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ECOLOGICAL CHARACTERISTICS OF RARE SPECIES: THE CASE OF PARASITIC HYMENOPTERA

ABSTRACT: Ecological characteristics of relatively rare (singleton) hymenopteran species sampled in a beech forest on limestone are studied. No marked differences between singleton and non-singleton species occurred in regard to guild membership, stratum of host attack and phenology. There was however a strong effect of sample size on the fraction of singletons. Body size and phylogenetic position also appeared to influence rarity, but it proofed to be difficult to separate the effects of both variables. Rare species appeared to have larger density fluctuations but – in line with the theory of local mate competition – lower sex ratios than more common species. Brachypterous and apterous species had lower fractions of singletons. This result contradicts theoretical expectations of metapopulation models.

KEY WORDS Hymenoptera, parasitoids, rarity, density fluctuations, beech forest, phylogeny

1. INTRODUCTION

The question why certain species of a community are rare and the similar question what causes observed patterns of rarity has recently gained growing interest (Gaston 1994, Kunin and Gaston 1997, Rosenzweig and Lomolino 1997, Papp 1998, Ferriere and Cazelles 1999, Benayas et al. 2000, Novotny and Basset 2000). Rarity may be defined in various ways (Rabinowitz 1981, Gaston 1994, Benayas et al. 2000) each time focusing on other aspects of life history traits. Often, habitat specificity, local or regional mean density, habitat occupancy, or relative abundances are taken as measures for rarity (see Gaston 1994 and 1997 for a broad discussion of various kinds to define rarity).

If we deal with samples from local habitats or a certain region a special case of relative rarity, the so-called 'mystery of singletons' (Novotny and Basset 2000) has come especially into the focus of interest. In samples out of larger assemblages there is often a considerable number of species represented by only one individual (shortly termed singletons) and we have to call these species relatively rare. High percentages of singletons characterize especially samples in the tropics (e.g. Morse et al. 1988, Novotny 1993, Stork et al. 1997). This fact led to the view that the underlying relative abundance distributions in the tropics differ from those in temperate regions, i.e. that they are more equal, and/or that tropical species have lower absolute densities (Schoener 1987, Price et al. 1995). However, detailed studies on absolute densities of tropical species, especially insects, and comparisons with patterns found in temperate habitats are largely missing. Several authors (Janzen 1988, Erwin 1995, Basset et al. 1997, Novotny and Basset 2000) attribute the assumed differences in

density between tropical and temperate habitats to insufficient samplings.

These problems notwithstanding the high number of singletons in samplings raise genuine questions about the causes of species' rarity. Have some species the intrinsic feature of being (relatively) rare and may this feature be explained by environmental, ecological or phenological traits, or is rarity caused by stochastic effects that influence densities and density fluctuations. In the first case we may identify a set of typical characteristics of rare species. In the latter case times of rarity may be found in all species (Ferriere and Cazelles 1999). The answer of these questions will have broad implications for our understanding of community processes but also for conservation biology. If rare species are really different they may also need different ways in conservation (Gaston and Kunin 1997).

Any study of rarity has therefore not only to deal with single samples in which some species are classified as being rare. Long-term studies are necessary to establish whether rarity is a genuine feature of a species. The present study results from seven years of sampling parasitic Hymenoptera in a temperate beech forest on limestone. It tries to give ecological characteristics of rare species (in this case of singletons) and to establish whether temporal patterns of densities differ between relatively common and relatively rare species. Such a study then allows comparisons to be made between patterns found in this temperate assemblage and others recently studied.

2. MATERIALS AND METHODS

The studies were undertaken from 1981 to 1987 on a chalk plateau in a mixed beech forest (420 m altitude, roughly 120 years old) on limestone near Göttingen (FRG). Eggert (1985), Schaefer (1990) and Ulrich (1987, 1988, 1998) gave detailed descriptions of the study area. Dierschke and Song (1982) characterized the vegetation as a Melico-Fagetum subassociation *Lathyrus vernus*. The herbaceous flora mostly consists of spring-geophytes that to a great extent disappear in the summer months. Most abundant are *Allium ursinum* and *Mercurialis perennis*.

Between 1981 and 1987 samplings were taken using ground-photo-eclectors. A detailed description of the sampling program is already given in Ulrich (1988, 1998), Schaefer (1990) and Hövemeyer (1985, 1992). Each year between 5 and 20 eclectors of 0.25 m² (1984, 85) or 1m² (other years) sampling area were used.

The sorting of the species into ecological guilds is the same as in Ulrich (1998). Detailed descriptions of the phenology and the temporal variability of the species are given in Ulrich (1999a, b, c, 2000). In total 36352 individuals out of 669 parasitoid species were found using ground-photo-eclectors.

Following Novotny and Basset (2000) this paper treats all species of which only one individual was found (singletons) as rare and compares these species with all other Hymenoptera of the beech forest under study. The study builds only on catches of those emergence traps (ground-photo-eclectors) that were taken at least 3 weeks after placing the traps. This procedure excludes transient or tourist species (sensu Moran and Southwood 1982) that (in tropical samples) may comprise up to 20% of all species collected (Basset 1997). Including them may give highly misleading results.

3. RESULTS

3.1. NUMBERS OF SINGLETONS

Of 669 parasitoid species found during the study period 176 (26.3%) were singletons. These species represent 0.49% of the total number of specimens (36352).

Of course, the fraction of singletons depends on the sample size. Sample size itself may be expressed in terms of densities and of area sampled. Both variables together determine the total number of specimens in the samples. A plot of yearly fractions of singletons versus density (individuals m⁻²) of the parasitoids and versus area sampled can be fitted either by a semi-logarithmic or by a linear model (Fig. 1 A, B).

The mean fraction of singletons per m² of forest floor was around 50% (Fig. 1 B). The fraction dropped below 1/3 above 100 m² sampled. Extrapolations with the semi-logarithmic and the linear regression models led to upper and lower limits of the area necessary to find no singletons. These values range between 0.4 and 56 ha and show mainly how difficulty it is to give estimates of
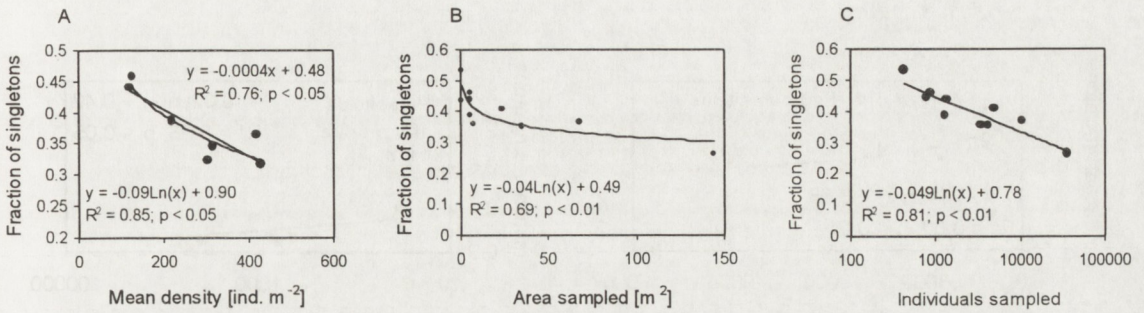
Fig. 1: Fraction of singletons in guilds of parasitoids in samples from ground-photo eclectors in relation to (A) mean density per guild (ind. m^{-2}), (B) area sampled [m^2], and (C) specimens sampled. Guilds are the same as in Fig. 2 A.

necessary sample sizes by extrapolation of limited samples.

A plot of specimens versus the fraction of singletons point to a semi-logarithmic dependence between both variables (Fig. 1 C). From an extrapolation of the regression we may infer that we need more than 800,000 specimens to get no further singletons.

3.2. HOST SPECIFICITY OF SINGLETONS

Fig. 2 A shows the fraction of singletons of important parasitoid guilds of the beech forest (guild associations are according to the classification in Ulrich 1998). It appears that the fraction of singletons was least in the parasitoids of miners and gall-makers, that means parasitoids of endophytophages. But, due to the above-described dependence of the fraction of singletons on sample size (Fig. 1 C) different total densities of the species of these guilds will result in different sample

sizes for each guild. Of the parasitoids of gall-makers, for instance, 11135 specimen were found, but of parasitoids of predators only 1109. We have therefore to compare the fraction of singletons per guild with the expected fraction assuming a regression as in Fig. 1 C. (Fig. 3).

The plot of fraction of singletons versus sample size (Fig. 3) shows that only the egg-parasitoids deviate from expectation. They have more than 60% more singletons than expected from the regression. This indicates that the community structure of the egg-parasitoids deviates from other parasitoids in having more rare species.

Fig. 2 B gives the fraction of singletons for the different host taxa. The Figure shows that extraordinary high fractions of singletons were only found in the case of parasitoids of Symphyta a result that holds even when again comparing the fraction of singletons with the expectation from the sample size (Fig. 3 B).
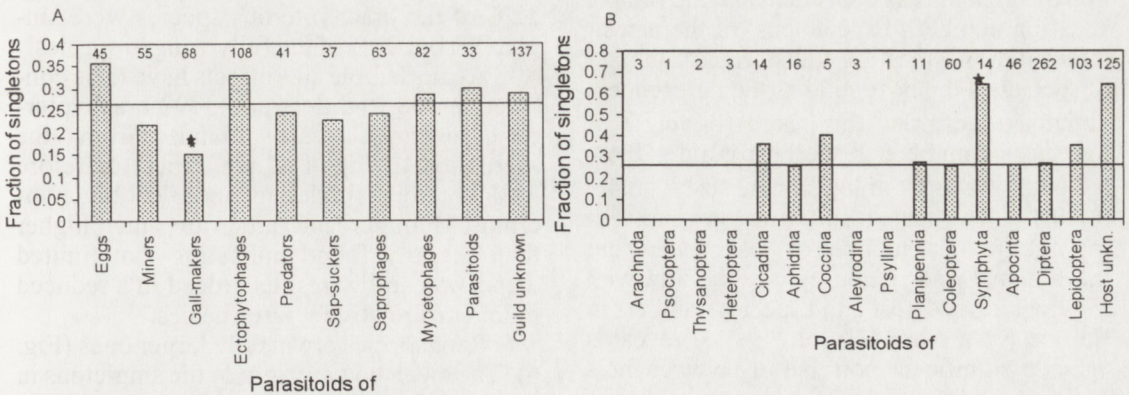

Fig. 2. Fraction of singletons in different parasitoid guilds after a sorting according to host guild (A) and host taxon (B). The numbers above the columns give the total number of species per guild. An asterisk marks significant deviations from the mean (indicated by the horizontal lines).
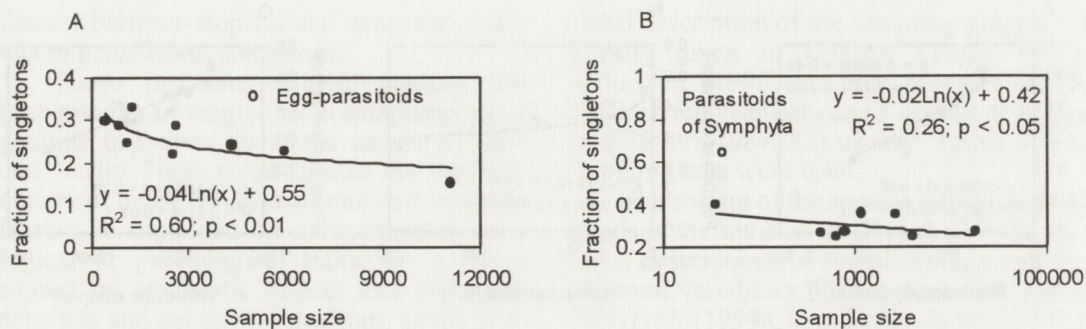
Fig. 3. Fraction of singletons in relation to the sample sizes (number of specimens) for the parasitoid guilds of Fig. 2 A (A) and Fig. 2 B (B). Open circles mark guilds that significantly deviate from the regression.

The fraction of singletons was neither correlated with the species number per ecological guild (Fig. 2. A) or host taxon (Fig. 2 B) nor with the respective species number of the local (beech forest: multiple regression with log sample size and log species number: β-weight of species number: 0.13, p = 0.68) or regional species pool (whole European fauna: β-weight of species number: 0.06, p = 0.88).

However, estimates of species numbers of host guilds (Schaefer 1991, Ulrich 1999b) revealed that the fraction of singletons depends on the size of the local and regional host guild (Fig. 4). Species rich host guilds like arthropod predators (about 250 species in the beech forest), ectophytophages (150 species), myceto- or saprophages (250 species), and the parasitoids itself (about 600 species) sustain parasitoid guilds that have higher fractions of relatively rare species than species poorer host guilds like sap-suckers (40 species), miners or gall-makers (about 50 species each). A multiple regression with the fraction of singletons as dependent and the sample size (log number of specimens) of the parasitoid guild and the (log-transformed) number of species of the host guild as the independent variables confirmed this result (β-weight of log species number in the host guild = 0.64, p < 0.05; β-weight of log sample size = –0.45, p = 0.14). The same result came up when taking not the local number of host species, but the regional one. A multiple regression with log-transformed host guild species numbers in Europe (data from Ulrich 1999b) revealed again a significant correlation between host guild size and fraction of relatively rare species of their hymenopteran parasitoids (β-weight of log European species number in the host guild = 0.65, p < 0.05).
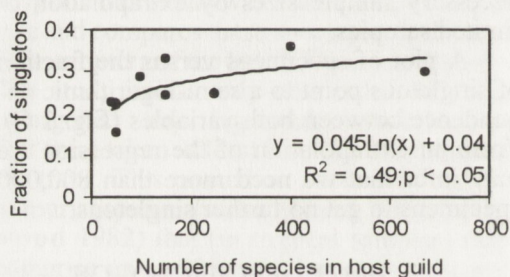

Fig. 4: Dependence of the fraction of singletons on the number of species in the host guild (guilds as in Fig. 2 A).

3.3. MORPHOLOGICAL AND PHYLOGENETIC CHARACTERISTICS OF SINGLETONS

Is rarity connected with the ability of dispersal? To answer this question I compared the fraction of singletons of fully winged, brachypterous and apterous parasitoid species (Fig. 5). It appeared that apterous species have the lowest fraction of singletons (16%). 22% of the brachypterous species were singletons, but 27% of the fully winged species.

Again sample size effects have to be considered. 358 flightless and 3792 brachypterous specimen were found. From the regression in Fig. 1 C we expect therefore 49% apterous singletons and 37% brachypterous. Both percent values are much higher than actually found indicating that limited dispersion ability results indeed in a reduced number of relatively rare species.

Rare species are mostly larger ones (Fig. 6). The mean body weight of the singletons in the beech forest was about 1.2 mg dry weight and exactly two times as high as the mean body weight of more abundant species. This result may be caused by the negative regres-
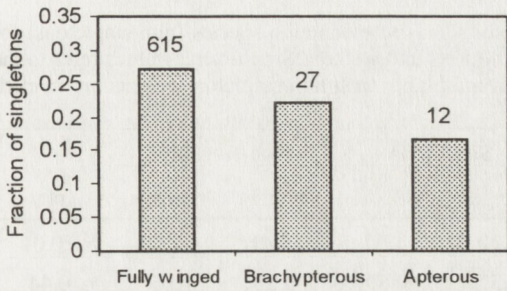
Fig. 5. Fraction of singletons of fully winged, brachypterous, and apterous parasitoid species. The numbers above the columns give in each case the total number of species.
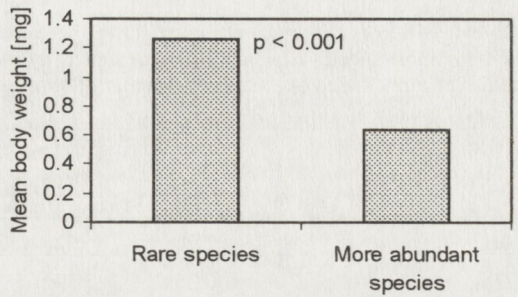

Fig. 6. Difference between singleton species (rare species) and more abundant species in regard to their mean body weight [mg dry weight]. The significance value refers to a two-tailed t-test.

sion of mean density on body weight (Ulrich 1999d). But a MANCOVA with sample size as covariate confirmed the picture of Fig. 5 (F = 5.11, p = 0.02). Rare species are in the mean larger than more abundant species.

Cotgreave and Pagel (1997) compared ecological characteristics of rare and common birds of Australia using the distribution maps of Blakers *et al.* (1984). Their main prediction was that rare species would typically belong to a phylogenetically old and/or primitive taxon. We may take the phylogenetic classification of Königsmann (1976, 1978) as a starting point to test whether this prediction also holds for parasitic Hymenoptera. Although the exact phylogenetic relationships are still unknown (Naumann and Masner 1985, Gauld and Bolton 1988) we can clearly identify more primitive and more derived taxa (mainly from the degree of reduction of wing venature). Ichneumonidae appear to be the most primitive group of Terebrantes. Ceraphronoi-

dea and some families of the Chalcidoidea (Aphelinidae, Eulophidae, Trichogrammatidae, Encyrtidae and Mymaridae) are highly derived. Fig. 7 gives a plot of the fraction of singletons in the 8 most species rich taxa of the beech forest versus their phylogenetic position (the gradient from more primitive to more derived: A) and sample size (B). It appears that more primitive taxa (Ichneumonidae and Braconidae) contain indeed higher fractions of singletons (above 30%). On the other hand, the highly specialized Ceraphronoidea and derived Chalcidoidea had less than 20% singletons. The last two taxa also appeared to have to few singletons when taking the sample sizes into account (Fig. 7 B). Ichneumonidae and Braconidae do not detectable deviate from expectation.

Unfortunately, reduction of body weight in the Hymenoptera is closely connected with the feature of being phylogenetically derived (Königsmann 1976, 1978). Primitive species are nearly always larger ones. Simple
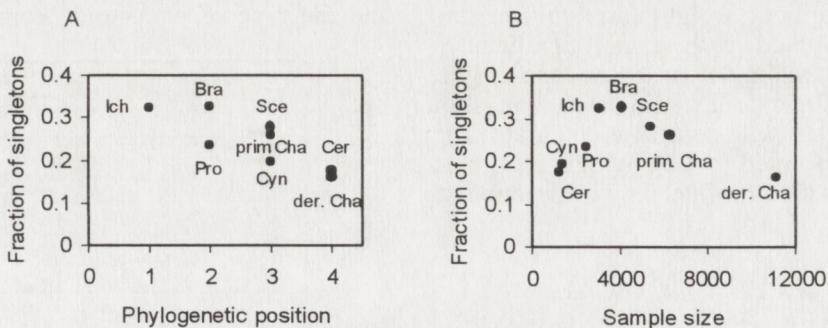

Fig. 7. Fraction of singletons in eight parasitoid taxa versus phylogenetic position and sample size. Ich: Ichneumonidae; Bra: Braconidae; Pro: Proctotrupoidea; Sce: Scelionoidea; Cyn: Cynipoidea; Cer: Ceraphronoidea; Prim. Cha and der. Cha: primitive and derived Chalcidoidea. The phylogenetic position follows the classification of Königsmann (1976, 1978). The most primitive group was given the position 1, the most derived the position 4.

Table 1. Difference in mean body weight [g] between singletons and more common species (non-singletons) for the eight most species rich taxa of Hymenoptera of the beech forest under study. Significance values refer to the results of a one-sided t-test. Mean weights of singletons that are higher than non-singleton weights are marked in bold type

Taxon	Mean body weight	Weight difference (max. / min.)	Singletons		Non-singletons		
			Weight	StDev.	Weight	StDev.	p(t)
Ichneumonidae	2.20	620	**3.10**	4.70	1.80	2.50	<0.01
Braconidae	0.36	394	**0.37**	0.80	0.35	0.60	0.44
Cynipoidea	0.20	54	0.14	0.16	0.21	0.24	0.26
Primitive Chalicidoidea	0.18	64	0.12	0.08	0.21	0.20	0.04
Derived Chalicidoidea	0.06	245	0.06	0.07	0.06	0.07	0.24
Proctotrupoidea	0.33	13	0.33	0.20	0.34	0.20	0.46
Scelionoidea	0.04	344	**0.05**	0.06	0.04	0.03	0.07
Ceraphronoidea	0.03	576	**0.06**	0.10	0.02	0.01	0.02

Table 2. MANCOVA to detect the dependence of the fraction of singletons on phylogeny (Taxa as in Tab. 1) and body weight. Mean density of the species served as covariate

Parameter	df Effect	MS Effect	df Error	MS Error	F	p(t)
Taxon	5	0.000106	533	3.75E-06	28.216	<0.0001
Body weight	1	1.86E-06	533	3.75E-06	0.496252	0.481
Combined effect	5	9.43E-06	533	3.75E-06	2.516582	0.029

comparisons as in Figs 6 and 7 do therefore not allow separating the effects of body weight and phylogenetic position on the fraction of singletons. For this task I undertook an intrataxon comparison of singletons and non-singletons (Tables 1 and 2). It appears from Table 1 that inside the eight taxa considered the body weight effect largely vanishes although this may be the effect of a to small difference in body weights. In two taxa singletons weighted in the mean significantly more than non-singletons, in one taxon (the primitive Chalcidoidea) this was opposite. A MANCOVA with density as covariate (Table 2) also pointed to the phylogenetic position as main factor influencing the fraction of singletons.

3.4. PHENOLOGICAL CHARACTERISTICS OF SINGLETONS

A classification of parasitoids into the stratum of host attack (canopy, herb-layer or soil – Ulrich 1998, 1999c) showed that parasitoids attacking hosts in the canopy region had the lowest fraction of singletons

(Fig. 8). This result holds when considering the sample size effect (MANCOVA with number of specimens sampled as covariate: F = 22.8; p < 0.0001).

A MANCOVA (again with the number of specimens sampled as covariate) did not detect differences between rare and more common species concerning the number of generations (MANCOVA: F = 0.06; p = 0.79) and the type of parasitoid (koinobiontic or
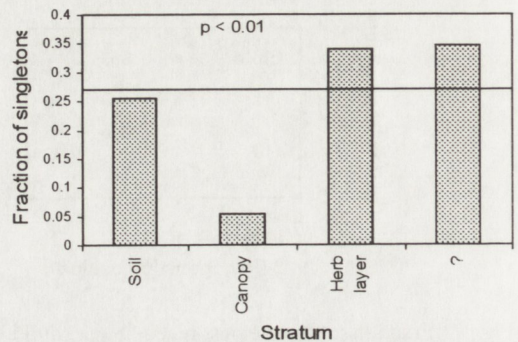

Fig. 8. Fraction of singletons in relation to the stratum of host attack. The significance value refers to a two-tailed t-test for a difference from the mean (indicated by the horizontal line).

idiobiontic: MANCOVA: $F = 0.08$; $p = 0.78$). But species hibernating as imago had a higher fraction of rare species (16%) than species hibernating as larvae or egg (11%) (MANCOVA: $F = 4.12$; $p = 0.04$).

More infrequent species proofed to have higher density fluctuations than more abundant species. Fig. 9 shows how many species had in one of the years densities that were more than 2 or more than 3 times the mean (ln-transformed) density of all species found in a given number of the study years. That means none of the species that were found in all of the seven study years reached densities above 2 times the ln-transformed mean densities (7.4 times the mean density) of that group. But 15% of the species that were found in only one of the study years had in that year a density above 2 times the mean of that group. 7% of these species had even a density above 3 times the mean ln-transformed density.
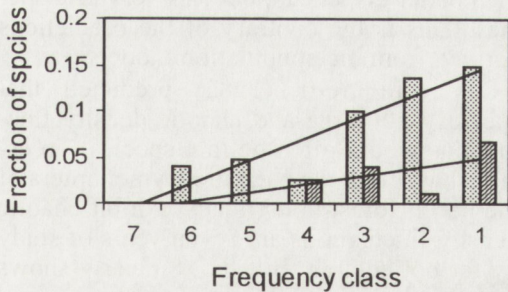

Fig. 10. Mean sex ratio (fraction of males of all individuals found) in relation to mean density per density class (ind. m^{-2}). These mean densities are computed separately for all species represented by only one individual (the singleton class, 176 species, numbers given at data points), 2 individuals (80 species), 3 individuals (92 species), and so on. The regression line refers to a best-fit model of the form $y = 0.7x / (0.007 + x)$.

Fig. 9: Fraction of species that had densities above 2 (gray bars) or 3 (stripped bars) times the mean density of his frequency class. The frequency classes are defined by the number of species that had been found in exactly 1, 2, 3...7 seven of the study years. Due to the high difference in densities ln-transformed densities were used for computation.

The theory of local mate competition (LMC, Hamilton 1967) states that rare species should reduce the fraction of males per habitat patch. Such a trend could indeed be detected for the parasitoids of the beech forest under study (Fig. 10). A comparison of the sex ratios of all singleton species (number of males / total number of individuals) with that for other density classes showed a positive dependence of sex ratio on mean density as predicted by the LMC theory. By extrapolating the regression we may estimate the density at which all species should be thelytokous. This boundary is below a density of 1 individual per 100 m^2 area.
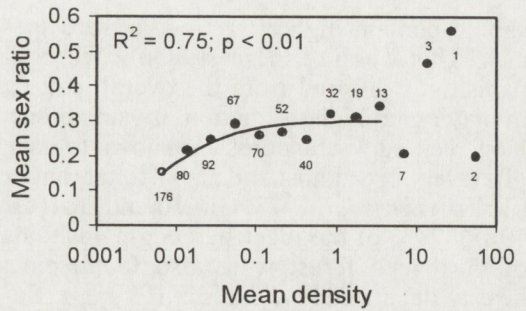
4. DISCUSSION

When studying rarity four main questions arise: What is rarity (Gaston 1994), what causes rarity (Gaston 1994, Kunin and Gaston 1993, 1997), is rarity predictable (Cotgreave and Pagel 1997), and are rare species different (Gaston 1994, Rosenzweig and Lomolino 1997, Novotny and Basset 2000)?

In the present study rarity was defined in terms of relative density. This is the most often used definition and has the advantage that it allows comparisons to be made with other studies.

Are rare species really different? Brown (1984) and Brown et al. (1995) argued that patterns of habitat use, niche breadth and degrees of specialization cause rarity. Narrow realized niches and a high degree of specialization result in local and – via the positive relation between local abundance and range size (Gaston 1996, Gaston and Curnutt 1998) – also regional rarity. The results of the present paper do not support this view. The fraction of rare species in more specialized koinobiontic species was not higher (in fact slightly lower) than in the less specialized idiobiontic ones (see Askew and Shaw 1986 for a review of these life history traits). Parasitoid guilds should also differ in respect to the fraction of rare species. Especially the more specialized parasitoids of concealed hosts and the hyperparasitoids

should contain higher fractions of rare species. This was not the case. Only the egg-parasitoids differed from the overall pattern in having a higher fraction of singletons. However, egg-parasitoids are known to have often very broad host and also habitat ranges (Trapitzin et al. 1978, Gauld and Bolton 1988). 29% of the identified egg-parasitoids of the beech forest were also found on a nearby dry meadow (Ulrich 1999 e, f; Soerensen index of species overlap: 0.34), but of all other species only 15% occurred in both habitats (Soerensen index: 0.22) (Ulrich 1999d). Unfortunately, there are no data on host densities and of most of the parasitoids the exact host range is unknown. Therefore, the influence of resource availability could not be studied.

Novotny and Basset (2000) studied ecological characteristics of singleton species in samples from New Guinean trees. They also rejected the specialization hypothesis and asked whether monophagous singletons (that means very specialized rare species) in fact exist?

Gaston (1994) and Blackburn and Gaston (1997) argued that the only clearly established pattern is that between rarity and body size. The present study again revealed a relation between both variables. Singleton species had on average 2 times the body weight than the more abundant species (Fig. 6). However, a more detailed analysis and a comparison with the phylogenetic position revealed a more complicated picture. The fraction of singletons was both connected with body size and with phylogenetic position. In a taxon like the Hymenoptera where phylogenetically derived groups show always a trend to body size reduction it appeared to be very difficult to separate the influence of both variables. The data of intrataxon comparisons of singleton and non-singleton body weights gave no clear answer (Table 1). Clearly, other studies on taxa that do not show a trend to body size reduction have to clarify the picture. However, the present study shows that we can not simply compare body sizes of species with different densities leaving other factors aside.

Judged from the published literature, it seems that there is a negative relation between dispersal ability and rarity. Metapopulation models often connect regional range sizes with dispersal ability (Hanski and Gilpin 1997, Hanski 1999). Additionally, the positive relation between local density and range size is well established (Holt et al. 1997, Gaston and Curnutt 1998, Hartley 1998, Thompson et al. 1998, Huston 1999). From this we may infer that good dispersers should also have higher local abundances and the fraction of relatively rare species should be small. Several studies found bad dispersers to be locally rare and to have smaller regional range sizes (Hedderson 1992, Oakwood et al. 1993, Gaston 1994, Novotny 1995). In beetles Crowson (1981) reported limited flight ability associated with restricted geographical range and from this we may also predict small local densities. The present study sheds a differentiated light on this view. Ulrich (1999d) found apterous and brachypterous species to have similar densities than fully winged ones. The data of Fig. 5 show that the fraction of relatively rare species (singletons) was significantly higher in the latter group. It seems that parasitoid species with low dispersion abilities have in the mean the same densities than better dispersers, but less very rare species. This is the contrary of the predictions derived from metapopulation models.

Vandermeer (1982) predicted that species with large and chaotic density fluctuations would often be rare species. To establish whether the parasitic Hymenoptera of the beech forest under study exhibit chaotic density fluctuations are seven years of study by far not enough. But Fig. 8 clearly shows that the degree of density fluctuation is related to the frequency of occurrence. Infrequent species – that means species that had been found in only a few of the study years – had relatively higher density fluctuations than more frequent ones.

At the end we may compare our results with that of the already mentioned study of singletons from tropical Bornean rain forest trees of Novotny and Basset (2000). They also found high proportions of singletons (45%) in leaf chewing communities. As in the present study little ecological differences between rare and more common species appeared. Guild membership did not seem to influence the fraction of singletons. Novotny and Basset (2000) reported that the fraction of singletons and the total species number in a guild were positively correlated. In the parasitoid guilds of the Göttingen beech forest no such dependence was found. But the fraction of singletons and the number of host species were positively correlated (Fig. 4).

Novotny and Basset (2000) also reported a logarithmic relation between the fraction of singletons and the sample size and extrapolated that more than 180,000 specimens have to be sampled to get no further singletons. The same relation was found in the present study (Fig. 1 C) and a similar extrapolation for the beech forest Hymenoptera gave more than 800,000 specimens. This difference indicates either a higher total species number of the beech forest (720 parasitoid species had been found, whereas Novotny and Basset reported 1050 species) or differences in the relative abundance distributions between the two communities with the beech forest having larger differences in density between most and least abundant species.

Is rarity predictable? Judged from the present and other mentioned studies the answer will largely be no. It appeared that rare and more abundant hymenopteran species differ markedly in only two ways. Individuals of rare species are more often larger than abundant ones and they have relatively larger density fluctuations. Guild membership and phenological traits seem to be of minor importance. Of course, in the case of parasitoid species host densities and their population dynamics have to be taken into account, but for this task more detailed analyses of whole food web structures are necessary. At the present time no such studies have been undertaken.

5. SUMMARY

Ecological characteristics of relatively rare (singleton) hymenopteran species sampled in a beech forest on limestone are studied. No marked differences between singleton and non-singleton species occurred in regard to guild membership, stratum of host attack and phenology (Figs 2, 3, 4, and 8). There was however a strong effect of sample size on the fraction of singletons (Fig. 1). Body size and phylogenetic position also appeared to influence rarity, but it proofed to be difficult to separate the effects of both variables (Figs 6 and 7, Tables 1 and 2). Rare species appeared to have larger density fluctuations (Fig. 9) but – in line with the theory of local mate competition – lower sex ratios (Fig. 10) than more common species. Brachypterous and apterous species had lower fractions of singletons (Fig. 5). This result contradicts theoretical expectations of metapopulation models.

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