

Flight Phenology of Parasitic Wasps (Hymenoptera: Ichneumonidae) in Georgia's Piedmont

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ABSTRACT We present monthly catches for the 22 subfamilies of Ichneumonidae ($n = 16,584$) collected in 5 Malaise traps at the Hitchiti Experimental Forest, GA (33° 03' N, 83° 43' W) in 1993 and 1994. Although average peaks of trap catches for koinobionts and idiobionts coincided, the phenological peaks of individual taxa within these parasitic groups often differed. The nocturnal parasitoid subfamily Ophioninae peaked in July 1993 and June 1994, whereas the nocturnal genus *Netelia* (Tryphoninae) peaked in April of both years. The most frequently caught subfamilies with hosts in the Lepidoptera and Symphyta peaked in late April–early May of both years (Campopleginae, Cryptinae, Ichneumoninae, Ctenopelmatinae, and Tryphoninae). In contrast, subfamilies with hosts in the Coleoptera had unsynchronized peaks in April (Tersilochinae) and June (Acaenitinae) 1993 and in September (Tersilochinae) and June (Acaenitinae) 1994. The subfamily Orthocentrinae, which attacks dipteran hosts, peaked in April 1993 and November 1994. The hyperparasitic subfamily Mesochorinae peaked in May 1993 and April and October 1994, corresponding in time to trap catches of their potential host subfamilies that attack Lepidoptera and Symphyta. We hypothesize that host seasonality is more important than other environmental factors and life history parameters in determining peak flight activity.

KEY WORDS Hymenoptera, Ichneumonidae, seasonality, koinobiont, idiobiont, parasitoid

THE HYMENOPTERA CONSIST mostly of parasitoids—parasites that eventually kill their hosts. The major hosts of these parasites are the larvae or pupae of holometabolous insects, particularly the Coleoptera, Diptera, Hymenoptera, and Lepidoptera (Gauld and Bolton 1988). Among the parasitic Hymenoptera one of the largest groups is the Ichneumonidae, consisting of an estimated 60,000 species worldwide (Townes 1969). Currently, much of the discussion on parasitoids concerns the biological factors governing their abundance (Nealis 1988, Gauld 1991, Thangavelu 1993). However, information on parasitoids is limited because of their elusive behavior and small size and because of a lack of researchers (Gauld and Bolton 1988). Thus, many of the questions that impinge upon higher-order processes remain unanswered. For example, What factors determine parasitoid flight activity? How much of this activity is determined by climatic variables, resource availability, or other factors?

The Ichneumonidae, composed of 35 subfamilies (Wahl 1993), are categorized 2 ways: either as ectoparasites versus endoparasites or as idiobionts versus koinobionts (Askew and Shaw 1986). Ectoparasitoids feed externally on the host whereas endoparasitoids

feed internally (Askew and Shaw 1986). Idiobionts kill or paralyze their host immediately after oviposition and host development does not continue. Hosts of koinobionts continue to develop after oviposition and are killed in a later stage of development. Idiobionts tend to have a wide host range (Spradbery 1968). Koinobionts are thought to have a more specialized host range because they must develop defense systems to fight the host's immune response (Salt 1968, Gauld 1988a). Most ichneumonid subfamilies are diurnal; however, 2 major groups are nocturnal: the subfamily Ophioninae and the speciose genus *Netelia* in the Tryphoninae (Gauld and Bolton 1988, Gauld 1991). It has been speculated that this strategy has evolved to combat the daily heat (Gauld 1988b), avoid diurnal predators (Gauld 1991), or hunt nocturnally active hosts, or all of these.

Owen et al. (1981) addressed the importance of host availability in ichneumonid seasonal abundance. Owen (1991) studied the phenology (seasonality) of ichneumonids in Leicester, England. She found that ichneumonid flight activity peaked in August, the warmest and one of the driest months of the year. She also found that many species of ichneumonids are common over longer periods of time than individual host species. Hence, she hypothesized that ichneumonid flight activity depends more on their niche specificity than on the phenology of individual host species.

Gauld (1991) studied the phenology of the ichneumonid subfamilies Ophioninae, Pimplinae, and Rhys-

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sinae in Costa Rica. Ophionines are endoparasitic koinobionts that attack Lepidoptera and are primarily nocturnal. Pimplines are either ectoparasitic or endoparasitic diurnal idiobionts that attack Coleoptera, Hymenoptera, Lepidoptera, and spiders. Rhyssines are diurnal ectoparasitic idiobionts that attack Symphyta (Hymenoptera) and Coleoptera. Gauld (1991) compared flight activity between the idiobionts (Pimplinae and Rhyssinae) and koinobionts (Ophioninae). He found that koinobionts peaked earlier than idiobionts and concluded that this may be a result of the koinobionts attacking the 1st flush of larvae early in the wet season and the idiobionts attacking later stages of host development later in the season. Flight activity is, therefore, expected to vary among parasitoids attacking different stages of host development, such as primary parasites and hyperparasites.

We analyzed 2 complete years of data (1993–1994) from 5 Malaise traps run in Georgia's Piedmont to answer the following 5 questions about ichneumonid flight activity: (1) Do koinobionts peak earlier in the year than idiobionts, as reported by Gauld (1991) in the tropics? (2) Are there different seasonal peaks between nocturnal parasitoids? (3) What is the relationship between host and parasitoid flight activity? (4) What is the phenological relationship between the number of specimens and the number of species? and (5) Do hyperparasitoids differ in flight activity peaks from primary parasites and their hosts?

Materials and Methods

Site Study. This study is part of a project examining the abundance of insects in the Hitchiti Experimental Forest (33° 03' N, 83° 43' W) in Jones County, GA (Lockard 1995; Gaasch 1996; Gaasch et al. 1995). The forest is located ~50 km from the fall line of the coastal plain in the lower Piedmont and consists of numerous managed and unmanaged forest stands. It is dominated by loblolly pine, *Pinus taeda* L.; flowering dogwood, *Cornus florida* L.; sweetgum, *Liquidambar styraciflua* L.; white oak, *Quercus alba* L.; and eastern hophornbeam, *Ostrya virginiana* (Miller) K. Koch. Five stands were sampled: a 1990 clear-cut stand, a 30- to 45-yr-old pine stand, a 60- to 85-yr-old pine stand with prescribed burning, a 60- to 85-yr-old stand without management, and a 70-yr-old riparian deciduous stand. For detailed stand descriptions see (Gaasch et al. 1995, 1996).

Trapping. One Townes-style Malaise trap was placed in each of the 5 stands (Townes 1972). These are tentlike traps that intercept insects during flight and collect them into a bottle containing 70% EtOH. We placed all traps in a N–S direction with the collecting jar facing south. We serviced these traps once a week in 1993–1994. We collected a total of 520 samples.

Barcoding. We mounted a total of 16,584 Ichneumonidae from the samples. To accurately analyze this large data set, we gave each specimen both a unique barcode and a conventional label. The barcode links

an individual with specific site information in the database, including location, trap, and sample dates.

Identification. We sorted all ichneumonids to subfamily. D. B. Wahl (American Entomological Institute) and C. Gaasch sorted members of the Campopleginae and Ichneumoninae to morphospecies, finding at least 117 and 100, respectively (Gaasch 1996). We determined certain specimens to species: Ichneumoninae, *Dusona* (Campopleginae) and *Casinaria* (Campopleginae). We deposited voucher specimens at the American Entomological Institute and the University of Georgia.

Data Analysis. Once identified, we electronically scanned specimens by taxon and sex into the database. We tallied specimens in each bulk sample by taxon. We calculated monthly totals for each subfamily by combining subfamily weekly totals from each month. If a week was divided between 2 mo, we proportionally distributed the specimens for that week between the 2 mo based on the proportional number of days of the week occurring in each month. For regression analysis, we log-transformed monthly counts. We added 0.5 to each count to allow the transformation of zero counts.

We calculated the proportion of species that occurred in each month in the same manner used to tally the subfamilies. We analyzed males and females separately to avoid the problem of linking males and females of sexually dimorphic species, as often occurs in the Ichneumoninae (Gaasch et al. 1995).

We used harmonic regression models (Bloomfield 1976) to describe the phenological pattern for each subfamily and to provide a basis for the estimation of T_1 and T_2 , the times of annual primary and secondary phenological peaks, respectively. Models that included terms for both 12- and 6-mo cycles (2 harmonics) had sufficient flexibility to capture primary and secondary phenological peaks in the data, should they exist. We did investigate single-harmonic models for each of the subfamilies, but we found significantly poorer fit for them relative to the 2-harmonic models (reduction in sums of squares, Rawlings [1988]) for 20 of the 22 subfamilies. Only the Lycorininae and the Poemeniinae exhibited single-peak behavior, but these subfamilies were among the sparsest sampled (Table 1). For the remainder of the analyses, we chose to use 2-harmonic models for all subfamilies.

We fit a 2-harmonic model to monthly data for each subfamily, and we included a term YEAR to allow an additive shift in the phenological pattern between 1993 and 1994. We also included interaction terms between YEAR and each of the harmonic components of the model to allow the patterns to vary by year. Testing the joint effect of the interaction terms (Rawlings 1988) allowed us to judge whether the subfamily possessed common (YEAR-additive, Fig. 1) or dissimilar (YEAR-interactive, Fig. 2) phenological patterns in 1993 and 1994. We investigated plots of model residuals to assess conformance of the models with least-squares assumptions and to identify areas of model weakness.

Table 1. Ichneumonid life history and trap catches of the subfamilies collected at Hitchiti Experimental Forest, GA, 1993–1994

Subfamily	No. trapped	K/I	N/C	Primary hosts
Acaenitinae	169	K	N	Col
Anomaloninae	191	K	N	Lep/Col
Banchinae	349	K	N	Lep
Campopleginae	2,517	K	N	Lep
Cremastinae	147	K	N	Lep
Cryptinae	5,159	I	C	Lep
Ctenopelmatinae	165	K	N	Sym
Diplazontinae	38	K	N	Dip
Eucerotinae	9	K	N	Hym
Ichneumoninae	2,308	I	N	Lep
Labeninae	79	I	C	>2 host orders
Lycorininae	13	K(?)	N(?)	Lep
Mesochorinae	231	K	N	Hym
Metopiinae	299	K	N	Lep
Ophioninae	264	K	N	Lep
Orthocentrinae	3,266	K	N	Dip
Pimplinae	504	I	N/C	>2 host orders
Poemeniinae	26	I	C	Col/Sym
Rhyssinae	15	I	C	Col/Sym
Tersilochinae	179	K	N	Col
Tryphoninae	598	K	C	Sym/Lep
Xoridinae	58	I	C	Col

Koinobiont (K), idiobiont (I), ectoparasitic (C), endoparasitic (N), Coleoptera (Col), Lepidoptera (Lep), Diptera (Dip), Symphyta (Sym), Hymenoptera (Hym).

For each model, we conducted a Newton–Raphson search (Press et al. 1986) for estimated phenological maxima \hat{T}_1 and \hat{T}_2 . YEAR-interactive models contained 4 potential maxima, 2 maxima in each year, whereas YEAR-additive models contained only 2 (i.e., maxima for 1994 were redundant with maxima for 1993, by definition of the YEAR-additive model). In

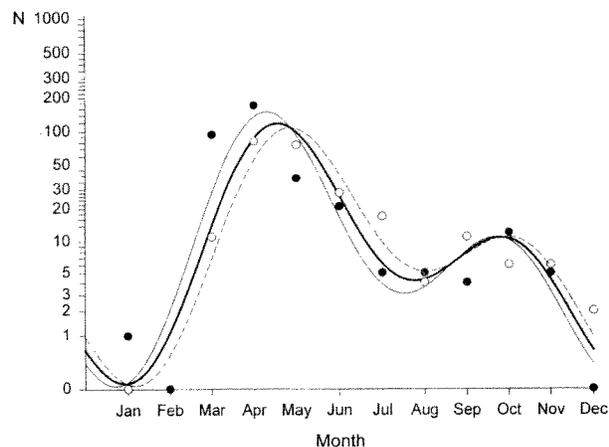


Fig. 1. Monthly counts of Tryphoninae (N) collected in Hitchiti Experimental Forest, GA, in 1993 (open circles) and 1994 (closed circles), superimposed with predictions from candidate 2-harmonic models. Predictions from the YEAR-interactive model show dissimilar phenology patterns for 1993 (light, dashed line) and 1994 (light, solid line) that are not statistically distinct from each other. Their average is expressed by the YEAR-additive model (2 overlaid heavy lines), in which predictions for 1993 and 1994 share a common phenology but at possibly different magnitudes. For Tryphoninae, the difference in magnitudes is by coincidence nearly 0, so the prediction lines overlay each other.

both kinds of models, \hat{T}_2 did not exist for some subfamilies (Fig. 3).

We estimated precision for the \hat{T}_i through parametric bootstrap sampling. For each model, we drew 1,000 pseudorandom parameter vectors from a multivariate normal distribution with mean $\hat{\mu}$, the vector of estimated regression model coefficients, and variance $\hat{\Sigma}$, the estimated variance-covariance matrix from the model. On each draw, we searched for the T_i and output their values. The T_i on a single draw resembled the estimated \hat{T}_i from the regression model, differed

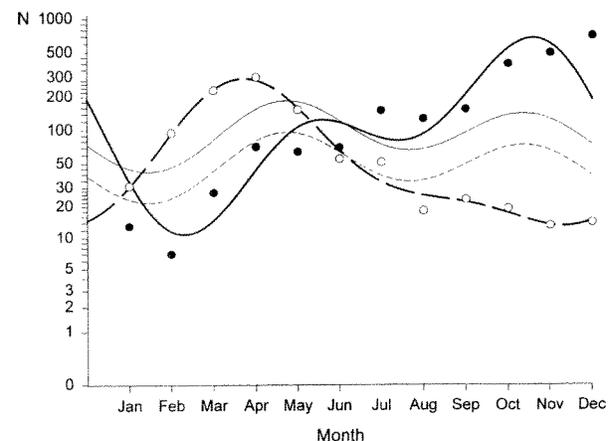


Fig. 2. Monthly counts of Orthocentrinae (N) collected in Hitchiti Experimental Forest, GA, in 1993 (open circles) and 1994 (closed circles), superimposed with predictions from candidate 2-harmonic models. Orthocentrinids followed distinct phenological patterns in 1993 (heavy dashed line) and 1994 (heavy solid line). For this subfamily, the YEAR-additive model (light lines) is clearly an inappropriate model.

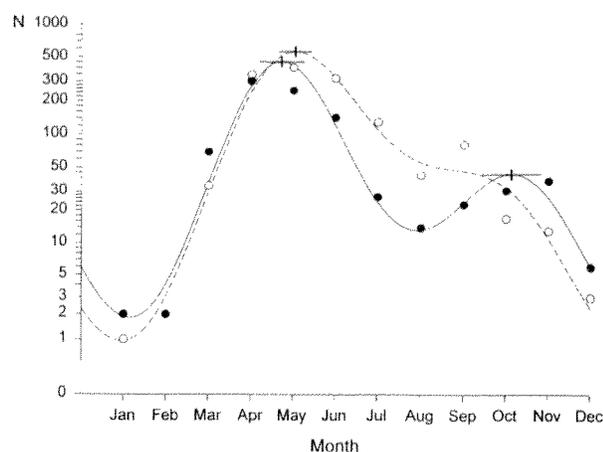


Fig. 3. Monthly counts of Ichneumoninae (N) collected in Hitchiti Experimental Forest, GA, in 1993 (open circles) and 1994 (closed circles), superimposed with predictions from YEAR-interactive model in 1993 (dashed line) and 1994 (solid line). Locations of phenological peaks are indicated by crosshairs, along with 95% CI estimated by bootstrap simulation. Note the absence of a secondary peak for 1993.

from the model \hat{T}_1 in regard to seasonal location of the primary peak, or differed from the model \hat{T}_1 in regard to existence of \hat{T}_2 (Fig. 4). Sample variances of the bootstrap-generated T_i served as our estimates of variance of the \hat{T}_i , $\hat{\sigma}^2(\hat{T}_i)$.

Before we analyzed the \hat{T}_i among subfamilies, we obtained means of \hat{T}_1 and \hat{T}_2 for those subfamilies to which the YEAR-interactive model was fit. We assumed independence between annual estimates of \hat{T}_1 or \hat{T}_2 , and we calculated variances for the means as

$$\hat{\sigma}^2(\bar{T}_i) = \text{Var}(\hat{T}_i) + \bar{x}[\hat{\sigma}^2(\hat{T}_i)] \quad [1]$$

where $\text{Var}(\hat{T}_i)$, the component for year-to-year variability, is the sample variance of the point estimates \hat{T}_i , and $\bar{x}[\hat{\sigma}^2(\hat{T}_i)]$, the component for point estimate precision, is the mean of the estimated variances $\hat{\sigma}^2(\hat{T}_i)$. For those subfamilies to which the YEAR-additive model was fit,

$$\hat{\sigma}^2(\bar{T}_i) = \hat{\sigma}^2(\hat{T}_i). \quad [2]$$

We tested 2 types of hypothesis. In the first, we tested homogeneity among the primary peak times \hat{T}_1 within a group of subfamilies. We assumed that the \hat{T}_1 were normally distributed with variances $\hat{\sigma}^2(\bar{T}_1)$, then we used the contrast method of Sauer and Williams (1989) to fit and test the contrast of no difference among means. We tested this hypothesis for \hat{T}_1 within idiobiont and koinobiont classes and within Lepidoptera-host classes (hosting solely on Lepidoptera, hosting at least partially on non-Lepidoptera).

In the 2nd type of hypothesis, we tested equality between means of \hat{T}_1 or \hat{T}_2 for 2 groups of subfamilies. In these tests, we assumed the \hat{T}_i were random samples of a group, and we tested for differences between group means in a 2-sample *t*-test. We assumed errors were distributed normally with 0 mean and variance $\hat{\sigma}^2(\bar{T}_i)$, so we weighted each observation by

$1/\hat{\sigma}^2(\bar{T}_i)$. In this manner, we tested the hypotheses of no difference between idiobiont and koinobiont class means and no difference between endoparasitoid and ectoparasitoid class means. For the idiobiont and koinobiont comparison, we also used a chi-square test on all annual phenologies to test whether relative frequency of single versus double-peaked phenologies differed by idiobiont or koinobiont class.

Results and Discussion

Malaise trap catches depend on adult abundance, flight activity and behavior, species and sex-specific propensities to be captured, and trap design and condition. It should be emphasized that trap catches do not reflect actual abundances. We use taxon catch size as a phenological measure of the interaction between 2 variables, the taxon population abundance and flight activity level. Hence, we assume that the propensity of flying individuals to be captured does not change over time and that there is minimal deterioration in trap condition.

The 5 traps caught a total of 16,584 ichneumonids in 22 subfamilies. Table 1 lists the number of specimens caught and the certain life-history variables for each of these subfamilies. Table 2 presents monthly trap catches for each subfamily.

We fit coincident (YEAR-additive) phenology models to 12 subfamilies, and non-coincident (YEAR-interactive) models to 10 others (Table 3). Five of 22 subfamilies had at least 1 annual phenology that lacked a secondary peak; Lycorininae and Ophioninae lacked secondary peaks in both years (Table 3). Ranges of T_1 and T_2 were 3.54–9.67 (mean = 5.62) and 4.68–11.25 (mean = 8.94, Table 3) mo. Regression model fit was often high (median adj $r^2 = 0.780$, range 0.204–0.939), but plots of lagged residuals and Durbin-Watson statistics suggested some degree of negative autocorrelation in many of the models (median $\hat{\rho} = -0.357$; range, -0.679 – 0.001). Because negative autocorrelation introduces positive bias to the estimate of residual mean squared error, we perhaps failed to reject the null hypothesis of YEAR-additivity as often as we should have and, therefore, tended to underfit regression models.

Koinobionts Versus Idiobionts. The most frequently captured ($n > 500$) idiobiont subfamilies have similar phenologies (Tables 2 and 3). Cryptinae and Ichneumoninae had large peaks in May of both years whereas the Pimplinae peaked somewhat earlier in 1994. Cryptinae, Pimplinae, and Ichneumoninae typically had smaller peaks in September–October of both years. Among all idiobiont subfamilies, times of average primary peak were consistent (range, 4.39–6.22 mo, $\chi^2 = 6.54$, $df = 6$, $P = 0.366$).

In contrast, frequently captured koinobiont subfamilies have dissimilar phenologies (Tables 2 and 3). The 3 most frequently captured ($n > 500$) koinobiont subfamilies were Campopleginae, Orthocentrinae, and Tryphoninae. The Campopleginae had large peaks in May 1993 and April 1994, and small peaks in September of both years. The Orthocentrinae had

Table 2. Ichneumonid trap catches by month, Hitchiti Experimental Forest, GA, 1993-1994

Subfamily	1993												1994												
	J	F	M	A	M	J	J	J	A	S	O	N	D	J	F	M	A	M	J	J	A	S	O	N	D
Acaenitinae	0	0	0	2	7	35	5	0	4	1	0	0	0	0	0	0	1	31	82	2	0	0	0	0	
Anomaloniinae	0	0	3	7	12	5	6	6	18	34	5	0	0	0	0	10	12	13	14	8	4	6	15	10	1
Banchinae	1	0	7	18	29	39	16	2	7	7	1	1	1	1	0	20	40	84	34	8	2	12	19	3	1
Campopleginae	0	3	64	204	411	455	131	29	66	45	19	1	4	6	115	242	181	119	54	47	163	109	46	4	
Cremastrinae	0	0	1	3	14	12	16	6	20	4	1	0	0	0	0	6	11	7	5	8	26	7	2	0	
Cryptinae	7	10	75	373	957	493	314	98	104	60	33	13	6	5	215	783	704	404	172	100	86	92	39	16	
Ctenopelmatinae	0	0	2	18	28	10	2	0	4	0	1	0	0	0	14	56	26	1	0	0	0	2	0	0	
Diplazontinae	0	0	2	7	4	2	0	0	1	1	1	0	0	0	2	6	3	0	3	0	0	0	2	4	0
Eucerothinae	0	0	1	2	0	0	0	0	0	0	0	0	0	0	3	3	0	0	0	0	0	0	0	0	0
Ichneumoninae	1	2	34	348	403	323	130	43	82	17	13	3	2	2	70	304	251	143	27	14	23	31	38	6	0
Labeninae	0	0	0	1	4	6	0	0	1	3	0	0	0	0	15	20	1	9	2	0	0	0	3	0	0
Lycoriniinae	0	0	0	0	1	1	1	0	6	0	0	0	0	0	0	0	0	1	1	0	0	1	1	0	0
Mesochorinae	1	1	2	17	22	11	9	2	7	5	9	1	2	0	6	28	15	7	3	3	16	36	17	10	0
Melopiinae	0	0	1	7	65	50	26	6	9	2	1	0	0	0	7	28	32	22	11	10	12	9	1	1	
Ophiinae	0	1	3	7	10	45	49	28	7	0	0	0	0	1	15	5	20	46	14	1	6	4	2	0	
Orthocentrinae	31	95	228	300	152	55	51	18	23	19	13	14	13	7	27	71	64	70	150	126	153	393	492	701	
Pimplinae	0	0	48	61	81	30	24	10	10	10	6	1	2	3	48	37	31	15	4	2	9	36	30	4	
Poemeniinae	0	0	1	10	2	3	5	1	0	0	0	0	0	0	0	1	1	2	0	0	0	0	0	0	
Rhyssinae	0	0	0	4	1	2	0	0	0	0	2	0	0	0	0	1	2	2	0	0	0	1	0	0	
Tersilochinae	0	0	35	40	18	6	1	0	4	6	1	0	0	0	29	2	4	2	9	12	5	4	2	0	
Tryphoninae ^a	0	0	5	16	33	7	10	1	2	3	1	1	1	0	34	105	18	10	4	3	2	2	2	0	0
<i>Netelia</i>	0	0	6	66	43	21	7	3	9	3	5	1	1	0	60	66	20	11	1	2	2	10	5	0	
Xoridinae	0	0	4	9	8	3	1	0	0	0	0	0	0	0	7	2	0	3	14	2	2	1	0	0	

^a Excluding *Netelia*.

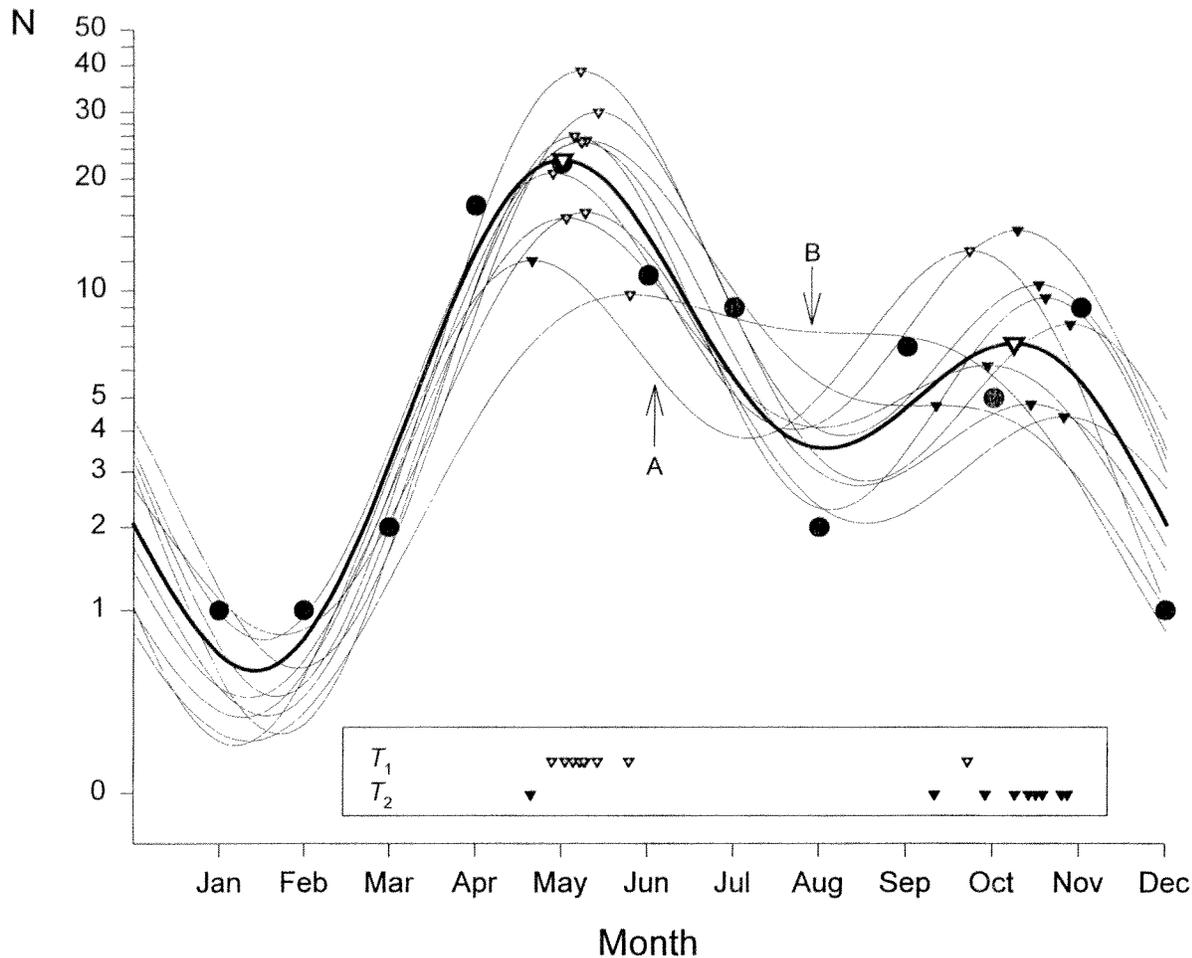


Fig. 4. Illustration of the parametric bootstrap sampling technique on monthly counts of Mesochorinae (N) collected in Hitchiti Experimental Forest, GA, in 1993 (closed circles). Predictions from the 1993 portion of the YEAR-interactive model (heavy line) are superimposed with symbols (large inverted triangles) indicating time of phenological peaks \hat{T}_1 and \hat{T}_2 . Predictions generated by each of 10 bootstrap samples of the model parameters are illustrated (light lines), with locations of primary (small open triangles) and secondary (small closed triangles) peaks superimposed. Note sample line A, in which seasonal locations of primary and secondary peaks disagree with model estimates, and sample line B, in which T_2 does not exist. Estimated variances for the \hat{T}_i were obtained as the variance of the temporal locations of the T_i from the bootstrap samples (arranged in the lower box).

large peaks in April 1993 and November 1994. The Tryphoninae had peaks in mid-April of both years. Among all koinobiont subfamilies, times of average primary peak differed (range, 3.54–9.67 mo, $\chi^2 = 74.7$, $df = 14$, $P < 0.001$).

Average times of peak flight were similar in idiobiont (mean = 5.02, SE = 0.81 mo) and koinobiont (mean = 6.05, SE = 1.08 mo) subfamilies ($t = 0.77$, $df = 20$, $P = 0.453$). Idiobiont (mean = 9.63, SE = 2.37 mo) and koinobiont (mean = 8.45, SE = 1.47 mo) subfamilies were similar in mean times of secondary peak as well ($t = 0.42$, $df = 18$, $P = 0.677$). We also found no difference between idiobiont and koinobiont classes in relative frequency of 1-peaked (10% among idiobionts, 20% among koinobionts) to 2-peaked phenologies ($\chi^2 = 0.50$, $df = 1$, $P = 0.478$).

The overall similarity between idiobionts and koinobionts and the differences found when individual subfamilies are considered indicates that differences

in phenological peaks may be determined by differences among individual subfamilies rather than by differences between idiobionts and koinobionts.

Nocturnality. Different flight activity in nocturnal ichneumonids with similar life-history variables supports the importance of phenological variation among subfamilies. Greatest counts of genus *Netelia* (Tryphoninae) occurred in April of both years, with smaller sample peaks in September and November 1993, and October 1994 (Table 2). Largest numbers of Ophioninae were observed in July 1993 and June 1994, and a smaller sample peak occurred in March 1994 (Table 2). Both groups are nocturnal koinobionts that attack Lepidoptera. They differ in their mode of parasitism; the Ophioninae are endoparasitic and *Netelia* are ectoparasitic. Among all subfamilies, average times of peak flight were similar in endoparasitic (mean = 5.97, SE = 1.04 mo) and ectoparasitic (mean = 5.05, SE = 0.87 mo) subfamilies ($t = 0.68$, $df = 20$, $P =$

Table 3. Estimated month of primary (\hat{T}_1) and secondary (\hat{T}_2) peaks in phenological models for ichneumonid subfamilies, Hitchiti Experimental Forest, Georgia, 1993-1994

Subfamily	Month of primary peak						Month of secondary peak						
	1993			1994			1993			1994			
	Model	Bootstrap results	Avg	Model	Bootstrap results	Avg	Model	Bootstrap results	Avg	Model	Bootstrap results	Avg	
\hat{T}_1	$\bar{\chi}(\hat{T}_1)$ $\hat{\sigma}(\hat{T}_1)$	\bar{T}_1 $\hat{\sigma}(\bar{T}_1)$	T_1	$\bar{\chi}(\hat{T}_1)$ $\hat{\sigma}(\hat{T}_1)$	\bar{T}_1 $\hat{\sigma}(\bar{T}_1)$	\hat{T}_2	$\bar{\chi}(\hat{T}_2)$ $\hat{\sigma}(\hat{T}_2)$	\bar{T}_2 $\hat{\sigma}(\bar{T}_2)$	\hat{T}_2	$\bar{\chi}(\hat{T}_2)$ $\hat{\sigma}(\hat{T}_2)$	\bar{T}_2 $\hat{\sigma}(\bar{T}_2)$		
Phenology not year-dependent													
Acaenitinae	5.65	1000	5.66	0.20	—	5.65	0.20	11.25	910	10.64	2.54	11.25	2.54
Anomaloniinae	9.67	1000	7.69	2.41	—	9.67	2.41	4.68	1000	6.66	2.48	4.68	2.48
Banchinae	4.85	1000	4.84	0.41	—	4.85	0.41	9.83	977	9.83	0.29	9.83	0.29
Cremastinae	8.60	1000	7.59	1.40	—	8.60	1.40	5.98	504	6.84	1.63	5.98	1.63
Cryptinae	4.97	1000	4.97	0.09	—	4.97	0.09	9.24	676	9.38	0.22	9.24	0.22
Diplazontinae	4.39	1000	4.41	0.41	—	4.39	0.41	10.26	1000	10.23	0.44	10.26	0.44
Eucerothinae	3.54	1000	3.54	0.23	—	3.54	0.23	9.54	984	9.55	0.41	9.54	0.41
Labeniinae	4.39	1000	4.39	0.24	—	4.39	0.24	9.95	961	9.94	0.54	9.95	0.54
Lycoriniinae	7.82	1000	7.75	1.07	—	7.82	1.07	—	330	4.75	3.35	—	—
Poemeniniinae	5.23	1000	5.23	0.32	—	5.23	0.32	10.54	463	9.76	3.37	10.54	3.37
Ryhssiniinae	4.94	1000	4.94	0.24	—	4.94	0.24	10.75	988	10.69	0.84	10.75	0.84
Tryphoninae	4.56	1000	4.56	0.15	—	4.56	0.15	9.80	996	9.79	0.25	9.80	0.25
Phenology year-dependent													
Campopleginiinae	4.86	1000	4.87	0.14	4.41	4.41	1000	9.17	820	9.23	0.26	9.47	1.19
Ctenopelmatiniinae	4.82	1000	4.82	0.22	4.17	4.17	1000	10.22	906	10.28	0.45	10.12	0.27
Ichneumoniniinae	5.04	1000	5.05	0.14	4.71	4.71	1000	—	343	9.25	0.28	10.12	0.16
Mesochoriniinae	5.00	1000	5.05	0.46	10.34	10.34	1000	10.23	972	10.20	0.53	4.64	10.00
Metopiinae	5.73	1000	5.74	0.19	4.88	4.88	1000	—	11	10.09	0.26	9.07	779
Ophiiniinae	6.87	1000	6.85	0.65	4.97	4.97	1000	—	75	2.65	1.42	—	454
Orthocentriniinae	3.72	1000	3.74	0.33	10.58	10.58	1000	—	415	9.23	0.73	5.61	919
Pimpliniinae	4.70	1000	4.71	0.19	4.29	4.29	1000	9.51	920	9.53	0.33	10.26	1000
Tersilochiniinae	4.20	1000	4.19	0.21	8.70	8.70	1000	9.88	998	9.87	0.30	3.90	889
Xoridiinae	4.60	1000	4.61	0.32	7.84	7.84	1000	10.40	688	10.33	1.38	3.46	751

Models differ for subfamilies by dependency of phenology on year. Parametric bootstrapping ($n = 1,000$) provided estimates of peak mean (\bar{x}) and standard error ($\hat{\sigma}$).

0.504). Mean times of secondary peak were also similar in endoparasitic (mean = 8.57, SE = 1.43 mo) and ectoparasitic (mean = 9.54, SE = 2.80 mo) subfamilies. Again, seasonal differences may be due more to differences among individual subfamilies within endo- and ectoparasitic types than to differences between endoparasitism and ectoparasitism.

Smythe's (1985) study on the seasonality of night-flying insects on Barro Colorado Island, Panama, demonstrated that Hymenoptera have an early wet-season peak followed by a late wet-season low and a small, early dry-season peak. Because Gauld (1991) used Ophioninae as the koinobiont representative and the Pimplinae and Rhyssinae as the idiobiont representatives, the early seasonal peak in koinobiont flight activity that Gauld found may further be explained by the nocturnal behavior of the Ophioninae.

Host Taxon. Among the most frequently captured subfamilies ($n > 500$), there is indication that subfamilies attacking the same host taxon may have similar flight activity. Similar peaks occurred in May of both years between the Cryptinae and Ichneumoninae, which both attack Lepidoptera (Tables 2 and 3; mean = 4.71–5.04, SE \leq 0.14 mo). The peak flight activity of the Pimplinae, a generalist subfamily that attacks numerous hosts, is spread over several months (Tables 2 and 3; mean = 4.29–4.70, SE \leq 1.58 mo). Estimated peaks of the Campopleginae (mainly Lepidoptera parasitoids) occurred in May 1993 and April 1994 (Table 3). The Orthocentrinae (Diptera parasitoids) peaked in April 1993 and November 1994 (Table 3). Greatest counts of the Tryphoninae (excluding *Netelia*) (Lepidoptera and Symphyta parasitoids) occurred in May 1993 and April 1994 (Table 2). This evidence suggests that the peak flight time of the campoplegines is more similar to the peaks of the idiobiont subfamilies that attack Lepidoptera (e.g., Cryptinae and Ichneumoninae) than to the peaks of other koinobiont subfamilies that attack other hosts.

Similar evidence is found for other host taxa. The 2 subfamilies with Symphyta hosts, the Ctenopelmatinae and the Tryphoninae, had equivalent estimated peaks in April–May of both years (Table 3). We estimated different peaks (Table 3) for the Acaenitinae (June) and the Tersilochinae (April 1993 and September 1994), the 2 most frequently trapped subfamilies with Coleoptera hosts ($n > 150$). However, the Acaenitinae attack mostly wood-boring beetles, in particular the Cerambycidae, and the Tersilochinae attack primarily Curculionidae, Chrysomelidae, and the superfamily Cucojoidea.

Among all subfamilies, however, we found evidence of heterogeneity among times of primary phenological peak within both the group of Lepidoptera-only parasitoids (range, 4.64–8.60 mo; $\chi^2 = 14.87$, df = 7, $P = 0.038$) and the group of all other parasitoids (range, 3.54–9.67 mo, $\chi^2 = 62.43$, df = 13, $P < 0.001$). Therefore, at least for lepidopteran hosts, we find no evidence that phenological activity is determined by host taxon. However, we are also cognizant that Lepidoptera is a large and heterogeneous taxon, and that at

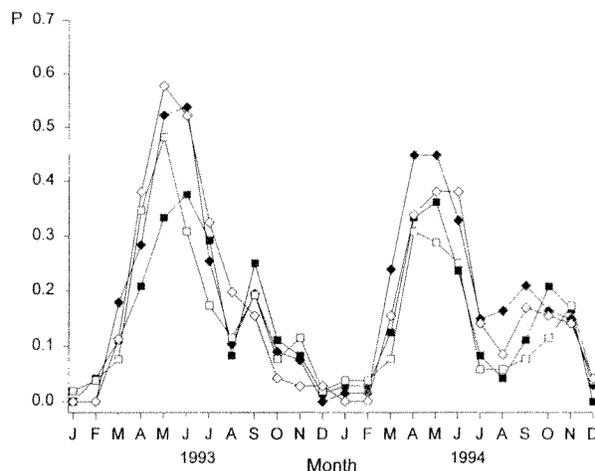


Fig. 5. Monthly proportion of species trapped (P) in the males (diamonds) and females (squares) of the subfamilies Campopleginae (closed symbols) and Ichneumoninae (open symbols) at the Hitchiti Experimental Forest, GA, in 1993 and 1994.

some finer taxonomic resolution, host taxon may determine phenological activity.

Specimens Versus Species. A potential methodological problem is that 1 or 2 common species would influence the seasonal peaks of its subfamily. To examine the relationship between the number of specimens and the number of species, we considered data for male and female campoplegines and ichneumonines. We used proportion of species collected per month to determine peaks in flight activity, as did Gauld (1991).

In the Campopleginae and Ichneumoninae, there is no evidence that 1 or 2 species are influencing the phenology of the entire subfamily. Figure 5 presents the peaks in proportion of species of males and females in both the Campopleginae and Ichneumoninae. Observed peaks in specimens (Table 2) bear a general similarity to these peaks in proportion of species, although they are not perfectly synchronized. We trapped peak numbers of campoplegine specimens in June 1993 and April 1994 (Table 2). Species proportions of both campoplegine males and females peaked in June 1993 (Fig. 5). In 1994, campoplegine males peaked in both April and May whereas females had a slightly larger peak in May than April (Fig. 5). The Ichneumoninae had observed peaks in May 1993 and April 1994 (Table 2). Species proportions of both ichneumonine males and females peaked in May 1993 (Fig. 5). In 1994, ichneumonine males peaked in both May and June whereas females peaked in April (Fig. 5).

Primary Parasites Versus Hyperparasites. Considering the tritrophic interaction between Symphyta, Ctenopelmatinae and Tryphoninae, and Mesochorinae, flight activity of hosts, primary parasites, and hyperparasites coincide at the level of resolution (monthly) that we consider in this study (Table 2). All 3 trophic levels—(1) Symphyta; (2) Ctenopelmatinae and Tryphoninae (excluding the genus *Netelia*),

which attack Symphyta; and (3) the Mesochorinae, which attack ichneumonoids that parasitize Symphyta and Lepidoptera—have identical peaks in flight activity (May 1993 and April 1994). The Mesochorinae also had later peaks in both years, especially notable in October 1994, which are coincident with the late-season peaks of many subfamilies of potential hosts that attack Lepidoptera.

In summary, our analysis of seasonal catch illustrates the difficulty in understanding the flight phenology of subfamilies with different biologies. Although many subfamilies have similar trends in seasonal flight activity, especially the ones that attack Lepidoptera and Symphyta hosts, it is impossible to formulate a single hypothesis to explain observed patterns.

Our results support the importance of host availability and variance between subfamilies. Evidence for koinobiont versus idiobiont parasitism, endo- versus ectoparasitism, nocturnality, and stage of host development affecting ichneumonid flight activity was not found. Because parasitoid species may have more than 1 host species, ultimately it will take large-scale studies of entire host-parasite communities to understand how climate, resource availability, mating patterns, and other factors affect flight activity and trap catches.

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