2005. The Journal of Arachnology 33:826–849

THE EMERGENCE OF MANIPULATIVE EXPERIMENTS IN ECOLOGICAL SPIDER RESEARCH (1684–1973)

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ABSTRACT. The history of spider ecology is discussed from its early beginnings in 1684 when the natural historian Martin Lister published his observations, to the post-war period up until 1973 when ecological spider research gathered momentum. While there have been many important observations since Lister, spider ecology appeared explicitly in the titles of papers only after the turn of the 20th century. However, much of what was published up until the 1950s is of little scientific value because these works contained natural history notes and conjecture, not manipulative experimentation. The exception was a paper written in 1939 by Pontus Palmgren who was not an ecologist but paradoxically a functional anatomist with a particular interest in ornithology. His paper was in the spirit of Ernst Haeckel's original definition of ecology that was seen as synonymous with physiology, a legacy that was detected in many of the papers decades after Palmgren. However, there was little evidence that ecological theory was being tested. Instead, theoretical inputs were largely ignored with most spider ecologists preferring to pursue the somewhat circular interest of basic observational studies. Eventually after some considerable delay, Charles Elton's theories of the niche and succession fed into spider ecology but the papers were often weak and invariably flawed due to the absence of experimental manipulations. Notably, it was not until the 1950s, when the elegant experiments of Edwin Nørgaard who manipulated the system in order to understand the interactions between spiders and their environment, that scientific spider ecology began. Edwin Nørgaard should be credited as the father of 'spider ecology', although Matthias Schaefer and Sven Almquist also made important contributions to the field and should not be overlooked. These researchers employed manipulative techniques during a period in which this experimental approach was not widely used in spider ecology. I conclude this review with a look to the future and predict that model selection will become much more prevalent, although it will never replace manipulative experimentation. One outstanding issue that has remained since 1684 has been the gift of ecological theory to the wider scientific community. Although spider ecologists have received theoretical frameworks from other disciplines such as botany and entomology, they have never reciprocated although they are now well placed to do so.

Keywords: Ecology, Nørgaard, inductive method, history of science

In this review, the aim is to trace the early advances in spider ecology to individual authors who were instrumental in shaping our current understanding of ecology as a modern science. The motivation for this paper is to reveal to the ecological community some of the best early research in the first half of the 20th century when it is believed that ecological spider experiments really began. This period has remained elusive to most researchers, because the majority of ecological literature pre-1970 is not available electronically and ecological research tends to have a short citation life-time which rarely extends beyond a decade. For example, there are two excellent, but very similar experiments on orientation in *Frontinella communis* (Hentz 1850) (Linyphiidae). The first by Pointing (1965) was not picked up by Suter (1981) or those who did the peer review and editing, simply because the reference was not in general electronic circulation (Robert Suter pers. comm.). This is not especially embarrassing because for most authors there has rarely been a need to look deep into the scientific literature—in fact, ecological journals positively discourage it.

Contrast this experience in ecology with that of spider taxonomy in which investigators can turn to a series of catalogues that list nearly all the publications since Clerck in 1757 (e.g., Platnick 2005). Taxonomists have the expectation that all important texts will be cited independent of date of original publication, even if a paper is drawn from the eighteenth century. Ecology would sometimes do well to embrace the citation ethos that taxonomy is unique in upholding. There is a strong argument to suggest that ecology may have come out of the doldrums much more quickly if studies were read, cited and then developed further. Instead, it seems that many of the individuals working during the embryonic phase in spider ecology, studied in isolation with few, if any, academic exchanges.

Ecology could be described as a new science because it is less than 150 years old and, for example, only one tenth the age of ''Aristotelian'' taxonomy. Its formal beginnings were in 1866 when this new branch of science was erected by Ernst Haeckel, a German invertebrate zoologist. Haeckel coined the word ''ecology'' in his book ''Generelle Morphologie der Organismen'' from the Greek, ''oikos'' meaning the study of the home. Ecology has always been defined quite loosely, but in this review it is defined as the scientific study of the abiotic (e.g., temperature) and biotic (e.g., competition) interactions between organisms and their natural environment. Implicitly, ecology contains a field component and is not purely laboratory based.

Defining ecological spider research as scientific.—There is a need to make objective judgments about which papers have scientific merit, versus those that have no scientific merit. To assess papers for scientific merit, there is a need to be clear about what parameters underpin science. Although there is general agreement that the first scientist was the 6th century B.C. Greek Thales of Miletus, the scientific method with which we are familiar today evolved during a revolution of thinking during the 16th century onwards. Ecologists generally follow the scientific protocol known as the inductive method, rather than the classical deductive method practiced by a handful of Bayesian ecologists and the great majority of physicists (Popper 1977; Murray 2001; Oksanen 2001). This distinction is important because ecologists are often not aware of the dichotomy between these approaches or the implications of applying either approach to their research. The replicated, randomized designs typical of the inductive methods are a vital tool to ecologists who will find the pervasive use of universal laws an anathema—the reverse is true for a deductivist. Oksanen (2001) criticizes such a clear distinction arguing for the hybrid approach in which ecologists switch scientific philosophies depending on the scale of the system and the constraints on replication and randomization. In the current climate, he has mild (Cottenie & De Meester 2003) or no support (Hurlbert 1984, 2004), but it will be interesting to see how, or indeed if, this debate will change the way ecological experiments are done in the future. Unlike physics, nearly all ecologists will argue that ''laws'' are absent from ecology because organisms cannot so easily be pigeon-holed. Consider the statement that ''all spiders are entirely carnivorous in the presence of a diversity of prey.'' This was the perceived view until very recently when it was found that a small minority of spiders intentionally supplement their diet with nectar and pollen (Jackson et al. 2001; Ludy 2004). That is not to say that all of ecology is without basic rules, since theorems are often used and are sometimes law-like in nature (Turchin 2001).

Not all ecologists are theory driven, but all recognize that ecology is empirical and therefore implicitly include at least one experiment. It is strongly argued by many that experimental ecology should include a hypothesis to formalize the procedure (Wise 1993 and see Ricklefs & Miller 1999 for approach). The approach to formalizing a hypothesis is poorly defined, not least because there are multiple opinions of what constitutes a hypothesis (Platt 1964; Connor & Simberloff 1986). In the context of this paper, I simply refer to hypotheses as questions or statements that are to be tested, accepting that this definition is not all-encompassing. Classically, hypotheses were of the null form (i.e., statement of no relationship; a negative statement), which have been heavily criticized in ecology and are now not widely used (Quinn & Dunham 1983; Turchin 1999; Anderson et al. 2000; Murray 2001). Instead, science now encompasses many variants including statistical (i.e., the use of predictors and probabilities to evaluate relationships) and alternative hypotheses (i.e., statement of a relationship; a positive statement), all of which I consider valid for the purpose of this review (Platt 1964; Johnson 1999; Anderson et al. 2000).

Ecological research that has gained the most credibility has been that which includes manipulative experiments to control more clearly the effects of a variable on a subject (Hairston 1989; Wise 1993; Ricklefs & Miller 1999; Hurlbert 2004). Without manipulation, ecology becomes very generalized and has very little explanatory power because it lacks the appropriate conditions and controls. Such studies that are without manipulation can only be suggestive, rather than explicit tests of hypotheses and tend to be observational. Observational studies occupy a ‘‘half-way house’’ between natural history and formal science (Lubchenco & Real 1991; Wise 1993). Observational studies have an empirical basis, but no treatment structure and represent much of what spider ecologists practice. While this method is not a test of a hypothesis, it forms the essential groundwork for later explicit testing and is a valuable scientific tool as long as the results are not overstated.

There is a need to make a distinction between ecology and other related disciplines. Natural history and faunistics often purport to be a branch of ecology and are sometimes referred to as ‘‘scientific.’’ Without exception these neither present any kind of hypothesis or manipulation and are without any rigid experimental framework. Further evolved is theoretical ecology which replaces the field component with mathematical simulation. Common to these three disciplines are that they can only generate new hypotheses and concepts, but they can never be a real test of them. Consequently, theoretical ecology, natural history and faunistics will not be at the center of this review, but are implicit in the evolution of ecology as a discipline and will be referred to throughout.

METHODS

Literature search.—In the trawl of ecological publications for this review, all empirical experiments up to 1973 have been considered. The process of deciphering whether hypotheses were apparent in a paper has been at times, extremely difficult and on other occasions quite straight forward. This is because some authors were quite explicit about their intentions expressing them in bullet form (e.g., Hypothesis 1, 2 and 3 etc.), while others were much more discrete. I have tried to highlight both cases, but will have inevitably failed to classify all types correctly. Thus, I offer my interpretations of what hypotheses are being tested as suggestive, but not conclusive. What was easier to assess was the quality of the empirical data as well as the subject or its environment being tested. In the review, I have drawn attention to some of the best manipulations and highlighted others that I have felt to be fundamentally erroneous. Until the 1950s, results were rarely rationalized through the use of any statistics, therefore I have not imposed the need for statistical tests so long as data have been given appropriate interpretation. Thus, the best examples I highlight follow a logical sequence of hypothesis statements, experimental manipulation, data acquisition and rationalization, which I identify as the benchmark for the purposes of this review.

For the review of the spider literature, Pierre Bonnet’s ‘‘Bibliographia Araneorum’’ (Bonnet 1945) which lists 8000+ papers from Aristotle to 1939 was used—all titles were read in combination with the online database JSTOR which covered the period 1684–1973. Post 1939, the Zoological Record replaced Bibliographia Araneorum. For both Bonnet and the Zoological Record, the search term ‘‘ecolog*’’ and its linguistic derivatives ‘‘ökolog*/ecologisch*/ekologitsch*’’ were selected as keywords that might appear in the title of an ecological paper. For the JSTOR search (1684–1973), all papers that included one or more of the following keywords ‘‘spider, spiders, ecology, ecological, aranea, araneae’’ were read. Additionally, the ‘‘Web of Science’’ online database was searched using the terms ‘‘aranea* OR spider* NOT mite* NOT monkey*’’ from 1970, the date of its inception, to 1973. While these keyword searches are not a ‘‘catch-all’’ of the entire ecological literature, it does strike at the center of the subject. Once papers were identified, they were critically examined for evidence of a hypothesis, experimental framework, manipulation etc, as described above. The limitation of this study is that papers published in non-European languages have not been analyzed.

THE HISTORY OF ECOLOGICAL SPIDER RESEARCH

The ecological spider literature between 1684 and 1956: a period of slow development.—The illusion that readers may have is that ecology started early in the 19th century, as a literature scan reveals a plentiful supply of ‘‘ecological’’ publications. For example, a paper by Boys (1880) on the influence of the tuning fork on the orb web of the garden spider appears to be a promising ecological investigation, detailing how he simulated the vi-

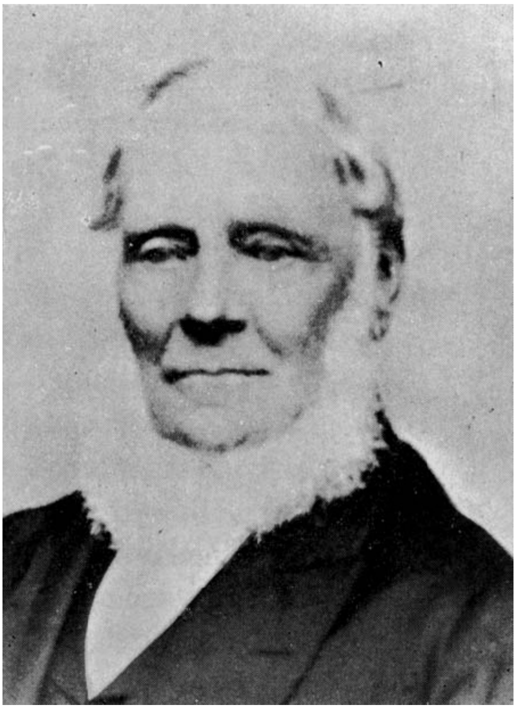

Figure 1.—John Blackwall (1790–1881) is credited as the first to recognize the taxonomic importance of the male palpus. Other than his taxonomic work, he also conducted behavioral experiments on spiders, including those on ballooning motivation, in which he referred to hypotheses. Additionally, he also wrote 15 papers on ornithology and is recognized as having made an important contribution to the study of bird migration. Source: Photo Bonnet (1945) plate IV. Note: The Natural History Museum, London holds many portraits of scientists, but the original of John Blackwall appears to have been lost. Bonnet (1945) now appears to be the only source (Peter Merrett pers. comm.).

brations of a trapped fly; a basic example of a manipulation. However, Boys (1880) was unable to interpret the effect of the tuning fork, nor did he collect any worthwhile data to present. Boys (1880) is not unusual for his time, as many articles are of a similar type. For example, John Blackwall (Fig. 1), the renowned English arachnologist who first discovered the taxonomic importance of palps and epigyna, could also have been the founder of spider ecology. Writing between 1827–1877, Blackwall was an independent thinker and not one to conjecture. To the ecologist, he will be best known for attempting to unravel the mechanics of ballooning spiders which had captured the attention of a number of eminent scientists since the 17th century, most notably Martin Lister (1684) who recognized that it was silk that dragged spiders into the atmosphere (Fig. 2).

Figure 2.—Martin Lister (birth not recorded, but baptized 1639, died 1712), a medic, is widely recognized as the ''father of arachnology.'' In 1685, Lister was elected as vice president of the Royal Society under the president Samuel Pepys, in recognition of his achievements in natural history. His interests did not stop at spiders, and perhaps his greatest accolade was for his research in conchology. He recognized the value of fossils and was the first to attempt a comparative anatomy of the Mollusca in his ''Exercitatio anatomica,'' ''Historia sive synopsis methodica conchyliorum'' and ''Historia conchyliorum,'' which have received lasting recognition. However, although he made plenty of observations of spiders and other organisms, he did not complete any formal experiments and he is best described as a taxonomist, natural historian and intellectual. Source: Photo supplied by kind permission of Basil Harley and John Parker, the authors of ''Martin Lister's English Spiders, 1678'' published by Harley Books.

It was not until later that Bon de Saint-Hilaire (1710) described the forces that cause lift. However, there was also some fanciful thinking that, for example, gossamer was the biproduct of evapotranspiration at harvest time or related to the vapors of the earth (Bechstein 1799). Blackwall was able to dismiss these and other nonsenses by experimentation (Blackwall 1827). He first described the tip-toe behavior and the ‘‘force’’ (i.e., drag) on the dragline which, through convection in the planetary boundary layer (which he termed ‘‘rarefraction of the air contiguous to the heated ground’’), allowed spiders to become airborne. Rather ground breaking was the recognition that spiders have some limited control over their excursion, either drawing in the line or allowing more silk out, though previously Lister (1684) intimated that this might be a possibility. Despite these leaps of knowledge, Blackwall never presented any data or described even his experiments in sufficient detail that they could be replicated. He did refer to hypotheses, but there was certainly no evidence that these were formally tested and thus it is difficult to judge the validity of his claims. It is arguable that whilst Blackwall was clearly a man before his time, he did not practice science, but instead published observation with limited interpretation and may best be described as a natural philosopher and taxonomist.

It may seem harsh to judge Blackwall according to procedures of contemporary modern science, but in fact ‘‘modern deductive science’’ was practiced 150 years before Blackwall—see exhaustive treatment of the history of science in Gribbin (2002). Arguably, the first practitioner of modern deductive science was Isaac Newton. Newton experimented at the same time that Martin Lister was active in arachnology and both were fellows of the Royal Society at its inception in 1662. One can only speculate whether Newton and Lister actually ever met as fellows in the rooms of the Royal Society, it being a breeding ground for new ideas. Lister’s big idea was that silk gave spiders lift, the number and length of the threads and the spider’s posture determined whether they were to be ‘‘carried into the air by an external force’’ (Lister 1684 p. 593). To understand principles of ‘‘drag,’’ which underpin ballooning, is complex and does require a rigorous understanding of Newtonian physics and a good manipulative experiment—Lister had neither. However, in terms of his thinking, Lister was a man before his time because, even in today’s research world with the most sophisticated technology at our disposal and with over 300 years of Newtonian physics behind us, quantifying Lister’s ‘‘external force’’ is at the cutting edge of current scientific discovery. We should reflect on the merits of Lister’s work in terms of his ground-breaking work on the taxonomy and classification of spiders and shells (Fig. 2), accepting that he also made a philosophical, but not an experimental contribution to dispersal ecology.

That there was an absence of scientific ecological experimentation until the mid part of the 20th century is not to dismiss the fact that there were many good practitioners of natural history during and after Blackwall’s period. Some of these individuals took the opportunity to publish beautifully illustrated taxonomic notes supplemented with limited aspects of spider behavior, many of which are now seen as ‘‘classics.’’ These included the Reverend Octavius Pickard Cambridge (‘‘Spiders of Dorset’’ published between 1879–1881), James Emerton (‘‘The Common Spiders of the United States’’ published 1902), and latterly B.J. Kaston (‘‘The Spiders of Connecticut’’ published 1948), W. Gertsch (‘‘American Spiders’’ published 1949) and George Locket & Arthur Millidge (‘‘British Spiders’’ published between 1951–1953). Others were more explicit about the natural history content, devoting most, if not all of their book to observation. These began in the latter half of the 19th century with Henry McCook (‘‘American Spiders and their Spinning Work’’ published between 1889–1894), Eugene Simon (‘‘Histoire Naturelle des Araignées’’ published between 1892–1903), Pelegrin Franganillo-Balboa (‘‘Las Arañas’’ published 1917), E. Nielsen (‘‘De Danske Edderkoppers Biologi’’ published 1928), Lucien Berland (*Les Araignées* published 1938) and William Bristowe (‘‘The Comity of Spiders’’ published 1939–1941). Some authors were able to reach a wider market by popularizing their work to a mass audience. Arguably, this began with John Comstock and his ‘‘The Spider Book’’ (published 1913) and followed much later by K. McKeown (‘‘Spider Wonders of Australia’’ published 1936) and John Crompton (‘‘The Spider’’ published 1950). Good though their observations may seem, prudence suggests that intimate ecological relationships are best described through a process of experimentation not just observation; the domain of journals not books.

Of all of the 8000+ papers in Bonnet's *Bibliographia Araneorum,* less than 0.1% of the journal papers mention the word ''ecology'' or its linguistic derivatives ''ökologie/ecologie/ecologische/ekologitschni'' in the title. Of those that do, it is evident that ecology as a discrete subject appeared in the first half of the 20th century (i.e., Shelford 1912; Adams 1915; Rau 1922, 1926; Weese 1924a, 1924b; Holmquist 1926; Peus 1928; Elliot 1930; Kolosváry 1930, 1933a, 1933b, 1937, 1938, 1939a, 1939b; Gebhardt 1932; Krogerus 1932; Ives 1934; Geijskes 1935; Kidd et al. 1935; Drensky 1936; Ksiazkowna 1936; Lever 1937; Petrusewicz 1938). One of the better papers of the above cohort is by Frank Elliott on spiders of a beech-maple forest published in 1930. Yet, this paper and all the aforementioned are nothing more than expanded field notebooks that include list upon list of spiders found in different strata or seasons. It is recognized that the early naturalists needed to lay foundations and simple principals to investigate the possibility of further testing. Yet, at the same time they had no focus, or apparent aim to their obsessional collecting sprees. While one can find merit in their observation, the lack of scientific rigor in the pre-1939 literature rarely invites close inspection for today's ecologists except to glean distribution and habitat data.

The lack of a scientific approach might be explained by the fact that only a few journals were dedicated to solely publishing ecological experiments, including ''Ecology'' (started 1920), ''Zeitschrift für Morphologie und Ökologie der Tiere'' (started 1924 but now known as Oecologia since 1968), ''Ecological Monographs'' (started 1931), ''Journal of Animal Ecology'' (started 1932) and later still, ''Oikos'' (started 1949). However, as has been evident throughout the screening process, finding a pre-1950s arachnological ''experiment'' worthy of publication in these international journals has been challenging.

One fundamental problem was that ecological concepts were rarely formalized until Charles Elton (Fig. 3), the so called ''father of ecology,'' who laid the foundations for further testing. In his seminal 1927 book titled ''Animal Ecology,'' Elton outlined several ecological ideas including food chains, nutrient cycles, ecological niches and the pyramid of numbers. If arachnologists had embraced these concepts and tested Elton's theories, then there would have been a plentiful supply of arachnological experiments worthy of international recognition. Instead, arachnologists set about producing a profusion of species lists, often without interpretation and making no attempt to relate their studies with current theory.

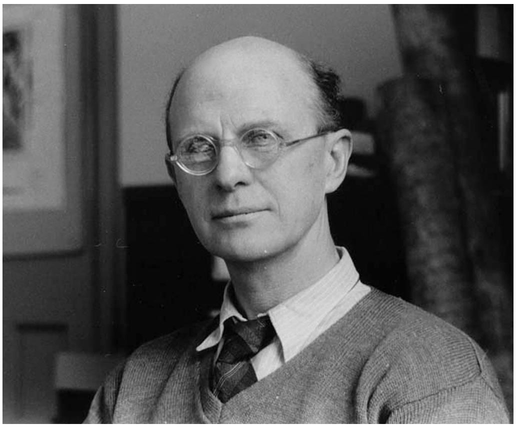

Figure 3.—Charles Elton (1900–1991) was educated at New College Oxford where he immersed himself in zoology. The catalyst for his radical thinking was a product of an expedition to Spitsbergen in 1921, where he was struck by the contrasting life histories of many animals living there. Elton produced his seminal work titled ''Animal Ecology'' in 1927 in which he described his theory of the niche and his pyramid of numbers. Elton had much greater impact in arachnology than his predecessors. This is particularly true of the American Victor Shelford (1877–1968), who despite formalizing ecology as a discrete science, was rarely cited by arachnologists. Source: Photo supplied by Catherine Dockerty, Reader Services Librarian, Charles Elton Library, Department of Zoology, Oxford University, UK.

Interpretation of data is greatly aided by statistical inference, but statistics were absent from ecology until the turn of the 20th century. The lack of statistical methodology was perhaps the biggest frustration to the early ecologists who were unable to rationalize their findings. Arguably, the most significant advance in statistical ecology was the appointment of Ronald A. Fisher (Fig. 4) in 1922 to Rothamsted Experimental Station. Fisher, the architect of modern statistical field ecology,

Figure 4.—Sir Ronald Aylmer Fisher (1890–1962), was a eugenicist and friend of Leonard Darwin, son of Charles, who himself was the president of the Eugenics Education Society for which Fisher wrote many articles. However, he is best known for shaping our understanding of statistical research methods in ecology. Fisher enforced the view that experiments need to have both treatments and a control. Furthermore, he stated that these must be properly replicated and randomized, outlining his ideas in books aimed at field ecologists. He will be perhaps best remembered in statistics for the ANOVA, which was developed as a result of his work in genetics. The ANOVA was first used to show that the inheritance of continuous traits could be fully explained by a Mendelian model. This valuable tool was used by arachnologists in the 1950s and thereafter continuously until the present day. Source: Photo supplied by Gavin Ross, Rothamsted Research, UK.

developed statistical solutions to complex field experiments, such as the ANOVA, and laid down concepts such as maximum likelihood. Uniquely, he was able to formalize his approach in readable texts for biologists. His seminal works were ‘‘Statistical Methods For Research Workers’’ and ‘‘The Design of Experiments’’ first published in 1925 and 1935 respectively. While it is true that these two texts made an impact in some areas of ecology soon after they were published (e.g., botany and entomology), these texts did not feed into spider research until the 1950s (e.g., Barnes & Barnes 1955; Kuenzler 1958).

For some unknown reason, theoretical and statistical hindrances did not deter entomologists who were beginning to make significant inroads in insect science. Of particular fascination to entomologists at that time were competitive interactions and fluctuations in insect populations. Mathematical descriptions of the rhythmic fluctuations in animal populations had been available since the 1920s (Lotka 1925; Volterra 1926; Nicholson & Bailey 1935). Later, Crombie (1945, 1946) was one of the first to test the model on insects. Working with two species of grain beetle from the genera *Tribolium* (Coleoptera, Tenebrionidae) and *Oryzaephilus* (Coleoptera, Silvanidae), Crombie was able to measure the equilibrium population densities and competition coefficients to show that coexistence did occur at the predicted levels, thus validating his model. Similarly, Varley (1947) should also be mentioned for his scientific approach to the study of the knapweed gall-fly, *Urophora jaceana* (Hering 1935) (Diptera, Tephritidae), in which he was able to determine the density dependent factors which affected mortality. Ecology appeared to be alive and well in entomology (see Varley et al. 1973) but was suffering from poor health in arachnology. Spider ecology’s deep malaise was only lifted by the intervention of a physiologist in 1939, although there were some encouraging philosophical beginnings after the turn of the 20th century.

The earliest ecological reference cited by David Wise (1993), the author of the only dedicated book on spider ecology, was Dahl (1906). Friedrich Dahl published over 60 papers on spiders between 1883–1927, but it was Dahl’s (1906) paper on mating success that showed he could think along ecological lines, stating ‘‘there are no two species of indigenous spiders that occupy precisely the same position in nature’s household’’ (quoted from Wise 1993). However, Dahl was a natural philosopher, a hypothesis generator, not a tester of his own ecological theories. Likewise, much the same could be said for Hermann Wiehle who studied the structure and function of the orb web for his PhD thesis at the University of Halle. He published continuously for nearly 50 years but 5 papers between 1927 and 1937, mostly for the journal

''Zeitschrift für Morphologie und Ökologie der Tiere,'' are notable (cited in Bonnet 1945). However, despite this prolific academic activity, Wiehle was only concerned with the construction of the web and its measurement, sadly ecology was never at the center of his observations (Samuel Zschokke pers. comm.). This is perhaps because Wiehle worked as a teacher and industrial worker after his PhD and had no resources to answer the ecological questions that must have arisen during his research. Questions regarding, for example, orientation and behavioral thermoregulation, would probably have been observed by Wiehle, although to answer these would have required a mathematical understanding, a good experiment and plenty of time. Two well executed examples came very much later. Both Pointing (1965) and Krakauer (1972) did have good experiments, but they were also reliant on the latest technology to make accurate temperature measurements. The level of accuracy allowed them to draw the same conclusion that web-spinning spiders use behavioral and physiological thermoregulation—something which Wiehle could not have concluded because of the lack of suitable apparatus and institutional support. However, Wiehle and his peers could have looked at simple habitat selection by web-spinning spiders and qualitatively noted the effect of independent variables (e.g., wind) in the same vein as Eberhard (1971) and Enders (1973). These were good but basic studies and ones that Wiehle and others could have executed; however, despite their obvious suitability, they did not appear until the 1960s.

Pontus Palmgren (Fig. 5), a distinguished Professor of Zoology at the University of Helsinki between 1940–1971, was best known for his anatomical research in ornithology (Koponen 1994). He was often heard repeating Galileo's motto ''to measure everything and make the immeasurable measurable'' (von Haartman 1994); this he applied rigorously to his work on the functional anatomy of bird's legs, spider muscles and trichobothria. Palmgren clearly enjoyed a diversity of disciplines, including ecology, publishing one scientific paper of note. Between finishing his PhD and his appointment to professorship, Palmgren turned his attention away from birds for a short while to investigate the ecology of a fishing spider in 1939.

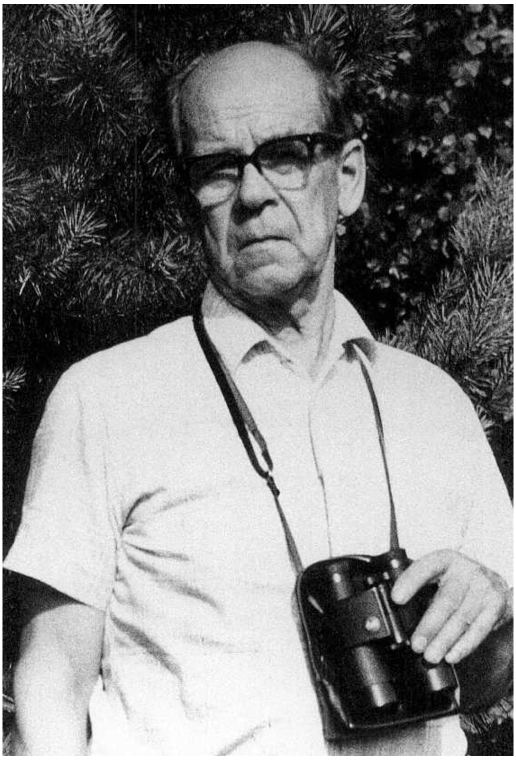

Figure 5.—Professor Pontus Palmgren (1907–1993), a physiologist who thought along ecological lines when trying to unravel the effect of environmental stimuli on *Dolomedes fimbriatus*. However, he will be best remembered for his groundbreaking work in ornithology, particularly that which relates to functional anatomy. Source: Photo supplied by kind permission of his son, Kaj Palmgren and with thanks to the Tvärminne Zoological Station, University of Helsinki, Finland.

Translated from its original German, Palmgren's (1939) paper was titled ''Ecological and physiological studies concerning the spider *Dolomedes fimbriatus* (Clerck 1757) (Pisauridae).'' It is immediately apparent that this paper is clearly a significant contribution to ecology. Furthermore, it is in the spirit of Ernst Haeckel's original definition of ecology that was seen as synonymous with physiology, a view espoused by the entomologist Victor Shelford and by others after the turn of the 20th century (McIntosh 1987). The paper includes a number of alternative hypotheses and manipulations both in the laboratory and the field. Palmgren (1939) demonstrated experimentally that *D. fimbriatus* was both positively phototaxic and negatively geotactic and was aware that *Dolomedes* preferred damp habitats. However, while he could demonstrate physiologically that individuals dehydrate quickly through the skin, he was unable to explain why individuals did not orientate themselves towards saturated air in his behavioral experiments in the lab. Palmgren then studied individuals into the field where he investigated the consequences of habitat conditions on spider mortality. Placing individuals in cages (4 cm × 2 cm) in four different habitats (10 individuals per habitat) of increasing dampness (i.e., 1. open pine forest with dry heath (*Calluna vulgaris* (L.)); 2. hazel (*Corylus avellana* L.) copse; 3. moist mixed *Alnus glutinosa* (L.)-*Betula verrucosa* Ehrh. wood and; 4. a *Sphagnum* moss carpet with other marsh plants), he then measured the climatic conditions and lifespans of the spiders in each treatment. Palmgren (1939) was fascinated to observe that individuals placed in the bog had the longest lifespans, despite the climatic conditions remaining roughly the same between the four habitats. This he attributed to the fact that in the bog there was always a constant availability of water, although one wonders why, if this were true, he never recorded completely saturated air most of the time. It is suspected that if these measurements were repeated with modern data loggers, that the variance in humidity would be different between the bog and the dry heath and may have changed the course of his discussion slightly.

It is perhaps not surprising, given that this paper is written in German and not electronically indexed, that it is rarely cited by modern scientists. In one sense, this is a mistake because Palmgren (1939) was way ahead of his peers. However, Palmgren's (1939) experiments do not always stand up to modern-day scrutiny. The physiological measurements are satisfactory, and the only thing that would change if repeated today would be the technology and the numbers of replicates. However, it is the fieldwork where the reader is left wanting. As would be commonplace in any study of its kind, the first step would have been to present the numerical case for spiders appearing to have some kind of habitat association. This could have been done with simple density estimates from selected habitats. The second step would have been to design an experiment that allowed spiders to exploit their environment naturally, observing their behavior and the frequency of mortality. The idea that caged spiders are a field test of what was observed in the laboratory is idiosyncratic. Modern ecologists do confine wandering spiders, but the tendency is for them to use large semi-natural enclosures (i.e., >1m^2), not small cages (i.e., 8cm^2).

It is clear to modern ecologists that Palmgren (1939) needed to make more connections between environment and spider mortality, which is suggestive of a correlation coefficient. The lack of statistical inference frustrated many ecologists including Shelford (1930, p. 236) who stated ‘‘often one sees papers containing weather data with no interpretation or correlation of the biological facts.’’ However, even though correlations were used in ecological studies of the period (e.g., Nash 1933), they were by no means commonplace. For example, even under the supervision of Ronald Fisher, Barnes (1932) overlooked the importance of using any statistics at all to support his study on fluctuating insect populations, which is remiss. It is true that Palmgren's (1939) study would have been greatly improved by the use of correlations, but statistics were not part of the culture of the majority of ecologists of the period, and Palmgren cannot be chastised for this omission.

Ecological theory seemed more palatable than statistics to arachnologists and finally showed signs of making an impact, particularly Elton's (1927) theories of the niche and succession. Elton's theories became the preoccupations for post-war arachnologists (e.g., Gibson 1947; Lowrie 1948; Muma & Muma 1949; Dowdy 1951 and many others not included here). One notable Eltonite was an American named Robert Barnes who examined the ecology of spiders in non-forested maritime communities for his PhD at Duke University, North Carolina. Barnes produced three notable papers loosely centered around niche theory and distribution (Barnes 1953; Barnes & Barnes 1954, 1955). Arguably, Barnes' most cited paper is his 1955 work titled ‘‘The Spider population of the abstract broomsedge community of the southeastern Piedmont.’’ This paper examined the spider community in terms of its homogeneity, density, population stability and range. Barnes used an ANOVA to form the view that of the 29 fields studied, the population structure was essentially the same—yet for all the paper's merits, a hypothesis was lacking. Despite this and other papers of that time being good examples of basic ecology, they fail to make the relationship between environment and the spider community, because they did not try to control or manipulate the system, severely weakening their conclusions. Barnes could have tried to deconstruct the abstract community by manipulating the stand-type to see which species were specifically related to the structure or physiognomy of the broomsedge. By doing so, the ecology of the community would have been more clearly understood. The work of Barnes and others of the time illustrate that many ‘‘observational studies’’ were apparent and that the value of manipulation was not generally recognized until later.

Duffey (1956) was one of the first to include a basic manipulation in his paper on ‘‘The aerial dispersal of a known spider population,’’ the subject of his PhD. For centuries, spiders had been observed ballooning, although it was not known what caused them to leave. Duffey set about attempting to understand the influence of population density and microclimate on ballooning success by using greased canes protruding from the sward of limestone grassland. While one can detect that Duffey excelled in the powers of observation, not all his conclusions are supported by his data. Fundamentally, Duffey should have manipulated the spider and microclimate and then, statements such as ‘‘temperature has a more important influence on aerial dispersal than have other microclimatic factors’’ (p. 111), could have be demonstrated probabilistically, not subjectively. Thus Duffey’s (1956) paper pertains to be a basic manipulative experiment which does not explain how or why they balloon or shed light on their relationship with the habitat and its role in dispersal. Duffey published several other ecological papers which tended to be observational studies of conservation management appeal, rather than of academic scientific interest.

Edwin Nørgaard (Fig. 6), a Danish primary school teacher, published two ground-breaking papers in the journal Oikos which are still cited fifty years after their publication (Nørgaard 1951, 1956). It was these and other contributions which were of particular inspiration to Toft (2002) who elucidated upon Nørgaard’s contribution to ecology in his opening address to the European Colloquium of Arachnology, Denmark 2000. Toft (2002) cited Nørgaard’s first ecology paper in 1951 paper as ‘‘unprecedented in the scientific approach’’ and that Nørgaard ‘‘combined field observations with detailed laboratory experimentation, turn[ing] natural history into the experimental science of ecology.’’ It is unequivocal that Toft (2002) believed that Nørgaard was the first arachnological ecologist, but he was not alone. The best textbook on animal ecology during the post war period, referred to Nørgaard’s work as ‘‘outstanding’’ (Macfadyen 1966, p. 63).

Figure 6.—Edwin Nørgaard (1910-present) the modern day father of spider ecology who understood the value of experimental design. His two papers published in Oikos are seminal works and continue to be cited 50 years after their publication. Educated as a school teacher, Nørgaard did his fieldwork during school holidays, managing to maintain parallel interests in teaching and natural history. He wrote 39 papers, articles, books and book chapters over a period of 1936–1998 and was editor of the Danish journal ‘‘Flora og Fauna’’ for 30 years. Although he has retired, he still continues to write popular articles for the Natural History Mueum, Aarhus. Source: Søren Toft, University of Aarhus, Denmark. Photo supplied by E. Nørgaard.

In his first paper Nørgaard (1951) presented a suite of experiments which sought to examine the distributional ecology of two co-occurring lycosids in a sphagnum bog. His scientific rigor was evident by his thorough experimental examination and manipulation of the microclimate. Having made microclimatic field measurements in the different zones of the sphagnum, he did not conjecture that microclimate was determining the differences between the distribution of *Pardosa pullata* (Clerck 1757) and *Pirata piraticus* (Clerck 1757) (Lycosidae). Instead, he went into the laboratory to manipulate these variables and examine more closely their effect on the spiders. By doing so, he linked the lab to the field to erect a probable ‘‘cause and effect’’ scenario. He elucidated upon these findings at length to conclude that ‘‘there exists a clear correlation between the microclimate conditions of the habitats and the spider's requirements.’’ Ideally, this statement needed underpinning with correlations between density estimates and average temperatures in the two layers of *Sphagnum*. Arguably, because there was an absolute zonation between the two species, density measurements could be viewed as redundant.

Nørgaard clearly demonstrated a scientific approach, but lacking in his first Oikos paper was an explicit hypothesis and a direct quantitative link to the environment. Implicit within his design was a statistical hypothesis statement that microclimate was predicted to be the cause of the distributions, written in the introduction as ‘‘differences in their distribution will be viewed in relation to the structure and microclimate of the sphagnum carpet.’’ Nørgaard's (1956) second paper in Oikos on the environment and behavior of *Theridion saxatile* (now *Achaearanea riparia* (Blackwall, 1834)) (Theridiidae) is quite outstanding but in addition, an explicit hypothesis was clearly stated. Furthermore, Nørgaard's 1956 paper is an improvement on his 1951 publication because he also provided quantitative data on the distribution of the spider. He set out to investigate whether Nielsen's (1932) claim that *T. saxatile's* ‘‘egg cocoons are sometimes suspended somewhat below the nest to be sunned,’’ was the real explanation of this behavior’’ (as quoted in Nørgaard (1956, p.160), itself a translation from Nielsen's Danish as found in his volume 1 on p. 189). Nørgaard (1956) took Nielsen's statement and made it his hypothesis and used it to design a suite of microclimatic experiments to test the role of temperature in the development and behavior of immature and adult spiders and their egg sacs. This eloquent set of experiments resulted in Nørgaard rejecting Nielsen's claim, instead accepting what was an alternative hypothesis that egg sac migration between 30–35 °C is an avoidance behavior to prevent thermally induced sub-lethal and lethal effects.

Nørgaard's achievements are best illustrated when they are compared with similar studies of that time, such as Shulov (1940) and Jones (1941). Shulov (1940) looked more generally at the effects of microclimate on the development in *Latrodectus tredecim-guttatus* (now *L. tredecimguttatus* (Rossi 1790)) and *L. pallidus* O. P.-Cambridge 1872 (Theridiidae) and Jones (1941) attempted to determine the effect of temperature and humidity on *Agelena naevia* (now *Agelenopsis naevia* (Walckenaer, 1842)) (Agelenidae). Both these papers are of an excellent high standard and they both manipulate the natural system. Where they both fail ecologically is that their experiments are purely laboratory based, and no data are taken from the field to support their laboratory measurements, although it should be noted that Shulov (1940) fills his paper with additional natural history notes. These papers illustrate the difference between biology which is ‘‘pure’’ and ecology which is ‘‘applied.’’ In this respect, ecology has always strongly supported applied fieldwork over laboratory measurements made in isolation and without reference to nature (Shelford 1930). Pure biology does not impose this constraint necessarily, insofar as abstract physiological measurements are valid and need not be couched in terms of what actually happens in the field.

It has been observed that in reading many papers from the period up until 1956 that most were concerned with physiological effects on spiders, not population ecology which appeared to be leading the charge in entomology.

The literature between 1956 and 1973: did spider ecologists engage in science?.—The volume of papers and the number of journals accepting them accelerated after the Second World War. This post-war period has already been reviewed by Turnbull (1973) and therefore it would be fruitless to re-review this period. Instead the purpose of this section is to examine whether the elegant experimentation that Nørgaard pursued was evident in others soon after 1956. To extend this trawl of the ecological literature up until the present day is beyond the scope of this review. Instead, although somewhat arbitrarily, I have chosen to confine my analysis of the literature to the actual publication date of Turnbull's 1973 review. However, in the case of Susan Riechert, where the author has had a single international publication footprint in the pre-1973 literature, I extend my search a little beyond the 1973 cut-off date because it is evident that she continues to have a lasting impact on spider ecology.

Of the 300+ papers treated by Turnbull, a minority relate to more general biological phenomena (e.g., the various headings detailing processes such as ''spider silk and spinning organs;'' ''development,'' etc.), which are not strictly ecological and hence are not considered further. Of the papers reviewed that do pertain to ecology, the heading ''population and community ecology of spiders'' is by far the largest section, followed by those related to ''spider feeding'' and ''webs.'' Very small sections refer to ''survival and mortality,'' ''reproduction,'' ''energy flow'' and ''dispersal.'' Surprisingly, a section devoted to competition is absent.

An analysis of the literature cited in Turnbull (1973) reveals a number of authors who will still be familiar to students today. John Cloudsley-Thompson (1957), for example, wrote an excellent paper on the then valid genus *Ciniflo* (now *Amaurobius* C. L. Koch 1837) (Amaurobiidae). He worked to an explicit alternative hypothesis that nocturnal behavior in primitive spiders was the result of competition with more modern, successful diurnal species. Cloudsley-Thompson (1957) went further than Shulov (1940) and Jones (1941) before him, demonstrating elegantly the relations between microclimate and amaurobiids. However, Cloudsley-Thompson was a physiologist by his own admission and although he discussed his results in an ecological context (e.g., ''the present work again stresses the importance of moisture on the distribution of spiders,'' pp. 150), he did not collect field data to support his analysis. Excellent though his work is, Cloudsley-Thompson's research is strictly physiological, of which there are many examples from the time (e.g., Lagerspetz & Jäynäs 1959; Miyashita 1968).

A number of authors continued to pursue ''observational studies'' in the post-1960s era, after the first wave of natural historians in the 1940s. This includes Turnbull's (1960) work on the stratification of spiders found in oak woods. This type of research, of which there are many, (e.g., Cherrett 1964; Duffey 1962, 1963, 1968; Huhta 1971; Sudd 1972) remains true to Elton's (1927) theory of the niche, but they are not an explicit test of it. Of considerable merit is the work of Sven Almquist (Fig. 7) who came much closer to understanding habitat selection than any of his peers, but who was completely overlooked by both Turnbull (1973) and by Wise (1993). Almquist, a Swede, studied at the University of Lund for his thesis titled ''Habitat selection and spatial distribution of spiders in coastal sand dunes,'' which was submitted in 1973. Almquist married laboratory tests of microclimate (Almquist 1970, 1971) with field experiments of habitat selection and association (Almquist 1973a, b). In his 1973b paper, which includes a field test of his earlier laboratory measurements of temperature and humidity, he writes: ''This paper deals with the correlations between the distribution of fifteen spider species of coastal sand dunes and the thermal tolerance and preference, and resistance to desiccation of each of those species under laboratory conditions'' (p. 134)—an understated alternative hypothesis. Almquist worked in the spirit of Nørgaard's research on microclimate two decades earlier. Understandably due to technological advances, Almquist's measurements are much more accurate than Nørgaard's, but most striking is the level of detail that is given throughout his work which is not technologically driven. Generally, Almquist concludes his 1973b paper, having compared actual densities with climatic differences in the field and underpinned by his early manipulative microclimatic research in the lab, by stating ''. . . habitat selection is fundamentally controlled by those requirements of the microclimate and the vegetation conditions. . . '' In the same year, on a different dune system, the Dutch scientist van der Aart (1973) independently substantiated the conclusions of Almquist using what is believed to be the first example of ordination in

Figure 7.—Dr Sven Almquist (1918-present) wrote an exceptional set of ecological papers of spiders from Swedish sand dunes, which was the product of his 1973 PhD thesis from the University of Lund. Like Edwin Nørgaard, Dr. Almquist took up teaching. He retired from his post as senior master in biology at Malmö grammar School in 1983 after 37 years of service. Dr. Almquist started publishing in 1970 and has written 9 papers and published one popular Swedish language spider book. Although he continues to publish, his interests are confined to the systematics of Swedish spiders. His study of the systematics of Swedish spiders is the subject of his three volume *magnum opus*, the first volume of which will be published soon. Source: S. Almquist (with the help of University of Lund).

spider ecology, although this was 16 years after its first use in botany (Bray & Curtis 1957). Van der Aart (1973) used principal components analysis (PCA) to investigate whether the hypothesis of the multidimensional niche space was valid for a community of dune-living wolf spiders. PCA is now known to fail to meet the requirements of most ecological datasets, and van der Aart (1973) is guilty of over-interpretation of his results. However, many studies agree with van der Aart's (1973) main findings that differences exist between seaward and landward spider communities, and that the spatial distribution of spider species is linked to vegetation structure.

The re-appearing figure of Charles Elton suggests that he was an extremely influential thinker, not least for his contribution on the role of habitats in animal ecology. Elton's (1946) work is evident in Tretzel's (1952, 1954, 1955) theory-driven spider research concerning competition, maturity, reproduction and phenology. Tretzel is perhaps best known for his writings on interspecific competition, although this theory is not his own but appeared explicitly in Nicholson & Bailey's paper on the ‘‘Balance of animal populations’’ in 1935 and implicitly in Volterra's paper in 1926. Within spider ecology, Tretzel has some influence and spawned a number of studies over several decades (e.g., Vlijm et al. 1963; Łuczak 1966; Vlijm & Kessler-Geschiere 1967; Merrett 1967, 1968, 1969; Den Hollander 1971 among many others not cited here). Tretzel's view was that interspecific competition explained many of the differences observed between closely related species, including their temporal (e.g., phenology) and spatial distributions (e.g., habitat). An early exponent of Tretzel's work was Edward Kuenzler (1958) who published a paper on niche relations of three species of *Lycosa* (Lycosidae) in South Carolina. Using mark-recapture, Kuenzler (1958) presented habitat selection, density and home-range data as well as some limited meteorological comparisons to associate with spider activity. He showed that whilst the niche relations of *L. carolinensis* (now *Hogna carolinensis* (Walckenaer 1805)) and *L. timuqua* (now *Hogna timuqua* (Wallace 1942)) could not be separated, *L. rabida* (now *Rabidosa rabida* (Walckenaer 1837)) did not overlap with the other two species because it accessed the vertical component of the habitat, rather than just remaining on the ground or in its burrow. It is of note that Kuenzler's (1958) research does not include manipulation and his meteorological correlations are highly speculative, even though he was aware of Nørgaard's more clinical approach.

Kuenzler and other studies that are a test of Tretzel's work are a paradox: they show considerable merit because they are a test of ecological theory yet present no explicit hypotheses. One is left wondering why? It seems as if many of the population studies at the time were hypothesis generating, as experiments were not a test of anything specific or at least anything that would suggest a hypothesis. This is not unusual, as McIntosh (1987) declares that ‘‘ecology, like biology, has commonly been criticized for its lack of an explicit and testable theoretical framework’’ (p. 257). For some reason, many of the population studies, which were in a similar vein to Kuenzler (1958), also chose lycosid spiders as their model organisms (e.g., Hackman 1957; Kajak & Łuczak 1961; Dondale et al. 1970; Kessler 1973). It is evident that there was a community of researchers working on lycosids who were interacting despite their disparate distribution across Northern Europe and America. Possibly because of the interaction and because lycosid spiders were a tractable model organism, a number of important advances in spider ecology materialized as a result of this research activity. It was relatively easy to demonstrate lycosid habitat choice in a simply designed natural experiment in grassland (e.g., Den Hollander & Lof 1972), but the many facets of habitat choice needed calibration and manipulation. Experiments of varying complexity showed that habitat choice provided a useful tool in explaining lycosid cannibalism (Hallander 1970), ballooning success (Richter 1967, 1970a, 1970b, 1971) frequency of feeding (Edgar 1970), reproductive rate (Richter et al. 1971) and courtship display (Hallander 1967), among others. While these studies should be noted, perhaps one lycosid study stands out above all other work for the period: Matthias Schaefer (Fig. 8) has been widely recognized as making a significant contribution to the study of spider competition and his work is exemplary. Schaefer’s (1972) research involved six years studying eleven dominant lycosid species that occurred in 17 different coastal habitats. His major conclusion was that species were ‘isolated’ either in space or time. Schaefer hypothesized that abiotic influences were having a much greater effect than competitive displacement, despite evidence from his laboratory experiments which suggested that there were strong biotic interactions between species. In a re-analysis of Schaefer’s work as summarized by Marshall & Rypstra (1999), Wise (1993) suggested that Schaefer was too conservative, in that he actually had compelling evidence of interspecific competition.

Figure 8.—Matthias Schaefer (1942-present) whose manipulative experiments concerning lycosid competition during the 1970s have been widely recognized as a significant contribution to the field. Matthias Schaefer has held a professorship at the Institute for Anthropology and Zoology, University of Göttingen since 1977. For the last 35 years, he has been an author of 131 scientific works spread across a broad research base. Notably, he has maintained a consistent and long standing interest in soil processes in beech forests, particularly that which relates to the involvement of invertebrates in the decomposition process. Source: Photo supplied by M. Schaefer.

Wise (1993) also revealed that, however good Schaefer’s findings may be, it was unfortunate that there was an oversight in the experimental design: Schaefer lacked a properly replicated control. It is, perhaps, important to state that statistical probabilities can be undermined if the experimental design is not robust, as highlighted by Ronald Fisher. Fisher identified the problems of a lack of replication and the absence of a control in the 1920s when he was confronted with analyzing the Broadbalk experiment at Rothamsted Experimental Station (Gavin Ross pers. comm). The importance of experimental design was highlighted in Fisher’s books designed for field-workers, but it is frustrating to see that these problems still plagued notable and widely cited works during the 1960s and 1970s. Problems of replication can be found in Clarke & Grant's (1968) manipulative experiment which attempted to investigate role of spiders as predators in a beech-maple forest. Identified by Wise (1993) as a classic, the study used enclosures in which they removed spiders to observe the effect on Collembola, their likely prey. However, at the admission of the authors (p. 1154), the experiment was not properly replicated (3 controls, 1 treatment), and suffered from pseudoreplication (Wise 1993), still a hotly debated issue in ecology (Oksanen 2001, 2004; Hurlbert 2004).

Conversely, Eliza Dąbroska-Prot's experiments did not suffer from a lack of replication or control and were large in number. In 300 separate experiments, she, along with her colleagues Jadwiga Łuczak and Kazimierz Tarwid at the Institute of Ecology, Warsaw, investigated spider-mosquito predator-prey ratios in a series of five papers (Dąbroska-Prot 1966; Łuczak & Dąbroska-Prot 1966; Dąbroska-Prot et al. 1966, 1968). The group was aware of the theoretical background to their work making reference to Hollings disc equation (Dąbroska-Prot et al. 1968), a widely used theoretical approach to predator-prey interactions. However, for all its merits, their experimental methods are difficult to follow and I remain uncertain as to how the experiments proceeded and their justification for certain idiosyncrasies. For example, the team used isolators (enclosures) that followed a split-plot design in which both a control and a treatment were nested within a single enclosure, separated by a screen. There were ten such enclosures into which spiders and mosquitoes were added and observed three times a day over a period of six months. For some treatments with particular species they used 40 mosquitoes per plot and for others 50, whilst in the control there were always 50 mosquitoes. Concurrently, the team varied the numbers of spiders introduced inconsistently between species and not all spider introductions happened at the same time, with one species being added on the 8th day of the experiment and the rest at the beginning. I also cannot find evidence of the 300 experiments to which they refer, and am of the belief that the word experiment may be misused and intended to refer to a replicate*treatment*species combination. However, despite these flaws, I don't believe their major finding that wandering spiders exert more pressure on mosquitoes than sedentary web-spinning spiders is contentious.

Dąbroska-Prot manipulated the system to allow direct observation of prey consumption, but this has not always been possible. Spider researchers have for a long time been much more likely to use indirect methods to detect prey proteins in the gut, such as precipitin test. Its first use was in mosquito research in 1947; later this knowledge was applied to spiders in the study of the spruce budworm in 1963. As the 1980s approached, the precipitin test was being replaced by the enzyme linked immunosorbent assay (ELISA), but in this intervening period, researchers were also experimenting with radioactive isotopes. Moulder & Reichle (1972) used Cesium^{137} at the landscape scale, introducing the isotope to the forests of the Oak Ridge reservation in Tennessee, USA. The method of application is poorly described in the paper, but Auerbach et al. (1964) describe how this radioactive tracer was applied to a 20m × 25m stand of trees. Uptake occurred through the bark, using water as a diluent. The build-up of radiocesium was traceable in the leaves of the canopy of 33 trees. When the leaves fell onto the forest floor, decomposers then bioaccumulated the radioactive cesium and it was then passed on to any predator that consumed them. On the assumption that these were ground active predators, pitfall traps were used to catch spiders. As indicated by the researchers, C^{137} has a half-life of 30 years, which formed the justification for choosing this over the much less radioactive C^{134}. Cynics would suggest that spiders were a viable measure of how to monitor bioaccumulation of radioactive isotopes for the United States Atomic Energy Commission (USAEC) and that the paper's ecological significance was merely a byproduct of their findings. That said, this byproduct showed that trophic-level food-chain interactions could be measured and that spiders were important predators in forest ecosystems. However, Moulder & Reichle (1972) failed to demonstrate that the bioaccumulation of Cesium^{137} had little or no effect on spider behavior. This failing had implications on the estimates of rates of consumption of the prey and the subsequent catchability of the spiders in the pitfall traps. If consumption rate and catchability were artifacts of the change in spider behavior following application of the tracer, the published data are likely to be a conservative estimate. The same criticism should be lodged at Van Hook (1971), in a related paper, who was also supported by the USAEC. Van Hook (1971) studied the uptake of the isotopes of calcium, potassium and sodium on a caged (0.25 m^2) grassland lycosid population. His energy flow diagrams are illuminating (e.g., fig. 7 in Van Hook (1971)), showing *Lycosa* at the top of the food chain and the interactions between it and its environment. However, the fundamental question remains, did the consumption of istope-tagged prey affect spider behavior? If so, then the study is drastically undermined.

David Quammen, widely recognized for popularizing ecology and biogeography, is in no doubt of the impact of one award winning experiment that is now ‘‘famous for its logical elegance, for its results and for its gonzo methods’’ (p. 428 Quammen 1996). There is further added praise from Lubchenco & Real (1991) in their review of classic papers in ecology, who suggested that it was ‘‘one of the most ambitious and successful large scale experiments attempted in ecological research’’ (p. 726). I am, of course, referring to the work of Dan Simberloff and Edward Wilson, who cast a shadow over all but a tiny portion of ecological research produced in the 1970s. Although spiders were not the specific focus of the work they, along with the rest of the arthropods collected, were a test of the equilibrium theory which was in need of empirical validation. Based in the Florida Bay, Simberloff and Wilson identified suites of mangrove islands which were each covered with a tent and ‘defaunated’ using methyl bromide fumigation (Simberloff & Wilson 1969; Wilson & Simberloff 1969). The fauna of six of these islands were censused before and after treatment, leading Simberloff & Wilson (1969) to conclude that recolonization curves approached a stable equilibrium with the exact number determined by the distance from the source habitats and the size of the island. Throughout, Simberloff & Wilson (1969) observed rapid species turnover and alluded to the fact that the majority of the fauna were ‘‘obligate transients,’’ which were at the mercy of the wind. This includes a discussion of ballooning spiders in which it is highlighted that the distances could not be calculated or correlated with wind measurements because of a number of technical issues.

It would be remiss not to mention the work of Susan Riechert who published her first paper in 1972 and her first international paper in the following year. Riechert has been prolific in her publishing and her contribution to ecology cannot be underestimated. For example, her paper regarding thermal balance and prey availability in *Agelenopsis aperta* (Gertsch 1934) (Agelenidae) remains one of the few papers to attempt to unravel the complexities of spider-habitat associations (Riechert & Tracey 1975). Riechert has maintained a focus on *A. aperta* for the past 30 years, starting with her PhD work published in 1973. Riechert et al.’s (1973) paper was not a manipulative experiment in itself, but it was well designed and presented a strong case to suggest that spiders and their habitat were correlated. What is apparent in retrospect was that her PhD research laid the groundwork for a multitude of studies which had a strong manipulative component and solid theoretical background. A monograph on the contribution of Susan Riechert is long overdue and would be extremely rewarding (but see Wise 1993 for a detailed overview of her research up until the early 1990s). Two other ‘‘appearing lights’’ beginning their research at the same time as Riechert were Frank Enders and William Eberhard whose work on web-site selection is still widely read today, and who began publishing their mainstream work in the early 1970s. I refer readers to Wise (1993) and to specific reviews on web-site selection for a proper treatment of their work, most of which extends beyond the cut-off date for this review.

To summarize the period of 1956–1973, there was a profusion of literature that did not engage science, but pursued an often circular interest of basic observational studies. Fundamentally, these often fell short of the scientific approach because they did not manipulate the system, or if they did, they manipulated to the wrong component. These studies are still informative but they must be treated with caution as some findings sway in the favor of conjecture, not substantive probability. For example, Chew’s (1961) natural experiment is a small study of spiders (n = 817 individuals) of a desert community. Surprisingly, it is still widely cited but is, in my view, erroneous. There are errors in the standardization of the sampling regime and wild conjectural statements made in the discussion which are unsupported by a formal analysis and an evidence-based manipulation (e.g., the role of temperature). When done well, observational studies are an extremely valuable resource to ecologists. Robinson & Robinson's (1973) study of the giant wood spider *Nephila maculata* (now *Nephila pilipes* (Fabricius 1793)) (Tetragnathidae), illustrates this point precisely. It is complete in its approach and does not suffer the illusion that it is anything other than a hypothesis generating autecological paper.

An overview of the literature sampled.— If I were to summarize what impact most of the papers included in this review have had on ecology, then I could do no better than to quote Turnbull's (1973, p. 333) synopsis of over 300 ''ecological'' studies: ''I wish I could also say that I had found no shortage of good papers, or good, well supported information on spider ecology. There are some excellent papers, but there are also large quantities of repetitious mediocrity. I am dismayed at the number of papers that, if they do not belong in ecology do not belong anywhere. [These papers] . . . leave me wondering why they were written, or if written, why any journal would publish them. They are often the product of the crudest methodology; they present data sets that cannot be analyzed; they come to no conclusions; and they are not put into any sort of relationship with general principles, ecological or otherwise.'' While I appreciate that spider ecology needed to go through a period of evolution, it is surprising that the mediocrity prevailed for so long and that the revolution appeared as late as the mid-twentieth century. Arguably, Turnbull did not expedite the rise of spider ecology by publishing cutting-edge research himself. Instead, he could be accused of being no different from his peers, in that his work was neither remarkable nor original; for those qualities, spider ecologists need to look to elsewhere.

Rainer Foelix, author of the ''Biology of Spiders'', wrote in the opening lines of his ecological chapter ''the interactions between spiders and their environment have been investigated systematically only within the past few decades'' (Foelix 1982, p. 232). If there was a need to be more exact, it is argued that arachnological ecology began with Pontus Palmgren in the late 1930s and was refined in the mid 1950s by Edwin Nørgaard with his experiments of microclimate. Both men understood that to manipulate the system is to understand the relationships between spiders and their environment more clearly. Edwin Nørgaard built on the experiences of Pontus Palmgren who worked in the spirit of Haeckel's physiological definition of ecology. However, Nørgaard's work was exemplary because he recognized the need to make both field and controlled laboratory observations. Sven Almquist and Matthias Schaefer also recognized the elegance of manipulation and their work is exceptional for the period.

CONCLUDING REMARKS

Spider research and experimental design.—I hope that through the course of this review, I have managed to convey at least two things: the power of hypothesis testing and the need for a manipulation of either the habitat or the spider, and sometimes both. I would like to encourage students in all branches of arachnology to consider the value of manipulative experiments that are part of a well planned design, and to move away from pure faunistics, which is provincial and therefore of little value. Furthermore, while I recognize that hypotheses are not always appropriate (e.g., when there are provisional data) and that when used imprecisely they seem rather drab, detectable hypothesis statements add a great deal of depth to most experimental designs. These statements need not be of the null form, but can include multiple dynamic alternatives.

Spider research and ecological theory.— It is evident that most studies included in this review had only a peripheral interest in testing ecological theory. This explains why spider ecology was in the doldrums and remained inward-looking during a period when other disciplines embraced the interaction between theory, experiments and empirical tests. For example, it has been argued by Statzner et al. (2001) that entomology has generated a number of general theories in ecology, but that botany has made the most significant contributions. Perhaps one of the most notable theories that has come directly from entomology and which had general appeal to ecologists is the Habitat Templet by the entomologist T.R.E

Southwood (1977). More recently, Ilka Hanski has had a similar impact with his Theory of Metapopulations derived from extensive butterfly studies (Hanski 1999). While it is easy to demonstrate the positive impact spider research has had on other science disciplines such as biochemistry (e.g., spider silks feeding into our understanding of arthropod silks and their evolution), it is difficult to find a single example where this has happened in ecology pre-1973.

I have consulted fellow scientists in numerous countries on the thorny issue of the impact of spider research on other science disciplines. International scientists were even asked if they could give an example of a theory that was not restricted by the 1973 cutoff date—none were forthcoming. Why should this be so? During the embryonic phase of spider ecology, it could be argued that spiders were dealt with as a second taxon to the insects. Indeed, whereas entomologists were likely to be snapped up by institutions wishing to employ them, arachnologists were not. It is also evident that communication between research groups and individuals was poor. For example, it has been observed by scientists both sides of the English Channel that, due to language barriers, papers written in anything other than the mother tongue of the author were largely ignored. All these factors would have meant that an exchange of hypotheses were all the more difficult. We know that hypotheses drive theory and thus theoretical spider ecology must have suffered as a result.

But what is our excuse now that we are in the 21st century? We meet regularly at conferences, congresses and seminars and for some of the ecology journals we even have pre-publication access to papers as well as a wealth of electronic media and back issues. Furthermore, spiders are well distributed, often in abundance and available for study throughout much, sometimes all of the year. It is not as if we do not have our hand on the pulse or have an obliging model organism. It seems to me as if there are no big questions in ecology which pre-dispose spiders to scientists in the search for their big ideas. Perhaps this is because we still do not know enough about our commonest spiders that would encourage sceptics to take a closer look. That was certainly true in agriculture as it has only been in the last three decades that spiders have stopped hiding behind the large, looming shadow of insect economic entomology and branched out in to the collective that is now known as ‘‘beneficial predators.’’ Howell & Pienkowski (1971), for example, give a short breakdown of experimental studies of spiders in American agriculture and show that, apart from a limited number of studies in sweet corn, sugarcane, sorghum and cotton, spider studies are otherwise absent. Post-second millennium, much has changed and there are now numerous groups around the world solely researching the role of spiders in agriculture.

I do believe that the lack of a new general theory applicable to ecology will not last for much longer. The reason for this confidence is because Susan Riechert (pers. comm.) has argued that, although spiders have not initiated new theory, they have proved important experimental subjects that have given support to our understanding and driven further general ecological developments. Thus, we are very theoretically aware and it is encouraging to find that we use theory in our research with some frequency. It is only the contribution to general ecology that we are lacking, so what could we do to encourage this? What to me seems critical is that we interact at the highest level, find paradigms of general applicability and do not present ourselves as a phylogenetic cul-de-sac where no one wants to stop and visit. Then, and only then will spider ecology cross over into general ecology in a major way.

What of the future of experimental spider ecology?.—Unlike physics, ecological relationships are difficult to define absolutely, which explains our addiction to statistical methods, but not necessarily to probabilistic tests. Spider researchers, like other ecologists, are confronted with a complex world of interactions that they have to untangle systematically. The traditional null hypothesis approach does not serve ecology well when complexity in nature is not met with complexity in statistical theory. It is now argued by an increasing band of ecologists, that null hypothesis testing should be curtailed and the use of P-values questioned when established via traditional approaches in some circumstances (Johnson 1999; Anderson et al. 2000; Eberhardt 2003; Johnson & Omland 2004). These authors propose an alternative called ‘‘model selection’’

(MS) which allows up to 20 multiple competing hypotheses to be weighted and compared. Model selection allows the possibility that more than one hypothesis might be true, allowing the researcher to rank their importance and identify more than one outcome (Johnson & Omland 2004). This is in stark contrast to the rather simple dichotomy of null hypotheses testing. I can find only one example where MS has been used in arachnology, in which the ecological traits of phytoseiid mites were assessed (Luh & Croft 1999). However, the likely outcome is that MS will become more prevalent in spider research, especially in the study of trophic relations and competition. However, I do not believe that, where clear and considered manipulations are possible, MS can ever replace manipulative experiments given that MS is founded on observational data mathematically expressed. Experimental ecology is here to stay and at the center of its development is manipulation, albeit somewhat scaled-up to what our forebears had in mind.

ACKNOWLEDGEMENTS

The views expressed here are my own and not necessarily supported by those from whom I have sought help. This paper has been six years in the making, but its relevance was crystallized as a result of discussions first with Margaret Hodge (USA) and subsequently with Søren Toft (Denmark) who fuelled my enthusiasm to look more closely. I am extremely grateful to the two anonymous referees who have improved the manuscript and presented an alternative view. I am appreciative to Emma Shaw (UK) for her help and thank Søren, Gernot Bergthaler (Austria), and Samuel Zschokke (Switzerland) for translations. Phil Wheater (UK), Gary Miller (USA) and Susan Riechert (USA) are thanked for their suggestions. I also thank Chris Felton (UK) and the British Arachnological Society library for providing me with translated reprints of Tretzel's work and Peter Merrett (UK) and Robert Suter (USA) for information. For photographic portraits, I acknowledge the help of Søren Toft, University of Aarhus (Denmark), Basil Harley (UK), John Parker (UK), Jamie Owen of the Natural History Museum, London (UK), Gavin Ross, Rothamsted Research (UK), University of Lund (Sweden), Sven Almquist (Sweden), Kaj Palmgren through the help of the Tvärminne Zoological Station, University of Helsinki (Finland). Thanks to Alison Haughton for proof reading the MS.

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Manuscript received 1 October 2005, revised 10 November 2005.