British Arachnological Society

The Newsletter No. 89 November 2000

Killing Power of the Orb-weaving Spider *Argiope bruennichi* (Scopoli, 1772) During a Mass Occurrence

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Argiope bruennichi (Scopoli, 1772) is one of Europe's largest and most conspicuous orb-weaving spider species. The female, 14–17 mm in length, reaches adulthood some time in late July, at which time it spins nearly vertical orb-webs, about 25 cm diameter, near ground level amongst tall grass (Wiehle, 1931). The species is sometimes found in large numbers locally. Mass occurrences of *A. bruennichi* have been repeatedly reported in the literature (Wiehle, 1931; Lohmeyer & Pretscher, 1979; Malt, 1996). An incidence of this type was witnessed by Lohmeyer & Pretscher (1979) during the exceptionally warm and dry summer of 1976 near Bonn, Germany in an old field of uncut grassland heavily infested with weeds: average numbers of 6 per m^2 were recorded in mid-August. (This figure refers to adult females found in webs.) Because adult females spin orbs with an average catching area of about 500 $\pm$ 36 cm^2 [mean $\pm$ SE] (see Nyffeler, 1982), one can extrapolate that the combined web area spun daily by the *A. bruennichi* population near Bonn may have been approximately 3,000 $m^2\,ha^{-1}$ grassland during August and September (except for rainy days). Such a huge web area would be expected to exert an enormous predation pressure on insects. Here I attempt to quantify the killing power of *A. bruennichi* during a mass occurrence, such as the one witnessed near Bonn.

Potential killing power

Large orb-weaving spiders have been observed to kill prey in excess of their nutritional needs ('superfluous killing' *sensu* Smith & Wellington (1986) and Riechert & Maupin (1998)). A single orb-web can catch up to 1,000 small insects per day (Kirchner, 1964; Naton, 1976). Maximum capture rates of up to seven medium-sized grasshoppers $web^{-1}\,day^{-1}$ by *A. bruennichi* have been recorded in the field (Nyffeler, 1982). Grasshoppers are the favourite food of *A. bruennichi* at many locations (Wiehle, 1931; Lohmeyer & Pretscher, 1979; Nyffeler, 1982; Malt, 1996). By multiplying the maximum killing capacity per web with the maximum web density reported in the literature, we get an idea of the magnitude of the killing power of these spiders occurring at high densities. Hence, large orb-weaving spiders during a mass occurrence theoretically could kill:

$$[7 \text{ grasshoppers } web^{-1}\,day^{-1}] \times [60{,}000 \text{ webs } ha^{-1}] = 420{,}000 \text{ grasshoppers } ha^{-1}\,day^{-1}.$$

The grasshopper species referred to have an estimated average fresh weight of about 145 mg per individual (see Malt, 1996) and the combined weight of 420,000 grasshoppers $ha^{-1}\,day^{-1}$ is therefore roughly 60 kg $ha^{-1}\,day^{-1}$.

During a dry summer (i.e. rain-free apart from sporadic evening thunderstorms), an orb- weaver population is expected to catch prey uninterruptedly for 61 days (in August and September), whereas their activities may be limited to about 40 days under less favourable weather conditions (see Malt, 1996). Hence, by multiplying the daily prey biomass (60 kg $ha^{-1}\,day^{-1}$) with the number of days available for foraging one would expect a theoretical maximum prey kill of around 3,660 kg $ha^{-1}\,season^{-1}$ during a dry summer (and about 2,400 kg $ha^{-1}\,season^{-1}$ under less favourable weather conditions). The estimate of 2,400–3,660 kg prey $ha^{-1}\,season^{-1}$ is purely speculative.

Nevertheless, this hypothetical calculation demonstrates the enormous potential killing power of these orb-weaving spiders (regardless of whether or not this potential is fully achieved in the real world).

Actual killing power

What then is the actual prey kill of *A. bruennichi* during a mass occurrence? Considering the food requirements of an adult female and assuming that these requirements were met in the investigated grassland near Bonn during the summer of 1976, I would expect an actual prey kill of around 200–300 kg ha^{-1} $season^{-1}$. This assumes that an average adult female catches 80–90 mg prey web^{-1} day^{-1} for 40–60 days in August/September. This estimate is based on 10–17 webs (depending on availability) of adult females monitored from 09.00 to 18.00 hours on three consecutive days in early August 1976 in a field study near Zurich (Nyffeler, 1982). At this prey capture rate, adult females of *A. bruennichi* appeared well-fed (Nyffeler, unpublished). However, in Lohmeyer & Pretscher's (1979) study the adult females were of noticeably small body size which indicates that they were feeding below their requirements. It seems that during a mass occurrence of large orb-weaving spiders a predation pressure is exerted of such proportions that prey numbers inevitably collapse (because of overexploitation of the food resources owing to intraspecific competition: see Kajak *et al.* (1968)). Hence it follows that the underfed population near Bonn was catching prey at a much lower rate than the well-fed adult females near Zurich which occurred at 12–20 times lower densities, which suggests that the prey kill was in reality less than 200 kg ha^{-1} $season^{-1}$. Malt (1996) estimated that the prey kill of an *A. bruennichi* population during a mass occurrence near Jena, Germany, was about 85 kg ha^{-1} $season^{-1}$. Usually spider numbers are reduced significantly in the year following a mass occurrence (see Wiehle, 1931; Lohmeyer & Pretscher, 1979; Malt, 1996).

Conclusions

Because of the limitation of the food supply, extraordinarily high prey kill, as theoretically predicted by Turnbull (1973), is unlikely to be found in nature (at least not in the case of *Argiope* spp., which depend almost exclusively on larger-sized insects as a food source). For the sake of argument one could assume an ecosystem with unlimited food supply (e.g., due to allochthonous input, see Polis & Hurd, 1996). In such a scenario, excessive feeding would presumably be followed by the spiders spinning webs of smaller size and/or rebuilding them less frequently (see Witt *et al.*, 1968). (The spider is no longer hungry and consequently the amount of energy invested into foraging is reduced.) Here again mechanisms come into play that would set limits. The upper limit of the prey kill estimates published in the literature are of the order of 200 kg ha^{-1} yr^{-1} (see Robinson & Robinson, 1974; Nyffeler, 2000). It cannot be ruled out, however, that there are systems somewhere, so far undiscovered, where large orb-weaving spiders, occurring at high densities, are filtering huge numbers of mosquitoes, caddis flies, stoneflies, mayflies and other tiny insects from the aerial plankton originating from nearby aquatic ecosystems. In such situations the prey biomass killed by spiders may exceed the values previously reported in the literature. Evidently large orb-weaving spiders can exert significant predation pressure on insect populations (see Kajak *et al.*, 1971; Nyffeler & Benz, 1989; Malt, 1996), even though only a fraction of their enormous killing potential (of 2,400–3,660 kg prey ha^{-1} $season^{-1}$) is achieved in the real world.

There is also indirect evidence for the significance of orb-weaving spider predation: quite a number of insect species have evolved morphological and/or behavioural adaptations to reduce the risk of being entrapped in spider webs (see Eisner *et al.*, 1964; Nentwig, 1982). Wise (1993) commented '. . . spider predation has been intense enough to mold the evolution of prey characteristics.'

Acknowledgements

I would like to thank Drs Matt Greenstone, Christian Kropf and Keith Sunderland for helpful comments.

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