

# INFLUENCE OF THE MATING SYSTEM OF THE EURASIAN DIPPER ON SEX-SPECIFIC LOCAL SURVIVAL RATES

GILBERT MARZOLIN,<sup>1</sup> 14 rue de la Latte, 57155 Marly, France

**Abstract:** The mating system of the Eurasian dipper (*Cinclus cinclus*) involves males defending resources, such as nesting sites or food, and females choosing sites based on quality. Strong territoriality and unequal quality of sites may induce polygyny. Depending on stream flow, external factors such as floods or drought may alter the quality of some breeding territories, leading to breeding dispersal. Emigration resulting from breeding dispersal should be reflected in annual local adult survival rates. In a study of the Eurasian dipper in northeastern France from 1981 to 1998, I verified that pairing and territoriality may influence local survival and that site choice may be mediated significantly by variation in extrinsic factors using mark–resighting data and selection of models using an information–theoretic framework. I found a decrease of about 0.09 in the annual adult local survival rates for both sexes of Eurasian dippers during flood years. During dry years and for monogamous dippers settled along <2m-wide brooks, female annual local survival rate decreased from 0.56 to 0.39, possibly reflecting permanent emigration, whereas the male resighting probability fell from 0.97 to 0.59, indicating delays in male breeding or temporary emigration. Unlike monogamous breeders, polygamous birds had constant local survival estimates and resighting probabilities, suggesting that they bred in sites secure from both flood and drought. Because the Eurasian dipper adapts poorly to environmental stress, I encourage managers to shorten stream diversions and other water management practices affecting stream flow.

*JOURNAL OF WILDLIFE MANAGEMENT* 66(4):1023–1030

**Key words:** breeding dispersal, *Cinclus cinclus*, drought, Eurasian dipper, flood, France, mating system, polygyny, survival.

The Eurasian dipper (hereafter, dipper) lives along streams and rivers throughout the year. It favors running streams lined with deciduous trees (Buckton and Ormerod 1997), secure nest sites above water, and access to food (Wolf 1981, Schmid and Spitznagel 1985). In my study area, nests of dippers are nearly always in wall cavities or protected above by bridges. Limited choice of such permanent sites (Marzolin 1996) and predictability of the resources (Sweeney 1984:57) may result in adult individuals returning to or remaining in the same territories year after year (Cody 1985:29), for breeding as well as for wintering (Holmqvist et al. 1999). This strong site fidelity results in a mating system in which males defend resources and females choose sites according to quality. In such a system, when food or nesting places are unevenly distributed and male parental investment is limited, a small percentage of males defend sufficient resources to attract >1 female (Emlen and Oring 1977), as has been noted in several populations of dippers (Marzolin 1988, Wilson 1996). Survival may differ between polygamous and monogamous birds because of differences in habitat quality. Moreover, factors such as temperature and rainfall likely alter the quality of some sites depending on the stream

flow and the structure of the channel. Floods may wash some nests away (Price and Bock 1983:70 for the American dipper [*Cinclus mexicanus*], Spitznagel 1996), carry many dipper prey items downstream with the substrate materials (Newbury 1984:341), and increase the energetic cost of foraging (Bryant and Tatner 1988). Rainfall scarcity may result in silting of the stream bed and drift of aquatic insects, and may reduce the carrying capacities of breeding territories (Wiederholm 1984:516). Pollution effects of agricultural runoff in small streams may be intensified in dry years by decreased dilution (Marzolin 1996). My objective is to demonstrate that floods or droughts altered breeding-site choice due to sex-dependent permanent or temporary emigration. Such emigration should be reflected by differences in the local adult survival rates of the dippers, stratified by sex, mating status (monogamous vs. polygamous birds), and the nature of the breeding-site stream and river channels.

## STUDY AREA

The study area was part of a 3,500-km<sup>2</sup> region in northeastern France described elsewhere (Marzolin 1988). The elevation ranges from 150 to 420 m. Streams emerge from limestone hills at about 350 m and are about 12 km long. They flow into the main rivers Meuse or Moselle, both between 30 m and 200 m wide. My sampling area was on

<sup>1</sup> E-mail: g.marzolin@wanadoo.fr

>150 stretches of 40 different streams. These sections, each about 400 m in length, may be separated by stream stretches not used by dippers; they constitute the potential breeding locations in the region.

## METHODS

### Survival Estimation

As local survival rates of immature birds from the same population are reported elsewhere (Clobert et al. 1990), I focused on the survival rates of breeding birds by means of observational data. Dippers were captured as nestlings or by placing a net across the stream, individually color banded, and resighted as breeders in each subsequent breeding season. They were sexed (female dummy variable SEX) according to morphometrics and breeding behavior at banding (Marzolin 1990).

Using Cormack-Jolly-Seber models (Cormack 1964, Jolly 1965, Seber 1965), I followed standard methodology in parameter estimation (Lebreton et al. 1992). I modeled 2 components: the probability ( $\phi_i$ ) of a bird surviving from year  $i$  to year  $i + 1$  and remaining in the study area to breed in year  $i + 1$ , given it was breeding in the population in year  $i$  (local survival probability); and the probability ( $p_i$ ) of being identified in year  $i$ , given it was breeding that year in the population (resighting probability). Recapture histories of the breeding birds were used to estimate year-dependent values of  $\phi$ ,  $p$ , and 95% confidence intervals, separately for each sex or based on characteristics of the breeding site.

A bird that either (1) temporarily emigrated, (2) was identified in year  $i$  as a nonbreeder, or (3) began a clutch but left the study area before it was identified, was recorded as 0 in the recapture history for year  $i$ . These gaps in its recapture history were used to derive annual values of  $p$ . I surveyed river stretches every year and identified all breeders. Thus, for breeding dippers exhibiting site fidelity, recapture probability = 1. Unlike many mark-resight studies, the resighting probability was not a nuisance parameter of the model. When  $p$  differed from 1 in any given year, it indicated that some birds did not breed that year or temporarily emigrated.

In this sample, 2–13% of the breeders were polygamous annually. As the mating status (monogamous or polygamous) of a bird varied with year, I used 2-state multistate models to examine differences in the local survival rates of

the birds stratified by the type of mating (MONO). These models include the probabilities of making Markovian transitions between states from 1 year to the next (Brownie et al. 1993, Schwarz et al. 1993). When the probability of survival from year  $i$  in state  $r$  to  $i + 1$  in state  $s$  only depends on initial state, it is the product of the probability that a bird breeding in year  $i$  in state  $r$  is alive and breeding in year  $i + 1$  whatever the state ( $S_i^r$ ) by a state-transition probability ( $\psi_i^{sr}$ ; notation similar to Lebreton and Pradel [2002]).

### Data Collection and Analysis

I collected meteorological data at a station (elevation of 350 m) 15 km NW of Metz (49°08'N, 06°10'E) near the center of the study area. The standard deviation of rainfall in 12 10-day periods from March through June (RAINDEV) was used to assess the regularity of the spring rain. The mean of daily minimum temperatures from December to February indicating possible delay of invertebrate growth (Sweeney 1984:61), the mean of daily average temperatures from March to June (start of vegetation growth), and for July and August (hot summers) were also recorded (Table 1). The mean flow rate of a spring-supplied stream was used to describe the rainfall in the interbreeding season (Sep–Feb) and the nest-building period (Mar–May).

Extensive rainfall from October 1982 to May 1983 caused 2 major floods in the middle of the breeding period, flooded out a number of nests, caused bridge collapses, and was expected to have altered both the 1982–1983 and 1983–1984 survival rates as well as the 1983 resighting probability. To incorporate effects of the flood on 1 value for stream flow but on 2 for annual survival rates, I pooled hydrologic variables into discrete classes. In addition, the low values of RAINDEV and the permanent high water levels over the spring of 1995 impaired the site quality and were expected to influence the 1994–1995 survival. Hence, I introduced the dummy variable FLOOD (FLOOD = 1 in 1982, 1983, and 1994). As floods occurred at the very beginning of the study, my a priori hypotheses about flood or drought effects were stated well before the whole data set was collected.

Field observations were supported by a cluster analysis based on the 6 climatic and hydrologic variables, placing in a single class the years 1988 to 1992, 1995, and 1997. These years were characterized as having hot summers and low mean flows from September to the following May and were represented by the dummy variable DRY.

Table 1. Hydrologic and climatic characteristics in northeastern France, 1981–1998. The number of sites (*N*) occupied by breeding pairs of Eurasian dippers is included for comparison.

Year <sup>a</sup>	Mean stream flow (l/sec)		RAINDEV <sup>b</sup>	Mean daily temp (°C)			<i>N</i> <sup>c</sup>
	Sep to Feb	Mar to May		Jul to Aug	Dec to Feb	Mar to Jun	
1981	885	443	14	22.0	-2.3	10.8	—
1982	486	1,114	33	24.5	-0.4	10.2	—
1983	371	529	20	28.5	-1.2	8.8	47
1984	276	434	14	24.5	-4.2	10.0	38
1985	177	627	20	23.5	-3.0	10.2	33
1986	332	466	23	22.5	-2.8	9.1	35
1987	562	730	22	22.5	0.1	10.7	33
1988	170	722	19	23.5	0.9	11.5	38
1989	344	405	18	24.5	0.8	11.3	32
1990	395	205	12	25.0	-2.1	10.0	22
1991	125	252	16	26.5	-1.8	11.3	22
1992	209	110	13	25.5	-0.9	11.8	15
1993	838	556	16	22.5	0.2	11.3	15
1994	554	1,387	15	26.0	1.1	10.4	18
1995	135	169	14	25.5	-2.3	10.0	22
1996	358	463	26	23.0	-2.1	11.2	26
1997	297	456	20	25.0	0.3	11.8	26
1998	349	624	18	22.5	-0.3	11.6	22

<sup>a</sup> To estimate survival from year *i* to year *i* + 1, the row of year *i* displays the mean flow from Sep *i* to Feb *i* + 1 and from Mar *i* + 1 to May *i* + 1 of a spring-supplied stream, the mean temp from Jul *i* to Aug *i*, from Dec *i* to Feb *i* + 1, and from Mar *i* + 1 to Jun *i* + 1.

<sup>b</sup> Standard deviation of rainfall in 12 10-day periods from Mar *i* + 1 to Jun *i* + 1.

<sup>c</sup> Number of sites occupied by breeding pairs each year among 60 selected sites (unavailable data denoted by “—”).

I monitored each breeding site from January through June by 2 visits/month. I used 60 potential breeding sites surveyed in 1983 and still suitable for breeding in 1998 to assess the variation in the annual numbers of breeding pairs; density in 1981 and 1982 was not assessed (Table 1).

The habitat of each nesting location (SITE) was categorized as: (1) Type 1, permanent sites in old mills or under bridges secure from floods, along >7-m-wide clay channels, where the water depth limited food availability in some places; (2) Type 2, sites along flood-prone streams from 2 to 7 m wide, flowing faster on sandy or stony beds; or (3) Type 3, temporary sites along <2-m-wide spring-supplied brooks. Dippers that changed territory types (*n* = 36) were given the SITE category of their first-breeding site, which was also the most often used (Table 2).

### Model Selection

Using prior knowledge of the dipper, I built a set of candidate models that included the variables expected to influence survival. Because I expected sex-specific behavior during the dry years, I considered models whose resighting component only included the indicator variable of males breeding in Type 3 sites during dry years. The survival component of the global model (A) comprised the

main effects of factors SITE, SEX, FLOOD, and DRY, and all their interactions. The survival component of the sub-models was constrained by factors FLOOD and SITE (model A1), along with either: (1) variable *U* (*U* = SITE(3) × SEX × DRY) to check a dry effect on female survival (model A2); (2) variables *U* and *V* SEX (*V* = SITE(2) FLOOD) to check sex-specific flood-effect on Type 2 sites (model A3); or (3) variables *U* and *V*, but without FLOOD, to check a flood effect only along Type 2 sites (model A4). To test for differences in survival rates among site types, I constructed models in which SITE was replaced with either SITE(3) (models B1, B2, and B3), or SITE(2) (model C; Table 3).

Table 2. Numbers of Eurasian dippers breeding in the study area in northeastern France, 1981–1998, classified by sex and breeding site type.

Sex	Site <sup>a</sup>			Total
	Type 1	Type 2	Type 3	
M	96	234	84	414
F	102	247	91	440
Total	198	481	175	854

<sup>a</sup> Type 1: permanent habitats along rivers, Type 2: sites along medium-wide streams with stony beds, and Type 3: temporary sites along brooks prone to drought.

Table 3. Structure of the components of models estimating survival probability in a Eurasian dipper population in northeastern France, 1981–1998, as function of breeding site type (see Table 2), sex, and climatic factors (flood years or dry years).

Model	Structure of survival component
A <sup>a</sup>	SITE*SEX*FLOOD*DRY
A1	SITE + FLOOD
A2	SITE + FLOOD + U <sup>b</sup>
A3	SITE + FLOOD + U + SEX × V <sup>c</sup>
A4	SITE + U + V
B1	SITE(3) + FLOOD + U
B2	SITE(3) + FLOOD + U + V
B3	SITE(3) + FLOOD + U + SEX × V
C	SITE(2) + FLOOD + U

<sup>a</sup> Notation similar to Lebreton et al. (1992).

<sup>b</sup> U = SITE(3) × SEX × DRY.

<sup>c</sup> V = SITE(2) × FLOOD.

I used program MARK (White and Burnham 1999) for parameter estimation and an information–theoretic framework to rank the models. For each model with  $n$  captures or resightings, that program computed its deviance and Akaike's Information Criterion corrected for small  $n$  ( $AIC_c$ ) or for extra multinomial variation ( $QAIC_c$ , with  $\hat{c}$  as the coefficient of overdispersion; Lebreton et al. 1992). It also ranked all models in a set based on  $AIC_c$ , calculated the differences in  $AIC_c$  ( $\Delta_i$ ) between each model  $M_i$  in the set and the model with the lowest  $AIC_c$ , and computed Akaike weight of each model ( $w_i$ ), where  $w_i = \exp(-\Delta_i/2) / \sum_k \exp(-\Delta_k/2)$ . An Akaike weight is the estimated probability that model  $M_i$  is the best model (in minimizing the information loss) for the data given the set of models (Burnham and Anderson 1998:123). An optimal model of the set is 1 with the smallest  $AIC_c$  that fits the data. The goodness-of-fit of model  $M_i$  was measured with a parametric bootstrap procedure;  $N$  replicates of each of the recapture histories in the data set were randomly drawn through the estimates yielded by model  $M_i$ . Then model  $M_i$  was fit to each of the  $N$  replicates and the  $N$  deviances were compared with that of model  $M_i$  fit to the initial data (Burnham et al. 1987:399). To get estimates conditioned on the model set, I used the Akaike weights to average the estimates produced by the models of the set. I used the formula from Buckland et al. (1997) for the confidence intervals to include a variance component for model-selection uncertainty.

Program MARK estimated  $S$ ,  $p$ , and  $\psi$  for multistate models of mating status. I expected the sites of polygynous pairs to be secure from flood

or drought, in contrast to that of some monogamous birds. I considered a set of 5 models, all with transitions only state-dependent, with survival components including the effects of FLOOD, MONO, or MONO × FLOOD in turn, and with either MONO or MONO × DRY in the resighting component. I performed the goodness-of-fit bootstrap procedure on the model in which  $S$ ,  $p$ , and  $\psi$  were only state-dependent using MARK in connection to a spreadsheet for 100 replicates.

## RESULTS

### Survival Rates by Sex and Breeding-Site Type

From 1981 to 1998, about 50 breeding pairs of dippers were present each year in the stream stretches. From there, 854 breeding birds were marked (Table 2; lifespan from 1 to 9 yr) resulting in exactly 1,600 effective captures or resightings. About 67% of these birds were immigrants to the sampling area.

The global model of survival fit the data (goodness-of-fit: in 38/100 bootstrap replicates, the deviance exceeded that of the model fit to the data,  $\hat{c} = 1.07$ , deviance df = 206.34). Among the 9 models of the set, model A2 had the lowest  $QAIC_c$ , with  $w_i = 0.34$  (Table 4). Model-averaged parameter estimates and confidence intervals were conditioned on the model set (Table 5). The annual local survival rate of all birds, independent of sites, declined by 0.09 in flood years compared with other years and was always higher

Table 4. Models estimating survival probability of Eurasian dippers in northeastern France, 1981–1998, as function of breeding site type (see Table 2), sex, and climatic factors (flood years or dry years).

Model <sup>a</sup>	$-2\ln(L)$	$K^b$	$QAIC_c^c$	$\Delta_i^d$	$w_i^e$
A2	2,347.4	7	2,212.2	0	0.338
A1	2,351.4	6	2,213.9	1.732	0.142
A3	2,347.2	8	2,214.0	1.854	0.134
B1	2,351.7	6	2,214.2	2.038	0.122
C	2,352.3	6	2,214.7	2.572	0.093
A4	2,350.9	7	2,215.5	3.289	0.065
B3	2,351.1	7	2,215.6	3.426	0.053
B2	2,351.4	7	2,215.9	3.720	0.053
A	2,341.1	20	2,232.8	20.60	0.000

<sup>a</sup> See Table 3. Resighting probability was modeled as SITE(3) × (1-SEX) × DRY.

<sup>b</sup> Number of parameters estimated.

<sup>c</sup> Akaike's Information Criterion corrected for small sample size and overdispersion ( $QAIC_c$ ).

<sup>d</sup> Increase over the lowest observed value of  $QAIC_c$ .

<sup>e</sup> Akaike weight: likelihood of a model to be the best in the set of candidate models given the data.

Table 5. Model-averaged survival estimates and 95% confidence intervals (including a component for model-selection uncertainty) of Eurasian dippers in northeastern France, 1981–1998, as a function of sex, breeding site type (see Table 2) and climatic variables (normal years, flood years, and dry years). Values are derived from the models in Table 4.

Sex	Site type	Type of year	Estimate (95% CI)
M + F	1	Flood	0.52 (0.44, 0.60)
		Normal + Dry	0.60 (0.54, 0.65)
M + F	2	Flood	0.46 (0.39, 0.54)
		Normal + Dry	0.56 (0.52, 0.59)
M + F	3	Flood	0.44 (0.34, 0.54)
		Normal	0.52 (0.44, 0.60)
M	3	Dry	0.52 (0.44, 0.60)
F	3	Dry	0.39 (0.25, 0.54)

in Type 1 than in Type 3 sites. Estimated survival was lowest for females breeding at Type 3 sites during dry years ( $\hat{\phi} = 0.39$ ) and highest for both sexes breeding at Type 1 sites outside of flood years ( $\hat{\phi} = 0.60$ ). The estimated model-averaged resighting probability was 0.97 (CI = 0.95, 0.98) for all the birds except males in Type 3 sites during the dry years, for which it was 0.59 (CI = 0.40, 0.76). These results agree with the decrease in the number of sites observed occupied by breeding pairs during the dry years (Table 1) and suggest that site choice is mediated by environmental factors.

### Survival Rates in Relation to Mating Status

The multistate model with S,  $p$ , and  $\psi$  only depending on state MONO (Table 6) fit the data (goodness-of-fit: in 30/100 replicates, the deviance exceeded that of the model fit to the data,  $\hat{c} = 1.08$ , deviance df = 161.5). Incorporating  $\hat{c}$ , I averaged the models of the set. Estimated survival probability of monogamous and polygamous birds was equivalent in normal and dry years but 0.08 lower in monogamous birds during flood years (Table 7). Estimated transition probability from monogamous to polygynous states = 0.11 (CI = 0.09, 0.13) and from polygynous to monogamous = 0.61 (CI = 0.51, 0.71). As polygamous birds did not show any significant breeding delays or permanent emigration, they may not be influenced by flood or drought.

### DISCUSSION

These survival rate estimates fall well within the range of survival rates reported elsewhere for similar-sized bird species (Peach 1993). Balat (1964) estimated a mean age of 2.33 years for 6 breeding male dippers of the Moravian Karst, and

2.5 years for 6 females, implying an annual survival rate of 0.47 for males and of 0.51 for females through Cormack's (1964) formula. In Scotland, Hewson (1969) found a minimal mean age of 2.68 years for 12 males and of 2.93 years for 10 females, which results in annual survival rate estimates of 0.55 and 0.59, respectively. Galbraith and Tyler (1982) used 185 recaptures and recoveries to estimate an adult annual survival rate = 0.54 using Haldane's method. With a mass of 60 g, the allometric relationship between survival and body size of European birds (Saether 1989) yields a survival rate for dippers = 0.55, which agrees with the previously estimated rate. Other Eurasian dipper studies using mark-resight methods are an unpublished study in Scotland by J. Logie (Bryant and Newton 1996), in which the survival rates ranged from 0.50 to 0.65 (mean = 0.53), a study in southern Norway in which the mean apparent survival rate was 0.52 (Loison et al. 2002), and the examples in Lebreton et al. (1992) using the first 7 years of data from this study.

Temporal variation in relative fitness associated with different types of sites is expected to result in temporal variation in between-site movements (Pulliam 1988). The decline in survival during flood years may reflect a combination of mortality and permanent emigration. Despite some nest destruction, flood effects were relatively ephemeral. Shortly following a flood, some birds were observed building new nests and some dead birds were recovered. Thus, I assumed that most movements were confined to the study area. In a Welsh population, only 3.6% of adult breeders moved

Table 6. Multistate models of survival probability of Eurasian dippers in northeastern France, 1981–1998, as function of their mating status (monogamous vs. polygamous birds) and climatic factors (flood years or dry years).

Model <sup>a</sup>	-2ln(L)	K <sup>b</sup>	QAIC <sub>c</sub>	$\Delta_i^d$	w <sub>i</sub> <sup>e</sup>
S(MONO × FLOOD), $p$ (MONO)	3,046.4	5	2,830.9	0	0.645
S(MONO × FLOOD), $p$ (MONO × DRY)	3,046.1	6	2,832.7	1.82	0.260
S(·), $p$ (MONO)	3,053.4	4	2,835.4	4.47	0.069
S(MONO), $p$ (MONO)	3,053.3	5	2,837.4	6.46	0.026
S(FLOOD), $p$ (MONO)	3,083.2	5	2,865.0	34.1	0.000

<sup>a</sup> The transition probabilities of these 2-state multistate models only depend on state MONO.

<sup>b</sup> Number of parameters estimated.

<sup>c</sup> Akaike's Information Criterion corrected for small sample size and overdispersion (QAIC<sub>c</sub>).

<sup>d</sup> Increase over the lowest observed value of QAIC<sub>c</sub>.

<sup>e</sup> Akaike weight: likelihood of a model to be the best in the set of candidate models given the data.

Table 7. Model-averaged estimates of survival (S) and resighting (p) probabilities (with 95% confidence intervals) of Eurasian dippers in northeastern France, 1981–1998, as a function of their mating status (monogamous vs. polygamous birds) and climatic factors (normal years, flood years, and dry years). Values are derived from the models in Table 6.

Model parameter	State	Type of year	Estimate (95% CI)
S	MONO	Flood	0.47 (0.39, 0.54)
	MONO	Normal + Dry	0.55 (0.52, 0.58)
	POLY	All years	0.55 (0.52, 0.59)
p	MONO	Normal + Flood	0.95 (0.92, 0.97)
	MONO	Dry	0.94 (0.91, 0.97)
	POLY	All years	0.99 (0.84, 0.99)

>2.5 km to breed from 1 year to the next, and none moved >5 km (Tyler et al. 1990). Given strong site fidelity, the computed survival probabilities of dippers in normal years were assumed to be good estimates of the true survival.

During the dry years, when brooks were partly invaded by vegetation, all the dipper nesting sites along some streams became unsuitable for several years. After the loss of their first broods, no females renested, as was observed for the American dipper in similar conditions (Price and Bock 1983:72). In my study area, the scarcity of natural and artificial breeding sites limited the distribution of the dipper. Fey (1992) noticed a similar limitation in a hilly district in Westphalia, Germany. As individuals may disperse only when local suitability deteriorates below a certain threshold (Danchin et al. 2001:251), the decrease in female local survival during dry years may be attributable to a combination of permanent emigration and decreased apparent survival. The decrease in the resighting probability of males could be attributed to breeding delays or temporary emigration, which reflects their strong fidelity to nesting sites. This supports the idea that males defend resources and territories, whereas females might disperse to locate better-quality territories. This sex-specific dispersal agrees with Greenwood (1980, 1989:216), who noted that such a mating system may lead to asymmetries in the costs and benefits of dispersal. The sex that is most involved in territory acquisition benefits from philopatry by making better use of local resources or having greater chance of obtaining a mate; competition for territories among males is strong, whereas females benefit from dispersal. Even if the proximate causes differ, territory knowledge also is used differently by the sexes of the collared flycatcher (*Ficedula albicollis*), also a

non-colonial and hole-nesting species in which males are territorial and polygyny occurs. Males use the reproductive success of conspecifics as an index of future territorial competition, whereas females use it as an indicator of resources. High-quality males do not seem to be influenced by that index, low-quality males tend to leave high-index woodlands, and all females emigrate from low-index woodlands (Doligez et al. 1999).

The observed decline in the density of dipper breeding pairs during the dry years supports the dispersal model of Gadgil (1971), which implies a reduction in the population size when there is an increase of variability of territory quality among patchy habitats. A decline in the numbers of dippers also has been noticed in South Wales after 1988, following either wet or very dry summers (George 1993, Tyler and Ormerod 1994). In southern Norway, along small streams, the size of a dipper population varied synchronously with the water flow in spring (Åhlund et al. 1999). In contrast to my study, in the same area, due to a shorter duration of ice cover on the streams from 1989 to 1992 (a North Atlantic Oscillation effect), there was a pronounced peak in the size of a dipper population (Saether et al. 2000).

According to the theoretical polygyny model of Orians (1969), beyond a threshold in the variability of the site quality, the best-quality sites are first occupied by mated pairs, then some males of these sites can attract a second female, even if lower-quality breeding sites remain vacant. Therefore, in view of my results, the good-quality sites for the Eurasian dipper are secure from both flood and drought. This is consistent with the fact that dippers depend mainly on the stream beds to forage. In addition, the survival difference between birds of different mating status supports the prediction that, in this study area, dipper habitats are scattered and of unequal quality.

## MANAGEMENT IMPLICATIONS

I suggest that the decrease in local survival probability of both sexes during flood years and of females during dry years was due to deterioration of the breeding territories. Emigration and true mortality indicated the poor adaptability of the Eurasian dipper and its sensitivity to environmental stress and site destruction. The increasing abstraction of water for urban and agricultural use reduces flows in rivers, resulting in changes in substratum type and distribution in prey species. The regulation of rivers results in poor habitats for dippers because of the replacement of forag-

ing areas by concrete channels. The construction of balancing reservoirs removes territories. I therefore encourage managers to restrict dam construction, stream diversions, and other water management practices affecting stream flow.

#### ACKNOWLEDGMENTS

The French Centre de Recherches sur la Biologie des Populations d'Oiseaux initiated this study, and the Centre de Metz de Météo-France provided the climatic data. I acknowledge the assistance of D. R. Anderson and J. Blakesley. I thank J. Clobert, E. Danchin, J. D. Lebreton, S. A. H. Osborn, and anonymous reviewers for comments on earlier drafts.

#### LITERATURE CITED

- ÅHLUND, M., R. BÖRJESSON, E. ENGBLOM, M. O. G. ERIKSSON, P. E. LINGDELL, K. STRÖM, AND I. ÅHLUND. 1999. Strömstaren *Cinclus cinclus* och försurning: beståndsutveckling, häckningsresultat och födoval i sydvästra Sverige. *Ornis Svecica* 9:47–58. [In Swedish.]
- BALAT, F. 1964. Breeding biology and population dynamics in the dipper. *Zoologické Listy* 13:305–320.
- BROWNIE, C., J. E. HINES, J. D. NICHOLS, K. H. POLLOCK, AND J. B. HESTBECK. 1993. Capture–recapture studies for multiple strata including non-Markovian transitions. *Biometrics* 49:1173–1187.
- BRYANT, D. M., AND A. V. NEWTON. 1996. Dominance and survival of dippers *Cinclus cinclus*. *Behavioral Ecology and Sociobiology* 38:173–181.
- , AND P. TATNER. 1988. Energetics of the annual cycle of dippers *Cinclus cinclus*. *Ibis* 130:17–38.
- BUCKLAND, S. T., K. P. BURNHAM, AND N. H. AUGUSTIN. 1997. Model selection: an integral part of inference. *Biometrics* 53:603–618.
- BUCKTON, S. T., AND S. J. ORMEROD. 1997. Use of a new standardized habitat survey for assessing the habitat preferences and distribution of upland river birds. *Bird Study* 44:327–337.
- BURNHAM, K. P., AND D. R. ANDERSON. 1998. Model selection and inference: a practical information–theoretic approach. Springer-Verlag, New York, USA.
- , ———, G. C. WHITE, C. BROWNIE, AND K. H. POLLOCK. 1987. Design and analysis methods for fish survival experiments based on release–recapture. American Fisheries Society, Bethesda, Maryland, USA.
- CLOBERT, J., J. D. LEBRETON, AND G. MARZOLIN. 1990. The estimation of local juvenile survival rates and of age-specific proportions of breeders in bird populations. Pages 199–213 in J. Blondel, A. Gosler, J. D. Lebreton, and R. McCleery, editors. *Population biology of passerine birds: an integrated approach*. Springer-Verlag, Berlin, Germany.
- CODY, M. L. 1985. An introduction to habitat selection in birds. Pages 4–56 in M. L. Cody, editor. *Habitat selection in birds*. Academic Press, London, United Kingdom.
- CORMACK, R. M. 1964. Estimates of survival from the sighting of marked animals. *Biometrika* 51:429–438.
- DANCHIN, E., D. HEG, AND B. DOLIGEZ. 2001. Public information and breeding habitat selection. Pages 241–258 in J. Clobert, E. Danchin, A. A. Dhondt, and J. D. Nichols, editors. *Dispersal*. Oxford University Press, Oxford, United Kingdom.
- DOLIGEZ, B., E. DANCHIN, J. CLOBERT, AND L. GUSTAFSSON. 1999. The use of conspecific reproductive success for breeding habitat selection in a non-colonial, hole-nesting species, the collared flycatcher. *Journal of Animal Ecology* 68:1193–1206.
- EMLEN, S. T., AND L. W. ORING. 1977. Ecology, sexual selection, and the evolution of mating systems. *Science* 197:215–223.
- FEY, J. M. 1992. Die Wiederbesiedlung des Rahmede (Märkischer Kreis) durch die Wasseramsel (*Cinclus cinclus* L.) und ihre Stellung im Ökosystem des Stadtbaches. *Charadrius* 28:82–100. [In German.]
- GADGIL, M. 1971. Dispersal: population consequences and evolution. *Ecology* 52:253–261.
- GALBRAITH, H., AND S. J. TYLER. 1982. The movements and mortality of the dipper as shown by ringing recoveries. *Ringling & Migration* 4:9–14.
- GEORGE, D. G. 1993. Impacts on freshwater systems. Pages 47–53 in M. G. R. Cannell and C. E. R. Pitcairn, editors. *Impacts of the mild winters and hot summers in the United Kingdom in 1988–1990*. Her Majesty's Stationery Office, London, United Kingdom.
- GREENWOOD, P. J. 1980. Mating systems, philopatry and dispersal in birds and mammals. *Animal Behaviour* 28:1140–1162.
- . 1989. Inbreeding, philopatry and optimal outbreeding in birds. Pages 207–223 in F. Cooke and P. A. Buckley, editors. *Avian genetics*. Academic Press, London, United Kingdom.
- HEWSON, R. 1969. Roosts and roosting habits of the dipper. *Bird Study* 16:89–100.
- HOLMQVIST, N., P. OLSSON, R. OTTVALL, AND G. FLYCKT. 1999. The winter occurrence of the dipper in Scania. *Anser* 38:1–8.
- JOLLY, G. M. 1965. Explicit estimates from capture–recapture data with both death and immigration–stochastic models. *Biometrika* 52:225–247.
- LEBRETON, J. D., K. P. BURNHAM, J. CLOBERT, AND D. R. ANDERSON. 1992. Modeling survival and testing biological hypotheses using marked animals: a unified approach with case studies. *Ecological Monographs* 62:67–118.
- , AND R. PRADEL. 2002. Multistate recapture models: modelling incomplete individual histories. *Journal of Applied Statistics* 29:353–369.
- LOISON, A., B. E. SAETHER, K. JERSTAD, AND O. W. RØSTAD. 2002. Disentangling the sources of variation in the survival of the European dipper. *Journal of Applied Statistics* 29:289–304.
- MARZOLIN, G. 1988. Polygynie du cincle plongeur (*Cinclus cinclus*) dans les côtes de Lorraine. *L'Oiseau et la Revue Française d'Ornithologie* 58:277–286. [In French.]
- . 1990. Variabilité morphométrique du cincle plongeur *Cinclus cinclus* en fonction du sexe et de l'âge. *Alauda* 58:85–94. [In French.]
- . 1996. Caractéristiques de l'habitat et variations de la distribution du cincle plongeur (*Cinclus cinclus*) en plaine lorraine. *Ciconia* 20:65–80. [In French.]
- NEWBURY, R. W. 1984. Hydrologic determinants of aquatic insect habitats. Pages 323–357 in V. H. Resh and D. M. Rosenberg, editors. *The ecology of aquatic insects*. Praeger, New York, USA.

- ORIAN, G. H. 1969. On the evolution of mating systems in birds and mammals. *American Naturalist* 103:589–603.
- PEACH, W. J. 1993. Combining mark–recapture data sets for small passerines. Pages 107–122 in J. D. Lebreton and P. M. North, editors. *Marked individuals in the study of bird population*. Birkhäuser Verlag, Basel, Switzerland.
- PRICE, F. E., AND C. E. BOCK. 1983. Population ecology of the dipper (*Cinclus mexicanus*) in the Front Range of Colorado. *Studies in Avian Biology* 7:1–84.
- PULLIAM, H. R. 1988. Sources, sinks, and population regulation. *American Naturalist* 132:652–661.
- SAETHER, B. E. 1989. Survival rates in relation to body weight in European birds. *Ornis Scandinavica* 20:13–21.
- , J. TUFTO, S. ENGEN, K. JERSTAD, O. W. RØSTAD, AND J. E. SKÅTAN. 2000. Population dynamical consequences of climate change for a small temperate songbird. *Science* 287:854–856.
- SEBER, G. A. F. 1965. A note on the multiple recapture census. *Biometrika* 52:249–259.
- SCHMID, W., AND A. SPITZNAGEL. 1985. Der sexuelle Größendimorphismus süddeutscher Wasseramseln (*Cinclus c. aquaticus*): Biometrie, Funktion und mögliche Ursachen. *Ökologie der Vögel* 7:377–408. [In German.]
- SCHWARZ, C. J., J. F. SCHWEIGERT, AND A. N. ARNASON. 1993. Estimating migration rates using tag-recovery data. *Biometrics* 49:177–193.
- SPITZNAGEL, A. 1996. Why dippers dip—on the adaptive significance of fitness-signalling and predator-pursuit deterring movements in birds. *Zoologischer Anzeiger* 235:89–99.
- SWEENEY, B. W. 1984. Factors influencing life-history patterns of aquatic insects. Pages 56–100 in V. H. Resh and D. M. Rosenberg, editors. *The ecology of aquatic insects*. Praeger, New York, USA.
- TYLER, S. J., AND S. J. ORMEROD. 1994. *The dippers*. T. & A. D. Poyser, London, United Kingdom.
- , ———, AND J. M. S. LEWIS. 1990. The post-natal and breeding dispersion of Welsh dippers *Cinclus cinclus*. *Bird Study* 37:18–23.
- WHITE, G. C., AND K. P. BURNHAM. 1999. Program MARK: survival estimation from populations of marked animals. *Bird Study* 46 (Supplement):S120–S138.
- WIEDERHOLM, T. 1984. Responses of aquatic insects to environmental pollution. Pages 508–557 in V. H. Resh and D. M. Rosenberg, editors. *The ecology of aquatic insects*. Praeger, New York, USA.
- WILSON, J. D. 1996. The breeding biology and population history of the dipper *Cinclus cinclus* on a Scottish river system. *Bird Study* 43:108–118.
- WOLF, M. E. 1981. Der Brutbestand des Wasseramseln (*Cinclus cinclus*), des Eisvogel (*Alcedo atthis*) und der Gebirgsstelze (*Motacilla cinerea*) im östlichen Wienerwald. *Egretta* 24:22–38. [In German.]

Received 20 February 2001.

Accepted 16 May 2002.

Associate Editor: Block.