Atti del 6° Convegno Italiano di Ornitologia (Torino, 8-11 ottobre 1991) | Mus. reg. Sci. nat. Torino, 1994

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Blackbird survival rates studied with capture-recapture methods in Piedmont (NW Italy)

ABSTRACT

Captures and recaptures of Blackbirds at a ringing station near Bra (NW Italy) were analyzed with the main aim to estimate survival. Adult survival rate estimated by the open-population models implemented in the program JOLLY resulted similar between sexes and comparable to most european estimates based on ringing recoveries (55±4%); as usual young show a lower survival rate, even lower than other european estimates, probably because of the weak philopatry, a main problem in the survival estimations by capture-recapture.

Sex-ratio shows wide monthly variations, but seems balanced over the year, suggesting seasonal differences in mortality between sexes. This problem could be addressed with specifically planned capture-recapture experiments.

Introduction

The four fundamental processes concerned with changes in abundance of animal populations are natality and immigration (that represent the gains), mortality and emigration (that represent the losses) (Krebs 1985). According to Lack (1954, 1966), in particular, mortality, acting in a density dependent way, is likely to play a critical role in the regulation of animal number.

In Italy, however, studies directed to assess bird mortality (or its complement, survival) were surprisingly neglected until now and essentially restricted to released gamebirds (Prigioni et al., 1977; Prigioni et al., 1986, Montagna et al., 1990; Boano e Silvano, in pubbl.); only very recent works dealing with wild birds (Boano e Cucco, 1991; Fracasso, 1994; Fraticelli, 1994).

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In ornithology mortality (or survival) estimates are currently derived from analyses of ring recoveries (i.e. recoveries of marked birds, usually found dead, made by the general public from a large geographic area) (Lack, 1943; Haldane, 1955; Brownie et al., 1986) and, more recently, by radiotelemetry methods (Kenward 1987), but also the recaptures or resightings of live marked birds (i.e. control of marked birds, usually made at a local study area, by new captures or sightings) are now widely used in association with proper stochastic open-population models (Cormack 1964, Seber 1982, Clobert et al. 1985, Pollock et al. 1990; Nichols, 1994).

A major drawback in estimating mortality from capture-recapture studies at a local site arises from the possibility of permanent emigration: if a significant part of the population, although alive, does not return at the sampling site in the subsequent sampling times, then mortality estimate will turn out positively biased. Estimates of the philopatry rates (the conditional probability that an animal alive at the time of recapture sampling effort is in the local area exposed to these effort) are therefore very useful and may be inferred by comparisons with survival estimates made from ring recoveries (Pollock et al. 1990). In any case estimates derived from capture-recapture experiments are better regarded as minimal survival rates. On the other hand survival estimates arising from local studies are valid for a clearly defined population, which is not the case in large-scale recovery studies, and at such a local scale other biological phenomena can be easily studied, supplying good opportunities to test hypotheses of ecological and methodological interest (Clobert et al. 1985).

In this paper we analyze the Blackbird (*Turdus merula* L.) capture-recapture data obtained from 1984 to 1990 at a NW-Italy ringing station. Our main aim is to provide survival estimates, but we also show estimates of other population parameters and descriptive statistics of the sampled population.

Study area and Methods

Study area

Data were collected at the ringing station of "Priore" farm (the residence of the senior Author) near Sanfrè (Coord. 44°45'N, 07°49'E) managed by the Museum Craveri of Natural History of Bra (CN) and working from 1976 onward, whith 10349 ringed birds of 91 species to its credit up to 1990 (Tibaldi e Molinaro, 1991). The station lies in a low hilly area at about 300 m on the sea level; the average annual rainfall is 700 mm (150 of which in the three summer months) and the habitat is a mosaic of broadleaved woods, pastures, orchards and fields.

Field tecniques

From 1984 to 1990 mist netting operations were made on the annual cycle nearly daily (with only a few major interruptions in July 1985 and in the last two autumns).

Ten (6-12 m long; 32-36 mm mesh) were spread in mixed woodlots (black locust, oak, hornbeam, chestnut) and hazel orchards around the farm in fixed positions; a few other nets were opened irregularly in space and time.

We stress that the station activity was not specifically designed for survival studies, but we selected a posteriori the data trying to minimize violations of the method assumptions as later explained.

The complete data base is made by 1735 captures of 871 individual Blackbirds ringed as adults or fledged young with INBS metal rings and aged and sexed according to Svennson (1984). Birds in juvenile plumage were not sexed because of the ascertained possibility of sexing errors. Age at ringing was given according to the EURING code, but for the purposes of survival estimates we took into account only two age classes, namely young (euring code 3) and adults (all the other birds).

Birds were immediately released after usual ringing operations and measurements (wing, third primary, bill, tarsus, weight).

Data analysis

Data were extracted from the ringing files of the Museum Craveri where they are stored in a DBASE format. In order to show the yearly and monthly distribution of captures as the sex and age ratios, we use only first captures (adding recaptures does not cause significant differences).

Demographic parameters were estimated using Jolly-Seber and related stochastic models (Jolly 1965; Seber 1965; Brownie et al. 1986; Pollock et al. 1990). These models include parameters for both survival (s) and capture probabilities (p). Survival probability is the probability that a bird alive at the period i is still alive and in the area exposed to sampling efforts at the period $i+1$. As with all capture-recapture sampling, the complement of survival probability estimates- includes both mortality and permanent emigration. Capture probability is the conditional probability that an individual is caught in period i, given that the individual is alive and in the area exposed to sampling effort at the time of sampling. Survival estimates based on these models differ from estimates equating survival and recapture rates, because the models explicitly include the possibility that an individual is alive and in the population being sampled, but simply not caught. In contrast, methods equating survival and recapture rates require the assumption that capture probability is 1, and they yield unbiased estimates of survival only in the very unusual condition in which every marked animal still in the population is actually caught (Nichols and Pollock 1983). Other parameters estimated by the models are the number (n) of birds present in each sample period in the study area and the recruitment (i.e. the number of birds entering the population between the sample *i* and the sample *i*+1). This last parameter is not further considered here.

The basic Jolly-Seber model assumpions are discussed by Seber (1982), the most important being the following: (1) Every bird present in the population at the time of sampling in period i has the same probability of capture. (2) Every marked bird present in the population immediately after sampling period *i* has the same probabillty of surviving until period *i* + 1. (3) Marks are not lost or overlooked. (4) All emigration is permanent (5) Sample is instantaneous (i.e. sampling time is negligibile in relation to the intersample period).

Biased estimates of the parameters of interest may derive from any departure from the above assumptions. Unfortunately, heterogeneity among individuals in either survival or capture probabilities is likely to affect animal populations (Jonshon et al. 1986). If survival probabilities vary among individuals, then estimates will also be biased. If both capture probabilities and survival probabilities vary among individuals, and are correlated, the captured animals will not be representative of the general population with respect to survival rate.

Heterogeneity among animals within a population can arise from several sources, some of which often associated with a measurable variable as age or sex. For this reason we have stratified our population by age and sex to account for this sources of heterogeneity and to seek differences in the population parameters among homogeneous groups. Another problem influencing capture probabilities is trap response. For example previously ringed birds may have a lower capture probability (because of net-shyness) than unmarked birds. We are aware that the all-days ringing schedule adopted at the station could induce trap-shyness and, as a consequence, a positive bias in population size estimator. However we point out that Jolly-Seber survival estimator is unaffected by permanent trap response (Nichols et al. 1984).

Every ringer can easely understand why the assumption (5) can never be completely met in practice, however most capture-recapture studies on an annual cycle are based on two-three months of sampling effort (Nichols et al. 1981, Karr et al. 1990). As our data are collected all over the year, to allow for assumption (5), we selected a shorter sample period, but still retaining an adequate bird sample. Excluding the main Blackbird migration periods (February-April and September-November) and winter, we restricted our analysis to birds captured in the months from May to August (to have an adequate sample of young and adults together) and from May to July (when only adults are considered), so our estimates are to be referred to the breeding population of the sampled area. As only one capture per single sample period is considered, the number of captures effectively used was 649 of 538 individuals (May-August samples) and 312 of 242 individuals (May-July samples).

All the estimates were obtained using the computer programs JOLLY and JOLLYAGE (Pollock et al. 1990). These programs provide parameter estimates under the basic Jolly-Seber model (Model A) and other related models which either generalize or further restrict assumptions about capture and survival probabilities (assumption 1 and 2) (Tab. 1). The programs also provide goodness-of-fit tests and specific tests for individuals assumptions.

The imput format here adopted consists in the capture histories of all the birds, coded with 0 (not captured in the sample period) and 1 (captured almost once in a sample period).

Table 1 - Summary of models in JOLLY and JOLLYAGE.

Jolly Models *	**	*Definitions*
A	st, pt:	standard Jolly-Seber model permitting time specific capture and survival probability
B	s, pt:	reduced-parameter model with time specific capture probability, but survival probability assumed constant
D	s, p:	reduced-parameter model with constant capture
2	st, s*, pt:	the most general model, similar to the model A, but permitting also different survival probabilities for newly banded birds (s*) versus previously ringed birds.
JOLLYAGE (Models A2, B2, D2)		As the corresponding A, B, D JOLLY models, but allowing for differences in capture and/or survival probabilities in two age classes (s = adult survival rates, s* = young survival rates).

* After the notations of Pollock et al. (1990).
** After the notations of Clobert et al. (1985).

Lacking other survival estimates at local or national level in Italy, we compare the results with some estimates obtained from ring recoveries in other european countries: Great Britain (Coulson 1961, Batten 1973), Germany (Erz 1964), Belgium (Van Steenbergen, 1971); Czechoslovakia (Beklova, 1972) and France (Pasquet et al. 1981).

All the above estimates were made with the Haldane's (Haldane 1955) or similar methods, only the last being computed with modern stochastic methods. We excluded from the comparisons the higher survival rates recorded for some urban Blackbird populations (Snow, 1958; Ribaut, 1964; Erz, 1964; but see Batten, 1973).

Results

The number of Blackbirds ringed per year varied between 75 and 175 (on average 124.4), the most marked changes being due to the variable number of young captured in July-August of each years (Fig. 1).

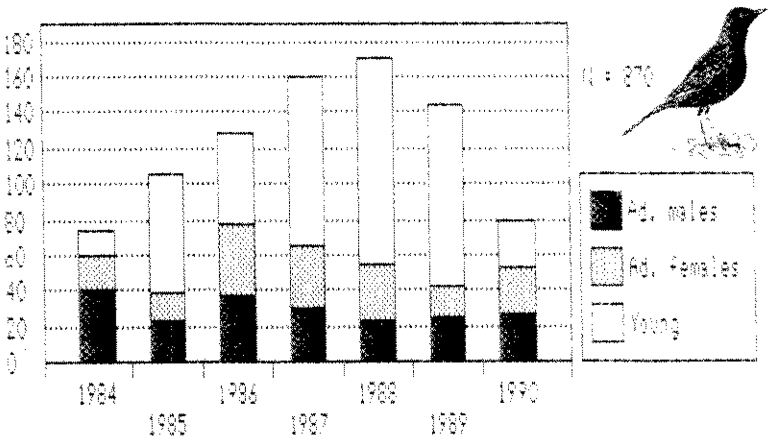

Fig. 1 - Number of Blackburds ringed per years in the study area.

The capture distribution shows a main peak in the summer months, mainly due to young, and two secondary peaks in march and october, due to migrant birds. We note that very few birds overwinter in the study area, but recoveries of breeding birds ringed there are until now lacking. Hence we do not know if this population follows the same migration routes as the Blackbirds ringed elsewhere in Piedmont (mainly during the postbreeding migration), whose winter recoveries come mainly from Corsica and Sardinia (Tibaldi e Molinaro, 1991). The adult sex ratio is not significantly different from the unit on the sampled population as a whole, but there are pronounced seasonal differences. In April we note a significant predominance of females ($\chi^2 = 8.27$, $P < 0.005$), on the contrary males outnumber females in May ($\chi^2 = 20.01$, $P < 0.001$) (Fig. 2).

Jolly-Seber estimates

We first examine the two age classes data set with JOLLYAGE. The test for age-dependence of survival and capture probabilities developed by Pollock (1981) and implemented in the program finds strong evidence of an age-dependent effect ($\chi^2 = 18.62$, 6 d.f., $P = 0.0048$); therefore there is a need for the class of age-dependent models. From the results of the subsequent goodness of fit tests and tests between the age-dependent models (A2, B2, D2), we select the model D2 as the more precise and still appropriate model; as the test between D2 and B2 is near the acceptations limits ($P = 0.0564$) we present also the estimates obtained under the model B2 (Tab. 2).

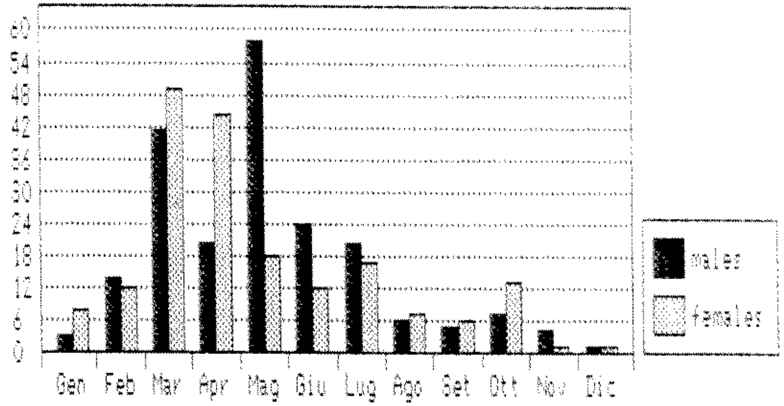

Fig. 2 - Monthly adult sex-ratio (males = 202; females = 188).

Table 2 - Survival rate estimates for young and adult Blackbirds (Periods: may-august 1984-1990) (S = Adult survival; S' = young survival).

	S	S.E.(S)	S'	S.E.(S')
Model D2	0.535	0.039	0.239	0.043
Model B2	0.560	0.045	0.263	0.050

Let now consider the adults alone. We first consider males and females separately. JOLLY's estimates under the model D result appropriate for both the sexes (Tab. 3). Survival and capture probabilities of males and females compared with z test (Brownie et al. 1985) show no significant differences. Therefore we cumulate the adults data and in this case too we are able to retain the estimates under model D. The goodness-of-fit tests suggest no strong violations of the Jolly-Seber models assumptions notwithstanding the continuous netting effort (Tab. 4).

Table 3 - Survival rate estimates for adult males and females Blackbirds (Periods: may-july 1984-1990) according to JOLLY Model D (S = Survival; P = Capture probability).

	S	S.E.(S)	P	S.E.(P)
Males	0.547	0.050	0.377	0.061
Females	0.571	0.081	0.266	0.073
Males + Females	0.548	0.042	0.339	0.048

Table 4 - Goodness-of-fit tests of the JOLLY's Models.

Model	Chi-square	DF	Probability
A	8.7558	5	0.1192
B	10.1241	9	0.3405
C	16.6194	14	0.2770

The population size estimates are shown in Fig. 3, and, separately for adult males and females in Tab. 5, but we cannot extrapolate densities because we do not know the area from which birds come to the ringing station.

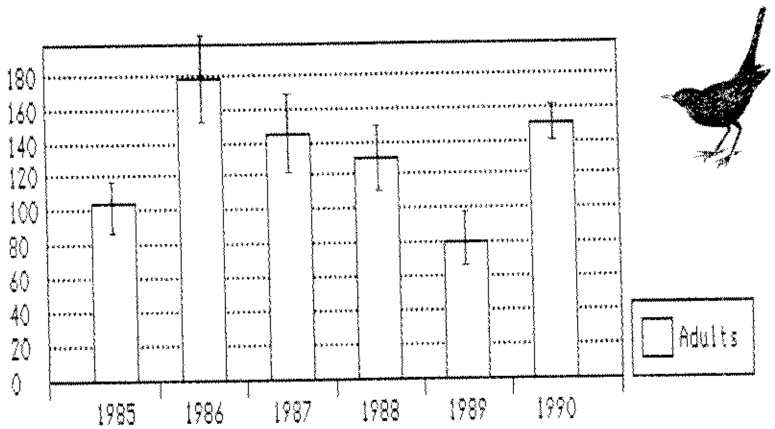

Fig. 3 - Blackbird population estimates (± standard errors) at the Bra ringing station.

Table 5 - Population estimates for adult males and females according to JOLLY's Model D.

	MALES		
Year	N	S.E.	95% Confidence interval
1985	69.60	13.69	42.78 - 96.43
1986	96.13	18.06	60.73 - 131.53
1987	91.06	16.90	57.95 - 124.18
1988	70.52	14.06	42.96 - 98.08
1989	52.24	11.75	29.21 - 75.28
1990	82.16	17.80	47.26 - 117.05
	FEMALES		
Year	N	S.E.	95% Confidence interval
1985	35.13	12.27	11.08 - 59.19
1986	84.13	26.63	31.93 - 136.32
1987	55.68	17.17	22.02 - 89.33
1988	65.44	20.82	24.64 - 106.24
1989	29.42	11.42	7.05 - 51.80
1990	75.27	25.03	26.21 - 124.34

Discussion

Tab. 6 and 7 compare our results with some survival estimates made by ringing recoveries. Our adult estimate agreed with most single ring recoveries estimates as well as with their average (53%). Only the date of Batten (1973) for rural southern England are significantly greater; nevertheless in the suburban London area Batten (1973) found a value (58% +/– 1%) more similar to ours.

We conclude that the adult Blackbirds of our population show a strong breeding philopatry and that the complement of the survival estimate is close to the true mortality.

On the contrary the young survival rate is lower than the compared estimates, although the differences with the recoveries studies are not all significant. However it is well known that natal dispersal in birds is much more widespread than breeding dispersal (Greenwood in Campbell and Lack, 1985); so we think that not a negligible part of the young, although alive, do not return to the ringing site in the subsequent years. The Blackbird is believed to have a marked tendency to breed where reared (natal philopatry rate is estimated as high as 72% after Wert, 1947, quoted by Cramp, 1988). If we adjust our young survival rate by dividing the unadjusted rate by the above probability of return to the natal area, then we obtain a value close to the ring recoveries estimates (i.e. 33%).

Table 6 - Survival rates estimates (values in percent) for adult Blackbirds from ringing recoveries compared to the results of this study.

S	S.E.	Country	Reference
55	2	France	Pasquet et al., 1981
56	1.5	Great Britain	Coulson, 1961
65	0.5	South. England	Batten, 1973
48	2	Belgium	Van Steenbergen, 1971
51		Germany	Erz, 1964
42		Finland	Haukioja, 1969
55	4	NW Italy	This study

Table 7 - Survival rates estimates (values in percent) for young Blackbirds from ringing recoveries compared to the results of this study.

S	S.E.	Country	Reference
31	3	France	Pasquet et al., 1981
50	5	South. England	Batten, 1973
32		Czechoslovakia	Beklova, 1972
24	4	NW Italy	This study

Biased sex ratio in Blackbird, commonly recorded (Snow, 1958; Simms, 1978; Sorace, 1990), is not confirmed on an annual basis by our data: and we have failed to find significant differences between sexes in the total number of ringed birds and in survival rates. Similar annual survival rates between sexes in Blackbird were reported also by Coulson (1961) and seem common in passerines (Dobson 1987), suggesting balanced sex ratios.

Instead we have observed marked differences of abundance between sexes in some months and lower female capture probabilities (although not statistically significant). It seems likely that in April, in our study area, there is a noticeable influx of migrating females, that overwinter at more southern latitudes than males (Simms, 1978; Lancini et al. 1994). According to this view, we obtain a lower capture probability (i.e. 0.177 +/– 0.061) for the females if we include April instead of July in the sample period analyzed with the program JOLLY.

The bigger number of males ringed in May is more difficult to explain and perhaps is partly related to floating birds in search of vacant territories. Also the JOLLY's population estimates suggest a male biased sex-ratio in breeding period, have too a low precision to allow strong inferences.

The differences in phenology and in capture probabilities suggest us that biased sex-ratios derived from count of birds observed or mist-netted in specific periods may also be spurious results due to differences in behaviour or habitat use. In fact Sorace (1990) recorded significant differences in feeding habitat choice in an urban park, the females being more tied to the wooded areas in breeding season.

However we do not exclude important sexual seasonal differences in mortality (hence in sex ratio), that do not necessarily involve differences in annual rates. For example egg-laying and incubating females are likely to be more exposed to the mammalian predators and physiologically stressed (Dobson 1987), while males overwintering at northern latitudes could experience greater winter mortality (Ketterson and Nolan, 1982).

This last question could be properly adressed with capture-recapture experiments designed to estimate survival rates corresponding to specific portions of the year.

Nevertheless our results confirm that with a reasonable capture effort, it is possible to obtain within a few years as good a precision in annual survival estimates as in long-term studies using recoveries. Yet increasing the capture effort in a suitable shorter sample period, we could probably obtain even better precision in few years. However we stress that information from other studies, especially involving recoveries, are very important to weigh or even to adjust the estimates obtained from capture-recapture methods.

As the Blackbird is one of the commonest bird ringed in Italy (with a mean of 2770 individuals ringed per year from 1980 to 1986, Bendini e Spina 1990), other local capture-recapture studies and analyses of the Italian recoveries may now be possible.

The results of such analyses and comparisons could be very interesting also in the light of the compensatory mortality hypothesis (Anderson and Burnham 1976; Nichols et al. 1984) as suggested by the dramatic diversity of hunting pressure on Trushes in different european country: the Britain, mainly sedentary, Blackbird population experience in fact a negligible hunting mortality (0.2% after Coulson 1961), while in France the hunting is one of the main mortality factors (Pasquet et al. 1981). In Piedmont the Blackbird has been protected from 1978 by the regional game law, but in most other italian regions and especially in the mediterranean areas there is a strong hunting pressure on all the *Turdus* species.

AKNOWLEDGEMENTS

We are indebted to Dr. J. Nichols for his advice and helpful comments and to Dr. M. Cucco and M.V. Cocito for the help with the English.

RIASSUNTO

Si sono analizzati i dati di cattura e ricattura di Merli inanellati nell'ambito della stazione ornitologica di Cascina Priore, Bra (CN), allo scopo precipuo di stimarne la sopravvivenza annuale. Le catture per inanellamento sono avvenute sull'intero ciclo annuale, ma i dati utilizzati per la stima della sopravvivenza riguardano solamente il periodo riproduttivo. La sopravvivenza degli adulti è risultata pari al 55% (S.E. 4%), valore comparabile a quelli ottenuti in altri paesi europei tramite l'analisi di tutte le segnalazioni di ripresa dei soggetti inanellati. Il valore ottenuto per i giovani è invece inferiore a quello delle suddette analisi, probabilmente a causa della scarsa tendenza dei giovani a tornare sul luogo di nascita. In effetti gli studi di cattura-ricattura, equiparando mortalità ed emigrazione permanente, sottostimano la sopravvivenza per specie o popolazioni scarsamente filopatriche.

Lo studio ha inoltre evidenziato un rapporto numerico fra i sessi variabile mensilmente, ma complessivamente paritario; ciò può far supporre una mortalità variabile stagionalmente a seconda del sesso, fatto che potrebbe essere indagato con esperimenti di cattura-ricattura appositamente programmati.

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