

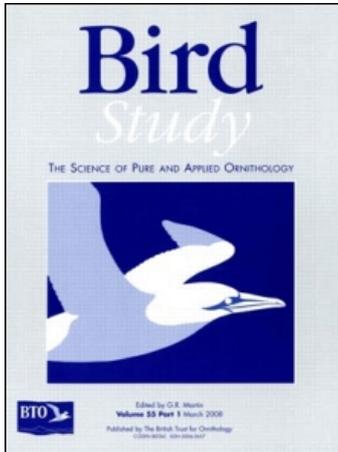
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The diet of Dippers *Cinclus cinclus* wintering in the catchment of the River Wye, Wales

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The diet of Dippers *Cinclus cinclus* wintering in the catchment of the River Wye, Wales

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We studied the diet of Dippers in the River Wye catchment by faecal analysis during the winters of 1983/84 and 1984/85. Diptera, Trichoptera, Ephemeroptera and Plecoptera comprised respectively 34, 23, 18 and 11% of 4650 items recorded from over 350 faecal samples. The Simuliidae (Diptera) and Baetidae (Ephemeroptera) were the commonest macroinvertebrate families recorded despite their small size. Fish and trichopteran larvae comprised respectively an estimated 63 and 19% of the diet by weight. By contrast with Dippers foraging for nestlings, the proportions and reconstructed weights of items appearing in faeces strongly reflected those in stream samples. Birds probably fed opportunistically. Consequently, Dippers feeding on hard water streams ingested more calcium-rich prey than those on soft-water streams. The results are discussed in relation to the influence of stream acidity on aspects of Dipper ecology.

In view of recent concern over the influence of stream acidification on the prey available to Dippers *Cinclus cinclus* in parts of Wales (Ormerod *et al.* 1985a; Ormerod *et al.* 1986) and Scotland (Fry & Cooke 1984), a full knowledge of the species' diet would be useful. However, most published information on the diet of Dippers relates to the breeding season (e.g. Jost 1975a; Ormerod 1985a,b; Ormerod & Perry 1986). For other times of the year, data are available only from small samples collected on mainland Europe (Vollnhöfer 1906; Jost 1975a). This paper describes the diet, assessed largely by faecal analysis, of Dippers in the catchment of the Welsh River Wye during the winter periods of 1983/84 and 1984/85. It forms part of a continuing autecological investigation (Ormerod *et al.* 1985a, 1986; Ormerod *et al.* 1985b; Ormerod 1985a,b; Tyler & Ormerod 1985) and the study area has been described elsewhere (Edwards & Brooker 1982; Ormerod *et al.* 1985b).

METHODS

Faecal collection and analysis

Unpredictable patterns of weather, river-flow and local bird movements prevented any systematic collection of faeces. Nevertheless, samples representing over 50 birds were taken throughout the catchment at 38 sites incorporating a wide range of chemical and physical conditions; most faeces were collected in January and February (Table 1). In order to assess errors due to differences between prey in digestibility and gut throughput, remains in faecal and regurgitated pellets were compared at 7 sites.

Samples were analysed using the methods of Ormerod (1985a,b): most macroinvertebrates were identified to family and quantified by counting mouthparts at $\times 40$ and $\times 100$ magnification. Molluscs were identified from shell fragments and quantified by counting shell spires. Fishes were identified from scales

Table 1. The numbers of Dipper faecal pellets collected in each month of the study (pooled for 1983/84 and 1984/85)

| Month | Number of faecal pellets |
|-----------|--------------------------|
| September | 5 |
| October | 6 |
| November | 28 |
| December | 61 |
| January | 109 |
| February | 147 |
| March | 12 |
| Total | 368 |

or vertebrae (Maitland 1972; Webb 1974) and quantified by counting the latter (28 vertebrae = one fish, shown by dissection). Worm chaetae were not found in any faecal sample.

The composition of the diet by weight was estimated by multiplying the number of faecal occurrences of each prey type by its geometric mean dry weight in stream samples. For fish, a geometric mean dry weight for Bullheads *Cottus gobio* (the commonest fish recorded in faeces) was given by UWIST (1978).

In order to examine prey-size selection within taxa, dry weights of individual prey-items from the most commonly occurring

families were reconstructed from faeces using regressions of weight on mandibular dimensions (Table 3). The latter were highly significant ($P < 0.001$ for each, Table 3). Mean weights were compared with those of the same taxa in stream samples using *t*-tests (Sokal & Rohlf 1981).

Intensive faecal collections (more than 20 pellets per site) were made at nine sites at which prey availability was also assessed (Table 2). Comparisons between the proportionate composition of available and ingested prey were made for major taxa using Wilcoxon signed rank tests (*w-s* test) (Siegel 1956). Prey preferences were also assessed using Jacobs' (1974) index (see Appendix) which gives values ranging from -1.0 , indicating avoidance or inaccessibility of prey items, to $+1.0$, indicating active selection. This index has several advantages over other proposed preference measures (Jacobs 1974; Cock 1978).

Macroinvertebrate collection

An earlier study of the diet of Dippers in relation to available macroinvertebrates involved quantitative sampling in riffles alone (Ormerod 1985a). However, this method failed to represent some taxa which were associated with

Table 2. The location and characteristics of sites used to study prey selection and between-site differences in the winter diet of Dippers

| Site | National Grid Reference | Altitude <i>m</i> O.D. | pH | Total hardness (mg CaCO ₃ l ⁻¹) | Date kick-sampled |
|-----------------------|-------------------------|------------------------|----------------|--------------------------------------------------------|--------------------|
| Upper Irfon | SN 835 556 | 420 | 5.41 (0.62;28) | 7.71 (1.52;27) | 4.2.85 |
| Upper Cammarch | SN 916 520 | 214 | 6.48 (0.27;6) | 16.43 (1.72;6) | 12.2.84 |
| Irfon, Llangammarch | SN 934 470 | 170 | 6.74 (0.31;7) | 18.81 (2.57;9) | — |
| Cammarch, Blackbridge | SN 934 473 | 175 | 7.05 (0.53;21) | 25.54 (7.22;18) | 26.1.85 |
| Marteg | SN 952 715 | 266 | 7.27 (0.42;7) | 26.37 (8.04;6) | — |
| Lower Chwefru | SN 997 530 | 160 | 7.16 (0.42;20) | 39.96(16.49;18) | — |
| Upper Duhonw | SO 044 487 | 160 | 7.27 (0.37;19) | 59.66 (16.76;17) | — |
| Lower Duhonw | SO 062 508 | 122 | | | |
| Upper Ithon | SO 085 793 | 310 | 7.51 (0.37;22) | 69.35 (20.91;20) | 19.2.84 |
| Bach Howey | SO 104 428 | 110 | 7.54 (0.33;16) | 85.28 (17.47;14) | 31.1.85 |
| Edw, Cregrina | SO 123 518 | 180 | 7.80 (0.37;18) | 89.02(22.0;17) | 31.1.85 |
| Monnow, Craswall | SO 277 361 | 291 | | | |
| Monnow, Forge | SO 503 137 | 21 | 8.10 (0.31;28) | 150.51 (39.5;26) | 2.2.85 |
| Angidy | SO 506 002 | 85 | 8.17 (0.29;25) | 168.71 (16.24;24) | 29.1.84; 2.2.85 |

Figures for pH and total hardness are arithmetic means from winter determinations (October–March inclusive) provided by Welsh water.

Figures in parentheses are standard deviations and sample sizes.

Table 3. Regressions of dry weight on mandibular dimensions for macroinvertebrate taxa preyed upon by Dippers

| Taxon | Equation | x variable | n | r ² |
|-----------------------|----------------------|--------------------------|----|----------------|
| Baetidae | $y = -2.41 + 0.068x$ | Width of right mandible | 52 | 0.88 |
| Leuctridae/Nemouridae | $y = -1.73 + 0.065x$ | Width of right mandible | 19 | 0.94 |
| Hydropsychidae | $y = -0.96 + 0.022x$ | Length of right mandible | 36 | 0.63 |
| Simuliidae | $y = -1.74 + 0.038x$ | Length of mandible | 26 | 0.89 |

$y = \log_{10}$ dry weight (mg); x variables is $\mu\text{m} \times 10^{-1}$

other riverine habitats and which were important prey. Consequently, food availability was assessed in this study using a standardized kick-sampling technique (one 3 min sample per site; net mesh aperture 400 μm) across the range of microhabitats in which Dippers feed. Although kick-sampling does not permit estimates of absolute density, it probably represents faithfully the proportionate composition of macroinvertebrate faunas in fast-flowing streams (Armitage *et al.* 1974; Weatherley *et al.* 1985). Ormerod (1985a) has described the laboratory methods used. Sub-samples of 3 to 86 individuals of important prey were dried at 80°C and weighed individually to 0.01 mg using an autobalance. Mandibular dimensions of Simuliidae (Diptera) and Leuctridae/Nemouridae (Plecoptera) were measured using a calibrated eyepiece and regressed against individual dry weight; similar regressions for the Baetidae (Ephemeroptera) and Hydropsychidae (Trichoptera) have been given previously (Ormerod 1985a).

RESULTS

Faecal and regurgitated pellets

At the 7 sites where both regurgitated and faecal pellets were analysed, there was a strong correlation between their compositions (Fig. 1) and errors resulting from a dietary study based largely on faeces are probably small. Only molluscs were slightly under-represented in faeces by comparison with regurgitated pellets.

Dietary composition

In total, 368 faecal pellets and 7 regurgitated pellets were collected, containing the remains of 4850 prey from over 26 macro-invertebrate

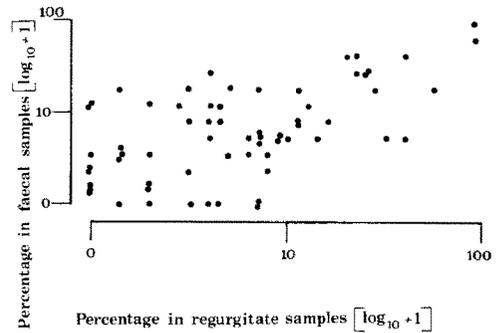


Figure 1. The percentage composition of Dipper faecal and regurgitated pellets at seven sites in the Wye catchment during winter. Each point represents the proportionate contribution by a macroinvertebrate family at a particular site (note log scale).

families (Table 4). Larval simuliids (Diptera), baetids (Ephemeroptera), leuctrids/nemourids (Plecoptera) and hydropsychids (Trichoptera) were the commonest families recorded despite their small size (under 1.5 mg geometric mean dry weight) (Table 4). Limnephilids (Trichoptera) also occurred widely in small numbers.

Similar rank orders of importance were apparent for prey taxa in their percentage frequency of occurrence and their percentage contributions to faeces (Spearman's rho = 0.895, $n = 27$, $t = 10.03$, $P < 0.001$; Table 4). At least for Dippers, therefore, percentage frequency of occurrence, which is easily assessed, probably provides an accurate indication of dietary importance.

Contributions by weight

Fish, notably Bullheads, comprised over 60% of the diet by weight and were the most important component. Trichopteran larvae,

Table 4. The diets of Dippers wintering in the catchment of the Welsh River Wye (based on the analysis of 368 faecal pellets and seven regurgitated pellets)

| <i>Taxon</i> | <i>Geometric mean dry weight (mg)</i> | <i>Number¹ (%)</i> | <i>Frequency² (%)</i> | <i>Weight (%)</i> |
|-----------------------|---------------------------------------|-------------------------------|----------------------------------|--------------------|
| Mollusca | | 5.2 | | 6.1 |
| <i>Ancylus</i> | 4.24 (2.03;3) | 4.6 | 20.7 | 3.5 |
| <i>Lymnaea</i> | 21.71 (1.22;4) | 0.6 | 4.7 | 2.6 |
| Crustacea | | 5.4 | | 3.2 |
| <i>Gammarus</i> | 3.25 (1.41;21) | 5.4 | 25.3 | 3.2 |
| Ephemeroptera | | 18.0 | | 3.2 |
| Ephemeridae | 7.4 (1.71;7) | 0.1 | 1.5 | 0.1 |
| Baetidae | 0.86 (1.17;86) | 14.7 | 62.1 | 2.3 |
| Leptophlebiidae | 0.95 (2.66;4) | 0.4 | 5.7 | 0.1 |
| Ecdyonuridae | 1.51 (1.34;15) | 2.7 | 33.1 | 0.7 |
| Ephemerellidae | 1.21 (3.25;5) | 0.1 | 0.5 | < 0.1 |
| Plecoptera | | 11.3 | | 1.3 |
| Leuctridae/Nemouridae | 0.53 (1.40;35) | 10.5 | 40.4 | 1.0 |
| Perlidae/Perlodidae | 2.46 (2.63;14) | 0.6 | 16.0 | 0.3 |
| Chloroperlidae | 0.39 (1.12;12) | 0.2 | 2.1 | < 0.1 |
| Hemiptera | | 0.3 | | (<0.1) |
| Corixidae | 1.61 (1.24;7) | 0.3 | 4.1 | < 0.1 |
| Trichoptera | | (23.3) | | (19.4) |
| Rhyacophilidae | 3.67 (1.38;15) | 2.1 | 33.2 | 1.4 |
| Glossosomatidae | 1.74 (1.30;27) | 2.5 | 34.7 | 0.8 |
| Hydropsychidae | 1.42 (1.22;66) | 9.3 | 68.3 | 2.4 |
| Polycentropodidae | 1.14 (1.72;4) | 0.1 | 0.3 | < 0.1 |
| Limnephilidae | 11.28 (1.98;18) | 3.6 | 63.2 | 7.3 |
| Odontoceridae | 5.41 (1.17;7) | 0.1 | 1.3 | 0.1 |
| Sericostomatidae | 8.12 (1.31;12) | 4.8 | 18.6 | 7.0 |
| Goeridae | 2.92 (1.41;12) | 0.4 | 8.2 | 0.2 |
| Leptoceridae | 1.92 (1.21;12) | 0.4 | 0.5 | 0.1 |
| Coleoptera | | (0.1) | | (< 0.1) |
| Elminthidae | 0.22 (1.20;15) | 0.1 | 1.0 | < 0.1 |
| Diptera | | (33.4) | | (3.1) |
| Simuliidae | 0.51 (1.17;53) | 33.6 | 65.8 | 3.0 |
| Chironomidae | 0.27 (1.7;32) | 0.7 | 8.9 | < 0.1 |
| Others | 2.48 (2.37;12) | 0.1 | 0.8 | < 0.1 |
| Fishes ³ | 213.0 (N.A.;1011) | 1.7 | 38.3 | 63.7 |
| Totals | | 4850 items | | 27 069.3 mg |

Notes:¹Total number of items recorded.

²Percentage of pellets with at least one of that prey.

³13.5% were salmonids, the rest Bullheads.

Values in parentheses are standard deviations and sample sizes (note geometric mean).

Table 5. Preference indices (Jacobs 1974) for Dippers feeding during winter at sites in the Wye catchment (Qualification-occurrence in prey and kick-samples at > 3 sites)

| <i>Taxon</i> | <i>Mean</i> | <i>1 sd</i> | <i>Range</i> | <i>n of sites</i> |
|-----------------------------|-------------|-------------|--------------|-------------------|
| Mollusca | | | | |
| Ancylidae | 0.15 | 0.78 | -0.00; 1.00 | 6 |
| Crustacea | | | | |
| Gammaridae | -0.41 | 0.72 | -0.97; 1.00 | 6 |
| Ephemeroptera | | | | |
| Baetidae | 0.26 | 0.54 | -0.23; 1.00 | 8 |
| Ecdyonuridae | -0.54 | 0.71 | -1.00; 1.00 | 7 |
| Plecoptera | | | | |
| Leuctridae/Nemouridae | -0.18 | 0.78 | -1.00; 1.00 | 8 |
| Perlidae/Perlodidae | -0.54 | 0.87 | -1.00; 1.00 | 5 |
| Trichoptera | | | | |
| Rhyacophilidae | 0.28 | 0.44 | -0.38; 1.00 | 6 |
| Glossosomatidae | 0.43 | 0.62 | -0.62; 1.00 | 6 |
| Hydropsychidae | -0.26 | 0.75 | -1.00; 1.00 | 8 |
| Limnephilidae | 0.60 | 0.45 | -0.29; 1.00 | 9 |
| Sericostomatidae | 0.00 | 0.78 | -1.00; 0.86 | 7 |
| Diptera | | | | |
| Simuliidae | 0.06 | 0.73 | -1.00; 0.99 | 9 |
| Others (excl. Chironomidae) | -0.73 | 0.44 | -1.00; 0.17 | 7 |

notably the case-bearing families Limnephilidae and Sericostomatidae, were second (Table 4).

Differences in diet between sites

Systematic differences in diet were examined only between those 14 sites from which more than 5 faecal pellets had been collected (pooled for all sampling occasions) and from which a range of environmental data was available (Table 2). Plecopteran nymphs were scarcer in diet, whilst *Gammarus*, molluscs and dipteran larvae (mostly Simuliidae) were more frequent at sites with harder waters. No such trends were apparent for other taxa or other environmental factors (Fig. 2).

Selection in relation to available prey

Chironomid larvae and Elminthidae, which consisted mostly of small individuals (< 0.3 mg dry weight, Table 4), were scarce or absent in faeces despite forming a large proportion of the animals collected at some sites. These taxa

were excluded prior to the following calculations of prey selection.

Most macroinvertebrate taxa appeared in similar proportions in both faecal and kick-samples and most groups showed no consistent deviation from the lines of no selection (Fig. 3). However, plecopteran families and other Diptera were proportionately scarcer in faecal samples than in kick-samples, whilst trichopteran families were slightly more abundant in faeces (Fig. 3). Mean values of Jacobs' index were positive for 3 trichopteran families. However, values were highly variable between sites and only in a few cases were there significant differences from zero preference (Table 5).

Prey-size selection within taxa

The sizes of simuliids and baetids taken by Dippers were similar to those available. By contrast, ingested individuals in the Hydropsychidae and Leuctridae/Nemouridae were larger than those available but the difference was statistically significant only for the former (Table 6).

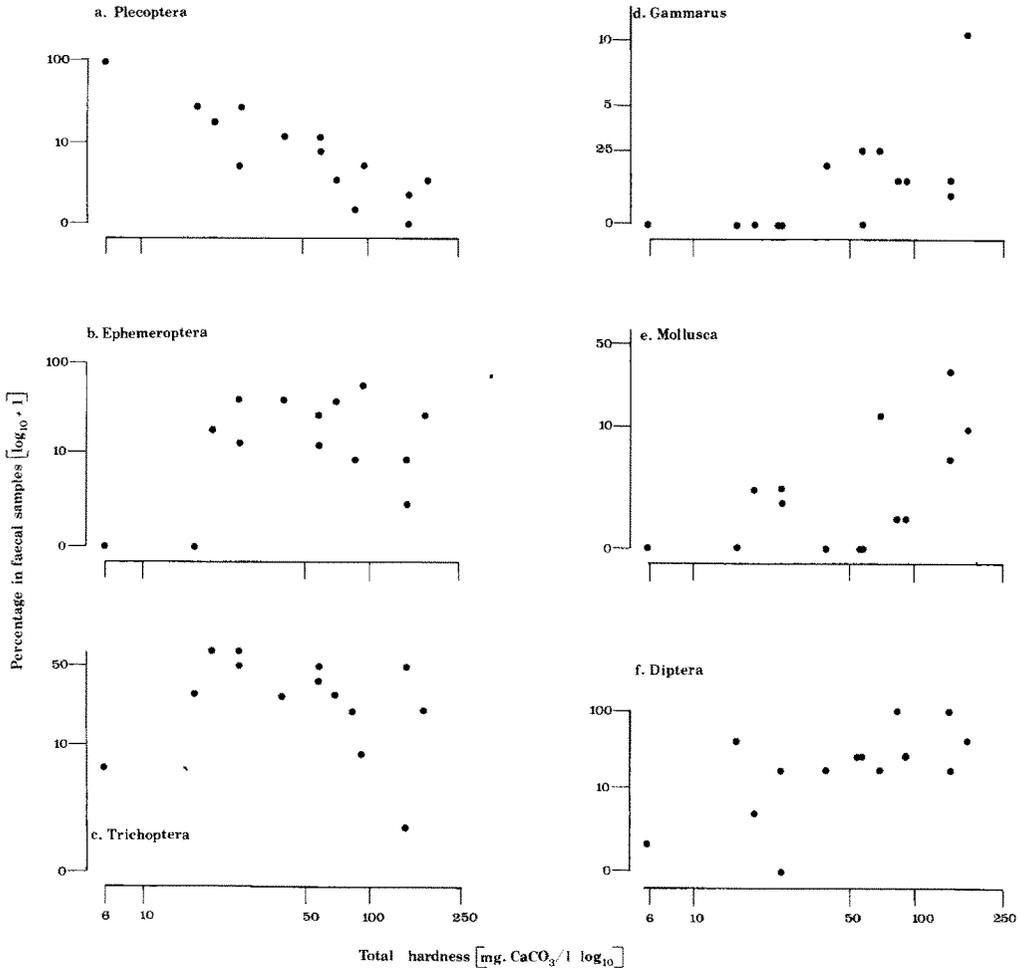


Figure 2. The percentage contributions by various prey to Dipper faecal samples at 14 sites in the Wye catchment in relation to total hardness during winter. Contributions by Plecoptera (Spearman's $\rho = -0.857$, $P < 0.01$), *Gammarus* ($\rho = 0.673$, $P < 0.01$), molluscs ($\rho = 0.562$, $P < 0.05$) and dipteran larvae ($\rho = 0.566$, $P < 0.05$) all correlated significantly with total hardness.

DISCUSSION

Only two studies have previously provided data on the diet of European Dippers in winter. Jost (1975a,b) analysed 330 regurgitated pellets collected from the upper Fulda (central Germany) between September and March (1965–69); 90% consisted mostly of *Gammarus* remains whilst the rest contained mostly trichopteran larvae. Despite a rich and diverse macroinvertebrate fauna in the streams concerned, only a small range of prey was identified (*Gammarus*, trichopterans, coleopterans,

gastropods and fish) and Jost (1975a) noted difficulties in identifying items which were fragmented. In Hungary, Vollnhofer (1906) examined the guts of 145 Dippers collected between September and February; 264 items were recorded of which 50% were trichopteran larvae, 25% were *Gammarus* and 11% were plecopteran nymphs. However, such a small number of items from so many guts (cf. Thut 1970 on *C. mexicanus*) indicates that only large and whole prey were identified. Published information on the diet of other *Cinclus* spp. is also scarce (e.g. Thut 1970).

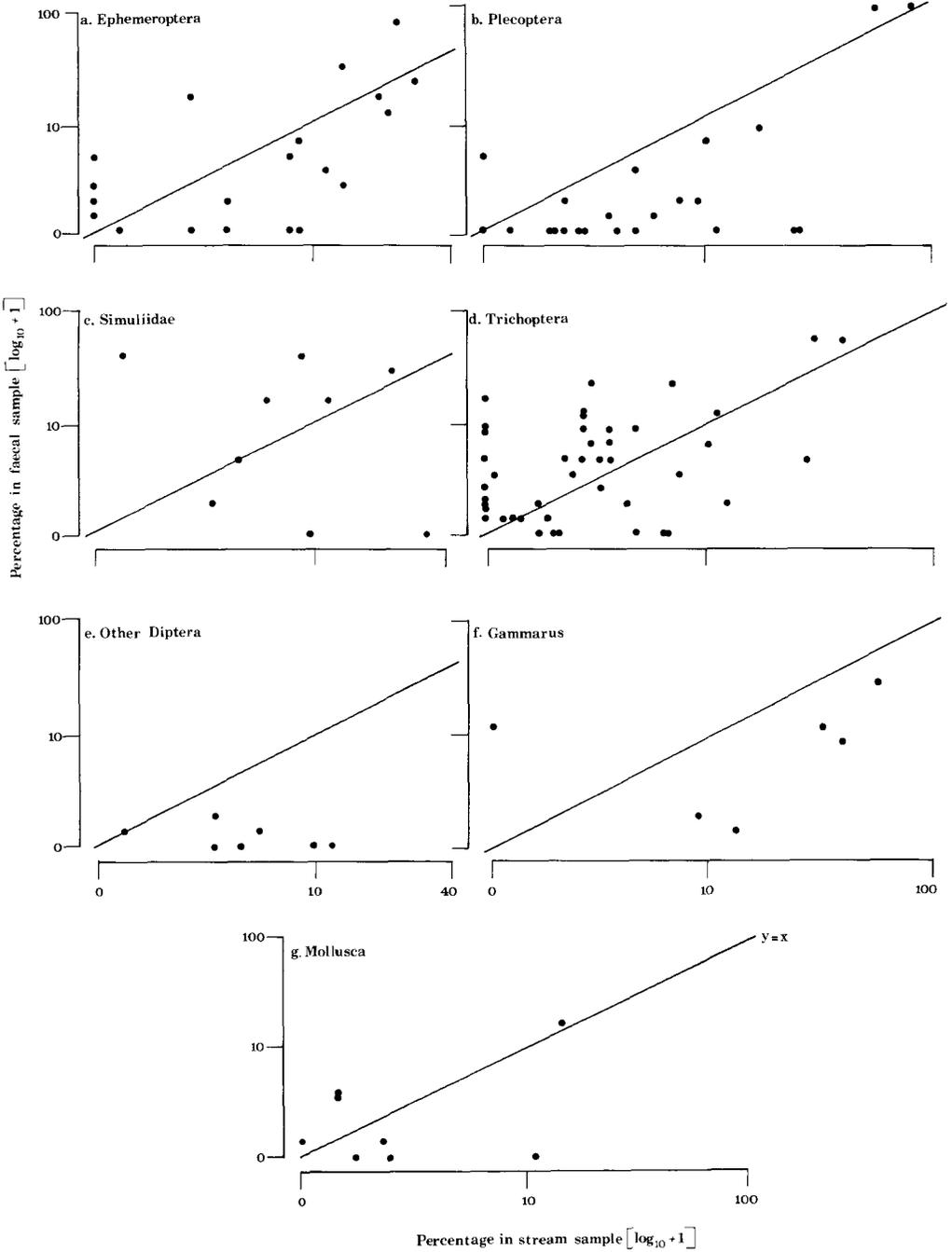


Figure 3. The percentage contributions by various taxa to faecal and stream samples at nine sites in the Wye catchment during winter. Each point represents a particular family at a particular site. The diagonal indicates $y = x$ and represents a line of no selection. Contributions by Plecoptera (*w-s* test, $T = 54$, $n = 23$, $P < 0.01$), other Diptera (*w-s* test, $T = 1$, $n = 7$, $P < 0.05$) and Trichoptera (*w-s* test, $T = 304.5$, $n = 44$, $2 = -2.275$, $P < 0.01$) all deviated significantly from the diagonal.

Table 6. The dry weights of prey in stream samples and in the diet of Dippers wintering in the Wye catchment

| Family | Dry weight (mg) | | t | P |
|-----------------------|----------------------|-----------------------|-------|-------|
| | In stream sample | In faeces | | |
| Leuctridae/Nemouridae | 0.54 (0.38–0.76; 35) | 0.82 (0.59–1.15; 21) | 1.40 | 0.08 |
| Baetidae | 0.86 (0.74–1.01; 86) | 0.81 (0.68–0.96; 103) | -0.46 | 0.64 |
| Hydropsychidae | 1.42 (1.16–1.73; 66) | 2.43 (1.76–3.35; 27) | 2.85 | 0.006 |
| Simuliidae | 0.51 (0.44–0.60; 53) | 0.46 (0.42–0.51; 94) | -1.01 | 0.32 |

Weights of items in the faeces were estimated from mandibular dimensions (see text and Table 3). Values shown are geometric means, with 95% confidence limits and sample sizes in parentheses. (The limits are asymmetric because the means are geometric). *t* is Student's *t* for the difference between two means, calculated on log-transformed data. *P* is the corresponding probability.

Fish provided the dominant component of the diet by weight and, as in the upper Fulda (Jost 1975b), those most frequently taken in the Wye were Bullheads. They are present in tributaries of the Wye at densities of 0.25–2.3 per square metre (Edwards & Brooker 1982), are more benthic and less mobile than salmonids (Mills & Mann 1983) and are probably more easily caught by Dippers.

Although simuliid larva were present in the upper Wye during spring and summer at densities over 10,000 per square metre (Scullion *et al.* 1982), they provided less than 2.5% of the items eaten by breeding adult and nestling Dippers (Ormerod 1985a,b; Ormerod & Perry 1986). By contrast, simuliid larvae were numerically dominant in the winter faecal samples (33%, Table 4). Simuliid larvae have a markedly patchy distribution and form dense mats on the upper surfaces of some stones within riffles (Armitage 1976; Scullion *et al.* 1982). It is possible that Dippers can profitably use such patches during winter, when spates and accompanying turbidity prevent foraging on other benthic macroinvertebrates. However, the winter diet generally reflected the range of prey available and there was little or no evidence of significant prey selection (Fig. 3, Table 5). This contrasts markedly with Dippers foraging for nestlings when active prey selection is apparent and correlates strongly with prey weight (Ormerod 1985a,b). Apparent variation in selection between sites (Fig. 3, Table 5), particularly pronounced for simuliids (Fig. 3), may merely reflect random or opportunistic use of prey patches. Such opportunism may have considerable advantages to a species

feeding in a changeable and heterogeneous environment where events such as spates can influence feeding behaviour (Da Prato 1981).

The apparent size-selection of larval Hydroptychidae was probably also determined by microdistribution and availability rather than active choice. Hydroptychids in Welsh rivers exhibit a marked bimodality between species in weight and instar development during winter: the smallest individuals (*Hydropsyche instabilis*, *H. siltalai*) occur in smaller interstices and in faster currents than larger ones (*H. pellucidula*) (Hildrew & Edington 1979).

Differences in diet in relation to water hardness (see Fig. 2) also reflect differences in the range of prey available: numerically, plecopterans dominate the insect fauna in soft-water acidic streams in the Wye catchment and elsewhere, whilst the abundance of *Gammarus* and most molluscs increases with increasing total hardness (Sutcliffe & Carrick 1973; SJO, pers. obs.). Since Dippers occurred along some acidic streams during this study, stream acidity appears less likely to influence their distribution than during the energetically demanding period of breeding (Ormerod *et al.* 1985a, 1986). However, unproductive soft and acidic water may still provide inferior habitat to wintering Dippers. High calcium demands have been noted in other species prior to breeding (Maclean 1974; Jones 1976; Turner 1982) and Dippers feeding on *Gammarus* (which contain 107–124 mg Ca g⁻¹ dry weight) and molluscs are less likely to encounter a shortfall in this mineral than when feeding predominantly on plecopterans (1.7–11.3 mg Ca g⁻¹ dry weight; Sadler & Lynam 1985). The

consequences of calcium scarcity for Dipper productivity are unknown, although birds breeding along calcareous tributaries in the southern Wye catchment are known to lay particularly large clutches (Tyler & Ormerod 1985). Further investigations of breeding performance in relation to stream acidity and calcium concentration are now in progress.

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APPENDIX

Jacobs' (1974) index of feeding preference

Called *D* by Jacobs (1974), this index is given as:

$$D = \frac{Ne/Ne' - N/N'}{Ne/Ne' + N/N'}$$

The notation follows Cock (1978), in which: *Ne* is the number of items of prey type 1 eaten, *Ne'* is the number of items of all other prey types eaten, *N* is the number of items of prey type 1 available, *N'* is the number of items of all other prey available.

Values range from –1, indicating avoidance or inaccessibility of prey type 1, to +1, indicating active selection of that type.

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ERRATUM

Tyler, S.J. & Ormerod, S.J. (1985) Aspects of the breeding biology of Dippers *Cinclus cinclus* in the southern catchment of the River Wye, Wales. *Bird Study*, **32**, 164–169

The legend to Fig. 4 (page 167) is incorrect. It should read as follows:

Figure 4. Seasonal (a) and annual (b) patterns in clutch (closed symbols) and brood sizes (open symbols) from this study (triangles) and from Shaw (1978; squares). The points joined are means, with vertical lines showing 95% confidence intervals, headed by sample sizes.