

Ecological impact of spider predation: a critical assessment of Bristowe's and Turnbull's estimates*

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Summary

Decades ago, Bristowe (1939, 1947, 1958) and Turnbull (1973) tried to quantify the ecological impact of spider predation upon insect populations by means of extrapolations. Both came to the conclusion that spiders, occurring in high numbers, would kill astronomical quantities of insects. Bristowe's and Turnbull's density and prey kill estimates have been quoted frequently in the arachnological literature; however, they have never been proven true or false. In this paper, these estimates are critically analysed in the light of current knowledge of spider ecology. Bristowe estimated that the annual prey kill of all British spiders would exceed the combined weight of all humans in Britain (which he assessed at $\approx 80 \text{ kg ha}^{-1}$). However, more recent comprehensive studies conducted on agricultural land have resulted in distinctly lower prey kill values ($\approx 1\text{--}40 \text{ kg ha}^{-1} \text{ yr}^{-1}$). Since Great Britain consists predominantly of agricultural land, it follows that Bristowe probably over-estimated the overall mean prey kill of the spiders. Turnbull's hypothetical calculation (based on a very high assumed average food consumption) resulted in a prey kill value of $42,500 \text{ kg ha}^{-1} \text{ yr}^{-1}$; this latter value is of the same magnitude as the net primary production, which is irreconcilable with ecological theory.

Introduction

Spiders are among the most abundant insectivorous predators of terrestrial ecosystems (Nyffeler & Benz, 1987; Wise, 1993). They have been reported to occur in peak numbers of more than 1,000 individuals per m^2 (Ellenberg *et al.*, 1986). At the same time, they are one of the most diverse arthropod orders, with over 30,000 species and exhibit a great variety of foraging strategies (Coddington & Levi, 1991; Foelix, 1996). The spiders' diet is made up primarily of insects from various taxa, and also of other spiders (Nyffeler, 1999). Eggs, larvae, and adults of many different insect pests are eaten by spiders (e.g. Whitcomb, 1974; Nyffeler *et al.*, 1990; Young & Edwards, 1990). Because of their high abundance and insectivorous feeding habits, spiders are suspected of playing an important role in the balance of nature (see reviews by Whitcomb, 1974; Gertsch, 1979; Luczak, 1979; Young & Edwards, 1990; Wise, 1993; Nyffeler *et al.*, 1994a,b).

Decades ago, two pioneers among arachnologists, W. S. Bristowe from England and A. L. Turnbull from Canada (both experts on the feeding and population biology of spiders), tried to quantify the ecological impact of spider predation by means of extrapolations, the annual feeding rate of an "average spider" being multiplied by the overall mean number of spiders per

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area unit. [This was basically the approach used by Darwin (1881) to demonstrate the enormous ecological impact of earthworms as decomposers in the soil.] Using this approach Bristowe and Turnbull both came to the conclusion that spiders kill astronomical numbers of insects.

Bristowe (1947) stated: "The spider population of England and Wales can, of course, only be guessed at. My guess is an average of 2.2 billions. At a very conservative estimate each spider destroys insects at the rate of a hundred per annum, so we arrive at a yearly insect consumption in England and Wales of 220,000,000,000,000 (two hundred and twenty billions)". With regard to this density estimate Gertsch (1979) concluded: "The overall effect of such a large fauna of predators must be a very significant one." Bristowe (1958) calculated that the weight of insects consumed by the entire British spider fauna would exceed the combined weight of all the humans in Britain. Wise (1993) commented on this: "The full implications of this finding are yet to be determined."

Another extravagant claim of this type was made by Turnbull (1973) in his review paper which laid the foundations of modern spider ecology. According to his estimate, the average total weight of food consumed per year by spiders would amount to 42,500 kg per hectare.

The density and prey kill estimates of these two researchers have been quoted in several standard works of spider biology (e.g. Stern & Kullmann, 1975; Gertsch, 1979; Wise, 1993; Foelix, 1996); however, they have never been proven true or false. In the following, these estimates will be critically analysed.

Methods

In order to find out whether the estimates of Bristowe and Turnbull relate to the real world, or whether they are pure speculation, they were compared with more comprehensive assessments made by other researchers (Teal, 1962; Kirchner, 1964; Kajak *et al.*, 1971; Van Hook, 1971; Robinson & Robinson, 1974; Luczak, 1975; Pühringer, 1979; Nyffeler, 1982; Imhasly & Nentwig, 1995). Some authors presented their data in terms of energy flow through the spider community (Table 1), and others as prey biomass killed (or ingested) in the course of a year per area unit (Table 2).

For purposes of comparison, all values (including those expressed in terms of energy flow) were converted to prey kill rates (in $\text{mg fresh weight m}^{-2} \text{ yr}^{-1}$, or in $\text{kg ha}^{-1} \text{ yr}^{-1}$). Values were converted, taking into account a prey water content of $\approx 75\%$ (see Hagstrum, 1970; Edgar, 1971; Humphreys, 1975) and a caloric equivalent of prey of $\approx 23.5 \text{ J/mg dry weight}$ (mean value from literature data, see Hagstrum, 1970; Moulder & Reichle, 1972; Pühringer, 1979). Thus, 1 mg fresh weight prey biomass equals approx. 5.875 J.

After having captured and killed a prey item, a large portion of its biomass is sucked out (i.e. ingested in fluid form) by the spider, whereas certain indigestible parts of the exoskeleton are discarded (Moulder & Reichle, 1972). Some authors assessed the quantity of food

Habitat, author(s)	Prey ingested (energy flow) $J \text{ m}^{-2} \text{ yr}^{-1}$	Prey killed (energy flow) $J \text{ m}^{-2} \text{ yr}^{-1}$	Prey killed (fresh weight) $\text{mg m}^{-2} \text{ yr}^{-1}$
Winter wheat field, Nyffeler (1982)			
Soil surface-dwellers	—	1,760–6,850*	300–1,166
Foliage-dwellers	—	50–650*	8–111
Combined	—	1,810–7,500	308–1,277
Winter wheat field, Imhasly & Nentwig (1995)			
Rye field, Łuczak (1975)	599–1,048*	749–1,310	127–223
Potato field, Łuczak (1975)	1,173*	1,466	250
<i>Festuca</i> grassland, Van Hook (1971)	28,324*	35,405	6,026
Salt marsh, Teal (1962)	117,320*	146,650	24,962

Table 1: Prey kill estimates originally presented as energy flow (original and converted values, respectively). *Original values as presented in literature.

ingested (e.g. Teal, 1962*; Van Hook, 1971; Łuczak, 1975), others the entire prey kill (e.g. Kirchner, 1964; Robinson & Robinson, 1974; Pühringer, 1979; Nyffeler, 1982; Imhasly & Nentwig, 1995). The assessments of Kajak *et al.* (1971) refer to food ingested in the case of the soil surface-dwelling spiders and to prey kill in the case of foliage-dwelling spiders. Food ingested values, if presented in the literature as such, were adjusted to prey kill rates by multiplication by a factor of 1.25, assuming that approx. 80% of the killed prey is ingested (see Edgar, 1971; Moulder & Reichle, 1972). The original values from the literature as well as those converted are presented in Tables 1 and 2.

Results and discussion

Prey kill of spiders (based on various authors)

In the following the estimates of Bristowe and Turnbull are compared with the data of other authors. The weight of prey killed by spiders per hectare per year in various habitat types is compiled in Table 3. The authors referred to in the table used in part very different methods in their assessments.

One group of authors estimated relatively high prey kill values (≈ 100 – $250 \text{ kg ha}^{-1} \text{ yr}^{-1}$) which refer to woodland, marshland, and unmanaged grassland (see Teal, 1962; Kirchner, 1964; Kajak *et al.*, 1971; Nyffeler, 1982). Kajak's group was studying a *Stellario-Deschampsietum* grassland, whereas the investigation of Nyffeler took place in a *Valeriano-Filipenduletum* grassland. These are largely undisturbed natural or semi-natural systems where spiders can forage and reproduce with little interference by man all year long. High prey kill ($\approx 160 \text{ kg ha}^{-1} \text{ yr}^{-1}$ by web-building spiders) was also estimated in an insecticide-free coffee plantation in the tropics; it was assumed that the estimated value of prey kill in this plantation might be about twice as high (roughly $300 \text{ kg ha}^{-1} \text{ yr}^{-1}$) if the hunting spiders were included in the assessment (see Robinson & Robinson, 1974).

A second group of authors, who conducted their studies in intensively managed meadows and crop fields,

*Teal's value was taken from an energy flow diagram; I have assumed that he assessed the food ingested, and not the entire prey kill.

found much lower values (≈ 1 – $10 \text{ kg ha}^{-1} \text{ yr}^{-1}$) (see Łuczak, 1975; Nyffeler, 1982; Imhasly & Nentwig, 1995). These are habitats in which spider populations are affected drastically by various agricultural practices such as mowing, grazing, combine harvesting, ploughing, fertilising, and application of pesticides (see Kajak, 1978; Łuczak, 1979; Young & Edwards, 1990; Gibson *et al.*, 1992). Such highly disturbed systems are colonised primarily by small-sized pioneer species (Linyphiidae). Though they may occur in high numbers, their combined biomass remains low, resulting in reduced energy flow (see Łuczak, 1975; Kajak, 1978). The maximum estimates of spider prey kill in crop fields ($\approx 10 \text{ kg ha}^{-1} \text{ yr}^{-1}$) refer to conditions where no insecticides were applied (see Imhasly & Nentwig, 1995; Nyffeler, unpubl.). Prey kill values of the same magnitude as in crop fields were recorded in the *Phragmites* reed belt of a European lake (Pühringer, 1979).

A third group of authors found intermediate values, which refer to less intensively managed grassland habitats. The prey kill of spiders in a meadow of the Arrhenatheretalia type, mown twice a year, was estimated at approx. $40 \text{ kg ha}^{-1} \text{ yr}^{-1}$ (Kajak *et al.*, 1971). For comparison, the spiders inhabiting a *Festuca* grassland which had not been managed for several years, were estimated to kill approx. $60 \text{ kg ha}^{-1} \text{ yr}^{-1}$ (Van Hook, 1971).

Bristowe's estimate compared with data of other authors

Bristowe based his assessment of spider predation on the assumption that the total number of spiders in England and Wales would amount to 2.2 billion individuals. This enormous number (which relates to a geographical area of approx. $150,000 \text{ km}^2$) corresponds to 14.5 individuals per square metre. In Table 4 this figure is compared with the density estimates of various British authors. It must be borne in mind that several different collecting methods were used, each having its bias (see Duffey, 1962, 1974, pers. comm.). This comparison shows that Bristowe's value is approx. ten times lower than the overall mean value presented in the table (14.5 vs. 152.1 individuals m^{-2}); thus, the estimate of 2.2 billion spiders for England

Habitat, author(s)	Prey ingested (dry weight) mg m ⁻² yr ⁻¹	Prey killed (dry weight) mg m ⁻² yr ⁻¹	Prey killed (fresh weight) mg m ⁻² yr ⁻¹
Arrhenatheretalia meadow, Kajak <i>et al.</i> (1971)			
Soil surface-dwellers	840*	1,050	4,200
Foliage-dwellers	—	54*	220
Combined	—	1,104	4,420
Stellario-Deschampsietum, Kajak <i>et al.</i> (1971)			
Soil surface-dwellers	2,630*	3,288	13,152
Foliage-dwellers	—	2,482*	9,930
Combined	—	5,770	23,082
<i>Phragmites</i> reed belt, Pühringer (1979)	—	—	600–1,200*
Valeriano-Filipenduletum, Nyffeler (1982)	—	—	>15,000*
Woodland, Kirchner (1964)	—	—	10,000*
Insecticide-free coffee plantation, Robinson & Robinson (1974)	—	—	16,000*

Table 2: Prey kill estimates originally presented as prey biomass (original and converted values, respectively). *Original values as presented in literature.

and Wales must be considered a very conservative estimate.

The question arises as to what Bristowe intended to show with his claim that the weight of insects consumed by the entire British spider fauna exceeds the combined weight of all the humans in Britain. To answer this question we need to know the weight of the human population of Great Britain at the time when Bristowe made his assessment. In one of his books he stated that the weight of the human population of Great Britain would amount to 32.8 kg per acre, or 81 kg ha⁻¹ (see Bristowe, 1939). Thus, he was suggesting that the British spider fauna would capture more than 80 kg fresh weight prey per hectare per year.

This figure is of the same magnitude as the prey kill estimates of some other researchers who studied natural or semi-natural habitats (see Teal, 1962; Kirchner, 1964; Kajak *et al.*, 1971), whereas considerably lower values were found in agroecosystems (see Łuczak, 1975; Imhasly & Nentwig, 1995). As indicated in Table 3, prey kill values vary considerably depending on the habitat type investigated. It is therefore crucial to examine the percentage cover of different habitat types in Britain when considering whether low or high spider predation impact can be expected.

The land area of Great Britain is covered by approx. 30% arable land and approx. 50% managed grassland. Less than 10% of Britain is covered by woodland. A little over 10% is covered by roads, buildings and industry (E. Duffey, pers. comm.); some spider species have adapted to living in man-made structures (Bristowe, 1939; Duffey, 1997). These land coverage percentages have not changed drastically since the time when Bristowe wrote (see “Agricultural Statistics—England and Wales”, June Census for the yrs 1930–1996, published by the Ministry of Agriculture, Fisheries and Food, London). Thus, the British landscape was (and is) dominated to about 80% by habitat types (i.e. disturbed systems) in which the spiders are assumed to have reduced predation impact (Table 3), suggesting that the overall mean prey kill of British spiders may be rather low.

To demonstrate this quantitatively, the weighted average prey kill of the spiders of Great Britain was calculated based on prey kill estimates of other researchers for four habitat types, the percentage cover of these habitat types being used as weighting factors. The data used in this calculation refer to European studies which had been done in cereal fields not treated with insecticides and in Arrhenatheretalia meadows

Habitat type	Prey kill kg ha ⁻¹ yr ⁻¹	Reference
Average value, World	≈42,500	Turnbull (1973)
Average value, UK	>80	Bristowe (1958)
Woodland, Europe	≈100	Kirchner (1964)
Salt marsh, USA	≈250	Teal (1962)
Insecticide-free coffee plantation, New Guinea	≈160(–300)	Robinson & Robinson (1974)
Unmanaged grasslands (Stellario-Deschampsietum and Valeriano-Filipenduletum, respectively), Europe	≈150–230	Kajak <i>et al.</i> (1971); Nyffeler (1982)
<i>Festuca</i> grassland (old field), USA	≈60	Van Hook (1971)
Arrhenatheretalia meadow (mown twice a year), Europe	≈40	Kajak <i>et al.</i> (1971)
<i>Phragmites</i> reed belt, Europe	≈5–10	Pühringer (1979)
Intensively managed meadows (mown 4–6 times a year) and agricultural fields, Europe	≈1–10	Łuczak (1975); Nyffeler (1982); Imhasly & Nentwig (1995)

Table 3: Estimated prey kill (fresh weight per hectare per year) by spiders in various habitats (based on data from Tables 1 and 2; values rounded).

mown (only) twice a year (see Kajak *et al.*, 1971; Nyffeler, 1982; Imhasly & Nentwig, 1995); these studies may compare with the conditions of less intensive agriculture between 1930 and 1960 when Bristowe wrote. Based on these data a weighted average prey kill of the order of $30 \text{ kg ha}^{-1} \text{ yr}^{-1}$ was found (Table 5). [If we consider that today's agriculture is managed in a distinctly more intensive manner, meadows being mown 4–6 times a year and cereal fields sprayed with insecticides (which is having negative effects on spider populations), it follows that the weighted mean prey kill of the spiders in modern times is likely to be less than $30 \text{ kg ha}^{-1} \text{ yr}^{-1}$.] This value is much lower than the $80 \text{ kg ha}^{-1} \text{ yr}^{-1}$ claimed by Bristowe, which means that his claim, that the weight of insects consumed by the entire British spider fauna exceeds the combined weight of all the humans in Britain, was an exaggeration. Nevertheless, his assessment of the impact of spider predation is not entirely unrealistic when compared with the estimates of some other researchers (see Teal, 1962; Kirchner, 1964; Kajak *et al.*, 1971; Nyffeler, 1982).

Turnbull's estimate compared with data of other authors

According to Turnbull's calculation the average prey kill by spiders is:

$$[131 \text{ ind. m}^{-2}] \times [89 \text{ mg ind.}^{-1} \text{ d}^{-1}] \times [365 \text{ d yr}^{-1}] = \\ 4.25 \text{ kg m}^{-2} \text{ yr}^{-1} = 42,500 \text{ kg ha}^{-1} \text{ yr}^{-1}.$$

His hypothetical calculation yields a value which is higher than any other estimate by a factor of more than 100 (Table 3). His calculation is based on the assumptions that: (1) the overall mean spider density is 131

individuals m^{-2} , (2) an "average spider" captures daily $\approx 89 \text{ mg}$ prey, (3) spiders feed at a constant rate all year long. In the following these assumptions are analysed.

First, Turnbull used an overall mean spider density of 131 ind. m^{-2} in his evaluation (based on data from 37 different literature sources). A comparison of this figure with the density values published by various British researchers (Table 4) suggests that Turnbull's estimate of average spider numbers is quite accurate. Similar values have also been reported for other geographical areas (see Nyffeler, 1982; Ellenberg *et al.*, 1986; Curry, 1994).

Secondly, he used Robinson & Robinson's (1970) data on the feeding rate of a tropical orb-weaver of the genus *Argiope*. These are large spiders, which can reach a body weight of about 500 mg. Most spiders, however, are much smaller and lighter. In the temperate and northern zones, spider communities consist mainly of dwarf spiders (family Linyphiidae), which weigh only 1–3 mg (see Nyffeler & Benz, 1987, 1988). Small-sized individuals from other families dominate the spider communities in more southern latitudes (e.g. Nyffeler *et al.*, 1987). It is generally known that individuals of small size (including large percentages of immatures) numerically dominate spider faunas in the field (see Moulder & Reichle, 1972; Luczak, 1975; Nyffeler, 1982). Such small-sized spiders have a very low individual feeding capacity. Since spiders in general are known to consume daily the equivalent of approx. 10–20% of their own body weight (Foelix, 1996), one can assume that a linyphiid of 1–3 mg weight usually feeds at a rate of $<1 \text{ mg}$ per day. The very low feeding rate of these tiny spiders has been confirmed by visual observations in the

Habitat type	Spiders m^{-2}	Collection and extraction method	Reference
Grassland (undisturbed)	101	Tullgren funnel	Ford (1935)
Grassland (cut)	62	Hand collecting	Bristowe (1939)
Grassland (cut)	161	Hand collecting	Bristowe (1939)
<i>Dactylis</i> grassland (undisturbed)	171–560	Hand collecting	Bristowe (1939)
Grassland plots	39–171	Flotation	Baweya (1939)
Grassland (grazed)	142	Flotation	Salt <i>et al.</i> (1948)
Oak-beech forest litter	15–110	Tullgren funnel	Gabbutt (1956)
Oak forest (all strata)	2–53	Tullgren funnel, beating, and sweeping	Turnbull (1960)
Rough sheep pasture	38–215	Hand collecting	Roy (1961)
Limestone grassland (<i>Festuca turf</i>)	320–842	Lateral heat extraction	Duffey (1962)
Limestone grassland (<i>Brachypodium</i> sward)	130–400	Lateral heat extraction	Duffey (1962)
Limestone grassland (grazed)	29–77	Lateral heat extraction	Cherrett (1964)
Moorland (<i>Calluna/Eriophorum</i>)	133–155	Lateral heat extraction	Cherrett (1964)
Moorland (<i>Juncus squarrosum</i>)	213–470	Lateral heat extraction	Cherrett (1964)
Moorland (<i>Festuca/Nardus</i>)	283–482	Lateral heat extraction	Cherrett (1964)
Grassland (cut)	77	Suction trap	Southwood & van Emden (1967)
Grassland (undisturbed)	69	Suction trap	Southwood & van Emden (1967)
Chalk grassland (undisturbed)	253	Tullgren funnel	Morris (1968)
Chalk grassland (grazed)	22	Tullgren funnel	Morris (1968)
Chalk grassland (grazed)	12	Hand collecting	Duffey (1974)
Chalk grassland (mown once a year)	35	Hand collecting	Duffey (1974)
Chalk grassland (undisturbed)	53–62	Hand collecting	Duffey (1974)
Grass heath (extensively grazed)	234	Tullgren funnel	Workman (1978)
Cereal fields	≈ 12 –103	Suction trap and hand collecting	Sunderland (1987)
Cereal fields	≈ 10 –120	Suction trap and hand collecting	Topping & Sunderland (1994)
Overall mean \pm SE	152.1 ± 28		

Table 4: Spider numbers per square metre in various habitats in Great Britain.

Habitat type	Land use (%)	Prey kill kg ha ⁻¹ yr ⁻¹	Reference
Arable land	30	10	Imhasly & Nentwig (1995) (data for winter wheat)
Meadows, pastures	50	40	Kajak <i>et al.</i> (1971) (data for mown meadow)
Woodland	7	100	Kirchner (1964)
Other land	13	10	Value arbitrarily chosen (based on Nyffeler's [1976] data for urban areas)
Total	100	—	—
Weighted average (WA)*	—	31.3	Nyffeler (unpubl.)
For comparison, Bristowe's estimate (average prey kill)	—	>80	Bristowe (1958)

Table 5: Estimated weighted average prey kill of the spiders of Great Britain based on data from literature (percentage cover of British land area by different habitat types used as weighting factors). *WA=(0.30 × 10)+(0.50 × 40)+(0.07 × 100)+(0.13 × 10)=31.3.

field (see Nyffeler & Benz, 1988). This suggests that the “average spider” is feeding at a much lower rate than the amount assumed in Turnbull’s calculation. He himself admits that: “... *Argiope argentata* is a larger than average spider and 0.089 g is probably more than the average daily consumption of food by spiders”.

Thirdly, the activities of spiders are strongly affected by the weather. Especially in the northern and temperate zones spiders have to adjust to the harsh conditions of the winter season which is characterised by cold, dampness, flooding, snow, lack of food, etc. (see Foelix, 1996). Only a small percentage of spiders are “winter active” (see Aitchison, 1987; Schaefer, 1987). Most spiders go without food during the winter months. The aspect of reduced feeding during the winter in parts of the world was not taken into consideration in Turnbull’s evaluation.

These points can be summarised as follows: Turnbull used density estimates which are realistic, but highly overrated the average annual feeding rate of spiders. He therefore produced a prey kill estimate that is much too high.

The 42,500 kg prey ha⁻¹ yr⁻¹ (=4.25 kg m⁻² yr⁻¹), claimed by Turnbull, corresponds to an energy equivalent of ≈25,000 kJ m⁻² yr⁻¹ (assumption: 1 kg fresh weight equals ≈5,875 kJ; see Methods section). For comparison, the net primary production of agricultural fields, grassland, marshland, and woodland usually

ranges from ≈5000 to 50,000 kJ m⁻² yr⁻¹ (Table 6). This suggests that Turnbull’s value is of the same magnitude as the net primary production of terrestrial ecosystems. According to energy flow studies, only a very small fraction (approx. 1%) of the net primary production is available to carnivorous animals, including spiders (see Odum, 1971; Van Hook, 1971; Ellenberg *et al.*, 1986). In conclusion, Turnbull’s estimate of 42,500 kg is much too high, irreconcilable with ecological theory.

Conclusions

(1) Bristowe’s claim that the weight of insects consumed by the entire British spider fauna exceeds the combined weight of all the humans in Britain, must be considered an exaggeration. Nevertheless, his prey kill estimate (of more than 80 kg ha⁻¹ yr⁻¹) is within the range of values published by various authors, indicating that his idea was not entirely unrealistic.

(2) Turnbull’s hypothetical calculation of the global spider prey kill, based on the assumption of an excessively high average annual feeding rate, yielded a value which is physically an impossibility.

(3) Estimates of spider prey kill published by various authors vary strongly depending on the habitat type investigated. The highest realistic estimates are of the order of approx. 200 kg ha⁻¹ yr⁻¹. Such high values indicate that spiders may indeed exert high predation pressure under conditions favourable to them, though Greenstone (1978) cautioned that the facts that spiders can achieve phenomenal densities and consume huge quantities of insects are not sufficient on their own to demonstrate a significant role for them in the regulation of insect populations.

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	kJ m ⁻² yr ⁻¹	Reference
Prey kill of spiders:		
Global value	≈25,000	Turnbull (1973)
Net primary production:		
Old field, USA	≈5,000	Van Hook (1971)
Soybean fields, Canada	≈10,000	Odum (1971)
Oak pine forest, USA	≈21,000	Odum (1971)
Rice fields, Japan	≈23,000	Odum (1971)
Winter wheat fields, Switzerl.	≈25,000	B. Feil (unpubl.)
Potato fields, Switzerl.	≈25,000	B. Feil (unpubl.)
Beech forest, Germany	≈29,000	Ellenberg <i>et al.</i> (1986)
Young pine plantation, UK	≈31,000	Odum (1971)
Salt marsh, USA	≈34,000	Teal (1962)
Sugar cane fields, Hawaii	≈50,000	Odum (1971)
Mature rain forest, Puerto Rico	≈54,000	Odum (1971)

Table 6: Turnbull’s estimate (42,500 kg ha⁻¹ yr⁻¹=approx. 25,000 kJ m⁻² yr⁻¹) compared with net primary production of terrestrial ecosystems.

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Sixteen hundred new county records of British spiders

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Summary

A list of about sixteen hundred new county records of British spiders is presented, recorded during the period between June 1994 and June 2000.

Introduction

The county records which follow are additions to those shown on the distribution maps in Locket, Millidge & Merrett (1974) and in subsequent published lists (Merrett, 1975, 1982, 1989, 1995), and have been recorded during the period between June 1994 and June 2000. The counties listed are those which existed before the boundary revisions of April 1974. Records for islands are treated as described in Locket *et al.* (1974: 132). The nomenclature and species order is the same as that used in the revised check list by Merrett & Murphy (2000).

The list includes both published and unpublished records, the principal contributors of the latter being Martin Askins, John Crocker, Stan Dobson, Tom Faulds, Adrian Fowles, Peter Harvey, Dick Jones, Michael Kilner, Edward Milner, David Nellist, Jennifer Newton, Wayne Rixom, Craig Slawson, Jim Stewart and Jim Wright. Many valuable records have also been contributed by other collectors who are too numerous to name, but I wish to thank them all.

Although records are being collected on a 10 km square basis for the spider recording scheme, I think it is still worthwhile to continue keeping the county records up-to-date, and I should therefore be pleased to receive any additional new county records for publication in future lists.

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Family Atypidae

A. affinis Suff., Chesh., Caern.

Family Dysderidae

D. crocata Heref.

Family Uloboridae

H. paradoxus Somer., Dorset, Heref.

Family Scytodidae

S. thoracica Heref., Worcs., Shrops., Leics.

Family Nesticidae

N. celullanus Suff., Heref., Worcs., Warw., Monm., Brecon

Family Pholcidae

P. phalangioides Leics., Notts., Chesh., Montgom.

Family Theridiidae

E. angulatus Heref., Warw., Notts., Pembs., Denbigh

P. simoni Beds., Worcs., Pembs.

E. truncatus Essex, Warw., Glam., Caern.

Family Segestriidae

S. senoculata Brecon, Radnor

E. flavomaculata Heref., Warw., Monm., Down

S. bavarica Hants., Anglesey

D. inornata Suff., Cards.

S. florentina Somer., Essex

C. guttata Heref., Montgom.

S. phalerata Heref., Notts., Lancs., Monm., Brecon

Family Oonopidae

O. pulcher Wilts., Heref., Islay

O. domesticus Wilts., Radnor

Orchestina sp.? Essex

Family Mimetidae

E. cambridgei Heref., Brecon, Radnor, W.

Lothian, E. Lothian

E. furcata Islay

E. aphana Hants., Surrey

E. tuberculata Warw.