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HOST BREADTH AND VOLTINISM IN GALL-INDUCING LEPIDOPTERA

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ABSTRACT. Because of specialized life systems and host relations, gall-inducing insects are believed to have narrower host breadth and lesser voltinism than other endophagous insects. These expectations were tested here using a sample of 136 species of British Lepidoptera consisting of 29 gallers in 11 families and 107 taxonomically matched endophagous nongaller controls. Gallers and nongallers were compared using biological data assembled and published by A. M. Emmet. Host breadth, scored as number of host genera, averaged 1.21 for the gallers, and 1.48 for the nongallers, and the difference is statistically significant, thus confirming host breadth expectation for this sample of Lepidoptera. This difference was generated mostly among Gelechiidae, Nepticulidae, Tortricidae, and Sesiidae. Voltinism, scored as number of generations developing per year, did not differ between gallers and nongallers. This outcome does not necessarily refute the hypothesis underlying the expectation. The cool British climate may inhibit multivoltinism, and thereby minimize differences in voltinism between gallers and nongallers.

Additional key words: Gelechiidae, Nepticulidae, Tortricidae, Sesiidae, Britain.

Galls induced by Lepidoptera vary from simple swellings to fruitlike bodies that bear little resemblance to supporting host parts. The galls are organ specific, most developing on host stems, but some developing on host reproductive structures, leaves, and roots. With few exceptions, larvae rather than ovipositing adults induce the galls. Worldwide, 352 morphospecies of gall-inducing Lepidoptera are known, of which 179 have been identified to genera and species in 20 families (Miller 2004). Greater numbers and taxonomic diversity of lepidopteran gallers are anticipated as tropical areas are explored.

Gall-inducing insects, including Lepidoptera, are believed to have narrower host breadth and to develop fewer annual generations than other endophagous insects (Cornell 1990, Raman 1994, Miller 2004). Narrow host breadth is expected because evolutionary adjustments between gall inducer and host foster foodplant specialization, a corollary of the reputed host specificity of gall inducers (Mani 1964, Shorthouse & Rohfritsch 1992, Harris & Shorthouse 1996). Lesser voltinism is expected because gall inducers seem to synchronize their phenology with that of their hosts, which would ensure that larvae have access to reactive tissues necessary for gall development, as during rapid plant growth in spring. Physiological mechanisms that might mediate this synchrony have not been investigated. These host breadth and voltinism expectations for lepidopteran gall inducers would acquire added strength if empirical tests confirmed them.

Cornell (1990) compared voltinism and other life history traits between gall inducers and leaf miners. His voltinism sample consisted of 28 species–12 leaf miners, mostly lepidopteran, and 16 gall inducers, mostly dipteran and hymenopteran. He found that voltinism averaged 1.4 generations/yr for the gall inducers and 2.5 generations/yr for the leaf miners, which is consistent with the expectation of lesser voltinism among gall inducers. In contrast to voltinism, host breadth of gall inducers in one or any combination of insect orders does not seem to have been compared empirically with that of endophagous nongallers.

Reported here are comparisons of host breadth and voltinism between gallers and nongallers in a large sample of Lepidoptera, an order poorly represented in previous cecidological studies (Miller 2004). The source of the data analyzed is Emmet's (1991) extensive life history tabulation for more than 2400 species of British Lepidoptera, the most extensively known lepidopteran fauna in the world.

MATERIALS AND METHODS

To test the hypotheses that gall-inducing Lepidoptera have narrower host breadth and lesser voltinism than other endophagous Lepidoptera, I assembled a study sample of 29 gallers and 107 endophagous nongaller controls, 136 species in all. All known British gallers were included, as listed by Spooner and Bowdrey (1995), with emendations as follows: *Argyresthia retinella* Zeller, unaccountably absent from the list, was added (Robbins 1992), and *Paranthrene tabaniformis rhinglaeforme* (Hübner), now considered synonymous with *P. tabaniformis* (Rottemburg), was removed (Špatenka et al. 1999).

The 107 endophagous nongallers were those marked in Emmet's (1991) tabulation exclusively with *b* for borer or *m* for miner, and, for *Heliozela* only, also with *c* for casebearer to match the casebearing *Heliozela* gallers. Taxonomic matching was possible at the generic level for gallers in 10 genera, and at the subfamily level for gallers in six genera, in line with principles of the comparative method (Harvey & Pagel 1991). For example, matches for the two *Ectoedemia* (Nepticulidae) gallers consisted of the 15 nongalling endophagous *Ectoedemia*, and the match for the galler *Adaina microdactyla* (Hübner) (Pterophoridae, Platyptiliinae), which has no British congeners, was *Leioptilus carphodactyla* (Hübner), the only other endophagous British member of the subfamily Platyptili-

TABLE 1. Host breadth and voltinism of British gall-inducing Lepidoptera and taxonomically matched endophagous nongallers. Data from Emmet (1991) except where noted otherwise. Family sequence follows Kristensen (1999).

Family	Species as numbered in Emmet's tabulation	N	Mean scores: Host breadth	Mean scores: Voltinism
Nepticulidae				
Gallers	23, 24	2	1.00	1.00
Nongallers	25–32, 34–39, 41	15	1.27	1.00
Heliozelidae				
Gallers	154, 157	2	1.00	1.00
Nongaller	156	1	1.00	1.00
Incurvariidae				
Gallers	138, 139	2	1.00	1.00
Nongallers	133, 136	2	1.00	1.00
Yponomeutidae				
Gallers	411, 415	2	1.50	1.00
Nongallers	401, 404, 405, 407, 410, 412, 418, 420, 422	9	1.33	1.00
Elachistidae				
Galler	906	1	1.00	1.00
Nongaller	905	1	1.00	1.00
Coleophoridae				
Gallers	486, 889, 891, 892, 893a[1]	5	1.00	1.25
Nongallers	487, 880–884, 887, 888, 890	9	1.00	1.33
Gelechiidae				
Gallers	728, 755	2	1.00	1.00
Nongallers	723–727, 727a, 729, 730, 735, 737, 744, 744a, 746–748, 753, 757, 808, 811–813, 816, 817, 821, 822, 823a, 825	27	1.71	1.33
Sesiidae				
Gallers	372, 377, 380	3	1.33	0.67
Nongallers	373–379, 381	8	1.50	0.75
Tortricidae				
Gallers	966, 1137, 1167, 1190, 1195, 1256, 1258, 1266	8	1.37	1.06
Nongallers	962, 964, 965, 967, 1168, 1192, 1194, 1196, 1197, 1199, 1200, 1200a, 1201, 1202, 1240, 1242, 1243, 1245–1247, 1249, 1253–1255, 1257, 1259–1261, 1264, 1265, 1267, 1268–1270	34	1.56	1.06
Pterophoridae				
Galler	1517	1	1.00	2.00
Nongaller	1519	1	2.00	2.00
Crambidae				
Galler	1359	1	2.00	1.00
Nongallers	1375	1	1.00	2.00
Summary				
Gallers		29	1.21	1.07
Nongallers		107	1.48*	1.11

[1] *Mompha bradleyi* Riedl, whose discovery in Britain (Harper 1994) postdates Emmet (1991).
* Mann-Whitney $U_{134df} = 1280.0$, $p_{one\ tailed} < 0.05$.

inae. Nongallers outnumber gallers in the study because plausible matches were often more numerous than the gallers matched, all being included to avoid selection bias.

Host breadth and voltinism data were extracted for both the gallers and nongallers from Emmet's (1991) tabulation. Data for one galler subsequently discovered in Britain, *Mompha bradleyi* Riedl, was obtained from Harper (1994). Host breadth was scored as number of recorded host genera. This is a stringent measure in that no distinction was made between one and more than one host species in the same genus; however, the problem of appropriately scaling and integrating genus and species scoring was thereby avoided. Scoring by species alone could not be done because the source did not consistently list numbers of host species within genera. Voltinism was scored as number of annual generations, with the case of less than one annual generation (one generation every two years) being scored as 0.5. This case had minimal impact because it occurred in only 3 of the 29 gallers (2 sesiids and 1 tortricid) and 4 of the 107 nongallers (all sesiids).

Student's t, Mann-Whitney U, and statistical summaries were computed with SYSTAT (1992) software. Homogeneity of variance between galler and nongaller groups was examined before analysis as outlined by Sokal and Rohlf (1981).

RESULTS

The 29 British gall inducers represent 11 of the 20 families of identified lepidopteran gall inducers worldwide (Table 1; Miller 2004). Stem galls are induced by 21 of the gallers, petiole galls by 5, and reproductive-structure galls by 3 (Robbins 1992, Spooner & Bowdrey 1995).

Mean host breadth was 1.21 genera for gallers compared to 1.48 genera for endophagous nongallers. The difference, 0.27, is in the expected direction of fewer host genera for gall inducers, and is significant (U-test, Table 1). The nonparametric U-test was used because galler and control variances proved divergent. Host breadth ranged 1–2 for the gallers, and 1–4 for the nongallers.

The difference in host breadth between the two groups originated mainly within Gelechiidae, Nepticulidae, Tortricidae, and Sesiidae. In these families, host breadth means for nongallers exceeded those for gallers by 0.71, 0.27, 0.19, and 0.17, respectively (Table 1).

Mean voltinism was 1.07 annual generations for the gall inducers, compared to 1.11 annual generations for the nongallers (Table 1). The difference, 0.04, although in the expected direction, is not significant ($t_{134df} = -0.53$, $p_{one\ tailed} = 0.30$). Galler and nongaller variances for voltinism proved to be homogeneous, which permitted the use of the parametric t-test. Voltinism ranged 0.5–2 for both gallers and nongallers.

DISCUSSION

Analysis of number of host genera supports the expectation of narrower host breadth for gall inducers than for endophagous nongallers among British Lepidoptera. This result (Table 1) might have been stronger had more elaborate scoring captured the intrageneric component of host breadth, but no objective method for combining or integrating genus and species scoring was available, and species counts alone could not be used because the source did not fully elaborate host species. Actual host breadth might also be stronger than indicated by the analysis for yet another reason: galls undoubtedly attract more interest and attention than other signs of insect infestation, so that host breadth of nongallers might be underreported compared to that of gallers, which could reduce the apparent difference.

Narrow host breadth is a trait that is highly desirable in biological control agents of weeds, one which, other things being equal, enhances the biological control potential of gallers (Harris & Shorthouse 1996, McEvoy 1996). Gelechiidae and Tortricidae, which are among the four families here with strongest differences between gallers and nongallers in host breadth (Table 1), are also the families with the greatest numbers of known gallers (Miller 2004).

Analysis does not support the expectation of lesser voltinism among gallers. This result (Table 1) contradicts Cornell's (1990) finding of lesser voltinism in gallers than leaf miners, but does not necessarily refute the hypothesis giving rise to the expectation. The British climate is cool–temperate and rainy, with the warmest month averaging less than 22°C (Lewis 1994). Such a climate may inhibit multivoltinism so that differences in voltinism between gallers and nongallers are minimized. By contrast, in eastern North America, a temperate land mass much larger than Britain, lepidopteran voltinism markedly increases as latitude decreases (Fracker 1920, Tauber et al. 1986). Multivoltinism in lepidopteran gall inducers, when it occurs, seems influenced more indirectly than directly by climate; that is, protracted growth seasons in warm temperate regions and in tropical wet cycles expand temporal availability of reactive host tissues for gall development (Miller 2004). Although Cornell (1990) did not taxonomically match gallers and leaf miners in comparing their voltinism, he reported no statistical connection between taxonomy and analytical outcome, and his result unequivocally shows lesser galler voltinism. Further testing of the voltinism expectation would be desirable. Possible mechanisms underlying galler–host phenological synchrony might include higher thermal thresholds for galler than nongaller development, and differing diapause reactions.

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