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Analysis of the diet of Daubenton's bat *Myotis daubentonii* in Ireland

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The diet of Daubenton's bat *Myotis daubentonii* (Kuhl, 1817), which takes prey by aerial hawking and from the surface of water, was investigated by analysis of faeces collected in summer at 7 roosts, all close to rivers in pastoral land, in three widely-separated districts in Ireland. Forty-seven categories of arthropod prey were identified; several were insect taxa found in and around water. Most categories were recovered at most roosts, but mainly in small amounts. The main categories were the same throughout, accounting for 82% of the diet by percentage frequency in droppings for pooled data: Chironomidae/Ceratopogonidae 24% (adults 14%, preadult stages 10%), other nematoceran Diptera 21%, other Diptera 10%, and Trichoptera 26% (adults 20%, preadult 6%). A quarter of the prey had evidently been obtained from the water's surface (eg aquatic insects, their larvae and pupae). Although consumption of several food items varied significantly by month at one or more roosts, little of such variation was consistent between roosts.

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Introduction

Daubenton's bat *Myotis daubentonii* (Kuhl, 1817) is usually found close to water, and whereas it also feeds around trees at heights up to 5 m, it often hunts at 30 cm above water. Prey are caught by aerial hawking or are taken from the water surface – either seized by the feet or scooped up by the interfemoral membrane (Jones and Rayner 1988, Kalko and Schnitzler 1989).

The biology of this species has been reviewed by Bogdanowicz (1994). In contrast to other species of bat in Europe, Daubenton's bat is widely reported to be increasing in numbers (Racey *et al.* 1998). Kokurewicz (1995), who reported a five to eightfold increase in numbers between 1950 and 1991 in parts of Poland, suggested that this might be because increased eutrophication had resulted in more insect prey. However, Racey *et al.* (1998) tested this hypothesis and found little difference in insect abundance over a large oligotrophic river and a small eutrophic one.

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There have been only 4 systematic analyses of prey remains in the faeces of Daubenton's bat in which the relative proportions have been expressed numerically (Vaughan 1997). Of these, Taake (1992), working in NW Germany, analysed prey remains in 36 faecal pellets to order with some to family. Beck (1995) examined 306 pellets from various sources in Switzerland but, while listing families and sub-families, gave overall figures only for orders. Swift and Racey (1983) examined a regular sample (n = 25) of droppings on each of 8 nights from a nursery roost in Scotland and compared the results (to family) with insects available to the bats on each night, as sampled with a suction trap. Finally, Sullivan *et al.* (1993) processed a total of 120 faecal pellets over 3 months, to family, from a roost in the west of Ireland.

The present study was undertaken partly to provide further detailed data on the diet of the species, but particularly to obtain a fuller picture of the prey taken in summer in Ireland. In it we present data from 1091 pellets from 7 different roosts, including, for one, results for each month from April to September over 2 years.

Study roosts

The land around all of the roosts, which are all at less than 150 m above sea level, is of good quality and pasture predominates, as it does on most agricultural land in Ireland. The fields are generally small and bordered by well-developed hedgerows with at least some trees.

The first 5 roosts are all in the catchment of the Blackwater River in the extreme south of Ireland, the water here being classified mainly as unpolluted (Lucey *et al.* 1999). In the surrounding district there are numerous hedgerow trees and also many blocks of both deciduous and coniferous woodland. The first three roosts are associated with the River Blackwater itself, which here is 40–50 m wide, its banks densely clad with deciduous trees. The roost at Convamore House (52°8'N, 8°25'W) is in the wine cellar of a ruined mansion, within 100 m of the river. That at Glencairn Abbey (52°8'N, 8°0'W) is in an underground passage, 3–5 m in height, again within 100 m of the river. This was the only verified nursery roost. The roost at Ballyhooly Bridge (52°8'N, 8°24'W) was in the stonework of the bridge which spanned the Blackwater River. The remaining two roosts were also in the stonework of bridges: Araglin Bridge (52°10'N, 8°13'W over the River Araglin, 15 m wide), and Licky Bridge (52°0'N, 7°48'W over the River Licky, 10 m wide).

Dysert Bridge (52°47'N, 7°13'W), in which the bats also roost in the stonework, is in SE Ireland and spans the Dinin River, 30 m wide at this point, with thick herbaceous cover on its banks. A recent survey reports water quality in the various stretches of this river as varying between unpolluted and slightly polluted (Lucey *et al.* 1999). At all the aforementioned bridges, the roosts are either wholly or partially in peripheral arches, through which the river did not flow over at least part of the summer. Blacksessiagh Bridge (54°33'N, 7°21'W), in Northern Ireland, spans the River Owenreagh, 15 m wide here. The roost is in a blindly-ending arch, 1.5 m high, some 100 m from the bridge itself. Water quality here is good (unpublished Government data). The Blackwater, Dinin and Owenreagh Rivers are slow-flowing; the Araglin and Licky rivers are fast-flowing.

Material and methods

Droppings were collected on polythene sheeting, except at Glencairn Abbey where, because of high humidity, curtain netting was used instead. There was only 1 collection at Blacksessiagh Bridge, from 15 June to 1 August 1997. At all the other sites, polythene/netting was laid at the beginning of April 1997, or, at bridge sites where water was flowing under the roost, at the beginning of the first month after the arch was dry. Polythene was removed at the end of each month, or at the beginning of the next one, and replaced until the end of September; thus each collection of faeces could be assigned to a particular month. However, because of flooding, some months were unrepresented at the bridge sites.

Table 1. Number of faecal pellets analysed from each month at each site (total 1091). Where < 40 is shown, all intact pellets in the batch were analysed. A dash indicates that no sample was available. Apart from Glencairn Abbey, all material was collected in 1997. The sample from Blacksessiagh Bridge included part of June and July.

Site	April	May	June	July	August	September
Glencairn Abbey 1997	40	40	40	40	40	40
Glencairn Abbey 1998	40	40	40	40	40	40
Convamore House	40	40	40	40	–	–
Araglin Bridge	40	40	–	40	–	–
Licky Bridge	–	40	40	40	–	–
Ballyhooly Bridge	23	–	–	–	28	–
Dysert Bridge	40	40	–	40	–	–
Blacksessiagh Bridge	–	–	–	40	–	–

The bats deserted Convamore House in July. In 1998 further monthly collections were made at Glencairn Abbey from April–September.

Each collection of droppings was oven dried at 50°C and stored in an airtight glass jar with a few crystals of para-dichlorobenzene to kill coprophages. A sample of 40 intact pellets was selected at random or, if there were less than 40, all available intact pellets. The numbers of pellets examined from each site on each month are given in Table 1. All recognisable arthropod fragments were extracted from each pellet, mounted in glycerinated gelatine and identified using the methods of Shiel *et al.* (1997), various publications on insect morphology, and an extensive reference collection of arthropods. As lepidopteran scales may persist in the guts of bats for long periods, only droppings with abundant scales or other characteristic structures, which were nearly always recovered when scales were abundant, were scored for Lepidoptera.

The present data – presence or absence of food categories in each dropping – were expressed in two ways: (1) percentage occurrence – the number of droppings n in which a category c occurred (n_c), divided by the total number of droppings examined × 100, and (2) as percentage frequency – n_c divided by Σn_c for all categories × 100. Percentage occurrence follows a binomial distribution and is independent of other categories. It is therefore used here to express seasonal variation. Variation between months was examined using the χ^2-test on numbers of occurrences. But percentage occurrences do not sum to 100%, unlike percentage frequencies, which have therefore been used to express the diets as a whole.

Most fragments were identified to family or superfamily. However, with some it was impossible to go further than order (eg Ephemeroptera, Lepidoptera) or, in the case of Chilopoda, to class. Fragments which obviously belonged to a particular order, for which we were usually able to determine the family or superfamily, but could not in a particular dropping, were categorised as "unidentified" (unidentified Diptera and Coleoptera). All fragments of Trichoptera which were not limnephilid, leptocerid or hydropsychid were categorised as "other Trichoptera". Because it was often not possible to distinguish between Ceratopogonidae and Chironomidae, these, the biting and non-biting midges, were considered as a joint food category. In collections at some sites/years, larvae and pupae of midges were noted separately, at others they were combined and recorded as "preadult". This was also the case with larval and pupal Trichoptera.

Results

The percentage frequency of each food category at each locality, pooled for each year is given in Table 2. Ignoring composites (such as unidentified Diptera, other

Table 2. Percentage frequency of each food category in the samples of droppings pooled for each year and site. Total occurrences for all droppings = 4834. In some collections of droppings larvae and pupae were recorded separately, in others combined as preadult. + = < 0.5%. The following other categories were recorded at levels of < 0.5% only: order Collembola (A), order Plecoptera: Leutricidae (ABE), order Hemiptera: Psylloidea (B), order Neuroptera: Hemerobiidae (ABG), order Coleoptera: Haplipidae (ADE), Dytiscidae (D), Hydrophilidae (E), order Diptera: Psychodidae (ABCE), Drosophilidae (B), order Hymenoptera: Chalcidoidea (BDE), Apoidea (G), order Opiliones (E), class Chilopoda (E).

Food category	A Glencairn Abbey 1997	B Glencairn Abbey 1998	C Con-vamore House	D Araglin Bridge	E Licky Bridge	F Bally-hooly Bridge	G Dysert Bridge	H Blackses-siagh Bridge	Pooled data
1	2	3	4	5	6	7	8	9	10
Class Insecta									
Order Ephemeroptera	+	1	0	1	2	0	+	2	1
Order Dermaptera	1	1	1	4	1	1	2	1	1
Order Hemiptera									
Suborder Heteroptera									
Corixidae	1	0	+	2	+	1	4	2	1
Veliidae	1	+	+	1	1	0	1	0	1
Suborder Homoptera									
Delphacidae	+	0	0	0	1	0	0	0	+
Aphidoidea	0	4	0	+	1	+	0	0	1
Order Coleoptera									
Suborder Adephaga									
Carabidae	+	+	0	+	1	0	+	1	+
Gyrinidae	3	+	2	1	1	0	1	2	1
Dytiscidae	0	0	0	+	0	0	0	0	+
Suborder Polyphaga									
Scarabaeidea	4	1	4	+	1	1	1	1	2
Chrysomeloidea	+	0	0	0	1	0	+	0	+
Scolytidae	0	+	0	1	2	0	0	0	+
Unidentified Coleoptera	1	+	2	1	1	+	0	4	1
Order Diptera									
Suborder Nematocera									
Tipulidae	1	7	1	2	3	2	4	6	4
Anisopodidae	12	6	6	6	5	5	11	14	7
Culicidae	2	6	4	4	4	7	2	15	4
Simulidae	9	5	1	1	1	0	0	0	3
Chiro/Cerato	15	15	22	12	8	16	20	16	14
Chiro/Cerato larvae	–	6	–	4	5	2	–	0	–
Chiro/Cerato pupae	–	9	–	4	7	3	–	0	–
Chiro/Cerato preadults	5	–	10	–	–	–	9	2	10
Suborder Brachycera									
Empididae	1	2	3	1	2	0	2	2	2
Suborder Cyclorrhapha									
Sphaeroceridae	2	1	+	1	2	0	3	0	1

Table 2 – concluded.

1	2	3	4	5	6	7	8	9	10
Calliphoridae	0	+	0	+	2	1	0	0	+
Scathophagidae	3	1	4	2	3	1	5	2	3
Ephydridae	0	0	0	1	+	0	+	0	+
Unidentified Diptera	5	4	6	7	7	4	8	2	6
Order Lepidoptera	1	2	1	+	2	1	2	2	2
Order Trichoptera									
Limnephilidae	2	1	+	3	1	2	1	4	1
Hydropsychidae	6	9	6	12	8	18	6	8	9
Leptoceridae	+	+	+	2	1	1	+	0	1
Other Trichoptera	13	7	23	6	7	11	9	11	10
Trichoptera larvae	–	+	–	3	1	5	–	–	–
Trichoptera pupae	–	4	–	12	8	16	–	–	–
Trichoptera preadult	2	–	0	–	–	–	1	0	6
Order Hymenoptera									
Suborder Apocrita									
Ichneumonidae	1	+	+	1	+	0	+	1	+
Class Arachnida									
Order Araneida	3	3	1	4	8	1	3	3	4
Order Acari	2	1	1	+	1	1	3	2	1
Order Pseudoscorpionida	0	0	0	1	+	0	0	0	+
Total occurrences	808	1326	453	571	851	218	485	122	4834

Trichoptera and composite preadult midges and Trichoptera), a total of 47 food categories were recorded in the droppings. Most of these were recovered at all sites, although usually only in small quantities. There is also a great degree of consistency between roosts in the major foods taken, figures for individual sites comparing well with those for pooled data. Indeed for most categories the extent of difference between sites is comparable to that between years at Glencairn Abbey. Rounded percentages for the major categories in the pooled data were midges 24% (adults 14%, preadult 10%), other nematoceran Diptera 21%, other Diptera (including unidentified) 10% and caddis flies (Trichoptera) 26% (adults 20%, preadult 6%), these major elements together accounting for 82% of the diet.

Significant seasonal variation is shown in Table 3. However, little of it showed any consistency between roosts. Moreover, little of the seasonal variation in the categories in the two years at Glencairn Abbey corresponded. However, on individual months at particular sites, some minor categories occurred at high levels, such as Dermaptera at Araglin Bridge and Ephemeroptera at Licky Bridge in May. At some sites/years there is also some indication that Culicidae and midges were taken more often early in the season (notably in April for midges) and Hydrophsychidae more frequently later, with perhaps a peak in July.

Table 3. Seasonal variation in prey categories significant at the 5% level (χ^2-test). Values are expressed as percentage occurrence in droppings. In some collections of droppings larvae and pupae were recorded separately, in others combined as preadult. Apart from Glencairn Abbey, all material was collected in 1997.

Food category and site	*p* <	April	May	June	July	August	September
1	2	3	4	5	6	7	8
Ephemeroptera							
Licky Bridge	0.05	–	30	18	5	–	–
Dermaptera							
Araglin Bridge	0.01	30	3	–	18	–	–
Corixidae							
Dysert Bridge	0.001	0	3	–	43	–	–
Scarabaeidea							
Glencairn Abbey 1997	0.05	15	0	15	15	15	28
Scolytidae							
Licky Bridge	0.01	–	3	10	28	–	–
Tipulidae							
Glencairn Abbey 1998	0.01	55	58	45	28	25	30
Licky Bridge	0.01	–	38	10	15	–	–
Anisopodidae							
Glencairn Abbey 1997	0.001	48	25	20	33	58	53
Glencairn Abbey 1998	0.01	33	38	15	23	35	58
Convamore House	0.05	25	28	5	13	–	–
Licky Bridge	0.01	–	38	50	13	–	–
Culicidae							
Glencairn Abbey 1998	0.01	45	40	43	28	20	10
Araglin Bridge	0.05	33	23	–	8	–	–
Licky Bridge	0.05	–	35	15	35	–	–
Ballyhooly Bridge	0.01	48	–	–	–	14	–
Simulidae							
Glencairn Abbey 1997	0.001	3	10	8	38	40	75
Glencairn Abbey 1998	0.001	0	0	15	23	50	90
Chiro/Cerato							
Glencairn Abbey 1997	0.001	95	45	35	38	40	43
Glencairn Abbey 1998	0.001	83	85	88	85	90	55
Convamore House	0.001	95	65	45	43	–	–
Araglin Bridge	0.001	90	68	–	18	–	–
Licky Bridge	0.001	–	55	30	75	–	–
Ballyhooly Bridge	0.01	91	–	–	–	50	–
Chiro/Cerato larvae							
Glencairn Abbey 1998	0.001	30	60	8	43	48	3
Araglin Bridge	0.001	45	5	–	0	–	–
Licky Bridge	0.001	–	40	13	55	–	–
Chiro/Cerato pupae							
Glencairn Abbey 1998	0.001	30	65	45	73	65	33
Araglin Bridge	0.001	52	8	–	0	–	–
Licky Bri-dge	0.001	–	60	20	78	–	–
Chiro/Cerato preadults							
Glencairn Abbey 1997	0.001	60	8	3	10	8	20
Convamore House	0.001	55	20	25	15	–	–
Dysert Bridge	0.001	80	30	–	3	–	–

Table 3 – concluded.

1	2	3	4	5	6	7	8
Scathophagidae							
Dysert Bridge	0.05	15	33	–	13	–	–
Unidentified Diptera							
Araglin Bridge	0.001	15	60	–	23	–	–
Licky Bridge	0.05	–	65	38	40	–	–
Lepidoptera							
Licky Bridge	0.001	–	35	5	5	–	–
Limnephilidae							
Araglin Bridge	0.001	0	43	–	5	–	–
Hydropsychidae							
Glencairn Abbey 1997	0.001	8	18	50	40	10	3
Glencairn Abbey 1998	0.001	63	38	73	75	50	3
Convamore House	0.001	0	10	18	40	–	–
Araglin Bridge	0.001	28	70	–	78	–	–
Dysert Bridge	0.001	0	28	–	50	–	–
Other Trichoptera							
Glencairn Abbey 1997	0.001	48	80	40	40	43	13
Araglin Bridge	0.01	18	25	–	48	–	–
Ballyhooly Bridge	0.05	26	–	–	–	60	–
Trichoptera pupae							
Araglin Bridge	0.001	25	73	–	70	–	–
Licky Bridge	0.01	–	63	68	33	–	–
Ballyhooly Bridge	0.001	39	–	–	–	93	–
Araneida							
Araglin Bridge	0.05	10	30	–	10	–	–

Discussion

Although the validity of analysis of faeces in determining the diet of bats has been disputed, and undoubtedly has its limitations, it is now considered a valid one (Whitaker 1988). The consistency in the present results suggests that they may give a good general indication of the diet of Daubenton's bat in Ireland, where the majority of land is similar to that at our study roosts – under agriculture and predominantly pastoral. Moreover the taxa of major importance in the only other Irish analysis of droppings of Daubenton's bat (Sullivan *et al.* 1993) are the same, although no preadult insects were noted. In analyses of droppings outside Ireland, the most frequently represented order and family have also been Diptera and Chironomidae (Vaughan 1997). Trichoptera have also been recorded in all such analyses (Vaughan 1997), but occurred sparingly in some (Taake 1992, Beck 1995).

Caddis flies and midges have aquatic larvae and pupae, and many of the adults here were probably caught around rivers, adult male chironomids commonly swarming above water. Adult Ephemeroptera and Plecoptera are also normally found near water (Chinery 1993). Nevertheless, larger adult Trichoptera may occur at some distance from water (Chinery 1993) and midges may breed in puddles and ditches or other standing water far from watercourses.

There is considerable evidence here that much of the prey was taken from the surface of the water. Of course, some such items, such as the Corixidae, can fly, but they spend relatively little time on the wing. Prey caught on the surface may be considered under three headings:

(1) Animals which live mainly at the surface of the water. These comprise midge larvae and pupae, the Veliidae, and the Gyrinidae;

(2) Aquatic animals which may appear on the surface, which comprise the Corixidae, water beetles of the families Haplipidae, Dytiscidae and Hydrophilidae and preadult stages of Trichoptera. Although the last are not usually considered surface dwellers, the pupae of some species come to the surface, break out of their casing, and swim to the shore before metamorphosing (J. O'Connor, pers. comm.), at which time they would be vulnerable to Daubenton's bats; pupal casings were often recovered from the droppings in the present study. Caddis larvae might be taken when they are isolated in shallow water at the edge of watercourses when the water level falls, and, on rainy nights, trichopteran larvae may crawl out of the water onto emergent vegetation, or onto that hanging into the river from the banks, to feed and still keep their gills wet (J. O'Connor, pers. comm.). All trichopteran larvae consumed by the bats were, of course, almost certainly of caseless forms;

(3) Arthropods which fall onto the water, either alive or dead. These include non-aquatic insects which strike the water and cannot fly off. These may form an important source of food for suitably-equipped predators. For example, trout *Salmo trutta* exploit them extensively (Maitland and Campbell 1992). In the present study, all Araneida which were not caught in the roost were presumably either aquatic spiders or terrestrial forms which had been trapped on the surface, and Opiliones and Chilopoda, if not caught in the roost, were also skimmed from the water's surface. Most Dermaptera fly little and are also included here. However, certain other taxa, which may seem worthy of inclusion on an empirical basis, have been rejected on strict criteria. Thus, whereas Acari and Pseudoscorpionida cannot fly, it is possible that they were eaten in association with other arthropods. Again, the Brachycera, Cyclorrhapha and Hymenoptera are all predominantly diurnal and seem unlikely to have been taken by aerial hawking. Nevertheless, in Ireland such taxa still feature in a minor way in the diets of other species of bat which apparently forage by aerial hawking alone (McAney and Fairley 1989, Sullivan *et al*. 1993, Shiel *et al*. 1998).

Together, these three groups constituted 25% of the diet in the present study (Table 2). Despite the possibility of a few such items having been caught at the roost or in flight, this figure still probably significantly underestimates prey taken from the surface of the water. Investigations of the diet of Irish trout suggest that aerial insects entrapped on the water surface may comprise a large proportion of available prey there. It is improbable that a bat such as Daubenton's, which is clearly capable of feeding from arthropods on the water surface, would ignore any aerial insects floating there.

The chief evidence for the abundance of aerial insects on the water surface in Ireland comes from analyses of the stomach contents of trout caught throughout the year at two sites in the east, in the catchment of the River Liffey: at Straffan ($n = 228$), on a lowland alkaline river, and at Ballysmuttan ($n = 349$), on an upland alkaline stream (Frost 1939). From May–October at Straffan, food taken at the surface made up two-thirds, and at Ballysmuttan a tenth, of the total. Furthermore, whereas throughout the year, larvae and pupae of Diptera together occurred at 14% at Straffan, calculated as percentage frequency in stomachs, and 9% at Ballysmuttan, the corresponding figures for adult Diptera were 10 and 7%, and for adult Diptera combined with adults of Ephemeroptera, Plecoptera, Trichoptera and Hymenoptera 28 and 20%. Analyses of smaller collections of trout stomach contents from four other sites on the Liffey catchment showed that aerial insects were often taken there too (Frost 1939). The rivers in the present study are not in the Liffey catchment, and it would be incorrect to infer that the food preferences of trout, and size range of insects taken by them, are the same as those of Daubenton's bats. Nevertheless, it can still reasonably be inferred from Frost's work that many adult aerial insects are available to, and may be taken by, Daubenton's bats as casualties on the surface of Irish rivers.

Rydell *et al.* (1996) noted that Daubenton's bat emerges 15–30 min after sunset and argued that earlier emergence was constrained by an increased risk of predation. They showed that emergence was after the dusk peak in flying insects, as determied by trapping. As Daubenton's bat takes such a large proportion of its prey from the surface of the water, both as living adult and juvenile insects and probably as casualties among non-aquatic forms, emergence of the bats after the dusk peak in flying insects may not be such a disadvantage as might at first be supposed.

As mentioned in the Introduction, Racey *et al.* (1998) investigated abundance of insects over a large oligotrophic river and a small eutrophic one and found little difference. However, the insects were sampled 1.5 m above the water surface. In the light of the findings in the present work, it would also be of interest to compare the relative numbers of insects actually on the water surface of oligotrophic and eutrophic rivers.

Because of the lack of consistency in seasonal variation between sites and years, few general conclusions can be drawn about this. However, the fact that at some sites Culicidae and midges (which are small insects) were taken more often early in the season, and Hydropsychidae (which are larger insects) later, with a possible peak in July, may represent maximization of return on catch effort later in the warmest part of the summer, when insects are generally most abundant. The peak in consumption of Ephemeroptera in May at Licky Bridge, where these insects were recorded in droppings in the highest numbers, probably represents a genuine peak in numbers during this month, when these insects are often most abundant, giving rise to their common name of "mayflies". In both 1997 and 1998 the greatest consumption of Simulidae at Glencairn Abbey, the only roost where they were commonly caught, was late in the summer, and may have corresponded with an autumn generation.

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