

## Diet of Dippers *Cinclus cinclus* during an early winter spate and the possible implications for Dipper populations subjected to climate change

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*The prey composition of the diet of Dippers Cinclus cinclus was shown to differ between baseflow and spate conditions. In southwest Ireland, faecal pellets were collected during a heavy spate in early winter 1991 and during a period of baseflow conditions three weeks later. The diet composition differed significantly between the two periods. During baseflow conditions diet was dominated by trichopteran larvae, especially Limnephilidae, whereas during the spate period diet was composed primarily of ephemeropteran nymphs, particularly Baetidae, and dipteran larvae of the family Simuliidae. Diet during the spate period also contained greater proportions of prey taxa of terrestrial origin. Enhanced hydrological cycles with greater precipitation, predicted under current climate change models, may have an effect on the diet of Dippers and this is discussed.*

Birds are known to show temporal and spatial variation in resource use (e.g. see papers in Morrison *et al.* 1990). Extreme weather may restrict access to food resources consumed during typical conditions and force birds to use foraging microhabitats and/or food taxa not normally exploited. For example, species that typically use flycatching techniques in pursuit of aerial insects are known, in cold and/or wet weather, to switch to gleaning insects from vegetation (Eastern Kingbirds *Tyrannus tyrannus*, Murphy 1987) or from old pine cones (Yellow-throated Warblers *Dendroica dominica*, Morse 1990). Carolina Chickadees (*Parus carolinensis*) switch from foliage gleaning to large-tree-limb foraging in cold, wet weather, probably to avoid the reduced insulative efficiency of wet feathers (Morse 1990). Such patterns of change in resource use are an important part of the ecology of a species (Recher 1990), yet most foraging behaviour or diet studies are undertaken on 'good' days (Morse 1990).

The dippers (Aves: Cinclidae) are closely associated with the aquatic environment. They

are adapted to feed in fast-flowing rivers (Goode 1959, 1960, Murrish 1970a, 1970b), eating mainly benthic macroinvertebrates and fish (review in Tyler & Ormerod 1994). The Dipper *Cinclus cinclus* forages by wading and diving in shallow riffles and river margins, and by diving and swimming in deeper riffles and pools (review in Tyler & Ormerod 1994). The frequency of diving declines at high river flows (Bryant & Tatner 1988, O'Halloran *et al.* 1990). High water velocity and turbidity during spates and floods, as well as increased depth, may prevent dippers feeding in riffles (O'Halloran *et al.* 1990). Alternatively, foraging efficiency and/or net energy gain may be sufficiently reduced to make it relatively more profitable to use different feeding methods and/or microhabitats. Diving is the most energetically expensive behavioural activity exhibited by dippers (Bryant & Tatner 1988). Da Prato (1981) observed the behaviour of one male Dipper which ceased feeding entirely during two winter spates, each of less than one day's duration. When prolonged spates occur, however, dippers must feed somehow to survive. As yet there are no published data on the diet of dippers during spate or flood events.

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The longer-term effects of spates and floods on Dipper biology are largely unknown. The local survival of adult Dippers in eastern France was found to be lower in years with winter flooding than in years without flooding (Clobert *et al.* 1990) and the loss of Dippers, especially first-year birds, following a heavy spate was recorded in southeast Scotland (Wilson 1996). In a population model of Dippers in southern Norway, however, Saether *et al.* (2000) found no effect of winter precipitation on Dipper population dynamics, but did find a positive correlation between recruitment rate and mean winter temperatures. They predicted an increase in Dipper population size in their study area under an estimated 2–3°C increase in mean winter temperature, as indicated by current climate change models (Houghton *et al.* 1995). In Ireland, with its warmer maritime climate, the role of spates and floods in the population dynamics of Dippers may be greater than in Norway.

Studies of General Circulation Models under conditions of increased atmospheric CO<sub>2</sub> have predicted enhanced hydrological cycles in many regions at northern latitudes, i.e. increased rates of precipitation, evaporation and runoff (Houghton *et al.* 1995), and such patterns have been recorded (e.g. Brutsaert & Parlange 1998). Kiely (1999) reported increases, since 1975, in annual precipitation and river discharges at eight precipitation sites and four discharge sites around Ireland. The precipitation increase was most notable in the west of Ireland and during the months of March and October. In addition, a much greater proportion of extreme precipitation events (approx. 75%) occurred in the years after 1975 (data set range 1940–90). Increases in precipitation extremes (frequency and/or magnitude) will probably lead to an increased incidence of flooding (Kiely 1999). No data on floods were available for Ireland, but Kiely (1999) found increases, since 1975, in the annual mean daily flows and March mean daily flows of four Irish rivers, including the Munster Blackwater at Ballyduff. This study compares the early winter diet of Dippers, during a spate event of approximately five days' duration, with the diet, during baseflow conditions, at the same sites three weeks later. Five of the six sites sampled for Dipper faecal pellets in this study were located on tributaries of the Munster Blackwater. The

possible impacts of dietary changes induced by spates and floods on the population biology of Dippers are discussed.

## METHODS

The study area, in southwest Ireland, is described in Smiddy *et al.* (1995). Fresh Dipper faecal pellets (<24 hours old, i.e. those still showing white uric acid, rather than creamy-yellow) deposited on emergent rocks in the rivers and along the rivers' edge were collected from six sites during two time periods in 1991. The first set of pellets, subsequently labelled 'Spate' pellets, were collected from 30 October to 1 November. During these three days, the rivers were in spate with high water levels and high turbidity (assessed visually); 15.4 mm of rain had fallen on 28–29 October, 34.8 mm on 30 October, 17.8 mm on 31 October and 31.7 mm on 1 November (Teagasc, Moor Park, Fermoy, Co. Cork). The second set of pellets, subsequently labelled 'Baseflow' pellets, were collected on 20–22 November. During these three days, water levels and turbidity were low relative to the Spate period. Only 0.33 mm of rain fell on 18 November, and none fell on 19–22 November. Dippers were territorial throughout the year at these sites (pers. obs.). Each site comprised one pair's territory and therefore pellets generally represented the diet of two birds at each site. Ten to 20 faecal pellets were collected from each site in each time period.

Pellets were preserved and prey remains were identified and counted at magnifications of ×40 to ×400, following the methodology of Ormerod (1985) and Taylor & O'Halloran (1997). Prey remains were identified to the taxonomic groups, usually family or order, shown in Table 2. No method for quantifying the number of oligochaetes was available. It was assumed that the presence of worm chaetae in a faecal pellet indicated that one worm had been eaten.

Diet data were classified as the percentage contribution by number of each taxon. The proportion of each prey category was determined separately for each faecal pellet. Diet composition was then calculated as the average of the proportions of each taxon in the 10–20 individual pellets collected at each site in each sample period (after Smith 1985). This resulted

in 12 diet 'samples': six spate diet samples (one for each site, each composed of the average of 10–20 faecal pellets), each with a corresponding Baseflow diet sample (each composed of the average of 20 faecal pellets). Diet was also classified as percentage occurrence, i.e. for each prey taxon, at each site in each time period, the percentage of faecal pellets containing that taxon was calculated.

A multi-response permutation procedure (MRPP), with a similarity index as the 'distance' measure, was applied to test for an overall difference in the proportional taxonomic composition of the diet between the Baseflow and Spate conditions (Good 1982). MRPPs are analogous to multivariate analysis of variance, although their applicability does not depend on the assumptions that the group means are normally distributed or that the variances are homogeneous under the alternative hypothesis (Good 1982).<sup>a,b</sup>

To investigate whether there were differences in the relative proportions of individual taxa in the diet, during Spate and Baseflow conditions, the percentage contribution of each taxon in the diet was compared using a *t*-test. The mean relative contribution of each taxon to the six Spate and six Baseflow diet samples was examined. The application of a parametric *t*-test requires the assumptions of normally distributed group means and equal variances under the alternative hypothesis. To relax these assumptions, which are difficult to meet with small sample sizes, the *t* statistic was calculated by the unequal variances formula (Manly 1991). Significance was determined by a permutation methodology equivalent to that of the MRPP, with significance calculated as the proportion of permuted *t* statistics as extreme or more extreme than the observed *t* statistic (Manly 1991).<sup>b</sup> No Bonferroni-type adjustment of  $\alpha$ -values was applied as the small sample size ( $n_1 = n_2 = 6$ ) reduces the power of the test, making a large difference between the two means and low within-group variances necessary to attain significance (Miller 1981).

## RESULTS

A total of 221 faecal pellets, containing 2450 prey items, were analysed. There were strong positive correlations between percentage occurrence and percentage contribution by

number (Table 1), and consequently only data as percentage contribution by number are presented below.

The overall proportional taxonomic composition of the diet samples differed significantly between the Spate and Baseflow time periods ( $L_{\text{observed}} = 0.61$ ,  $P = 0.002$ ,  $n_{\text{permutations}} = 924$ . 'Within' similarity: median = 67.2, 1st quartile = 53.9, 3rd quartile = 75.2. 'Between' similarity: median = 38.6, 1st quartile = 27.2, 3rd quartile = 52.3). Baseflow diets were dominated by the trichopteran larvae Limnephilidae, followed by the ephemeropteran nymphs Baetidae, the trichopteran larvae Hydropsychidae and Goeridae, and the amphipod Gammaridae (Table 2). The Spate diets, meanwhile, were dominated by Baetidae and the dipteran larvae Simuliidae, followed by Limnephilidae, the ephemeropteran nymphs Heptageniidae, the non-aquatic Diptera adults and the probably non-aquatic Oligochaeta. Baseflow diets contained significantly greater proportions of the trichopteran larvae Rhyacophilidae, Limnephilidae, Sericostomatidae and Goeridae than Spate diets (Table 2), while Spate diets had significantly greater proportions of the ephemeropteran nymphs Ephemeridae, Simuliidae and Oligochaeta. The apparently greater proportions of the ephemeropteran nymphs Heptageniidae and Baetidae in Spate diets approached statistical significance.

**Table 1.** Correlation of the percentage contribution by number of each prey taxon with the percentage occurrence of that prey taxon in the Dipper diet at each of the six sites during baseflow and spate conditions. Data are squareroot-arc sine transformed and *r* is Pearson's product-moment correlation coefficient.

	Site	<i>r</i>	<i>P</i>	df
Baseflow period	A	0.81	0.003	9
	B	0.91	<0.001	7
	C	0.97	0.032	2
	D	0.83	<0.001	10
	E	0.98	<0.001	6
	F	0.83	0.003	8
Spate period	A	0.94	<0.001	8
	B	0.92	<0.001	7
	C	0.96	0.001	5
	D	0.72	0.013	9
	E	0.92	<0.001	7
	F	0.96	<0.001	6

**Table 2.** Mean ( $\pm$  se) percentage contribution by number of each taxon in the diet during Baseflow and Spate conditions.  $t$  is the  $t$ -statistic for a two-sample test, the significance value of which is derived from a permutation procedure.<sup>b</sup>  $n$  = six sites in each of the Baseflow and Spate periods. N. = nymphs only, L. = larvae only, A = adults only.

Taxon	Mean percentage contribution by number		$t$	$P$
	Baseflow	Spate		
<b>Aquatic prey</b>				
Gammaridae	7.8 $\pm$ 4.3	0.2 $\pm$ 0.2	1.80	0.18
Helodidae L.	0	2.4 $\pm$ 1.5	1.58	0.45
Nemouridae N. <sup>1</sup>	0.8 $\pm$ 0.5	1.0 $\pm$ 1.0	0.20	1.00
Perlidae N. <sup>2</sup>	0.8 $\pm$ 0.8	0	1.00	1.00
Ephemeroidea N.	0	4.3 $\pm$ 1.9	2.20	0.05
Heptageniidae N.	1.5 $\pm$ 1.4	10.0 $\pm$ 3.7	2.15	0.08
Baetidae N.	12.1 $\pm$ 4.9	25.2 $\pm$ 4.3	2.01	0.07
Simuliidae L.	0	20.9 $\pm$ 8.9	2.34	0.02
Hydropsychidae L.	11.1 $\pm$ 3.7	3.7 $\pm$ 2.5	1.67	0.13
Polycentropodidae L.	2.9 $\pm$ 1.7	0	1.74	0.18
Rhyacophilidae L.	3.2 $\pm$ 1.1	0	2.87	< 0.01
Philopotamidae L.	2.3 $\pm$ 2.1	0.3 $\pm$ 0.3	0.98	0.72
Limnephilidae L.	34.6 $\pm$ 7.2	10.2 $\pm$ 3.7	2.99	0.02
Odontoceridae L.	0.3 $\pm$ 0.3	0	1.00	1.00
Sericostomatidae L.	4.1 $\pm$ 1.5	0	2.66	0.02
Goeridae L.	7.6 $\pm$ 3.3	0	2.27	0.04
Lepidostomatidae L.	2.4 $\pm$ 2.4	0	1.00	1.00
<b>Non-aquatic prey</b>				
Ephemeroptera A.	3.0 $\pm$ 3.0	0.2 $\pm$ 0.2	0.93	1.00
Plecoptera A.	2.3 $\pm$ 1.2	2.7 $\pm$ 0.9	0.24	0.83
Diptera A.	1.9 $\pm$ 1.9	8.0 $\pm$ 4.6	1.24	0.27
Trichoptera A.	0.5 $\pm$ 0.5	0.9 $\pm$ 0.4	0.72	0.55
Diploda	1.0 $\pm$ 1.0	0	1.00	1.00
Oligochaeta	0	7.2 $\pm$ 1.8	4.10	< 0.01
Isopoda	0	1.0 $\pm$ 0.7	1.38	0.45
Coleoptera	0	1.9 $\pm$ 1.4	1.31	0.45

<sup>1</sup>Includes the nymphs of the families Nemouridae, Leuctridae & Taeniopterygidae.

<sup>2</sup>Includes the nymphs of the families Perlidae, Perlodidae & Chloroperlidae.

## DISCUSSION

The worm chaetae found in the faecal pellets were large, robust structures, without teeth at the distal end, and were thought to be of the family Lumbricidae (earthworms). These oligochaetes were probably of terrestrial origin in this study, although an aquatic origin could not be ruled out. Chaetae were only found in the faecal pellets of the Spate period, although they were found at all six sites and in 19.8% of the total number of faecal pellets collected during this period. Chaetae were absent from over 5000 faecal pellets collected, in all seasons, during periods of seasonally normal river flow in 1991 and 1992 (Taylor unpubl. data). Studies

of Dipper diet in mid-Wales also examined faecal pellets for worm chaetae, but none were found (review in Tyler & Ormerod 1994).

Trichopteran larvae are thought to be the preferred food of Dippers in this study area. The birds exhibited the highest mean selection indices for this order, particularly for the families Limnephilidae and Hydropsychidae, in all seasons, over a two-year period (Taylor unpubl. data), and they were among the most common dietary items for much of this time. They were also frequent prey in other studies of Dipper diet (review in Tyler & Ormerod 1994). Baseflow diets were characterized by a dominance of trichopteran larvae, especially Limnephilidae. Spate diets were characterized

by a mixture of ephemeropteran larvae, dipteran larvae and non-aquatic prey. This may indicate that the Dippers were foraging more selectively during the Baseflow period, with preference for a trichopteran-dominated diet at all sites. During the Spate period Dippers appeared less selective, feeding on a wider variety of taxa, perhaps because the preferred trichopterans were less available and/or less energetically profitable during high water levels.

Studies in Wales (O'Halloran *et al.* 1990) and Scotland (Bryant & Tatner 1988) showed that Dippers forage predominantly by wading in shallow riffles and river margins, with some diving in deeper riffles and pools. The density of benthic invertebrates is highest in riffles (Rabeni & Minshall 1977) and many species of birds are known to concentrate foraging behaviour in microhabitats of greatest food abundance (Smith & Sweatman 1974, Zach & Falls 1979). The proportion of time spent diving, however, decreases at high river flows (O'Halloran *et al.* 1990), as the riffles become deeper and faster (Da Prato 1981). Energetic costs and physical constraints probably prohibit diving in deep water of high velocity (Bryant & Tatner 1988, O'Halloran *et al.* 1990). The turbidity of spate waters may also restrict feeding efficiency as Dippers are thought to be primarily visual foragers (Goodge 1960). The increase in the dietary proportion of Diptera adults and the inclusion of the terrestrial Isopoda and Coleoptera, and probably terrestrial Oligochaeta, during the Spate period in this study, suggests that the birds were either foraging on the bankside itself or collecting invertebrates which had been washed from the vegetation or soil into the slow eddies along the river margins. Spitznagel (1988), in Germany, observed Dippers flycatching and gleaning vegetation for invertebrates, but these behaviours were rarely exhibited (<2% of foraging observations). Tyler & Ormerod (1994) reported that, in Wales, terrestrial Coleoptera were found in Dipper faecal pellets during high river flows, although no data were presented.

Despite the increase in non-aquatic prey, however, Dipper diet during the Spate period was still dominated by aquatic prey, particularly Baetidae and Simuliidae (Table 1). These latter two taxa are known to inhabit stone

surfaces in shallow fast flowing water (Kohler & McPeck 1989, Scullion *et al.* 1982). Even during spate the water in some marginal microhabitats may still be shallow enough for insects on stone surfaces to remain accessible to Dippers. Switching to forage in much smaller and shallower tributary streams, as suggested by Tyler & Ormerod (1994), was also an option at some sites.

Further increases in spates and floods due to climate change could potentially affect the diet, survival and/or breeding productivity of Irish Dippers. Dippers are early breeders, especially in southwest Ireland: first-egg dates in southwest Ireland range from 22 February to 17 May, with 62% of first clutches at all altitudes started by 7 April (over 90% of nests were below 120 m, all were below 300 m, Smiddy *et al.* 1995). An increase in flooding in March, as predicted by Keily (1999), may prevent Dippers finding sufficient prey to achieve breeding condition. Nests, eggs and nestlings may also be at risk from high water levels. Dippers provision their nestlings principally with trichopteran larvae (Taylor unpubl. data, Ormerod 1985, Tyler & Ormerod 1994). This taxon is the largest invertebrate group, in terms of dry mass, available to the Dippers and probably allows parents to obtain a high rate of energy delivery to their nestlings. The present study suggests that trichopteran larvae become less available and/or less energetically profitable during high water levels and this could affect chick growth and survival. There were no trends in laying dates, clutch size or brood size of Dippers in southwest Ireland during the period 1983–92 (Smiddy *et al.* 1995). This does not rule out, however, the possibility of declines in these parameters and others, such as population density and survival, if the trend of increased precipitation and river flows continues. Further study is required into the relationship between spates/floods and the behaviour and population dynamics of Dippers and benthic macroinvertebrates in all seasons.

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## ENDNOTES

a. The geometric mean similarity (GS) index was applied:

$$GS = \Sigma (p_i q_i)^{1/2}$$

where  $p_i$  is the percentage contribution of the  $i$ th taxon in diet sample  $p$  and  $q_i$  is the percentage contribution of the  $i$ th taxon in diet sample  $q$  (Bhattacharyya 1946). If there are no differences in the taxonomic compositions of the two groups of diets (Baseflow and Spate), then the similarities between samples from the same group ('within' similarities) should have roughly the same values as similarities between samples from different groups ('between' similarities). If the taxonomic diet compositions differ between the Baseflow and Spate groups, then the 'within' similarities will be higher than the 'between' similarities. The test statistic is:

$$L = B/W$$

where  $B$  is the mean 'between' similarity and  $W$  is the mean 'within' similarity (Good 1982). For each group, a within-group mean similarity ( $G$ ) is calculated as the average of all the possible pairwise similarity measures ( $S$ ):

$$G_i = \Sigma S_i / [0.5n_i(n_i - 1)]$$

where  $n_i$  is the number of samples in group  $i$ . The overall mean within-group similarity ( $W$ ) is given by:

$$W = \frac{\sum_{i=1}^g n_i G_i}{N}$$

where  $N$  is the total number of samples and  $g$  is the number of groups.

The mean between-group similarity is given by the average of all the possible between-group similarity measures ( $T$ ):

$$B = \frac{\sum T_i}{\sum_{i=1}^g \sum_{j>i} n_i n_j}$$

where  $n_i$  is the number of samples in group  $i$  and  $n_j$  is the number of samples in group  $j$  (Smith *et al.* 1990).

b. The significance of the  $L$  statistic was determined by a permutation argument (Smith *et al.* 1990).  $L$  was calculated from the original data ( $L_{\text{observed}}$ ), and for all the  $N!/(n_1!n_2!\dots n_g!)$  possible permutations of the data ( $L_{\text{permute}}$ ), of which  $N!/\Pi[(i!)^{m_i}m_i!]$  are unique ( $m_i$  is the number of groups with  $i$  replicates): the  $N$  samples are reassigned to the  $g$  groups, keeping the numbers per group the same as in the original data. The null hypothesis is that the magnitude of the test statistic ( $L_{\text{observed}}$ ) is not different from that expected by chance (here approximated by the  $L_{\text{permute}}$  statistics). If there is a significant difference between the composition of the Baseflow and Spate diets, then, in the observed data, the 'within' similarities will be higher than the 'between' similarities and, hence,  $L_{\text{observed}}$  will be low relative to the  $L_{\text{permute}}$  statistics. The significance of  $L_{\text{observed}}$  is determined as the proportion of  $L_{\text{permute}}$  statistics less than or equal to  $L_{\text{observed}}$  (Smith *et al.* 1990).

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