

Bats and insects over two Scottish rivers with contrasting nitrate status

Paul R. Racey, Susan M. Swift, Jens Rydell and Laura Brodie

Department of Zoology, University of Aberdeen, Aberdeen AB24 2TZ, UK

(Received 8 July 1997; accepted 31 March 1998)

Abstract

The abundance of foraging bats (*Pipistrellus pipistrellus* and *Myotis daubentonii*) and flying insects over two rivers in north-east Scotland (Dee and Ythan), differing eightfold in nitrate levels, were compared by paired samples over three periods in summer 1995, during each of which 10 nights' sampling was undertaken using ultrasonic detectors and insect suction traps. Thirteen out of the 18 pairwise comparisons of bat passes, insect numbers, biomass and diversity were not significantly different. The oligotrophic Dee supported higher numbers of bats than the eutrophic Ythan in June, but this was attributed to an effect of adverse weather conditions affecting the Ythan. In July and August–September, neither bat abundances nor the abundance of Chironomidae and Trichoptera, the main food of the bats, differed significantly between the two rivers, although the Ythan showed higher total insect biomass than the Dee. The Ythan also showed a much higher abundance of small Diptera, mainly Psychodidae and Cecidomyiidae, associated with elevated nitrogen levels in the intensively farmed river valley. Thus a small eutrophic river can support as many bats and as high an insect density as a large oligotrophic one.

INTRODUCTION

Bats are the most common contributors to Britain's mammalian biodiversity and until recently 14 species bred in Britain although this number has recently increased to 16. The common pipistrelle *Pipistrellus pipistrellus* has now been separated into two phonotypes (Jones & Van Parijs, 1993) which are to be recognized as two species on the basis of the 11% DNA sequence divergence reported by Barratt *et al.* (1997) and assortative mating inferred by Park, Altringham & Jones (1996). A newly discovered maternity colony of *P. nathusii* (Russ, O'Neill & Montgomery, in press) supports recent suggestions that this species now breeds in the UK (Speakman, Racey, Hutson *et al.*, 1991; Barlow & Jones, 1996). Widespread concern about declining bat numbers throughout Europe (Stebbing, 1988) resulted in The Wildlife and Countryside Act 1981, which protects bats and their roosts. This has been reinforced recently by The European Bats Agreement 1991 (Hutson, 1991) which additionally seeks to protect foraging areas.

In contrast to declines in numbers of many bat species,

Daubenton's bat *Myotis daubentonii* is widely reported to be increasing in numbers throughout mainland Europe. In the Netherlands, Daan (1980) and Voûte, Sluiter & van Heerdt (1980) reported fourfold increases between 1945 and 1979, and more recently, Weinrich & Oude Voshaar (1992) recorded a 12-fold increase between 1940 and 1985. In the Czech and Slovak republics, Bárta *et al.* (1981) reported a doubling of numbers between 1969 and 1979, and in south-west Germany and the adjacent Sumava mountains, Van Helvesen *et al.* (1987) and Cerveny & Bürger (1990) reported sixfold increases during 1977–1987 and 1975–1990, respectively. In the Krakow–Czestochowa region of central Poland and in Lower Silesia in south-west Poland, Kokurewicz (1995) reported a five- and eightfold increase in numbers between 1950 and 1991, and 1964 and 1987, respectively. The geographical spread and unanimity of these reports, which are based mainly on counts of bats in hibernacula, suggest a real increase, which Kokurewicz (1995) has suggested is due to the eutrophication of fresh waters.

Daubenton's bat feeds almost exclusively over water (Swift & Racey, 1983; Rydell, Bushby *et al.*, 1994) where, in addition to catching insects in free flight, it gaffs prey from the water surface (Jones & Rayner, 1988). Pipistrelles (*Pipistrellus pipistrellus*), which are the commonest bats in Britain (Harris *et al.*, 1995) but not in mainland Europe, also feed in riparian situations

All correspondence to: Professor P. A. Racey. Tel: 01224-272858; Fax: 01224-272396; E-mail: p.racey@abdn.ac.uk. Present address for Dr J. Rydell: Department of Zoomorphology, University of Göteborg, Medicinargatan 18, S-413 90 Göteborg, Sweden

(Racey & Swift, 1985; Racey, 1988) and both species have similar diets (Swift & Racey, 1983; Swift, Racey & Avery, 1985; Vaughan, 1997) in which nematoceran Diptera and Trichoptera predominate. In the UK, therefore, any changes that affect numbers of Daubenton's bat through their food supply are also likely to affect pipistrelles.

Our study area in north-east Scotland provided an opportunity to investigate the effects of eutrophication on bat numbers since it contains two rivers with sharply contrasting nitrogen levels, one of which has recently been considered for designation as a nitrate-vulnerable zone in terms of the EC Nitrate Directive. Our aim, therefore, was to test the hypothesis that eutrophication results in an increase in numbers of Daubenton's and pipistrelle bats, by counting bat passes and trapping their insect prey over two rivers of contrasting nitrate status.

METHODS

The study area

The two rivers investigated here, the Dee and the Ythan, drain into the North Sea at *ca* 57°N near Aberdeen, north-east Scotland (Fig. 1). The Dee is 141 km long, has a catchment area of 2100 km² and drains mostly mountains (up to 1280 m above sea level (a.s.l.)), moorlands and permanent pasture, which are sparsely populated. The main enterprises along the river are sport fishing, shooting, forestry and hill farming. There are several small towns and villages on the banks but little polluting industry. The main river is oligotrophic, but some nutrient enrichment occurs close to Aberdeen (Wright *et al.*, 1991; North-east River Purification Board, 1993).

The Ythan is 63 km long and has a catchment area of 690 km². It drains mostly fertile, rolling farmland (up to 260 m a.s.l.), used for intensive arable and livestock farming. Although there has been an increase in sewage effluents from surrounding towns and villages as a result of rapid population growth in the area over the last 20 years, this contributes only a small proportion of the total nitrogen load in the river, which still supports some

salmon and trout fishing (Raffaelli, Hull & Milne, 1989; Wright *et al.*, 1991; North-east River Purification Board, 1993; Macdonald *et al.*, 1995).

The Ythan is more exposed to wind than the Dee, which is situated in a valley mostly surrounded by hills. Furthermore, while there is riparian woodland along *ca* 40% of the banks of the river Dee, there are trees along only *ca* 15% of the Ythan (estimated from Ordnance Survey Landranger maps, 1:50 000 scale). In September 1994, the average widths of the Dee and Ythan, respectively, were 58 and 15 m, as measured using ropes across the river at the 10 sampling sites. These values were probably close to the seasonal averages.

The nitrate levels, which indicate the degree of eutrophication in running waters, where phytoplankton production is only of minor importance (Wetzel, 1983), have been measured annually since 1958 in the two rivers by the former North-east River Purification Board in Aberdeen (now the Scottish Environmental Protection Agency), and show an eightfold difference between the two up to 1992 (Fig. 2). Significant increases in soluble nitrogen in the Ythan catchment from 1980 to 1992 have also been documented by Macdonald *et al.* (1995). The greatest seasonal increase occurs in spring, and is associated with agricultural intensification which has resulted in changes in cropping practice. As a result the Ythan has recently been considered for designation as a nitrate-vulnerable zone in terms of the EC Nitrate Directive 91.676.

The general 'Solway Weighted Water Quality Index' (WQI), varying from zero (worst) to 100 (best), is based on dissolved oxygen, biochemical oxygen demand, ammonium-nitrogen, total oxidized nitrogen, phosphate,

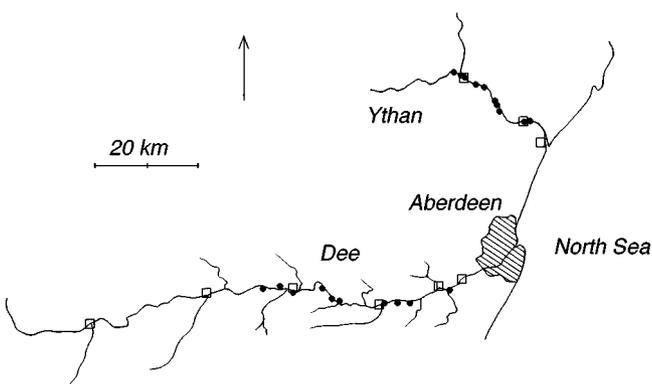


Fig. 1. The study area with major towns and villages along the rivers (open squares) and approximate locations of the sampling sites (filled circles).

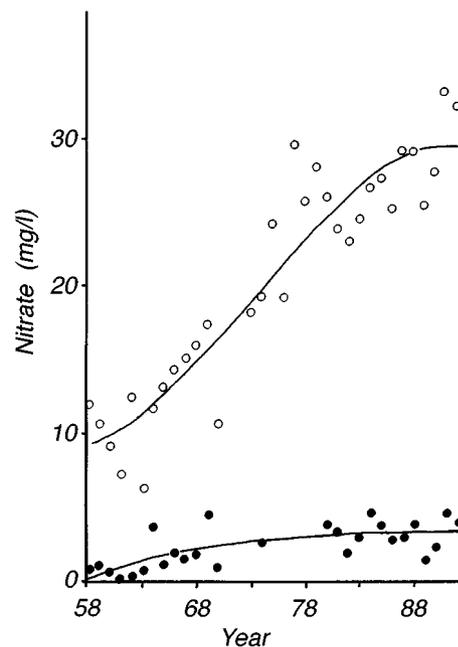


Fig. 2. Mean annual nitrate levels (mg/l) in rivers Dee (filled circles) and Ythan (open circles), Aberdeenshire, north-east Scotland, 1958–1992. Data courtesy of the North-east River Purification Board, Aberdeen.

pH, suspended soils, conductivity and temperature. In 1993, the average WQI score was 96 for the Dee and 79 for the Ythan. Likewise, the 'Biological Monitoring Working Party Index' (BMWP) assigns each site a value between zero (lowest) and 10 (highest), depending on the abundance of each bottom fauna taxon found there. The BMWP is then quoted as the average score per taxon (ASPT). In 1993, the ASPT was 6.8 for the Dee and 5.6 for the Ythan (North-east River Purification Board, 1993). Hence, the nitrate levels show major and consistent differences in water quality between the two rivers, which is supported by the two general indices.

In 1995, we sampled insects and measured the bat activity at 10 sites along the lower part of each river (Fig. 1). The sections of the rivers sampled were relatively shallow, in that the bottom was often visible, and there were occasional deep pools. The highest sampling sites were 150 m a.s.l. for the Dee and 15 m a.s.l. for the Ythan. We attempted to match the sites at the two rivers pairwise with respect to bottom conditions (two sites at each river were muddy, the rest had large stones or gravel), presence/absence of riffles (which are known to affect bats negatively by interfering with the echolocation; von Freneckell & Barclay, 1987), and the presence/absence of riparian trees, which may provide wind shelter and protection from predators. Matching the sites in this way, we aimed to facilitate the use of paired tests, thus as far as possible controlling for environmental factors other than water quality. We used each site once during each of the three sampling periods, comprising June, July and August–September, coinciding with pregnancy, lactation and post-lactation of the bats, respectively. At the start of each sampling period (22.30 in June and July, 21.00 in August and 20.00 in September, British Summer Time), we recorded air and water temperatures with a mercury thermometer, wind speed (none, slow, moderate, fresh, strong, very strong), wind direction, cloud cover (0–8 scale) and occurrence of rain and mist.

Bat activity

We counted Daubenton's bats *Myotis daubentonii* and common pipistrelles *Pipistrellus pipistrellus*, both occurring at high densities at the two rivers (Speakman, Racey, Catto *et al.*, 1991; Rydell, Bushby *et al.*, 1994). The two species are easily separated visually and/or by their echolocation calls. However, pipistrelles were separated into two phonic types, by the peak amplitude frequency of the echolocation calls used in search flight (*ca* 55 and *ca* 45 kHz, respectively; Jones & van Parijs, 1993). These phonic types have since been shown to be two species (although the new species has yet to be named) (Barratt *et al.*, 1997). Estimates of bat activity were obtained by counting the number of bat passes using Pettersson D-980 ultrasound detectors (Pettersson Elektronik, Uppsala, Sweden) and headphones. A bat pass was recorded when the increasing followed by the decreasing sound intensity from the detector output indicated that a bat had flown past. It was possible to dis-

tinguish two bats passing at the same time and bat activity was such that there were seldom more. The detectors were used in the heterodyne mode and were tuned to 55, 45 and 35 kHz for the two pipistrelle species and Daubenton's bats, respectively. The three bat species were counted separately during 5 min each, beginning at 22.45 in June and July, 21.15 in August and 20.15 in September. We first counted 55 kHz pipistrelles, then 45 kHz pipistrelles and finally Daubenton's bats. The process was then repeated 45 min later, to obtain a second count for each species. For analysis, the early and late counts were pooled. Daubenton's bats were counted last, because they emerge and start to feed later than pipistrelles (Jones & Rydell, 1994; Rydell, Entwistle & Racey, 1996). The range of the bat detectors was estimated as *ca* 20–30 m under most conditions encountered, but was reduced near riffles, which produce ultrasound (Ahlén, 1981).

To ensure that the bat counts were consistent between the two observers who made the counts (J.R. and S.M.S.) and also that the two bat detectors (each of which was used by the same person throughout) did not differ in sensitivity, we made eight parallel counts (five of pipistrelles and three of Daubenton's bats) at the river Dee two days before the first samples were taken in June and another 10 parallel counts (four of pipistrelles and six of Daubenton's bats) the day after the last samples were taken in September. During these counts, J.R. and S.M.S. stood 2–3 m from each other with the detectors pointed in the same direction towards the river (using headphones) and counted the bat passes during five minutes. Counts were usually identical and the difference was always less than 10%. A paired *t* test on all the counts (excluding the four zero counts) showed no significant difference ($t = 1.4$, d.f. = 13, $P > 0.1$).

Insect samples

Aerial insects were sampled with unmodified Johnson–Taylor insect suction traps (Southwood, 1978), placed in the water at the edge of each river with the fan *ca* 1.5 m above the surface of the water and operated simultaneously at maximum speed for 1.5 h each night. The traps were powered by Honda generators placed > 10 m away from the traps. They were started at 22.30 in June and July, at 21.00 in August and at 20.00 in September. These times were chosen to coincide as closely as possible with local bat activity, particularly over the rivers, as documented in earlier publications (Swift, 1980; Swift & Racey, 1983; Racey & Swift, 1985).

The insects were killed by a pyrethroid sprayed onto the catching device of the trap. They were identified at least to family and sorted into 'morphospecies' i.e. morphologically easily distinguishable kinds, using a dissecting microscope (Wild M5; at $\times 40$ maximum). The whole sample was then dried in an oven at 60°C for 18 h, and weighed on an electronic balance to the nearest 0.1 mg.

To ensure that the two insect traps did not differ in

catching efficiency, they were calibrated by placing them 1 m apart and then operating them simultaneously for seven 1 h periods over one day in the Cruickshank Botanical Garden in Aberdeen, shifting their positions each time a sample had been completed. The average catches were 90 and 89 insects/h for the 'Dee' and the 'Ythan' traps, respectively ($SD = 57$ and 47 , respectively; $t = 0.25$, $P > 0.1$; paired t test).

Statistical analysis

The distributions of the bat counts and the insect catches were skewed and therefore analyses were carried out on log-transformed data using paired t tests (SYSTAT 5.0; Wilkinson, 1990). Differences in environmental factors such as weather were analysed by t tests on untransformed data. As noted above, we used 10 different sampling sites at each river during each of three sampling periods. The samples were only statistically independent of each other within each 10 day sampling period, so the data from the three sampling periods were analysed separately. Two-tailed tests were employed throughout.

RESULTS

Weather

Generally, the weather was warm and dry in July but rather unsettled with rain and wind for much of the June and August–September sampling periods. The June sampling period was also rather cool (Table 1). The difference in flow direction of the two rivers (Fig. 1) had important consequences during the last six days of the June sampling period (7–12 June), the only time when windy conditions prevailed from the same direction for more than a day. A persistent fresh to strong wind from the north-west left the relatively flat and treeless area along the Ythan exposed, while the well-wooded Dee river valley behind the hills provided more shelter. The wind at the Dee during this period was intermittent and moderate to fresh. The air temperature, although not differing significantly between the two rivers in June, was on average 2.0°C higher at the Dee than at the Ythan in July and 2.3°C higher there in August–September. The

water temperature did not differ significantly between the two rivers in June, but the Dee was consistently the warmer of the two later in the summer, with a mean difference up to 3.4°C (Table 1).

Sampling during wet weather was avoided. Although isolated showers affected one or other river on occasions, there were no consistent differences in the occurrence of rain between river valleys. Five days of torrential rain in early September caused severe flooding in both river valleys. Although the rain did not affect the results directly, because no sampling was attempted during that period, the remaining high waters may have affected the insect catches and bat counts obtained subsequently (10–19 September). Indeed, the catches and counts were surprisingly low for this time of the year (*cf.* Rydell, Bushby *et al.*, 1994). However, the flooding appeared to affect the two rivers similarly.

Activity of bats

Differences in the activity of Daubenton's bats between the two rivers were not significant throughout the three sampling periods ($P > 0.05$; paired t tests; Fig. 3). The activities of both pipistrelle species were significantly lower over the Ythan than over the Dee in June ($P = 0.02$ and $P < 0.01$ for the 55 and 45 kHz phonic types, respectively). There were no significant differences between the rivers in the activity of pipistrelle bats during the two following sampling periods ($P > 0.05$, Fig. 3).

Insects

There were no significant differences in the numbers of insects caught over the two rivers in any of the three sampling periods (Fig. 3).

The dry weights (biomass) of the insects catches were significantly higher over the Ythan than over the Dee in July and also in August–September ($P < 0.05$; Fig. 4), but not in June ($P > 0.05$). The species richness of flying insects, as measured by the total number of morphospecies identified from each evening's sample, was significantly higher over the Ythan than over the Dee in July ($P < 0.005$; Fig. 4), but there were no such differences during the other two sampling periods ($P > 0.05$).

Table 1. Differences in (a) air and (b) water temperatures (means and SD) between the two rivers (Dee and Ythan) during the three sampling periods in 1995

(a) Period	Air temperature ($^\circ\text{C}$)		<i>n</i>	<i>P</i>
	Dee	Ythan		
June	9.0 ± 1.5	9.4 ± 1.5	10	> 0.05
July	16.3 ± 2.7	14.3 ± 2.4	10	0.005
August–September	15.5 ± 3.2	13.2 ± 1.3	10	< 0.01
(b) Period	Water temperature ($^\circ\text{C}$)		<i>n</i>	<i>P</i>
	Dee	Ythan		
June	11.5 ± 0.4	11.4 ± 1.0	7	> 0.05
July–September	20.0 ± 1.8	16.6 ± 0.8	7	0.001

n is the number of samples. *P* refers to the significance values obtained by paired t tests (two-tailed).

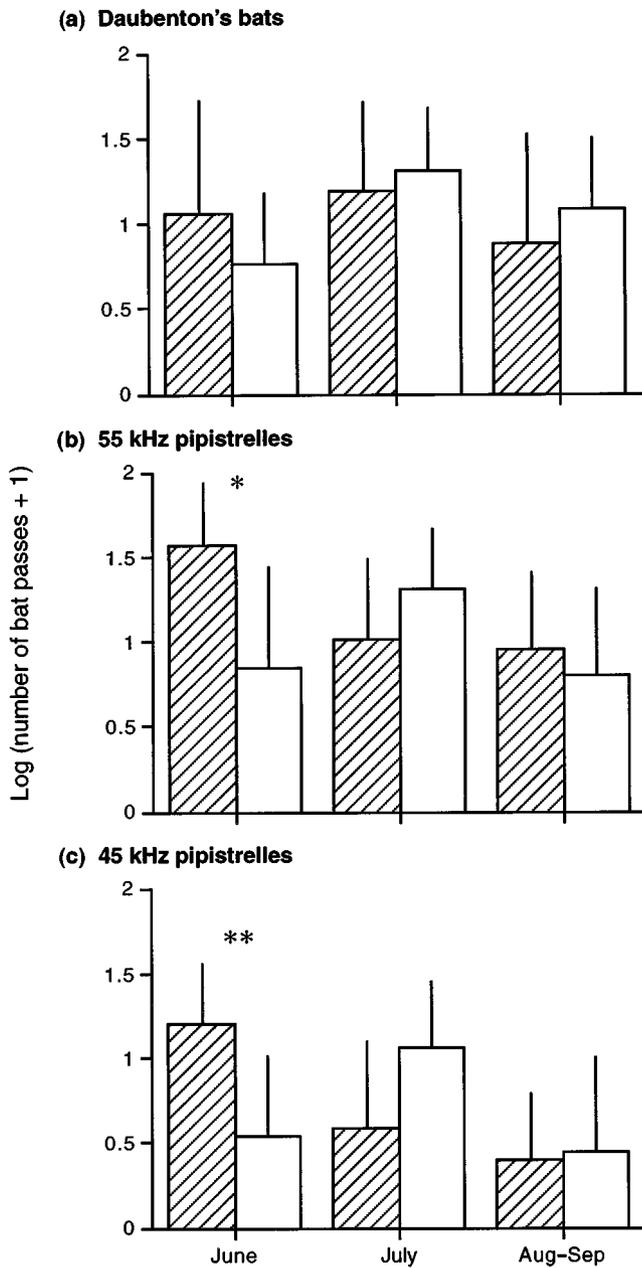


Fig. 3. Bat passes (means and SD) recorded during 10 × 30 min samples at the rivers Dee (hatched) and Ythan (white) during each of three sampling periods (June, July and August–September, 1995). Three bat species were monitored using Pettersson ultrasonic detectors: (a) *Myotis daubentonii*, (b) 55 kHz *Pipistrellus pipistrellus* and (c) 45 kHz *P. pipistrellus*. The counts were made simultaneously at the two rivers. * $P < 0.02$; ** $P < 0.01$.

Insect catches were divided into caddis flies (Trichoptera), chironomids (Diptera: Chironomidae) and others. The number of caddis flies did not differ significantly between the two rivers during any of the three sampling periods ($P > 0.05$; Fig. 5). This also applies to the chironomids in July and in August–September. In June, however, the chironomid catch was significantly higher over the Dee ($P = 0.05$; Fig. 5).

Other than chironomids and caddis flies, the insect

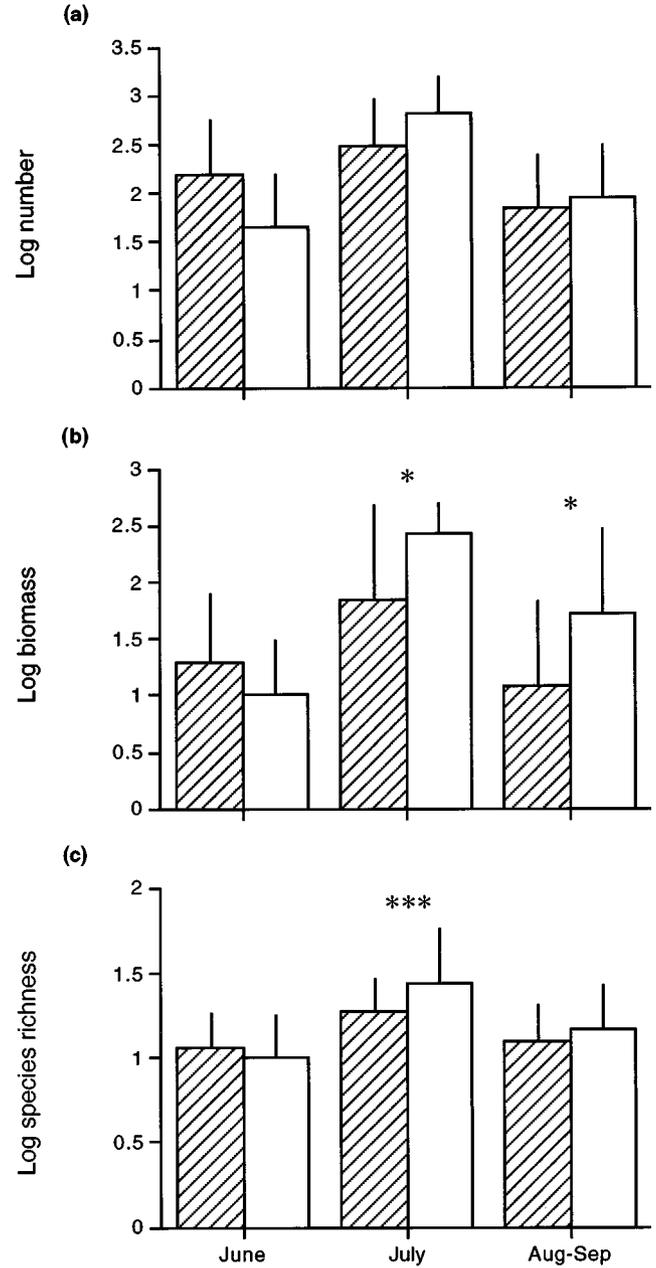


Fig. 4. Insect catches (means and SD) at the rivers Dee (hatched) and Ythan (white) obtained on 10 evenings during each of three sampling periods (June, July and August–September, 1995), expressed as (a) total number of insects per sample, (b) total biomass (mg dry weight) per sample and (c) 'species' richness (i.e. number of 'morphospecies') in each sample. The samples were obtained using Johnson–Taylor insect suction traps run at boost speed for 1.5 h at dusk and simultaneously at the two rivers. * $P < 0.05$; *** $P < 0.001$.

catches consisted predominantly (95 and 96% at the Dee and the Ythan, respectively) of small dipterans, most of which probably originated on the fertilized grasslands and drains away from the main river, including owl midges (Psychodidae), gall midges (Cecidomyiidae), biting midges (Ceratopogonidae), fungus gnats (Mycetophilidae) and Empididae. Owl midges were by far the most abundant within this group, particularly at the Ythan, followed by gall midges, together accounting for

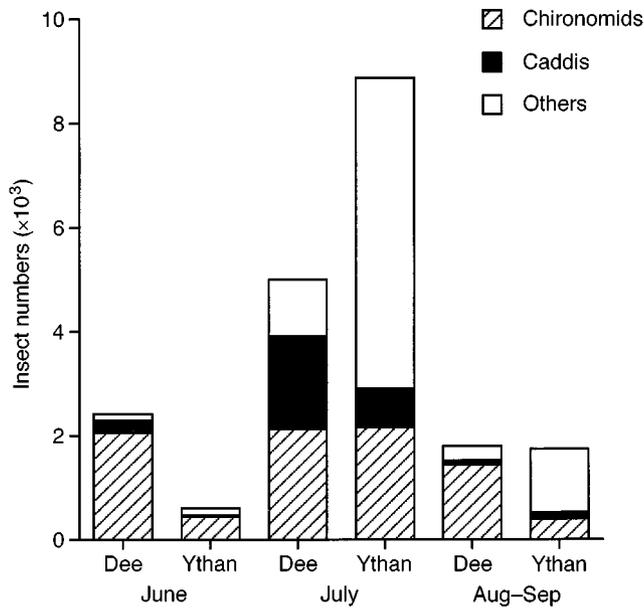


Fig. 5. Composition of the insect catches at the two rivers during each of the three sampling periods (June, July and August–September, 1995). The 10 samples obtained during each period were pooled, and the catches were divided into chironomids (Diptera, Chironomidae; hatched), caddis flies (Trichoptera; black) and ‘others’ (white).

92% of the ‘other’ category at the Ythan and 89% at the Dee. The remaining part of the ‘other’ category consisted of moths (Lepidoptera), mainly Geometridae and several families of microlepidoptera, representing 3% of the ‘other’ category at the Dee and 2% at the Ythan, and dipterans, mostly those with aquatic larvae such as crane flies (Tipulidae), mosquitoes (Culicidae) and black flies (Simuliidae), representing 2% of the ‘other’ category at each of the two rivers.

In summary, the most important difference between the aerial insect faunas (with any relevance to bats) at the two rivers appeared to be the much higher abundance and biomass of small flies, particularly owl midges and gall midges, at the Ythan in July and in August–September.

DISCUSSION

The most striking feature of this study is the similarity between the two rivers in the bat and insect parameters measured. Of the 18 pairwise comparisons (Figs 3 & 4) only five were significantly different. The only significant difference in bat passes between the two rivers occurred in June and almost certainly resulted from between-river differences in weather. Temperatures below *ca* 10°C tend to reduce the flight activity of insects and of the bats that feed on them, particularly when combined with strong winds and/or rain (e.g. Rydell, 1989). Windy conditions also tend to reduce the catching efficiency of insect suction traps (Southwood, 1978). Fresh-to-strong north-westerly winds blew down the Ythan for much of the June sampling period. They coincided with relatively low evening temperatures (*ca* 9°C at dusk),

and sometimes with rain as well, and, therefore, presumably reduced the insect catches and bat counts alike. At the same time, the Dee river valley remained relatively sheltered behind the hills.

In July, the lactation period of the bats, the wind conditions were more normal and the air temperature was well above that which affects the activity of insects and bats negatively. Therefore, the weather was unlikely to have influenced the comparison between the rivers. The bat counts suggest that the Ythan supported similar numbers of bats to the Dee in July and during the post-lactation period in August–September.

The most striking difference in the insect faunas at the two rivers was the much higher densities of owl midges (Psychodidae) and gall midges (Cecidomyiidae) at the Ythan in July, leading to significant differences in insect biomass. Although these insects are mostly very small (*ca* 2–5 mm body length and 5–8 mm wingspan), they are eaten both by pipistrelles and Daubenton’s bats (Swift & Racey, 1983; Swift *et al.*, 1985). Gall midges live on land plants during their larval stages (Colyer & Hammond, 1968). Most owl midges have aquatic larval stages, which breathe through air-tubes and can survive in almost totally deoxygenated waters. Owl midges occur in ‘astronomical numbers’ in sewage filters and are also common in farm drains and similar places (Hynes, 1960). Therefore, the higher biomass of flying insects over the Ythan in July and August was most probably an effect of the abundance of nitrogenous material resulting from the density of livestock and the intensity of arable farming in the river valley, rather than one of eutrophication in the river itself.

The data suggest however, that the eutrophication level in the river Ythan has not yet reached the stage where the most sensitive caddis flies, e.g. *Agapetus* spp. (Butcher, Longwell & Pentelow, 1937), disappear, and is therefore below the stage where deoxygenation-tolerant chironomids start to increase in numbers. Thus, the current level of nutrient enrichment of the Ythan may be below those encountered by the bats observed by Kokurewicz (1995).

Vaughan, Jones & Harris (1996) recently found that pipistrelle bats foraging over streams and rivers in England spent more time and emitted more feeding buzzes upstream from sewage works than downstream, hence indicating a negative effect of organic pollutants on this species. At the same time, however, Daubenton’s bats appeared to react in the opposite way, since they emitted more feeding buzzes downstream. This result appears somewhat puzzling in view of the fact that pipistrelles and Daubenton’s bats feed predominantly on Diptera (Vaughan, 1997), but may reflect different types of pollution in the two studies. Furthermore, the number of feeding buzzes may not provide a good estimate of the food intake of bats, and may not necessarily be correlated with the insect abundance. This is because few feeding buzzes may indicate either a low food intake, or that the bats feed on larger insects, which may require more time for searching and handling, thus resulting in fewer capture attempts per unit time. Second, pipistrelles

and Daubenton's bats usually feed over rivers, at least in Scotland (Swift & Racey, 1983; Racey & Swift, 1985; Rydell, Bushby *et al.*, 1994), and their diets are virtually identical (Swift & Racey, 1983; Swift *et al.*, 1985). Therefore, we would expect changes in the insect faunas over rivers to affect these bat species in the same way.

At present, both pipistrelles and Daubenton's bats occur at high densities over the Dee as well as over the Ythan and other rivers in Scotland (Speakman, Racey, Catto *et al.*, 1991; Rydell, Bushby *et al.*, 1994). Hence, in view of the present population density (more than 100 active roosts are currently known from the Dee valley alone; Racey (1998) and unpublished), the supposed decline of pipistrelle bats in Britain over the past 30 years (40%; Stebbings in Harris *et al.*, 1995) does not appear to apply to our study area. Moreover, the pipistrelle was considered rare in the Dee valley 100 years ago (Sim, 1903), suggesting, if anything, that the populations have been increasing and/or spreading considerably over the past century. Overall, the striking feature of this study is the apparent similarity between the two rivers — a small eutrophic river can support as many bats and insects as a large oligotrophic one.

Acknowledgements

We acknowledge all the landowners who gave us access to their properties, and also W. and M. Milne, F. Porteous, J. Russ and A. Williams for assistance during the field work. We also thank H. Smith, J. Loman and M. R. Young for statistical advice, and C. Brönmark, R. Gerell, K. Lundberg, D. Raffaelli, J. Stensson and M. R. Young for many constructive comments. The North-east River Purification Board kindly provided help with background information and permitted us to use their unpublished data. The study was funded by a NERC grant GR9/1712A. J.R. also acknowledges supports from the Swedish Natural Science Research Council and Lunds Djurskyddsfond. L. B. was supported by a Nuffield Foundation Undergraduate Research Bursary.

REFERENCES

- Ahlén, I. (1981). *Identification of Scandinavian bats by their sounds*. Swedish University of Agricultural Sciences, Department of Wildlife Ecology, Report 6.
- Barlow, K. E. & Jones, G. (1996). *Pipistrellus nathusii* (Chiroptera: Vespertilionidae) in Britain in the mating season. *J. Zool., Lond.* **240**: 767–773.
- Barratt, E. M., Deaville, R., Burland, T. M., Bruford, M. W., Jones, G., Racey, P. A. & Wayne, R. K. (1997). DNA answers the call of pipistrelle bat species. *Nature, Lond.* **387**: 138–139.
- Bárta, Z., Cerveny, J., Gaisler, J., Hanák, I., Hurka, L., Miles, P., Nevrlý, M., Rumler, Z., Sklenár, J. & Zalman, J. (1981). Results of winter census of bats in Czechoslovakia 1969–1979. *Sb. Oresniho muz. v Moste* **3**: 71–116.
- Butcher, R. W., Longwell, J. & Pentelow, F. T. K. (1937). Survey of the River Tees, III. The non-tidal reaches. Chemical and biological. *Tech. Pap. Wat. Pollution Res., Lond.* **6**: 1–187.
- Cerveny, J. & Bürger, P. (1990). Changes in bat population sizes in the Sumava Mts (south-west Bohemia). *Folia Zool.* **39**: 213–226.
- Colyer, C. N. & Hammond, C. O. (1968). *Flies of the British Isles*. 2nd edn. London: Frederick Warne & Co.
- Daan, S. (1980). Long-term changes in bat populations in the Netherlands. *Lutra* **22**: 95–105.
- Harris, S., Morris, P., Wray, S. & Yalden, D. W. (1995). *A review of British mammals: population estimates and conservation status of British mammals other than cetaceans*. Peterborough: Joint Nature Conservancy Council.
- Hutson, A. M. (1991). European bats agreement approved. *Bat News* **23**: 4–5.
- Hynes, H. B. N. (1960). *The biology of polluted waters*. Liverpool: Liverpool University Press.
- Jones, G. & Rayner, J. M. V. (1988). Flight performance, foraging tactics and echolocation in free-living Daubenton's *Myotis daubentonii* (Chiroptera: Vespertilionidae). *J. Zool., Lond.* **215**: 113–132.
- Jones, G. & Rydell, J. (1994). Foraging strategy and predation risk as factors influencing emergence time in echolocating bats. *Phil. Trans. R. Soc. Lond. Ser. B* **346**: 445–455.
- Jones, G. & van Parijs, S. M. (1993). Bimodal echolocation in pipistrelle bats: are cryptic species present? *Proc. R. Soc. Lond. Ser. B* **251**: 119–125.
- Kokurewicz, T. (1995). Increased population of Daubenton's bat (*Myotis daubentonii* (Kuhl, 1819)) (Chiroptera: Vespertilionidae) in Poland. *Myotis* **32–33**: 155–161.
- Macdonald, A. M., Edwards, A. C., Pugh, K. B. & Balls, P. W. (1995). Soluble nitrogen and phosphorus in the river Ythan system, UK: Annual and seasonal trends. *Wat. Res.* **29**: 837–846.
- North-east River Purification Board (1993). *Water quality review*. Aberdeen: North-east River Purification Board.
- Park, K. J., Altringham, J. D. & Jones, G. (1996). Assortative roosting in the two phonic types of *Pipistrellus pipistrellus* during the mating season. *Proc. R. Soc. Lond.* **263**: 1495–1499.
- Racey, P. A. (1998). The importance of the riparian environment as a habitat for British bats. In *Behaviour and ecology of riparian mammals*: 69–91. Dunstone, N. & Gorman, M. L. (Eds). *Symp. zool. Soc. Lond.* no. 71. Cambridge: Cambridge University Press.
- Racey, P. A. & Swift, S. M. (1985). Feeding ecology of *Pipistrellus pipistrellus* (Chiroptera: Vespertilionidae) during pregnancy and lactation. I. Foraging behaviour. *J. Anim. Ecol.* **54**: 205–215.
- Raffaelli, D., Hull, S. & Milne, H. (1989). Long-term changes in nutrients, weed mats and shorebirds in an estuarine system. *Cah. Biol. Mar.* **30**: 259–270.
- Russ, J. M., O'Neill, J. K. & Montgomery, W. I. (in press). An increase in mammalian biodiversity — a maternity colony of roosting *Nathusius' pipistrelle* bat (*Pipistrellus nathusii* Keyserling & Blasius, 1839) in Ireland. *J. Zool., Lond.*
- Rydell, J. (1989). Feeding activity of the northern bat *Eptesicus nilssonii* during pregnancy and lactation. *Oecologia* **80**: 562–565.
- Rydell, J., Bushby, A., Cosgrove, G. C. & Racey, P. A. (1994). Habitat use by bats along rivers in north east Scotland. *Folia Zool.* **43**: 417–424.
- Rydell, J., Entwistle, A. & Racey, P. A. (1996). Timing of foraging flights in three species of bats in relation to insect activity and predation risk. *Oikos* **76**: 243–242.
- Sim, G. (1903). *The vertebrate fauna of 'Dee'*. Aberdeen: Wyllie & Son.
- Southwood, T. R. E. (1978). *Ecological methods*. 2nd edn. London: Chapman & Hall.
- Speakman, J. R., Racey, P. A., Catto, C. M. C., Webb, P. I., Swift, S. M. & Burnett, A. M. (1991). Minimum summer populations and densities of bats in N. E. Scotland, near the northern borders of their distributions. *J. Zool., Lond.* **225**: 327–345.
- Speakman, J. R., Racey, P. A., Hutson, A. M., Webb, P. I. & Burnett, A. M. (1991). Status of *Nathusius' pipistrelle* (*Pipistrellus nathusii*) in Britain. *J. Zool., Lond.* **225**: 685–690.

- Stebbins, R. E. (1988). *The conservation of European bats*. London: Christopher Helm.
- Swift, S. M. (1980). Activity patterns of pipistrelle bats (*Pipistrellus pipistrellus*) in north-east Scotland. *J. Zool., Lond.* **190**: 285–295.
- Swift, S. M., & Racey, P. A. (1983). Resource partitioning in two species of vespertilionid bats (Chiroptera) occupying the same roost. *J. Zool., Lond.* **200**: 249–259.
- Swift, S. M., Racey, P. A. & Avery, M. I. (1985). Feeding ecology of *Pipistrellus pipistrellus* (Chiroptera: Vespertilionidae) during pregnancy and lactation. II. Diet. *J. Anim. Ecol.* **54**: 217–225.
- van Helversen, O., Esche, M., Kretzschmar, F. & Boschert, M. (1987). Die Fledermäuse Südbaden. *Mitt. bad Landesverwaltung Naturkunde und Naturschutz* **14**: 409–475.
- Vaughan, N. (1997). The diets of British bats (Chiroptera). *Mamm. Rev.* **27**: 77–94.
- Vaughan, N., Jones, G. & Harris, S. (1996). Effects of sewage effluent on the activity of bats (Chiroptera: Vespertilionidae) foraging along rivers. *Biol. Conserv.* **78**: 337–343.
- von Frenckell, B. & Barclay, R. M. R. (1987). Bat activity over calm and turbulent water. *Can. J. Zool.* **65**: 219–222.
- Voûte, A. M., Sluiter, J. W. & van Heerdt, P. F. (1980). De vleermuizen stand in einige zuidlimburgse groeven sedert 1942. *Lutra* **22**: 18–34.
- Weinrich, J. A. & Oude Voshaar, J. H. (1992). Population trends of bats hibernating in Marl caves in the Netherlands (1943–1987). *Myotis* **30**: 75–84.
- Wetzel, R. G. (1983). *Limnology*. Saunders College Publishing.
- Wilkinson, L. (1990). *SYSTAT: the system for statistics*. Evanston, IL: SYSTAT Inc.
- Wright, C. G., Edwards, A. C., Morrice, J. G. & Pugh, K. B. (1991). North east Scotland river catchment nitrate loading in relation to agricultural intensity. *Chem. Ecol.* **5**: 263–281.