

The spatial distribution of spangle galls (*Neuroterus* spp.) on oak (Hymenoptera, Cynipidae)

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In two sites of young oak trees the spatial distribution of spangle galls was analysed. *Neuroterus albipes* occurred more or less equally on trees and predominated base of leaves. *N. numismalis* and *N. quercusbaccarum* were most abundant in top and periphery of trees. Occurring separately on leaves the latter two species predominated apex, but on leaves with both species present *N. quercusbaccarum* was displaced towards base reflecting the possibility of interspecific competition on heavily galled leaves. The intimate relationship between leaf development and gall initiation is discussed. It is suggested that timing of life cycles of gall wasps in relation to leaf development of oak trees has reduced the effect of competition between the three species concerned.

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Introduction

The distribution of insects on host trees may reveal important general ecological aspects, e. g. intra- and interspecific competition, insect/plant relationships, timing of life cycles, host/ parasite relationships, etc. and several studies deal with the distribution pattern of forest arthropods (cf. Nielsen and Ejlersen, 1977).

In early autumn the undersides of oak leaves are usually occupied by the hard disc-like spangle galls, induced by the agamic generation of gall wasps of the genus *Neuroterus*. The galls develop during the summer and fall to the ground in autumn before leaf fall.

Variation in the extent of attack is observed from year to year and from locality to locality. Young oak trees are often heavy infested, the colonization of a particular leaf may reach a coverage of about 80–90 % of the lower surface. Such a high density may give rise to intra- and interspecific competition for the same host.

Lifecycles, appearance and distribution of spangle galls are described by Hough (1953a, b), Askew (1962) and Darlington (1974), however, due to discrepancies between results in the patterns of distribution further investigations are relevant.

In this paper the spatial distribution of spangle galls of *Neuroterus quercusbaccarum* L.,

N. numismalis Geoff. and *N. albipes* Schenck on oak is presented.

Localities

Two study-areas were selected. The first area, viz. the U-site, is situated in the University park of Aarhus, Jutland, containing rows and small groups of young oak trees *Quercus robur* L. (5–15 years) with canopy height about 2 m.

The second area, viz. the R-site, a mixed deciduous woodland predominated by sycamore *Acer pseudoplatanus* L. and oak *Quercus robur* L. of different ages and heights, is situated at Ryomgaard (Blegmose) about 40 km NNE of Aarhus. Young oak trees (5–10 years) with canopy height about 2 m were selected.

Methods

Sampling

The study was carried out during August and September 1974 and supplementary samples were collected in autumn 1975 and 1976. Based on pilot investigations in the two sites in early August 1974 a suitable number of sampling units (leaves), providing a reasonable compromise between an acceptable statistical accuracy and the cost of work, was calculated of each treatment in the planned sampling programme.

The vertical distribution of galls in oak canopy was analysed. Four trees in each site were chosen at random from infested trees and each tree was subdivided into three or four sections, viz. top, mid canopy, lower canopy, etc. A number of 50–100 leaves was collected at random from each section per tree, the galls were identified and the number per leaf was counted.

The horizontal distribution of galls in oak canopy was investigated. Four branches in each site, growing almost horizontally from the trunk, were chosen at random from mid canopy sections of infested trees, and each branch was subdivided into three sections, viz. apical third, middle third and basal third. A number of 25–50 leaves was collected at random from each section per branch and the number of galls per leaf was counted.

The number per leaf is not an absolute estimate, but a measure of intensity (Southwood, 1968), however, in the present case, if the distribution on similar trees is the primary concern, the intensity of galls is an acceptable estimate.

Finally, the distribution of galls on leaves was analysed. Leaves with galls of one species only and leaves with galls of more than one species present were selected at random in both sites. A number of 50 leaves was collected per species or species combination, and each leaf was cut at right angles to the midrib into four pieces of equal length. The number of galls per leaf section was counted and the areas of the corresponding leaf sections were estimated.

The application of an absolute estimate, i. e. number of galls per cm², to leaf treatment was required due to a large variation of the leaf areas.

Statistics

The significance of differences of mean gall density observed between sections of each tree, each branch etc., was tested by analysis of variance (one-way classification, level of significance $\alpha = 5\%$). In cases of significance a pairwise test was used to detect which section means were equal and which were different from each other (levels of significance $\alpha = 5\%$ or 1% , cf. Yamane, 1973).

The sampling distributions generally fit the negative binomial distribution and the $\log(x + 1)$ -transformation was applied to normalize the sampling data.

Bartlett's test for the homogeneity of vari-

ances and test for normality were applied to the transformed data to assure that the assumptions underlying the analysis of variance were fulfilled. A few cases of non-normality were ignored, since the powerful F-test appears to be little affected by the effect of minor deviations from normality in a one-way classification with equal sample size (cf. Snedecor and Cochran, 1968).

The computations were mainly performed according to the procedures of Davies (1971) and the detailed statistical analysis of data was presented by Ejlersen (1976).

Results

Galls of *Neuroterus numismalis*, *N. quercusbaccarum* and *N. albipes* were present in the samples, except in the U-site where the latter species was missing.

Pairwise test results are indicated in Figs 1–7 showing the paired comparisons between sections A₁ (basal part) to A₃ or A₄ (apical part) of trees, branches and leaves, respectively. The geometric sample means are presented in relative units setting maximum mean density equal to 100%.

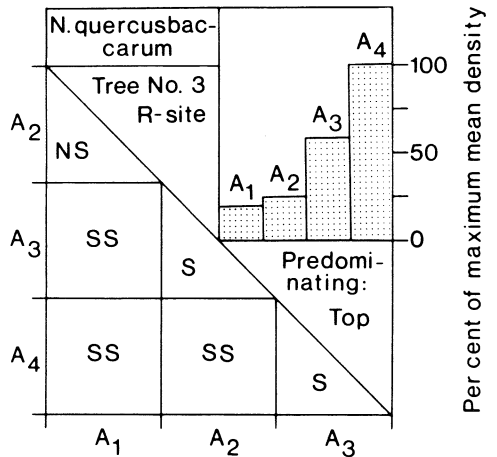


Fig. 1. Relative densities of *Neuroterus quercusbaccarum* on a tree – pairwise test. All trees in both sites showed similar trends. A₁ to A₄ represent the four sample sections from lower canopy to top. S and SS indicate significant differences at 5% and 1% levels of significance, respectively, NS indicates no significant difference.

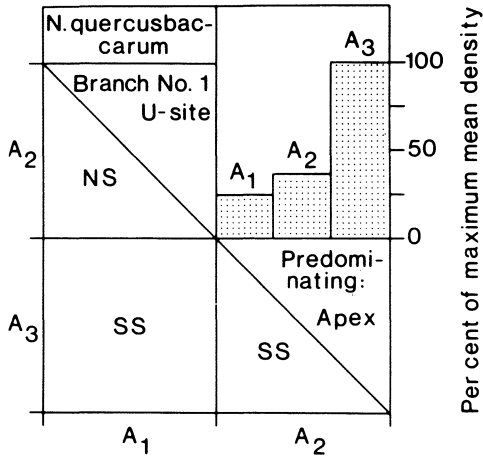


Fig. 2. Relative densities of *Neuroterus quercusbaccarum* on a branch - pairwise test. All branches in both sites showed similar trends. A₁ to A₃ represent the three sample sections from base to apex. Further explanation Fig. 1.

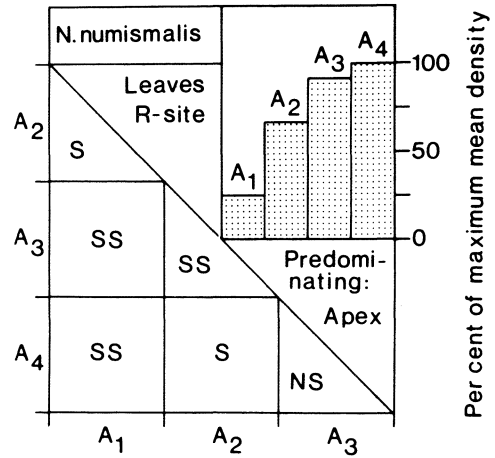


Fig. 3. Relative densities of *Neuroterus numismalis* on leaves - pairwise test. Leaves in the U-site showed similar trend. A₁ to A₄ represent the four leaf sections from base to apex. Further explanation Fig. 1.

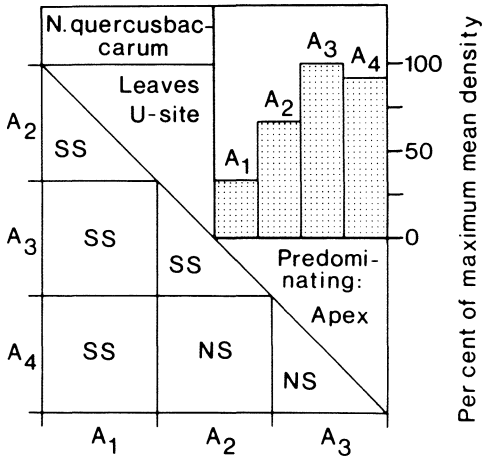


Fig. 4. Relative densities of *Neuroterus quercusbaccarum* on leaves - pairwise test. Leaves in the R-site showed similar trend. A₁ to A₄, as in Fig. 3. Further explanation Fig. 1.

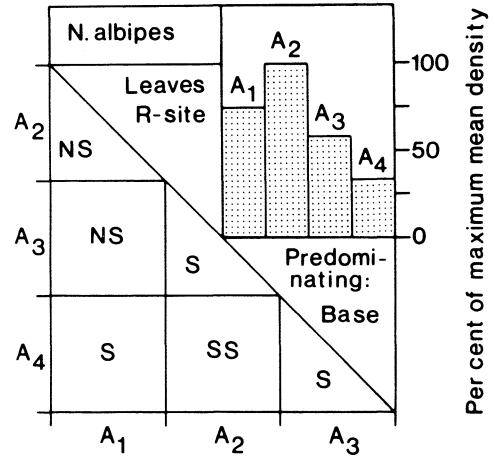


Fig. 5. Relative densities of *Neuroterus albipes* on leaves - pairwise test. A₁ to A₄, as in Fig. 3. Further explanation Fig. 1.

Vertical and horizontal distribution

In both sites *N. numismalis* was mainly present in samples from the top and periphery of each tree and no statistical tests were required.

The density of *N. quercusbaccarum* was significantly higher in the top of each tree and in the apical part of each branch in the two sites (Figs 1-2). Apparently *N. quercusbaccarum* showed a similar pattern of distribution to *N. numismalis*.

In the R-site no significant differences were

detectable of *N. albipes* between tree or branch sections.

The distribution on leaves

On leaves with one species only the densities of *N. numismalis* and of *N. quercusbaccarum* in both sites were significantly higher in the apical part (Figs 3-4). In the R-site the density of *N. albipes* was significantly higher in the basal part of the leaves (Fig. 5).

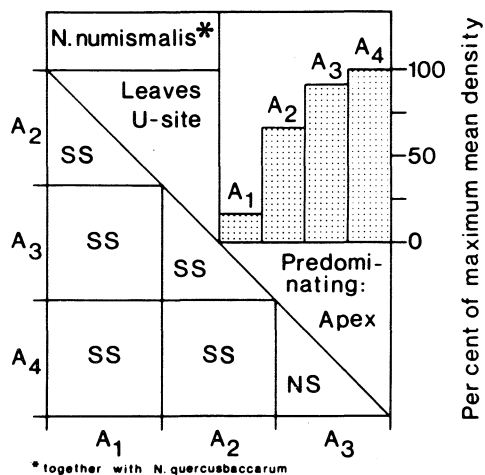


Fig. 6. Relative densities of *Neuroterus numismalis* on leaves with *N. quercusbaccarum* present – pairwise test. A₁ to A₄, as in Fig. 3. Further explanation Fig. 1.

On leaves with more than one species, viz. *N. numismalis* together with *N. quercusbaccarum* (U-site), the density of the former species was significantly higher in the apical part (Fig. 6), whereas the density of the latter species was significantly higher in the basal part of the leaves (Fig. 7).

When *N. quercusbaccarum* and *N. albipes* occurred together on leaves (R-site) the distribution pattern of each particular species was similar to the one valid for the same two species occurring separately.

Only a few leaves with *N. albipes* and *N. numismalis* and with all three species present were collected, hence lack of data affected the statistical accuracy and no results were satisfying.

The patterns of distribution recorded from the investigations in 1974 were confirmed by the supplementary samples in 1975–76.

Discussion

Comparison of samples from different trees generally requires application of a two-way analysis of variance to all data in order to detect inter- and intra-tree variation. However, some of the trees were only slightly infested whereas adjacent trees were heavily attacked. Consequently, it was not necessary to test for a significant inter-tree difference and data were only subjected to a one-way analysis of variance. The significance of statistical inter-

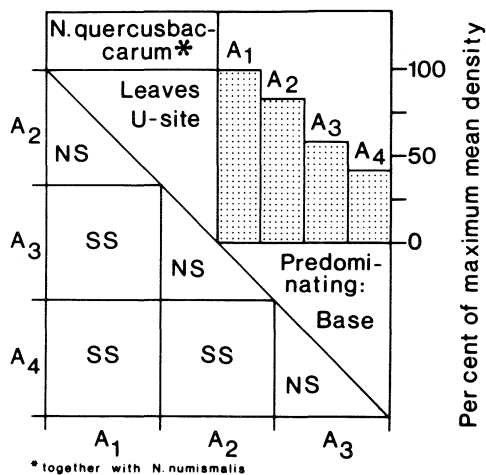


Fig. 7. Relative densities of *Neuroterus quercusbaccarum* on leaves with *N. numismalis* present – pairwise test. A₁ to A₄, as in Fig. 3. Further explanation Fig. 1.

action effects (trees × sections or branches × sections) could be detected by analysing individual trees and branches separately. However, there is insufficient evidence of interaction since the distribution of galls, as mentioned above, showed similar trends on all trees and branches in the two sites.

Spangle galls develop as a result of oviposition of sexual females. On trees galls of *N. albipes* are more or less equally distributed whereas galls of *N. numismalis* and *N. quercusbaccarum* are most abundant in top and periphery. As shown by Askew (1962) the adult sexual generation of *N. albipes* is the earliest arrival emerging immediately after leaf flush. When oviposition starts the leaves are small and leaf density is low implying more or less open canopy structure. The adult sexual generations of *N. numismalis* and *N. quercusbaccarum* appear later (Askew, 1962) and oviposit when most of the leaves have increased in size and leaf density is high implying a more or less closed canopy structure. The different distribution patterns observed may reflect a coincidence between variation in canopy structure and flight periods of the sexual generations. Within an open canopy structure any leaf at any level may have an equal probability of being selected by chance for oviposition by *N. albipes* contrary to a closed canopy structure, where females of *N. numismalis* and *N. quercusbaccarum* may be subject to an increased probability of accumulating

attack on leaves at upper and outer levels by chance encounter. Actually, the primary infestations of the latter two species are initiated at these levels. This was emphasized in a parallel investigation carried out in a third area, situated in a homogeneous forest of oak *Quercus robur* (55 years), canopy height 13–17 m in Tinning Wood, Frijsenborg, about 20 km NW of Aarhus.

In spring 1974 this area was heavily defoliated immediately after leaf flush by an attack of caterpillars, mainly *Tortrix viridana* L., and no spangle galls were observed in autumn, although spangle gall, collected from litter traps in 1973, was estimated to 7300 per m² (S. E. = ± 350). This absence was probably due to a destruction of sexual galls and/or lack of leaves at the time the sexual generations appeared.

In autumn 1975 a minor population of spangle galls had built up. By a fortunate coincidence a thinning of oak trees was carried out in the area in August and 20 felled trees were selected at random and intensively searched for galls. Only a few leaves with galls were observed per tree and *N. numismalis* and *N. quercusbaccarum* were only present on leaves in top and periphery indicating that oviposition commenced at these levels.

The distribution patterns recorded on trees are, except for *N. numismalis*, different from the results obtained by Askew (1962), who observed a basipetal and central concentration of *N. albipes* and *N. quercusbaccarum*, respectively.

Galls of *N. albipes* predominate basal leaf parts. Hough (1953a, b) infers that gall wasps in some way are able to insert ova in leaves at a suitable stage of development and tend to select regions of the lamina, which are expanding at the maximum rates. As mentioned above, sexual females of *N. albipes* oviposit newly flushed leaves, and since leaves in early stage of development generally show exponential growth (Maksymowych, 1973), each particular part of the leaf may be selected by chance for oviposition. Due to leaf growth galls of *N. albipes* will mainly occupy the basal parts of mature, fully expanded leaves in autumn.

Occurring separately on leaves galls of *N. numismalis* and *N. quercusbaccarum* predominate apical leaf parts. At the time their sexual generations appear growth of oak leaves are, according to Hough (1953b), different from the

early stages showing maximum growth and expansion at leaf apex, although a basipetal pattern of leaf growth has been recorded in other leaves (Maksymowych, 1973). However, newly gall-infested oak leaves, marked in spring with waterproof ink at about 3 mm intervals all over the surface, showed during a month a relative higher increase of elongation in apical direction (Ejlertsen, unpublished). Assuming maximum rates of growth at leaf apex and that the females are able to select these parts for oviposition, galls of *N. numismalis* and *N. quercusbaccarum* would be expected to predominate apical leaf parts. This conforms to the results obtained in this study and the distribution pattern of *N. quercusbaccarum* is similar to that observed by Hough (1953b).

When *N. numismalis* and *N. quercusbaccarum* occur together on leaves, they predominate apex and base, respectively. According to Askew (1962) sexual females of *N. quercusbaccarum* starts oviposition a little earlier than sexual females of *N. numismalis*, although both species overlap considerably. Since both females apparently prefer the apical part of leaves, the displacement of *N. quercusbaccarum* towards base may have developed as a result of competition between the two species. However, as in this study, the significance of interspecific competition in nature is rarely observed directly, but usually inferred from indirect evidence, and the distribution pattern recorded above may as well have developed in relation to apical growth of the oak leaves. An early attack of females of *N. quercusbaccarum* followed by a subsequent attack of females of *N. numismalis* may display a similar trend.

The similar distribution pattern of *N. albipes* and *N. quercusbaccarum* irrespective they occur together or separately on leaves may reflect the successively appearance of their sexual generations in relation to leaf growth, and although not recorded in this study, a similar trend would be expected on leaves with *N. albipes* and *N. numismalis* present. Consequently, although not recorded either, one would expect *N. albipes* to predominate base, *N. numismalis* apex and *N. quercusbaccarum* in between on leaves with all three species present. Actually, this was observed by Askew (1962).

The distribution patterns demonstrated on leaves agree with the results obtained by Askew (1962) except for leaves with only *N. quercusbac-*

carum present. In this special case he observed a concentration of galls towards the central leaf parts, contrary to the apical predominance recorded by Hough (1953b), Darlington (1974) and in this study. However, Askew (1962) did not apply any test of significance to his data, so probably this discrepancy is insignificant (cf. Fig. 4).

Apparently, the distribution patterns on leaves may reflect the significance of leaf development to gall induction and formation. The relationship between the gall-causer and its host plant is very intimate, but the mechanism of gall induction is not yet elucidated; however, in Hymenoptera nucleic acids may be involved (Went, 1970).

Incorporation of ^3H -thymidine into nuclear DNA of *Xanthium* leaves was higher in the near-vein region (Maksymowych, 1973) indicating that rates of lamina expansion on a micro-level are not evenly distributed throughout the lamina and that a near-vein region is a specialized growth center. Hough (1953a) observed that sexual females of *N. quercusbaccarum* tend to insert eggs by the side of a vein of second order.

It seems reasonable to assume that a specific interaction, probably on nucleic acid level, between host plant and gall wasp is of vital importance to gall initiation and then probably decisive of gall distribution on leaves.

The results in this study indicate that interspecific competition is fairly weak, although some may occur on leaves attacked by adult sexual females of *N. numismalis* and *N. quercusbaccarum* simultaneously. The timing of life cycles of gall wasps in relation to leaf development seems to have reduced the effect of competition between the three species concerned.

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Sammendrag

Fordeling af *Neuroterus*-galler på egetræer (Hymenoptera, Cynipidae).

Om efteråret forekommer ofte meget store mængder af knap- og linsgaller på undersiden af egeblade; op til 80–90 % af bladarealet kan være dækket. Disse galler induceres af den parthenogenetiske generation af *Neuroterus*-gallhvepse (Cynipidae). Der er stor variation i angrebets størrelse fra år til år samt fra lokalitet til lokalitet. Unge træer angribes som regel hårdt.

Populationer af forskellige arter, der lever i samme miljø, kan som bekendt påvirke hinanden på mange måder (konkurrence om føde, plads, etc.). På lokaliteter, hvor flere *Neuroterus*-arter forekommer sammen, kan der ved høj galletæthed opstå interspecific konkurrence om plads på bladet. En analyse af fordelingen af de enkelte arter kan bl. a. belyse dette forhold.

Undersøgelserne er koncentreret om de tre almindeligste arter, *Neuroterus quercusbaccarum* L., *N. numismalis* Geoff. og *N. albipes* Schenck på unge træer (5–15 år), dels i Universitetsparken i Århus, dels ved Ryomgård (Blegmose) på Djursland.

Bladene er indsamlet tilfældigt (random) fra for-

skellige niveauer på forskellige træer, gallerne er optalt, og resultaterne er behandlet statistisk – variansanalyse og parvis test (Ejlertsen, 1976) – med henblik på fordelingsmønstre. Blade med galler er sorteret fra, inddelt i fire zoner og behandlet på tilsvarende måde.

Resultaterne er præsenteret i fig. 1–7. *N. quercusbaccarum* og *N. numismalis* har samme fordeling på træerne, idet begge arter hovedsagelig forekommer i toppen og i kronens periferi (fig. 1 og 2), hvorimod *N. albipes* fordeler sig mere eller mindre jævnt i kronerne. På blade, hvor arterne optræder hver for sig, findes *N. quercusbaccarum* og *N. numismalis* primært

i spidsen (fig. 3 og 4), i modsætning til *N. albipes* (fig. 5), der optager de basale dele. Når flere arter forekommer på samme blad, fortrænges *N. quercusbaccarum* mod basis i konkurrence med *N. numismalis* (fig. 6 og 7).

Gallerens fordelingsmønstre kan forklares ud fra de enkelte arters livscyklus og egebladens vækst. En synkronisering af galhvepsenes livscyklus i forhold til bladvækst har muligvis nedsat effekten af den interspecificke konkurrence.

De opnåede resultater afviger på en række punkter fra de af Askew (1962) påviste fordelingsmønstre.

Anmeldelse

K. Dumpert, Das Sozialleben der Ameisen. »Pareys Studentexte« Nr. 18. 1978. 253 S., 95 Abb., Balacron brosch. DM 26.

Salomo's Ordsprog fra Det Gamle Testamente kap. 6, 6 »Du Lade! gak til Myren, see dens Veie, og bliv viis« står som indledende sætning til denne, overordentlig overskuelige oversigt over vor nuværende viden om myrernes naturhistorie. Bogen er sandsynligvis tilrettelagt for specialkurser ved universiteter og andre højere læreanstalter og henvender sig således primært til et ret beskeden publikum her i landet, men da den er affattet i et relativt ukompliceret sprog, vil en langt videre læserkreds kunne lære meget af den. Den er illustreret med enkle, særdeles informative tusch-tegninger (95), alle omtegnede af en enkelt tegner, hvorved der er opnået et fint, ensartet præg.

Forfatteren må være relativt ukendt blandt myrmecologer, men hans formåen til at samle og redigere den kolossale stofmængde, der ligger til grund for bogens tilblivelse, karakteriserer ham som dels en ypperlig skribent, der har evnet at simplificere mange, tidligere tørt og knudret formulerede forsøgsresultater, dels er hans eget lette sprog medvirkende til en kontinuitet, der gør, at bogen næsten kan læses som en roman. En distraherende brist er måske de mange, til dels overflødige, litteraturhenvisninger, især da mindst to review-lærebøger eksisterer, nemlig Wilson, E. O., 1971 »The Insect societies« og Schmidt, G. H., 1974 »Socialpolymorphismus bei Insekten«. Sidstnævnte voluminøse værk er, sært nok, ikke citeret af Dumpert.

Gennem fire indledende kapitler behandles følgende emner: Alm. morfologi, fylogeni, sanseorganer og orienteringsmekanismer. Argumentationen i det fylogenetiske afsnit er svag og langt fra i overensstemmelse med teoretiske overvejelser. D. Brothers' afhandling fra 1975 er ikke citeret.

Det morfologiske afsnit er særdeles udmærket og velskrevet, og mange fine »Rasterelektronmikroskopische Aufnahmen« (i.e. scanning billeder) giver et godt indblik i finstrukturen af f.ex. stridulationsapparat og »Borstenfelder«. Afsnittet om optisk orientering er – desværre – gjort næsten uforståeligt på grund af manglende illustrationer og for mange overflødige termer, der ikke anvendes i de følgende afsnit. Kapitlet bliver i særlig grad gjort uoverskueligt af, at forfatteren ikke har vurderet de hypoteser, der ligger til grund for forståelsen af den informationsbehandling, der foregår af de indkommende stimuli.

De følgende emner om duftspor, taktile sanser, alarmferomoner og kemisk kommunikation læses faktisk bedre i Wilson (1971), hvorfra også langt de fleste af eksemplerne og illustrationerne er hentet.

Til gengæld er næsten hele indholdet i Schmidt (1974) koncentreret på små 28 sider.

Fra side 132 og ud, dvs. ca. halvdelen af teksten, beskæftiger bogen sig med mangfoldighederne i myrernes biologi og deres almindelige naturhistorie. I dette essayistiske afsnit forstyrres de mange litteraturhenvisninger især, og det er helt uden proportionsfornemmelse at citere ikke færre end 13 forfattere for tilsammen 16 afhandlinger for at dokumentere det helt basale (= oprindelige) koloni-etableringsprincip, hvor kun en enkelt befrugtet dronning starter et nyt samfund.

De økologiske tilpasningsforhold mellem myrer/planter og myrer/andre dyr giver adskilligt godt stof til eftertanke, men den stadige anvendelse af termen »co-evolution« er distraherende og utilstrækkeligt defineret, da den giver indtryk af et synkroniseringsforhold snarere end et komplekst evolutionsmønster, hvor de involverede organismer gennem utallige mislykkede mutationsforsøg trods alt har formået at leve sammen til gensidig glæde.

Ole Lomholdt