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Apparent survival and dispersal in a White-throated Dipper (*Cinclus cinclus*) population from northern Iberia

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River systems are some of the habitats most drastically affected by climate change. Consequently, many riparian species are amongst the most threatened living organisms worldwide, making riparian areas a conservation priority. Demographic analyses destined to improve our comprehension of the population dynamics of riparian species are crucial in this context. The present work analyses the spatio-temporal demographic dynamics of a presumably well-preserved White-throated Dipper (*Cinclus cinclus*) population from northern Spain. Using multistate models where we considered the effects of factors such as mean water flow in winter, age, sex, hydrographical basin of origin and hatching date, we found that the population had a constant annual dispersal rate ($\psi = 0.038$; 95% CI: 0.022–0.065). The mean apparent survival of Dippers from first-order clutches was 0.18 (95% CI: 0.12–0.22), whereas for those hatched in second-order clutches was 0.07 (95% CI: 0.03–0.15). The mean annual apparent survival for adults was 0.64 (95% CI: 0.56–0.70). Although apparent survival varied from year to year, we found no effect of the average winter flow on this parameter. Recapture probability (p) varied among basins, probably reflecting a heterogeneous sampling effort. In conclusion, using multistate models were found that Dippers from three adjacent river basins in northern Spain had a very short-range natal dispersal rate, and a breeding dispersal close to zero, a trait that could be different from findings in other zones of Spain, where dispersal rates seem to be much higher.

1. Introduction

Demographic analyses constitute a basic piece of knowledge necessary to comprehend causes explaining bird population dynamics (Croxall & Rothery 1991, Lebreton *et al.* 1992, Newton 1998, Lebreton 2001). For instance, population models are fed with the corresponding estimate of the different age-classes survival rates (Garcias & Tavecchia 2018), and quantifying the effect of the multiple sources that might shape variation in survival is crucial because this allows a proper evaluation of the direction and magnitude of environmental drivers on bird population dynamics (Loison *et al.* 2002, Prieto *et al.* 2019). Dispersal is also one key parameter driving demographic processes in birds (Oro *et al.* 2011, Delgado *et al.* 2021), for instance due to source-sink dynamics mediated by natal or breeding dispersal (Greenwood & Harvey 1982, Senar *et al.* 2002, Pfeiffer & Schaub 2023). From a conservation standpoint, most studies are usually done in relatively small areas where dispersal (*i.e.* emigration/immigration) can play a role. Thus, if dispersal is important, protecting only isolated small areas might be insufficient to maintain populations, and in these cases approaches to conservation should involve actions at broader spatial scales (Baillie *et al.* 2000).

Climate warming is causing dramatic changes worldwide, with river systems being one of the most drastically affected habitats (Pletterbauer *et al.* 2018). Predictive models suggest changes in the air and water temperature, and in the amount and/or regularity of precipitation (Chiu *et al.* 2013, Royan *et al.* 2015). These climate alterations trigger processes that can alter river morphology (Ashmore & Church 2001), riparian vegetation (Dwire *et al.* 2018), nutrient dynamics (Johnson *et al.* 2012) or distribution and abundance of animal species (Timoner *et al.* 2021). Consequently, highly specialised riparian species are amongst the most threatened living organisms worldwide, making these areas a conservation priority (Capon *et al.* 2013, Zhang *et al.* 2023).

The White-throated Dipper (*Cinclus cinlus*)—hereafter to simplify referred to as ‘Dipper’—is a specialised small passerine bird associated with clean, well-oxygenated, fast-flowing streams living across much of Eurasia (Ormerod & Tyler 2005). Its dependence on such a well-preserved riparian ecosystem and its sensitivity to the pollution and alteration of the natural riparian systems have led to its consideration as a bioindicator (Ormerod *et al.* 1986, Ormerod & Tyler 1989, Ormerod *et al.* 1991, Vickery 1992, Nilsson *et al.* 2011, Morrissey *et al.* 2012). Studies on population dynamics of dippers are gaining increasing interest in the scientific community, given that their populations are suffering from the effects of climate change in many places worldwide, either due to droughts or an increasing number of extreme flooding episodes (Loison *et al.* 2002, Nilsson *et al.* 2011, Chiu *et al.* 2013, Sánchez *et al.* 2017).

The Cantabrian region in Spain constitutes, together with the Pyrenees, a capital bastion for the Dipper population in the Iberian Peninsula (Keller *et al.* 2020, Molina *et al.* 2022). Under the current climate change scenario, droughts and desertification are amongst the most serious threats to the conservation of Dipper populations in much of Spain (Galindo *et al.* 2003, Huntley *et al.* 2007). Therefore, Dipper populations breeding in those areas still maintaining well-preserved river basins might play a key role for the conservation of this species in southern Europe. In this context, all those studies aimed at determining the conservation status of Dipper populations, including analytical approaches to estimate demographic parameters such as survival or dispersal, are highly recommended. Although the Dipper is a relatively frequently ringed bird in Spain (Regla & Arizaga 2016), we know only one study in which survival is estimated (Sánchez *et al.* 2017). The average apparent annual survival of Dippers caught as adults in a nearby population (Gipuzkoa, Basque Country) was 0.56, and it varied annually slightly, in part explained by winter flooding episodes (Sánchez *et al.* 2017). Survival did not vary between sexes and the study, due to the nature of the used data set, was unable to estimate the survival of first-year birds (an essential parameter to feed population models) and did not test to what extent survival varied locally (*e.g.* between nearby river basins) or estimated dispersal. For this latter parameter, most analyses have been done by measuring directly distances from ring-recovery data (Tellería *et al.* 1999, Galindo *et al.* 2003, Campos *et al.* 2012, Regla & Arizaga 2016), a method which has often been questioned because the ringing effort is normally concentrated in very specific rivers or basins, what hampers from detecting longer-distance dispersal (*e.g.* Hernández *et al.* 2012). Although Dippers from Spain show on average short-range dispersal distances as compared to their northern European counterparts (Franks *et al.* 2022), there is still little knowledge of the characteristics of this trait for the Iberian Dipper populations.

The main goal of this study is to address the lack of information on Dipper population dynamics in Spain, contributing to investigate the environmental drivers that may influence variations in demographic parameters. In particular, we analysed the apparent annual survival and dispersal of an apparently well-preserved population of Dippers in northern Spain (Biscay, Basque Country, Cantabrian region), testing for the effects of factors such as mean water flow in winter (Chiu *et al.* 2013), age, sex, hydrographical basin of origin and hatching date. These parameters have been proved to affect Dipper population dynamics in previous studies (Bryant & Newton 1996, Loison *et al.* 2002, Middleton & Green 2008, Sánchez *et al.* 2017).

2. Material and methods

2.1. Study area and data collection

This study was carried out in three basins within the province of Biscay (Basque Country, Spain), from east to west: Artibai, Lea and Oka (Fig. 1). Overall, these basins cover an area of 458 km^2 with an accumulated length of *ca.* 90 km of rivers (tide-influenced stretches excluded). Most of the main rivers and their tributaries within the study area are protected under European regulations (Special Areas of Conservation: ES2130006, ES2130010 and ES2130011). Topographically, these three main rivers flow through valleys ranging from 0 to *ca.* 1000 m above sea level, though in the majority of the territory the altitudinal difference ranges from 0 to 200 m. The landscape is dominated by Atlantic native deciduous forest patches, timber plantations and countryside, with small scattered towns and farms.

We searched for nests during the breeding seasons of 2015 to 2022 (from mid-February to mid-May), trying to cover the whole study area and marking as many nestlings as possible. The population comprised from 54 to 68 pairs of adult, territorial Dippers. These were distributed equally and uninterruptedly throughout the three basins, from the sea level up to an altitude of

Fig. 1. River basins where the study was carried out. In the square right above, we show the location of these three basins within the province of Biscay (shaded in dark grey), belonging to the Basque Country (Spain). The small square shows the location of the Basque Country in the Iberian peninsula.

300 m. We estimate that we ringed 47.5% of the broods (n = 232 fledglings: Artibai=60, Lea=102, Oka=70). Given that the Dipper may lay a second clutch, each nest was monitored to determine whether the ringed nestlings came from the first or second clutch (in this last case we also included replacement clutches laid when the first one failed). During the subsequent breeding seasons we trapped adults using mist nets placed close to nests, captured when entering or leaving their nests to incubate or feed their offspring. Upon capture, each bird underwent ringing, and for adults, their sex was determined by assessing the presence of an incubating patch or employing the discriminant function as described by Arzak *et al.* (2014). Nestlings were ringed when they had an age of one to two weeks. Older nestlings were avoided because they tend to jump from the nest due to the manipulation, which would decrease their survival prospect.

The Basque Water Agency provided hydrological data. Because we wanted to assess the impact of extreme flooding in the months before the breeding season, we considered the mean values from November to February, just before the end of the interval between one season and the other (Sánchez *et al.* 2017). Dippers mostly feed on riparian macroinvertebrates (with a diet that include insects, molluscs, crustaceans and fish eggs and larvae) (Tyler & Ormerod 1994), Extreme flooding episodes, which in our sampling zones are more habitual in winter, can impact Dippers survival as they temporally hamper the access to food and reduce its availability by increasing the turbidity of the water and by favoring the washing of the river bed by strong currents. In particular, data were collected from three gauging stations located, respectively, in the basins of Lea (station of Oleta), Artibai (station of Berriatua) and Urdaibai (station of Muxika) (for details see Appendix 1).

2.2. Capture-mark-recapture models

We used multistate with only live recaptures models (Lebreton & Cefe 2002) to calculate the following parameters: apparent survival (ϕ: probability that a bird captured in time t is alive in t+1), recapture probability (p: probability of recapturing a bird which is alive at encounter occasion t+1) and transition probability (ψ, probability of moving from one of the states -in this work, river basin- to another one). Multistate models estimate local survival rates (apparent survival), since they cannot distinguish true mortality from permanent emigration. Models using a logit-link function were run in the software MARK 6.1 (White & Burnham 1999).

The original data sets (Dippers ringed either as nestlings or as adults—in their second year of life or later) were lumped into a single matrix with 868 rows (individuals) by 8 columns (years), where the birds ringed as nestlings or as adults were identified by considering two groups (a ‘marked as nestlings + marked as adults’ approach). In this matrix, we identified the river basin where the Dippers were captured or recaptured (A = Artibai, B = Lea, C = Oka). For instance, ‘A00B0BB0’ represents a bird ringed in A in 2015, not recaptured in 2016 and 2017, recaptured in B in 2018, not recaptured in 2019, recaptured in B in 2020 and 2021, and not recaptured in 2022.

Before starting to select models, we tested that the data fitted to the model assumptions. We used for that the software UCARE (Choquet *et al.* 2009). The global goodness-of-fit (GOF) for a matrix simplified to a single-site approach was significant ($\chi^2 = 94.25$, df = 33, $P<0.001$), due to the presence of transients ($Z=5.925$, $P<0.001$), and not trap-dependence ($Z=-0.915$, $P = 0.360$). Similarly, a multisite GOF test revealed a violation for the assumptions for the group of Dippers ringed as nestlings ($\chi^2 = 58.4$, df = 27, $P<0.001$), but not for those marked as adults ($\chi^2 = 2.26$, df = 10, $P = 0.994$). The presence of transients can be solved with matrices assuming age-dependence on CJS models (Pradel *et al.* 1997), considering the two-age class approximation.

Corrected small sample sizes Akaike values (AICc) were used for ranking the fit of alternative models to data (Burnham & Anderson 1998). Models with a ΔAICc < 2 were considered to fit the data equally well. Because models with additional unsupported parameters will be likely within 2 AICc units and these models are non-competitive unless the extra parameter leads to a reduction in AICc (Arnold 2010), we analysed in detail the *B*-parameters from all models having a ΔAICc < 2 from the top-ranked one in order to see if the parameters affected ϕ, but also the deviance. This is known as 'pretending variable', which is found when two models with similar AICc values and only one parameter of difference have an almost identical deviance, so the additional parameter is probably a 'pretending variable' with an artificial, not trustable, effect (Anderson 2008). Parameters with a 95% confidence interval (CI) including zero indicate a non-significant effect of the factor/covariate (Taylor *et al.* 2004) and the overlap with 95% CI of average survival estimates indicate a lack of significant difference between those means.

We ran a set of candidate models with various patterns in ϕ, p and ψ. Due to the huge amount of possible combinations (of thousands of models), we conducted a preliminary analysis to identify a global model structure with minimal or no estimability problems. Subsequently, we built a set of candidate models after fixing the best structure for parameter p (Burnham & Anderson 2002). These candidate models tested various hypotheses related to ϕ and ψ whilst p structure kept consistent.

Firstly, we built a first model assuming age-dependence on ϕ (considering two age

Table 1. M-array tables summarizing capture–recapture data from the Dipper Biscay population surveyed from 2015 to 2022. Data categories: Dippers ringed as nestlings or as adults, with sexes of the latter set segregated. Note that nestlings were ringed from 2015 onwards, whilst adults were ringed from 2017 onwards. The term R(*i*) refers to the number of Dippers released at each time (breeding season).

Year	R(*i*)	2016	2017	2018	2019	2020	2021	2022	Total
Nestlings									
2015	88	1	0	0	1	0	0	0	2
2016	50		6	5	0	0	1	0	12
2017	122			11	1	0	1	0	13
2018	174				15	1	3	0	19
2019	144					12	5	4	21
2020	129						8	5	13
2021	150							19	19
2022	28								0
Male									
2017	11			8	1	0	0	0	9
2018	14				9	0	0	0	9
2019	16					7	1	0	8
2020	17						9	1	10
2021	16							8	8
2022	10								0
Female									
2017	14			8	2	0	0	0	10
2018	16				7	2	0	0	8
2019	12					4	0	0	4
2020	15						3	0	3
2021	9							6	6
2022	9								0

categories: survival of first-years [*i.e.* during their first year of life] and of older birds [annual survival from the second year of life onwards], annotated as ϕ_{fy} and ϕ_{ad}), and constant ψ and p. We then checked whether p remained constant (ϕ_{fy}, ϕ_{ad}, p, ψ) or varied among basins [$p_{(basins)}$], given that the sampling effort was not homogeneous (we invested more effort in the Oka river basin than in the other two), between age classes [p_{fy}, p_{ad}], among years (*e.g.* time-dependence on p) [$p_{(year)}$] or taking into account interactions between basins, age classes and years. The model which considered an effect of river basin and age on p had a better fit than the rest of tested models, so we fixed the model [ϕ_{fy}, ϕ_{ad}, $p_{fy(basins)}$, $p_{ad(basins)}$, ψ] to test various hypotheses related to ϕ and ψ.

Secondly, we checked whether ψ was constant or varied between age classes (ψ_{fy}, ψ_{ad}), among basins [$\psi_{(basins)}$], in relation to clutch order [$\psi_{(clutch)}$] or considering a combination of both factors [$\psi_{(basins\times clutch)}$]. The model assuming age-dependence on ψ had a better fit to the data (Table 3), though it fitted to the data equally well than the one with constant ψ, suggesting a weak effect of age on ψ, also probably due to sample size constraints (only one adult was found to change of river basin; Table 2). Because of this, and given the small sample size for adult birds, we considered constant ψ for the models used to test effects on ϕ (next step). Time-dependence on ψ was ignored due to sample size constraints (for details see Tables 1 and 2).

Thirdly, starting from [ϕ_{fy}, ϕ_{ad}, $p_{fy(basins)}$, $p_{ad(basins)}$, ψ], we built various models testing for the effect of clutch order, basin, year and mean water flow in winter on ϕ. To test for the effect of flooding episodes on ϕ, we replaced year-dependence by the mean water flow measured during the months of November to February (Sánchez *et al.* 2017). Apart, and because the sex of most Dippers ringed as nestlings was ignored, we used a subset of the original matrix, comprised only by adults, in order to also test for the effect of the sex on ϕ. The alternative tested models in this case included constant-, time- (year) or sex-dependence on both/either ϕ and p. Due to sample size constraints, in this case we did not use multistate models, but Cormack-Jolly-Seber models with the data from the three sampling river basins pooled. The GOF test for this new dataset was not significant ($\chi^2 = 1.894$, df = 13, P = 0.999), nor the specific test to detect transients (Z=0.464, P = 0.642) or trap-dependence (Z<0.001, P = 0.999).

Table 2. Basic statistics of the number of Dippers ringed (also segregated by basins; A=Artibai, L=Lea, O=Oka) and recaptured (in a subsequent year of the ringing one). For those recaptured, we note whether they were recaptured within the same river basin where they were ringed (Recapt. no change) or in another river basin (Recapt. change). In this last case, we indicate the direction of the movement was done.

	Nestlings	Adults
Ringed	786	82
Basin: A	215	1
Basin: L	339	13
Basin: O	232	66
Recaptured	68 (8.65%)	53 (64.6%)
Recapt. no change	56	52
Recapt. change	12	1
Change: A to L	1	–
Change: A to O	2	–
Change: L to O	3	–
Change: O to A	1	–
Change: O to L	5	1

3. Results

From 786 Dippers ringed as nestlings, we only obtained 68 recaptures (8.65%). From them, 56 (82.4%) were recaptured within the same river basin where they were ringed, with only 12 dispersing to the nearby studied basins (for details see Table 2). The globally observed percentage of Dippers that moved outside their origin basin was on average 1.6% (referenced to the sum of Dippers ringed by basin), with this proportion being similar among basins ($\chi^2 = 2.56$, df = 2, P = 0.30). Once recruited in a new basin, birds were never recaptured in a third basin and they did not move again to the original one.

Models showed a higher fit to the data when dispersal rate (ψ) was age-dependent, though

Table 3. Top-ranked multistate with only live recaptures models used to test for the effect of several factors (age, year, winter flow, river basin) on survival (ϕ), recapture probability (p) and dispersal (ψ) across three river basins from the province of Biscay. Abbreviations: AICc=small sample sizes-corrected Akaike values; ΔAICc=AICc difference in relation to the top-ranked model within each case (candidate models on p, ψ or ϕ); np = number of parameters. For the column np, we show in parenthesis the number of real parameters that should be estimated (modified manually in MARK). This can be compared to the number of parameters actually estimated, as a result of sample size constraints.

Models	AICc	ΔAICc	np	Deviance
Candidate models on p				
$\phi_{fy}, \phi_{ad}, p_{fy(basins)}, p_{ad(basins)}, \Psi$	1022.02	0.00	9	303.25
$\phi_{fy}, \phi_{ad}, p_{(basins)}, \Psi$	1024.03	2.01	6	311.35
$\phi_{fy}, \phi_{ad}, p_{(basins\times year)}, \Psi$	1029.79	7.77	15(24)	298.71
$\phi_{fy}, \phi_{ad}, p_{fy}, p_{ad}, \Psi$	1044.29	22.27	5	333.64
$\phi_{fy}, \phi_{ad}, p_{(year)}, \Psi$	1045.49	23.47	10	324.68
$\phi_{fy}, \phi_{ad}, p, \Psi$	1050.61	28.59	4	341.98
Candidate models on ψ				
$\phi_{fy}, \phi_{ad}, p_{fy(basins)}, p_{ad(basins)}, \Psi_{fy}, \Psi_{ad}$	1020.80	0.00	10	299.98
$\phi_{fy}, \phi_{ad}, p_{fy(basins)}, p_{ad(basins)}, \Psi$	1022.02	1.22	9	303.25
$\phi_{fy}, \phi_{ad}, p_{fy(basins)}, p_{ad(basins)}, \Psi_{(clutch)}$	1024.05	3.25	10	303.23
$\phi_{fy}, \phi_{ad}, p_{fy(basins)}, p_{ad(basins)}, \Psi_{(basins)}$	1047.95	27.15	10(11)	327.13
$\phi_{fy}, \phi_{ad}, p_{fy(basins)}, p_{ad(basins)}, \Psi_{(basins\times clutch)}$	1074.45	53.65	10(14)	353.64
Candidate models on ϕ				
$\phi_{fy(year)}, \phi_{ad(year)}, p_{fy(basins)}, p_{ad(basins)}, \Psi$	1008.07	0.00	17(21)	272.86
$\phi_{fy}, \phi_{ad(year)}, p_{fy(basins)}, p_{ad(basins)}, \Psi$	1014.12	6.05	12(15)	289.21
$\phi_{fy}, \phi_{ad(flow)}, p_{fy(basins)}, p_{ad(basins)}, \Psi$	1016.75	8.68	10	295.94
$\phi_{fy(clutch)}, \phi_{ad}, p_{fy(basins)}, p_{ad(basins)}, \Psi$	1017.11	9.04	10	296.30
$\phi_{fy(flow)}, \phi_{ad(flow)}, p_{fy(basins)}, p_{ad(basins)}, \Psi$	1018.68	10.61	11	295.82
$\phi_{fy(year)}, \phi_{ad}, p_{fy(basins)}, p_{ad(basins)}, \Psi$	1018.88	10.81	15	287.80
$\phi_{fy(flow)}, \phi_{ad}, p_{fy(basins)}, p_{ad(basins)}, \Psi$	1023.74	15.67	10	302.93
$\phi_{fy(basins)}, \phi_{ad}, p_{fy(basins)}, p_{ad(basins)}, \Psi$	1024.76	16.69	11	301.90
$\phi_{fy}, \phi_{ad(basins)}, p_{fy(basins)}, p_{ad(basins)}, \Psi$	1025.76	17.69	11	302.90
$\phi_{fy(basins)}, \phi_{ad(basins)}, p_{fy(basins)}, p_{ad(basins)}, \Psi$	1028.06	19.99	12(13)	303.15

the fit to the data was as good as for the models assuming constant ψ (Table 3; see methods for more details). Thus, our top-ranked model provided a mean dispersal of 0.05 (95% CI: 0.026–0.086) for the first-year birds, and of 0.01 (95% CI: 0.002–0.070) for the adults (note that the 95% CI of the two age classes overlap). The second model provided a mean dispersal of 0.038 (95% CI: 0.022–0.065), *i.e.* on average 4% of Dippers moved outside their original basin.

Recapture probability (p) varied among basins and between age categories. Thus, models supported decreasing mean values from west to east (being lower in Artibai than in the other two basins), and for Dippers recaptured one year after having been ringed as nestlings than in older birds (Fig. 2).

The top-ranked model showed time-dependence on both ϕ_{fy} and ϕ_{ad} (Table 3), albeit a detailed exam of the parameter estimates showed that the model was unable to estimate most of the annual values for adults, clearly because of the lack of a sufficient amount of data (for details see also Table 1). For first-years, a plot of their annual survival rates together with their 95% CI indicate that, in fact, most of the variation was capitalized by the annual survival rates obtained for the nestlings ringed in 2015 (ϕ_{fy}=0.032, 95% CI: 0.008–0.116) and 2016 (ϕ_{fy}=0.270, 95% CI: 0.152–0.430), whilst for the rest of the years the mean annual survival remained relatively constant, around a mean of 0.16 (Fig. 3). Models assuming an effect of the mean water flow in winter on survival were lower-ranked and hence did not fit to the data as well as the models assuming time-dependence. Other models that were ranked also very high were those which included an effect of the clutch order on ϕ_{fy}. Thus, the mean apparent survival of Dippers from first-order clutches was 0.18 (95% CI: 0.12–0.22), whereas for those hatched in second-order clutches was 0.07 (95% CI: 0.03–0.15). The mean annual survival for older birds (ϕ_{ad}) was 0.64 (95% CI: 0.56–0.70).

For the data subset of adults, we observed that a model assuming sex-dependence on ϕ, constant *p* (AICc=237.71, deviance=46.36) fitted to the data as well as the one with constant ϕ (237.90, deviance=48.64). This slight difference must be interpreted as a weak, statistically null effect of sex on survival. Average survival for males was 0.82 (95% CI: 0.56–0.94), whereas in females was 0.52 (95% CI: 0.40–0.64), and *p* was 0.84 (95% CI: 0.70–0.93).

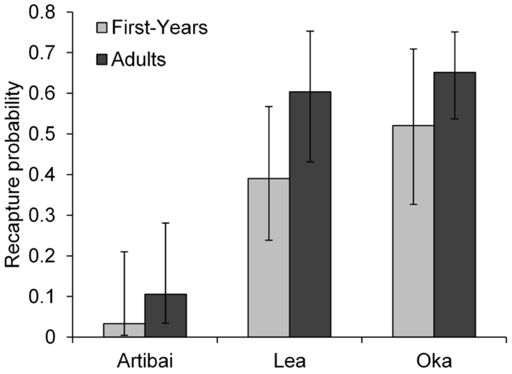

Fig. 2. Recapture probability (*p*; we show mean values ± 95% confidence interval) of Dippers ringed in three river basins (Artibai, Lea and Oka) from Biscay either as nestlings (first-years) or as adults. Estimates obtained from the top-ranked model (the one with the lowest AICc) shown in Table 3.

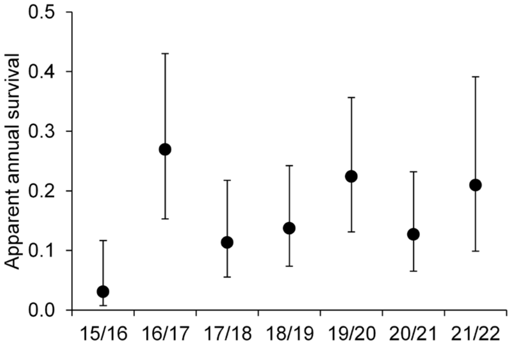

Fig. 3. First-year annual apparent survival of Dippers ringed as nestlings in Biscay. We show mean values (±95% confidence interval) obtained from the top-ranked model shown in Table 3.

4. Discussion

This is the first study estimating survival in a Dipper population of Biscay, and to the best of our knowledge the second one for Spain (Sánchez *et al.* 2017). Moreover, we used for the first time multistate models to estimate dispersal rates among river basins, an approach that is statistically more robust than assessing them directly from the raw data, because we control for the effect of other parameters, including recapture rate (Senar & Conroy 2004). Dippers from the three studied river basins had very low annual dispersal rates, with most being recaptured within the same river basin where they were ringed either as nestlings or adults. For adults, indeed, only one bird out of 53 was found to change basin. Our results suggest that the population had a very short-range natal dispersal rate, and a breeding dispersal close to zero, a trait that could be different from findings in other zones of Spain, where dispersal rates seem to be much higher (Hernández *et al.* 2018).

The mean dispersal rate among the three studied river basins was 4%, with models ignoring local variation among basins. Note that this estimation is higher than the observed 1.6% dispersal. This is caused by an imperfect detection of individuals. Indeed, the advantage of the use of multistate models is that we also estimated the detection probability (*p*) and, by doing so, we obtained a more robust estimate of dispersal. As the amount of recaptures of adult birds was nearly zero, and since birds did not move to third river basins once they were recaptured, the estimated dispersal can be considered as a true natal dispersal value for the studied Biscayan population. Although we cannot reject that the assessed 4% rate could be biased to a sample size limitation (*e.g.* models showed problems of convergence to estimate parameters in more complex contexts) and by the fact that our study was based on a data set of capture-recaptures obtained in a relatively small zone, so we could still ignore certain amount of dispersal to further distant basins, evidence supports that, overall, dispersal was truly low for our population (see below for more discussion). The biological conservation status of the three studied river basins was good, according to indicators of the composition and abundance of benthic aquatic macroinvertebrates, aquatic plant species or fish, as stated by European laws (López *et al.* 2021). Therefore, the lack of a clear flow from a given basin to others (*i.e.* a source–sink scenario) could also respond to the lack of an environmental variation promoting this potential flow (Senar *et al.* 2002).

Our estimated mean dispersal rate of *ca.* 4% is similar to the *ca.* 3% observed for all Spain using directly ring-recovery data (Hernández *et al.* 2018). However, this last number should be higher in case of applying multi-state models that control for aspects like recapture rate, which is likely to be very low for those birds moving outside their natal river basins (Regla & Arizaga 2016). Noteworthy, our estimated dispersal through models doubled the observed one. In this scenario, the dispersal for the studied population would be lower than the one possibly existing in other parts of Spain.

According to Hernández *et al.* (2018), ring-recovery analyses may underrepresent the true magnitude of the genetic flow between river basins in Spain, assessed to be *ca.* 14%. In that work, however, authors did not include any sample from the Cantabrian basins (northern slopes of the Cantabrian mountains), where due to the occurrence of more stable hydrological conditions Dippers could show lower dispersal rates than their southern (Mediterranean) counterparts. Noteworthy, Hernández *et al.* (2018) observed that the dispersal was smallest for the Dippers sampled in the southern slopes of the Cantabrian mountains. Moreover, we calculated an annual dispersal rate, whilst Hernández *et al.* (2018) pooled data from many years, hence they obtained some kind of accumulated (‘historical’) dispersal within each population, which is likely to be higher than an annual estimation obtained with a sample collected over eight consecutive years. We consider that our three-basin approach provides a robust design to estimate dispersal, but it would be useful for the future to (1) replicate our study in other basins and (2) to do genetics in order to estimate the genetic flow between basins and test the hypothesis that the Cantabrian populations might show lower dispersal rates than their Mediterranean or Pyrenean counterparts.

As expected, first-year survival was lower (almost 80%) than adult survival. This is because most bird species tend to show lower apparent survival rates in their first-year, either due to higher dispersal rates or because they are less experienced and then more vulnerable to predators and other causes of mortality (Newton 1998). Moreover, birds from first broods had a higher survival prospect than those hatching in second clutches, a phenomenon also reported in many other bird species (*e.g.* Parejo & Danchin 2006, Galarza & Arizaga 2014). There is a very large body of studies dealing with this behaviour (*e.g.* see for a review Newton 1998), and the occurrence of second clutches in short-lived species is ultimately driven by trade-offs between the current reproductive investment and the breeders’ future fitness assuming intra-generational costs (Dawkins & Ridley 1986). For our particular case, it would be interesting to address a finer comprehension about under which circumstances Dippers lay second clutches and to what extent these are critical to keep a sustainable (either stable or growing) population.

Female apparent survival was on average 0.3 points lower than males (0.52 versus 0.82), but the 95% confidence interval showed a slight overlapping, indicating that the difference was non-significant. We attribute this lack of significance to relatively small sample sizes, possibly linked to an also high variability of this parameter. Other studies dealing with larger data sets, however, were equally unable to detect sex differences in survival (Loison *et al.* 2002, Sánchez *et al.* 2017). If this difference between sexes would have biological significance within the survey area, it may be due to either lower survival rates in females (*e.g.* due to higher predation rates than males during the incubation period) and/or higher dispersal in females. Regarding this last possibility, it must be acknowledged that females from our population had slightly longer natal dispersal distances than males (Galarza *et al.* 2023), but anyway most Dippers ringed as nestling, including females, were recaptured at less than 5 km from their natal site. Given that our entire sampling region covered by far more than 5x5 square kilometres, it is unlikely that presumably lower apparent survival rates in the females may be due to emigration. This hypothesis is in line with findings obtained for all Spain using ring-recovery data (Regla & Arizaga 2016).

Overall, we found no effect on mean water flow regimens during the winter on annual survival, as observed in other cases, both in the Brown Dipper (Chiu *et al.* 2013) and the White-throated Dipper (Sánchez *et al.* 2017), although in this last case differences were subtle. It is possible that flooding episodes within the study area had a negligible effect on Dippers (*e.g.* birds could find alternative feeding sources during the days/weeks when their main used streams remained flooded; Chiu *et al.* 2013). Future research, focusing also on breeding parameters (such as clutch size or productivity), will be necessary to disentangle more finely whether the current flow regimens of the Cantabrian rivers have a significant impact on Dippers populations and, therefore, estimate more accurately the degree of vulnerability of such populations to climate warming.

Koskikaran (*Cinclus cinclus*) eloonjääminen ja levittäytyminen Pohjois-Iberian populaatiossa

Jokiympäristöt ovat erityisen herkkiä ilmastonmuutoksen vaikutuksille, ja monet niissä elävistä lajeista kuuluvat maailman uhanalaisimpiin. Tästä syystä jokivarsien suojelu on ensiarvoisen tärkeää. Demografiaan perustuvat analyysit voivat syventää ymmärrystämme jokivarsien lajien populaatiodynamiikasta ja edistää suojelutoimia. Tässä tutkimuksessa tarkastelimme koskikaran (*Cinclus cinclus*) populaatiodynamiikkaa ajallisesti ja alueellisesti Pohjois-Espanjassa. Tilastollisissa malleissamme huomioimme talvien keskimääräisen virtaaman, yksilön iän, sukupuolen, syntyperän valuma-alueen sijainnin sekä kuoriutumispäivän. Tuloksemme osoittivat, että populaation vuosittainen levittäytymisaste pysyi vakiona (ψ=0.038; 95% luottamusväli: 0.022–0.065). Ensimmäisen poikueen poikasten keskimääräinen eloonjäämisaste oli 0.18 (95% lv: 0.12–0.22), kun taas toisen poikueen poikasten eloonjäämisaste oli 0.07 (95% lv: 0.03–0.15). Aikuisten keskimääräinen vuosittainen eloonjäämisaste oli 0.64 (95% lv: 0.56–0.70). Vaikka eloonjäämisaste vaihteli vuosittain, talvivirtaamalla ei havaittu olevan merkittävää vaikutusta siihen. Uudelleenpyyntitodennäköisyys (*p*) vaihteli valuma-alueiden välillä, mikä saattaa johtua näytteenoton heterogeenisyydestä. Yhteenvetona voidaan todeta, että Pohjois-Espanjan kolmella vierekkäisellä valuma-alueella koskikaran syntymälevittäytyminen oli vähäistä ja aikuislevittäytyminen lähes olematonta. Tämä voi poiketa muista Espanjan alueista, joissa levittäytymisasteet ovat raportoidusti korkeampia.

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Appendix 1.

Mean discharge (calculated for the months of November to February of the next year, unit: m^3/s) in gauging station located in the basins of Urdaibai, Artibai and Lea (Bizkaia).

	2014/15	2015/16	2016/17	2017/18	2018/19	2019/20	2020/21	2021/22	Average
Muxika (Urdaibai)	206.6	122.1	93.0	282.2	96.1	154.8	190.3	212.5	169.7
Berriatua (Artibai)	756.0	396.8	334.5	1011.7	378.6	532.8	605.3	741.1	594.6
Oleta (Lea)	667.8	419.0	349.7	806.6	316.3	476.5	615.4	686.6	542.2
Total	1630.4	937.9	777.1	2100.5	791.0	1164.1	1411.1	1640.1	1306.5