacement clutches (70.0%, n = 10) were significantly different ($\chi^2 = 6.51$, df = 2, p = 0.039), a result imputable to an exceptionally high breeding performance of genuine second broods (individual component of $\chi^2 = 3.83$). Our data did not support any significant differences neither among stream stretches nor between nest-site characteristics, notwithstanding the higher success of nests built in artificial than natural sites (27.3% vs 17.5%). The mean annual productivity, computed as:

$$(n \text{ fledglings}/n \text{ successful nests}) \times \% \text{ nest success} \times (\text{mean } n \text{ of nesting attempts}/n \text{ pairs})$$

resulted in 5.39 ± 0.36 fledglings/pair, with no significant between-years variation (Table 4).

Relative nestling survival

In the 1991-95 period we mist-netted as many as possible fledged or full grown birds to evaluate the possible effects of reproductive parameters on the survival rate of ringed nestling Dippers. Out of 267 birds marked in the nest during the 1991-94 breeding seasons, 51 (19.1%) or 42 (15.7%) were recaptured at least one month after ringing and from 1st August onwards respectively. In comparison, the last value gives a better indication of survival, because it was referred to fully independent young, although the first one provided a larger sample size. Our data showed a highly significant increase in the chance of subsequent recapture of nestlings with the progress of the laying

season, up to a maximum around the end of April, and then a sharp decline (Fig. 6).

Greater recapture rates were found in replacement clutches, in brood sizes of 2-3 and 6 chicks and in nestlings ringed in the stream stretch C; conversely,

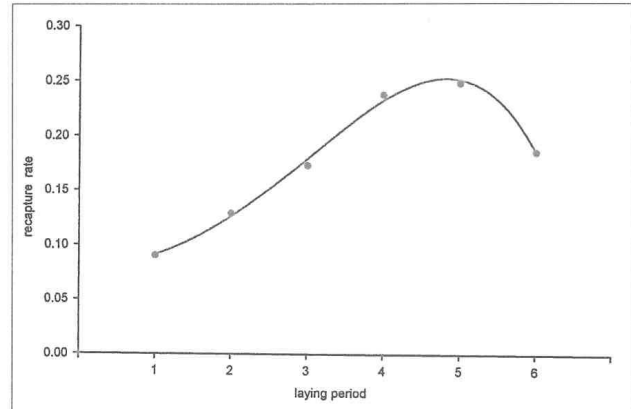


Figure 6. Seasonal variation in the recapture rate of nestling Dippers (n=51) in River Posina. The fitted curve was a third-order polynomial ($F_{2,3}=104.8$, $P=0.009$, $r^2=0.98$). Laying dates were divided into 6 periods of 20 days, starting from 1 February.

clutch size of 5 eggs produced fewer surviving young than 4- and 6-eggs clutches. After applying Bonferroni method to overcome the consequences of repeated tests on the same data set, the recapture rate of nestlings appeared to be significantly affected by brood size only (Table 5).

Population dynamics

The numbers of breeding Dippers captured and recaptured in 1992-95 are shown in Table 6.

Because of small sample size, we estimated the survival rate of adult birds for males and females combined. The model selection procedure proposed by SURGE let us exclude both the model St Pt (St Pt vs. St P: $\chi^2 = 0.325$, df = 1, p = 0.57; St Pt vs. S Pt: $\chi^2 = 0.213$, df = 1, p = 0.64) and the model St P (St P vs. SP: $\chi^2 = 0.889$, df = 2, p = 0.664) or S Pt (S Pt vs. SP: $\chi^2 = 1.103$, df = 2, p = 0.58). The simplest model that best described Dipper capture-recapture data was the

Table 4. Annual values of breeding success parameters in the Posina Dipper population.

Year	n fledglings / n successful nests	% nest success	mean n of nesting attempts / n pairs	mean productivity
1992	4.54	83.3	1.35	5.11
1993	4.50	79.3	1.65	5.89
1994	4.53	79.2	1.44	5.16
1995	4.72	83.3	1.37	5.39

Table 5. Recapture rates of Dippers in River Posina subdivided by different categories of some breeding or environmental variables. Recapture rates are expressed as percentage of nestlings recovered from 1st August onwards. Significance levels were corrected with the Bonferroni method.

Variable	recapture rate				χ^2	p
nesting attempt	first=0.12	second=0.16	subst.=0.32		6.78	ns
clutch size	4 eggs=0.20	5 eggs=0.09	6 eggs=0.26		7.07	ns
brood size	2-3 pulli=0.29	4 pulli=0.15	5 pulli=0.10	6 pulli=0.33	11.47	0.05
stream stretch	A=0.08	B=0.13	C=0.22	D=0.03	10.35	ns
pair age	juv/juv=0.10	juv/ad=0.21	ad/ad=0.16		1.86	ns

Table 6. Recaptures in subsequent nesting seasons of Posina Dippers initially captured as breeding birds.

Initial captures year	Totals recaptured in later years			
	Total	1993	1994	1995
1992	34	8	6	3
1993	25	–	9	4
1994	16	–	–	5
1995	28	–	–	–
Totals	103	8	15	12

one in which both survival and recapture probabilities were constant across years. The estimation of average annual adult parameters was 56.8% for local survival rate (34.5-72.6% asymmetric 95% confidence limits) and 51.7% for recapture probability (30.2-72.7% asymmetric 95% confidence limits).

It was possible to obtain the age structure of breeding population (Fig. 7), using the most complete age data set for nesting birds available for 1995. The oldest Dippers in the Posina breeding population were a male ringed as first-year bird and controlled in the last occasion when 6 years and 7 months old and a female ringed as full-grown and controlled when at least 7 years and 2 months old.

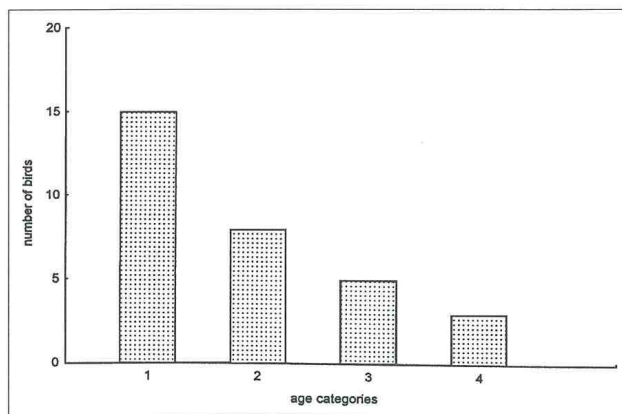


Figure 7. Age structure of adult Posina Dippers in the 1995 breeding season (1=first year birds).

Comparisons among years were only possible on the basis of age ratio first-year/all birds: in 1992 and 1995 there was a higher, but not significant, proportion of one-year old breeding Dippers (0.46 and 0.44) than in 1993 and 1994 (0.25 and 0.29).

Pooling the 1992-95 breeding seasons, the age composition of Dipper population was not homogeneous along the river, birds settled in tract C being more probably adult than first year ($\chi^2 = 13.99$, $df = 3$, $p = 0.003$).

Breeding-site fidelity

The Posina Dippers showed a high degree of territory fidelity both during one season and in subsequent years with no significant differences in sex-related movement (males 30%, $n = 10$ vs. females 10%, $n = 20$ dispersing, Fisher exact test $p = 0.19$). Considering genuine second broods ($n = 25$), all pairs but one bred in the same territory. After an unsuccessful first attempt ($n = 20$), 10 of known repeated nestings were made in the same site, only one pair shifting to an adjacent unoccupied tract. In the remaining 9 cases, we were unable to ascertain whether the pair did not lay a replacement clutch or renested outside the study area. High fidelity to breeding site is emphasized by the great number (83.3% of 30) of instances of birds not changing territory in subsequent years; of 5 Dippers moving, 2 settled within 400 m and 3 over this distance.

Natal-site fidelity

Only 11 of 267 marked nestlings were recaptured as breeding birds in the study area. The few available data give only a clue to differences in settlement distance between sexes. In terms of suitable territories interposed between natal and breeding sites, females tended to move at a greater extent (median = 4, range = 3-11 territories, $n = 5$) than male Dippers (median = 2.5, range = 0-7 territories, $n = 6$), although this difference was not significant (Mann-Whitney U-test).

Inter-seasonal movements

The percentage of adult Dippers (1-year old) moving

more than 400 m between autumn and breeding territories and reverse, was quite similar (82.6% and 83.3% respectively). Furthermore, considering autumn as extended from September to November or up to December, there were no significant differences in movements between male and female Dippers. Hence, all available data ($n = 41$) were pooled into a single frequency distribution (Fig. 8), showing that Dippers are largely sedentary.

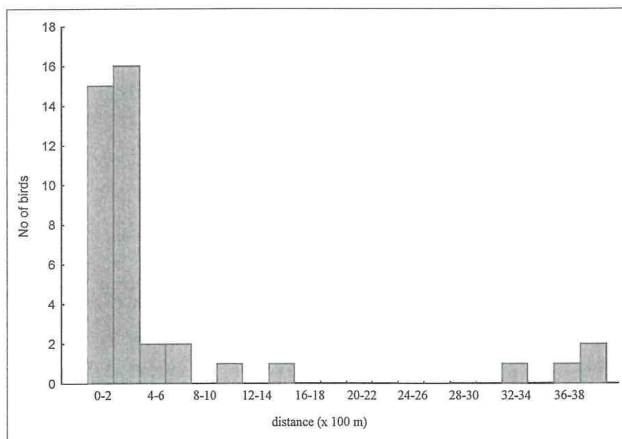


Figure 8. Frequency distribution of distances moved by Posina Dippers between autumn and previous or subsequent breeding season.

Discussion

Density

Large fluctuations over the years in local Dipper breeding densities are ascribed to strong natural events, such as hard winters or drought (Shooter 1970, Glutz and Bauer 1985), and artificial ones, such as river management (Glutz and Bauer 1985) or water acidification (Marchant *et al.* 1990). The overall year to year stability of breeding density observed in our study area could be explained by the lack of extreme environmental conditions in the catchment of the River Posina during 1991-96. By contrast, the average breeding density markedly varied along the stream, the highest value being three times greater than the lowest one. Food availability, gradient, morphological characteristics and permanence of watercourse, water quality, nest and roost site richness are considered the primary factors involved in determining breeding abundance (Tyler and Ormerod 1994). Most of these variables could not be investigated in our study. Sampling of macrobenthic fauna (pers. obs.; Salvati *et al.* 1997) allowed us to assess only the water quality of the studied stream tract, which entirely belonged to Quality Class I (standard E.B.I. method; Woodwiss

in Ghetti 1986). Nevertheless, very low density in stretch B was probably imputable to marked bank alteration and to apparently low number of suitable natural or artificial nest sites, whereas breeding territories in upper tract D were more spaced as a consequence of excessive steepness (gradient >25 m/km; Marchant and Hyde 1980) and narrowness of the waterway (Sokolowski in Tyler and Ormerod 1994; Wilson 1996). The supply of artificial supports for nesting, started in 1993 in previously occupied breeding sites, did not apparently affect the density, since the number of Dipper pairs remained nearly constant. Moreover, the number of used supports changed from year to year, whereas the wooden board availability increased during the study period.

Numerous studies revealed much variability and lack of geographical influence in Dipper breeding abundance throughout Europe (Table 7). Compared with more extensively studied areas, our 4-year average value appears to be high, on short stretches almost identical to the maximum density reported for the Alps (Breitenmoser-Würsten and Marti 1987) and slightly lower than the highest values for Europe (Schmid 1985a, Rockenbauch 1985).

Breeding season

Only few researches on Dipper breeding biology have been performed outside central and northern European countries. Comparing the start of breeding of different populations (Tab. 8), the average laying date of first clutches on River Posina was very early and similar to dates recorded in Limousine and Auvergne (Roché and d'Andurain 1995), French regions situated nearly at the same latitude of the present study area. Altitude is another commonly reported factor affecting the time of laying. Notwithstanding the narrow altitudinal range of our study area, the onset of reproduction was positively correlated with altitude only above 500 m. Here a delay of 39 days per 100 m was found, a much higher value than 5-6 days/100m reported by most authors (Balat 1964; Zang 1981; Schmid 1985b; Sackl and Dick 1988) and even greater than delays of 19-26 days/100 m cited by Breitenmoser-Würsten (1988) and Priemetzhofer and Priemetzhofer (1984) respectively. This deferred starting was unlikely to be linked only to altitude (explaining about 40% of variance in time of laying) and was apparently imputable to other characteristics of breeding habitat too. The morphology of the upper tract of the Posina valley determines prolonged icy conditions at the end of the winter, what could modify the seasonal availability of benthic preys. Besides, the lack both of manufactures and management activities on banks induced Dippers to nest more often in natural sites. Breitenmoser-Würsten (1988) showed that in Swiss

Table 7. Densities of Dippers breeding in different European countries. Range is given when more river tributaries were included in the study area.

Authors	Geographical area	Pairs/km
	Alps	
Wagner (1985)	Austria	0.24
Goller & Goller (1987)	Austria	0.57
Breitenmoser-Würsten & Marti (1987)	Switzerland	0.43-2.00
<i>Present study</i>	<i>NE Italy</i>	<i>1.46</i>
	N Europe	
Efteland & Kyllingstad (1984)	S Norway	0.14-0.22
Borgström (1991)	C Sweden	0.30-0.40
	Great Britain	
Cowper (1973) in Wilson (1996)	S Scotland	0.14-0.22
Shaw in Cramp (1988)	Scotland	up to 0.77-0.97
Wilson (1996)	S Scotland	0.18-1.66
Vickery (1991)	S Scotland	up to 1.00
Horn (1985) in Tyler & Ormerod (1994)	S Scotland	0.30-0.33
Sinton (1988) in Tyler & Ormerod (1994)	N England	0.71
Robson (1956)	N England	0.21-0.62
Round & Moss (1984)	Wales	0.12-0.27
Ormerod <i>et al.</i> (1985)	Wales	0.29-0.85
	C Europe	
Vangeluwe <i>et al.</i> (1993)	Belgium	0.49-1.30
Daulne (1990)	Belgium	0.22-0.87
Liedekerke de (1980)	Belgium	0.17-1.04
Wiesemes (1977, 1978) in Roché & d'Andurain (1995)	Belgium	0.40-0.49
Roché (1989)	France	0.13-1.20
Roché & d'Andurain (1995)	France	0.36-1.37
Kempf (1977) in Roché & d'Andurain (1995)	France	0.67-1.25
Joubert (1981) in Roché & d'Andurain (1995)	France	0.82-1.14
Marzolin in Roché & d'Andurain (1995)	France	0.04-0.92
Stuß (1972)	Germany	0.19-0.23
Rockenbauch (1985)	Germany	0.55-2.33
Schmid (1985a)	Germany	0.33-2.56
Klein & Schaack (1972)	Germany	0.12-0.36
Kaiser (1988)	Germany	0.02-0.29
Oelke (1975) in Wilson (1996)	Germany	0.07-1.00
Jost (1975)	Germany	0.11-0.37
Steffens & Sturm (1978)	Germany	0.07-0.24
Priemetzhofer & Priemetzhofer (1984)	N Austria	0.37
Dick & Sackl (1985)	N Austria	0.16-1.13
	S Europe	
Peris <i>et al.</i> (1991)	C Spain	0.14-1.50
Sarà <i>et al.</i> (1994)	Sicily	0.10-1.00

Alps Dippers nesting in natural conditions retarded the start of laying. In whole study area, egg laying started earlier in stretch C, where also breeding density, mean clutch and brood sizes and percentage of second attempts showed the highest values. All these breeding parameters, which were found likewise correlated in Welsh Dipper populations (Tyler and Ormerod 1994), suggest a better quality of territories held in this river tract.

Clutch and brood size

The mean clutch size (5.11) recorded in the present study is almost identical to the highest values found in Germany and Scandinavia (Table 8), confirming the observed lack of a clear link with latitude in Dipper populations of continental Europe (Breitenmoser-Würsten 1988; Wilson 1996), despite clutch-sizes in northern countries are constantly large. The high frequency of 6-eggs clutches (20.3%) in Posina Dippers is worth being stressed, as compared with the percentages reviewed by Breitenmoser-Würsten (1988) for the British Isles (3.8%) and continental Europe (15.6%), among which the value (51%) found in a German population (Baake 1982) stands out as an exception. The clutch size remains almost constant through most of the breeding season, weakly peaking in the second half of April, as a consequence of the occurrence of second attempts, which are larger in size, and then falling abruptly in May. This overall pattern is consistent with other authors' findings of no evident seasonal effect (Sackl and Dick 1988; Wilson 1996) or of lower size in very early and late clutches (Breitenmoser-Würsten 1988; Tyler and Ormerod 1994; Smiddy *et al.* 1995). However, a stronger evidence of seasonal decrease in clutch-size was demonstrated in other Dipper populations (Zang 1981; Schmid 1985b). The anomalous lack of clear-cut latitudinal and seasonal effects on clutch-size variation in Dipper populations could be explained by the relative stability of the peculiar habitat of this species and, furthermore, emphasizes the overwhelming importance of local water course conditions, as suggested by Wilson (1996) for British Dippers. This last hypothesis is supported by the occurrence of larger clutch size, earlier laying and higher second brood rate observed in the central tract C than in the remaining of our study area.

The mean brood size recorded in the present study was highest among those observed in European countries (Table 8). Even if we limit the analysis to mean brood size calculated by the same method, our value has to be taken with caution due to the variable age distribution of chicks ringed on a broad time period in the different studies.

Second broods

Comparisons of second brood frequencies reported in different populations can lead to misleading conclusions because some authors computed these values in relation to successful first attempts or total breeding pairs. Incidence of second nesting as well as clutch and brood sizes does not show a clear geographical pattern, e.g. ranging from 8% to 60% in the British Isles or from 12% to 56% in Germany (Table 8). Besides, the high yearly variability recorded on a same study area during long-term researches (Breitenmoser-Würsten 1988, Tyler and Ormerod 1994) could explain some very high values found in populations kept under short-term observation. It is apparent that only Fennoscandian populations are characterized by constantly low rate of genuine second broods, probably due to short breeding season at northern latitudes. Throughout Europe, Dippers are more likely to produce second broods in years when egg laying starts early (Breitenmoser-Würsten 1988, Smiddy *et al.* 1995, Wilson 1996, this study). The high rate of second brooding in our study area is likely to be imputable also to average altitude falling in the range found to be optimal for double nestings in other studies (Wagner 1984, Priemetzhofer and Priemetzhofer 1984, Schmid 1985b, Sackl and Dick 1988) and to high breeding rates in artificial sites. By decreasing nest failures, the latter let Dippers lay subsequent clutches as genuine second ones (Breitenmoser-Würsten 1988). Moreover, older pairs, settled in the best territories (C stretch), were more frequently involved in second nesting. Altitude, nest-site characteristics and pair age could actually affect indirectly the rate of second breeding through a calendar effect.

Breeding success

The overall breeding success, calculated as percentage of nests producing at least one fledged young, differed in most Dipper studies between subsequent nesting attempts. Some authors found first clutches being more successful than second ones (Zang 1981, Baake 1982, Tyler and Ormerod 1994), while others observed that first attempts were less successful than second (Priemetzhofer and Priemetzhofer 1984, Schmid 1985b, Breitenmoser-Würsten 1988) or second/replacement clutches (Rockenbauch 1985, Schnabel in Rockenbauch 1985). Our results agreed with the second pattern, despite repeat nestings were the least successful. Since the reproductive success would have to be computed as number of recruits in the breeding population, we used the recapture rate of ringed nestlings as an estimation of this parameter. This rate showed a progressive increase along the season, peaking when incidence of second and repeat

Table 8. Breeding parameters of Dipper populations in different European countries. Altitudinal range of each study area is included. Clutch dates are median or mean (#) values of first-egg laying. Clutch and brood sizes are means \pm sd, where available, of first, second and replacement breeding attempts. Brood size was calculated as number of nestlings at ringing age or as fledged young/found nest ($\dagger\dagger$) or as fledged young/successful nest (**). Sample size is given in parentheses. Percentages of second clutches were calculated as ratio between numbers of second and successful or total (§) first attempts (latter value in parentheses). Symbols: \dagger second and replacement nesting attempts, * unclear calculation method.

Authors	Geographical area	1st clutch date	2nd clutch date	Overall clutch date	Overall mean clutch size	Overall mean brood size	% 2nd clutches
	Alps						
Wagner (1984)	Austria 490-929 m	10-20/IV (32)			4.79 (33)		rare
Breitenmoser-Würsten (1988)	Switzerland 982-1700 m	29-30/IV (122)#	30/V (23)#		4.91 \pm 0.58 (87)	4.07 (87)	18.1 (127)§
<i>Present study</i>	<i>NE Italy</i> 400-600 m	<i>9/III</i> (72)	<i>23/IV</i> (27)		5.11 \pm 0.54 (64)	4.64 \pm 0.79 (87)	46.3 (54)
	N Europe						
Haartman von (1969)	Finland			May	4.67 \pm 1.04 (27)		
Pulliainen & Saari (1994)	N Finland			23/V (63)	4.93 \pm 1.02 (40)	2.71 \pm 1.89 (46) $\dagger\dagger$	
Andersson & Wester (1975)	S Norway				5.10 \pm 0.65 (14)		very rare
Efteland & Kyllingstad (1984)	S Norway				5.08 \pm 0.74 (74)	4.25 \pm 0.99 (72)	2.9 (69)
Mork (1975)	S Norway						6 (100) §
Borgström (1991)	C Sweden			a: 19/IV (38) b: 8/V (25) #	5.06 (105)	4.24 (68)**	5 (100)§
	Great Britain						
Hardy <i>et al.</i> in Tyler & Ormerod (1994)	N Scotland				4.55 \pm 0.79 (74)	4.16 (64)*	32.8 (58)*
Wilson (1996)	S Scotland 45-520 m	10/IV (302)	18/V (91) \dagger		4.63 \pm 0.66 (378)	3.88 \pm 0.99 (336)	19.3 (296)
Baines in Tyler & Ormerod (1994)	N England				4.34 \pm 0.99 (38)	3.50 \pm 1.19 (40)*	53.4*
Robson (1956)	N England 200 m			5-12/IV (75)	4.1 (92)	2.80 (92) $\dagger\dagger$	20 (70)§
Tyler & Ormerod (1994)	Wales 3-650 m			1-7/IV (364)	4.78 \pm 0.61 (222)	4.13 \pm 1.04 (286)	19.4 (403)§
Smiddy <i>et al.</i> (1995)	S Ireland 5-300 m	30/III (364)#	1/V (32)#		4.16 \pm 0.65 (467)	3.48 \pm 0.93 (348)	8.2 (404)§
	C Europe						
Roché & d'Andurain (1995)	C France 500-1000 m	10-17/III (24)	27/IV-4/V (11)		4.6 (10)#		28-45§
Marzolin in Roché & d'Andurain (1995) and in Breitenmoser (1988)	N France 170-300 m	25/III	9/V		4.64		49*
Pallier in Roché & d'Andurain (1995)	C France 430-930 m	4/III					38-43*
Baake (1982)	N Germany 240-418 m				5.36 \pm 0.74 (39)	3.44 (34)**	56 (25)§
Rockenbauch (1985)	S Germany 260-625 m	end March			5.02 (179)	4.15 (267)*	37 (265) \dagger
Schmid (1985b)	S Germany 350-550 m	25-26/III (67)#	13-14/V (45)#		4.72 (142)	4.03 (142)	49.0 (98)§

Segue: Table 8

Authors	Geographical area	1st clutch date	2nd clutch date	Overall clutch date	Overall mean clutch size	Overall mean brood size	% 2nd clutches
Jost in Rockenbauch (1985)	C Germany 235-750 m					4.17 (80)*	
Steffens & Sturm (1978)	C Germany				4.31±0.89 (29)	3.34 (44)††	10 (40)§
Ristow (1968)	N Germany 200-400 m	29/III-5/IV (19)	17-24/V (7)		5.08±0.89 (37)	4.11 (28)*	38.9 (18)
Haensel (1977)	N Germany 150-700 m			half/end March	4.56±1.33 (9)	3.42±1.30 (43)**	
Zang (1981)	N Germany 190-790 m			21/IV (83)	4.86±0.76 (98)	3.83±1.28 (75)	11.8 (68)§
Czapulak <i>et al.</i> in Horváth (1993)	S Poland				4.9 (20)	4.08*	33 (30)*
Horváth (1993)	Hungary			5-9/IV (98)	4.65±0.85 (126)	2.93 (136)††	37 (125)§
Balát (1964)	Czech. Rep. 242-343 m	early April			4.74±0.91 (46)	2.37 (38)††	14.3 (35)§
Priemetzhofer & Priemetzhofer (1984)	N Austria a: 430-550 m b: 650-700 m	a: 1/IV (7) b: 27/IV (12)			4.70±0.70 (27)	2.97 (29)††	38.9 (18)§
Sackl & Dick (1988)	N Austria 186-910 m	8/IV (37)			4.67±0.70 (55)	3.79 (44)	15.9 (63)†

laying was highest. In particular, this peak was strongly affected by the high recapture frequency of young from replacement clutches which were also larger in size. It is possible that Dipper females maximize their reproductive effort investing greatly in repeat nesting, having no time to rear a genuine second brood. The recapture probabilities of nestling Dippers was also related to clutch and brood sizes, according to a picture recalling Ormerod's (1993) findings from a Welsh population (cfr. Fig. 2a).

Although the "replacement-strategy" could explain the high success of 6-nestling broods, we were unable to identify the causes of the low success of 5-nestling broods, commonest in the study area, even when taking the recapture probability into account extended to the whole brood.

Among the causes of nest failure, the occurrence of three cases of probable infanticide is remarkable. An intruder Dipper was observed in one case removing the inner lining of a nest with newly hatched nestlings, owner pair alarming nearby; on next visit, the nest was empty and deprived of the inner cup. In the remaining two cases loss of both the content and cup of nests built in sites apparently safe from predators was observed. One of these nests was subsequently occupied by the neighbouring pair for the second brood. Infanticide by Dipper has been reported in Britain (Yoerg 1990, Wilson 1992) and related to polygyny, as

it would enhance extra-pair mating opportunities. Despite high capture rate of individually marked breeding males, in the Posina population no case of polygyny was recorded or suspected. The presence of single males not involved in nesting and captured in already occupied territories suggested the existence of "floaters" which in this way could increase their chance of mating.

Population dynamic

The annual survival rate of adult Dippers breeding in the Posina valley (56.8%) is comparable with the few estimates available from other countries: 53% or 55% (Galbraith and Tyler 1982) and 52.6% (Logie and Bryant in Bryant and Newton 1996) in the British Isles, 56.0% (Marzolin in Lebreton *et al.* 1992) in France, and 54.8% for the American Dipper *C. mexicanus* (Price and Bock 1983).

Data from Table 6 allowed us to compare the variation in local annual survival rate with other population parameters and formulate hypotheses on some aspects of dynamics of our Dipper population. Despite variation in annual survival rate, observations suggest that the breeding population remained stable across years. The proportion of first-year birds in the total breeding population reveals that the recruitment of this age class is not sufficient to compensate adult mortality. Moreover, the annual

value of this ratio appears not to be linked to the mean breeding success of the previous year, but fluctuate on a wider range, as reported by Balat (1964) and Wilson (1996). Table 9 supports the hypothesis that only a fraction of Posina Dippers start to breed when one year old, the proportion of two-year old birds in the whole breeding population being slightly smaller than the proportion of the same cohort, i.e. birds born in the same year, in the previous nesting season. These figures could be explained either by assuming that full breeding condition is reached by the Dipper at age two, as claimed by Clobert *et al.* (1990), or by the incoming of two-year birds having previously bred in suboptimal territories outside the study area. As consequence, the local annual adult mortality seems to be compensated just by the two-year age class, as shown by the ratios 2y/adult birds which varied inversely to the survival rates. We do not know the natal site of these two-year birds, because most of them were ringed as juveniles from July onwards, after the end of the breeding season. Therefore we were unable to ascertain whether there was a differential mortality between local breeders and non-breeders (first-year), or whether the adult mortality was compensated by birds crossing watersheds and immigrating from neighbour populations. As expected for a bird species so closely associated with streams, Dipper mortality is mainly imputable to extreme variations in river discharge through a reduction in macrobenthic prey availability. Heavy floods occurring in the course (Lebreton *et al.* 1992) or at the end of the breeding season, as well as drought in spring and summer (Tyler and Ormerod 1994), were found to lower survival rates. Major floods took place at the beginning of October during our study, a time when adult Dippers resuming territory defence are exposed to adverse environmental conditions at a greater extent than juvenile birds which are more likely to disperse in other river catchements.

Table 9. Demographic parameters of population dynamics in Posina Dippers.

	1992	1993	1994	1995
adult survival ¹		0.48 ₍₉₂₋₉₃₎	0.66 ₍₉₃₋₉₄₎	0.53 ₍₉₄₋₉₅₎
1y/tot ²	0.46	0.25	0.29	0.44
2y/tot ²		0.45	0.18	0.24
2y/ad ³		0.60	0.25	0.42
breeding success	5.11	5.89	5.16	5.39
breeding density	18	18	18	19

¹ annual adult survival as computed by SURGE; ² ratio of first-year (1y) or 2nd-year (2y) to total breeding birds; ³ ratio of 2nd-year to adult birds (age \geq 2 years).

Dispersal

Our results show that adult Dippers are strongly sedentary and defend the same breeding territory in successive years, also remaining within its boundaries or nearby during the autumn months. A similar behaviour is typical of populations breeding in areas where mild winter weather maintains streams unfrozen; conversely, with icy conditions birds are forced to move downstream (see Tyler and Ormerod 1994). Evidence was also found that territories located in the cold upper portion of the study area were entirely deserted by birds. Two males were repeatedly retrapped in central segments of River Posina 3.2 km and 3.8 km away from their respective breeding site. This favourable stretch was also used as wintering site by Dippers immigrating from marginal territories outside the boundaries of the study area, such as a male controlled here in autumn, at a distance of 4 km from its nesting place situated along a small tributary. Beside these three cases of inter-seasonal movements, we could confirm that females are more likely to move larger distances than males (Tyler *et al.* 1990).

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Riassunto - Tra gli anni 1991 e 1996 è stata studiata la popolazione di Merlo acquaiolo presente lungo il Torrente Posina (Prealpi vicentine). I risultati ottenuti sono stati confrontati con analoghe ricerche condotte in altre regioni europee. La densità delle coppie riproduttive (media = 1.46 \pm 0.04 coppie/km) si è mantenuta costante nell'arco della durata dello studio, ma sensibilmente variabile nei diversi tratti del torrente. Complessivamente sono stati rinvenuti 127 nidi, costruiti per la gran parte (81.1%) su strutture artificiali. Le date mediane di deposizione del primo uovo sono risultate il 9 marzo per le prime covate e il 23 aprile per le seconde. L'età della coppia e non ben identificate caratteristiche fisiche dei diversi tratti del torrente hanno influenzato l'inizio della deposizione nelle prime covate. Complessivamente la dimensione media di covata è stata di 5.11 \pm 0.54 uova, un valore relativamente alto e prossimo a quelli riscontrati in popolazioni settentrionali dell'Europa continentale. La dimensione media di covata è rimasta costante nel corso della stagione riproduttiva, a parte un brusco calo alla fine del periodo di deposizione (maggio). Dopo l'esito favorevole della prima covata, il 46.3% delle coppie ha intrapreso una seconda deposizione.

La percentuale dei nidi che ha prodotto almeno un involato è stata superiore nelle seconde covate rispetto alle prime ed alle sostituzioni, con un tasso complessivo dell'80.8%. I giovani nati da covate deposte verso la fine di aprile hanno registrato il più alto tasso di ricattura. Il tasso annuale di sopravvivenza degli adulti è stato stimato al 56.8%. Il controllo degli individui marcanti ha messo in evidenza la forte fedeltà territoriale sia nella stessa stagione riproduttiva sia in quelle successive.

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