RYAN PAUL BARTLETT

Efficiency of collection methods and flight activity of Ichneumonidae (Hymenoptera) in three sites in Guanacaste, Costa Rica

(Under the direction of JOHN PICKERING)

I compare Malaise trapping to rearing as methods for collecting Ichneumonidae in Guanacaste, Costa Rica. In total, 6707 Ichneumonidae were collected in the one year of Malaise trapping, while 2193 were collected in approximately 22 years of rearing. Malaise trapping found a total of 18 different subfamilies, while rearing yielded a total of 13 subfamilies. At the species level for subfamily Pimplinae, Malaise trapping yielded a total of 28 species (375 specimens), while rearing yielded a total of 13 species (108 specimens). Of these, six species were found by both methods, meaning that 22 were found only by Malaise trapping and seven were found only through rearing. I conclude that Malaise trapping is a more efficient way of collecting Ichneumonidae quickly than rearing. I also attempt to determine whether rainfall, host abundance and phenology, or other factors influence the magnitude and timing of flight activity of Ichneumonidae, as measured by Malaise trap catches. To this end I compare across three sites with differing amounts of yearly rainfall in Guanacaste, Costa Rica. Neither rainfall nor host abundance clearly has a significant effect on the magnitude and timing of ichneumonid flight activity, although there is some evidence that host abundance may play a role.

INDEX WORDS: Parasitoids, Guanacaste, Ichneumonidae, Pimplinae, Malaise trapping, Rearing, Rainfall, Host abundance, Tropical dry forest, Tropical rainforest, Phenology, Insect seasonality

EFFICIENCY OF COLLECTION METHODS AND FLIGHT ACTIVITY OF ICHNEUMONIDAE (HYMENOPTERA) IN THREE SITES IN GUANACASTE, COSTA RICA

by

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TABLE OF CONTENTS

INTRODUCTION AND LITERATURE REVIEW

Natural History and Taxonomy of the Hymenoptera

Hymenoptera is one of the four largest orders of insects, along with Coleoptera, Diptera, and Lepidoptera, with each of these orders containing over 100,000 described species worldwide (Mason and Huber, 1993). Gauld and Bolton (1988) characterize adult Hymenoptera as having two pairs of membranous wings, lepismatid ovipositors in females, and prominent antennae. Haplo-diploid sex determination is common to most Hymenoptera. This type of sex determination has the advantage of allowing a female to choose the sex of her progeny, as well as preventing lethal recessive mutations from being masked in males (Gauld and Bolton, 1988). Hymenoptera is divided into two suborders: Symphyta, the sawflies and horntails, and the much larger suborder, Apocrita, which contains ants, bees, and wasps. The larvae of Symphyta are generally caterpillar-like and use legs to crawl around on plants, while the larvae of Apocrita are generally legless and grub-like. The suborder Apocrita is often divided further into the groups Aculeata and Parasitica. Aculeata consists of stinging Hymenoptera such as ants, bees, and some wasps, while Parasitica contains the many groups of parasitic wasps. One of the superfamilies contained within Parasitica is Ichneumonoidea. This superfamily is further divided into two families, the Ichneumonidae and Braconidae, which are the two largest families in the Hymenoptera (Wahl and Sharkey, 1993). Family Ichneumonidae is the focus of the current study.

Natural History of the Ichneumonidae, with special reference to the Costa Rican fauna

With an estimated 60,000 species worldwide (Townes 1969; Gauld and Bolton 1988; Wahl and Sharkey 1993), Ichneumonidae is the largest family of Hymenoptera and one of the largest families of insects. Gauld (1997) currently divides family Ichneumonidae into 37 subfamilies, although this number has varied greatly over the past few decades and is still debated in the taxonomic community. The Costa Rican ichneumonid fauna is rather diverse, with 25 of the 37 subfamilies represented, with those not occurring being very small subfamilies containing about 40 or fewer species (Gauld 1991; Hanson and Gauld 1995). Ichneumonids are very common worldwide, having been collected as far north as 80º N latitude. They are known to occur in all vegetated terrestrial habitats in Costa Rica (Gauld 1991).

The vast majority of ichneumonids are parasitoids of holometabolous insects and spiders, with the majority attacking Coleoptera, Diptera, Lepidoptera, and Hymenoptera (Hanson and Gauld 1995, Gauld 1997). Most ichneumonids are primary parasitoids, although some, such as members of the subfamily Mesochorinae, are hyperparasites of other parasitoids such as tachinid flies or other ichneumonids. Those ichneumonids that attack insects generally parasitize the larval or pupal stages, although some do oviposit into eggs, completing development in later stages. Ichneumonids commonly use four different developmental strategies: ectoparasitism, endoparasitism, idiobiosis, and koinobiosis. Ectoparasites live on the outside of the host and feed through an integumentary wound, while endoparasites develop inside of a host and must overcome the immune system of the host to survive. Idiobionts kill or permanently paralyze the host at the time of oviposition, while koinobionts allow the host to develop after oviposition and do not kill the host until a later stage (Askew and Shaw, 1986). Idiobiont ectoparasitism is the strategy of most primitive ichneumonids, whose hosts usually are hidden within plant tissues, while endoparasitism represents a more evolutionarily advanced strategy (Wahl and Sharkey, 1993). Koinobiosis is a more advanced form than idiobiosis, and most koinobionts are also endoparasitoids (Gauld, 1991). Both gregarious and solitary larvae can be found in Ichneumonidae, although most species have solitary larvae.

According to Gauld (1991), adult ichneumonids are subjected to predator pressure, as would be expected for any exposed group of insects. As a result, a number of defensive traits appear to have evolved. A number of Costa Rican ichneumonid species in the genera *Neotheronia* and *Xanthopimpla* (subfamily Pimplinae) have tarsal claws with an internal poison-sac that is thought to function as a type of poison fang to deter predators (Gauld, 1991). In addition, other Costa Rican pimpline ichneumonids, such as members of the genera *Dolichomitus* and *Pimpla* appear to be Batesian mimics of stinging aculeates (Gauld, 1991).

Natural History of the Pimplinae

The Pimplinae, a subfamily of Ichneumonidae, is the most biologically diverse subfamily of Ichneumonidae (Gauld, 1991) and a focus of part of this study. The subfamily is divided into three tribes: Ephialtini, Pimplini, and Polysphinctini. All species of pimplines are generalist parasites (rather than specialists) that are able to feed on more than one species of host. The most primitive pimplines belong to the tribe Ephialtini and are idiobiont ectoparasitoids of other endopterygote insects (Salt, 1931;

Stuart, 1957; Fitton et al., 1988). Typically the host of these insects is concealed within plant tissues. Some pimplines within the tribe Pimplini are also idiobiont ectoparasitoids, while others are idiobiont endoparasitoids. Those pimplines of the tribe Polysphinctini are generally koinobiont ectoparasitoids who attach their eggs to live spider hosts (Nielsen, 1937). Most pimplines lay a single egg in a host, but a few species are gregarious (Gauld, 1991). Adult pimplines feed on honeydew, nectar, and other plant secretions (Leuis, 1960; Juillet, 1959). The Costa Rican fauna of Pimplinae is fairly diverse, with all of the pimpline genera from the Neotropical region having been found in Costa Rica (Gauld 1991).

Diversity of Tropical Ichneumonidae

In general for most insects, species richness increases with decreasing latitude (Stevens, 1989). However, forces governing the abundance and distribution of parasitoids are not very well understood (Hawkins et al., 1992), and this generalization of Stevens appears to be false for several groups of parasitoids, including the Ichneumonidae. Several preliminary studies show that it is unlikely that species richness increases with decreasing latitude for most Ichneumonidae (Owen and Owen, 1974; Janzen and Pond, 1975; Janzen, 1981; Gauld, 1986; Gauld, 1991; Gaston and Gauld, 1993; Skillen et al., 2000), and that, in fact, a peak in ichneumonid diversity seems to lie at mid-latitudes. Gauld (1986) reported that ichneumonids are not more diverse in the tropics than in temperate regions based on Australian data, and other studies showed similar results for additional parts of the world, including decreasing diversity from Europe to Africa and North to Central America.

Numerous explanations have been offered to explain this apparent trend. Janzen (1981) states that the species richness of ichneumonids appears to be higher in the mid-latitudes of Virginia than nearer the equator in Florida and predicts that increased host diversity in lower latitudes reduces the carrying capacity of the environment. In this explanation, the huge diversity of potential hosts and fragmentation of host populations make it too difficult for parasitoids to specialize on many hosts. A popular alternative hypothesis, the “nasty host hypothesis” (Gauld et al. 1992; Gauld and Gaston 1994) predicts that the reduction in diversity of some groups of ichneumonids may be caused by a tritrophic interaction in which toxic secondary compounds in plants (which are thought to be more common in tropical than temperate plants) are sequestered by herbivores, making those herbivores unavailable as potential parasitoid hosts. Other explanations include abiotic factors (Hawkins, 1990; Gauld, 1991, Hawkins et al. 1992), predation (Rathcke and Price, 1976; Price et al., 1980), and competition (Hawkins, 1990).

However, some researchers have found that species richness does increase in the tropics for certain groups of parasitoids (Hespenheide, 1979; Noyes, 1989). Notably, Gauld and Gaston (1994) point out that species richness increases for many idiobiont pupal parasitoids, such as the Pimplini, from temperate to tropical areas. They point out that it is primarily a reduction of koinobionts, such as the Campopleginae and Banchinae, which make numbers of tropical Ichneumonidae lower than those in temperate areas.

Phenology of Tropical Insects

Most studies of insect seasonality have been performed in temperate regions. Although these studies have allowed some speculation about the seasonality of tropical insects, few data are available as of yet to verify these speculations. Dobzhansky (cited in Wolda, 1978a) first suggested in 1950 that insect populations should be fairly constant over time in the tropics because of the absence of climatic catastrophes. Owen and Chanter (cited in Wolda, 1978b) supported this hypothesis, finding that *Charaxes* butterflies in Sierra Leone showed little fluctuation. However, other studies have since shown that Charaxes butterflies are an exception and most tropical insect abundances do fluctuate with seasonality (Wolda, 1978a). Wolda (1978a) suggested that insect populations fluctuate more in regions with low and unpredictable rainfall; stable insect populations are more likely to be found in areas without seasonality in climate. Wolda's study supported Dobzhansky's hypothesis that climates with greater stability had smaller fluctuations in species abundance.

Some studies have shown a definite seasonal influence of the abundance of insect groups in the tropics. Penny and Aria (cited in Lovejoy and Bierregaard, 1982) concluded in their observation of the Reserva Ducke in Brazil a higher abundance within insect populations in December and April. Some of the insect families in this study demonstrated strongly seasonal abundances. In areas with a pronounced dry season, insect abundance was low during the whole of the dry season, while insect abundance decreased in the dry season and increased in the wet season in areas with a less extreme dry season (Wolda, 1978b). Areas with an intense dry season have a noticeable movement of insects into moist areas during the dry season (Janzen, 1981). Some insect groups vary in abundance during different seasons among different species, as shown by Cicadoidea (Homoptera) (Wolda and Ramos, 1992). One species was most abundant during the early dry season, another during the late dry season, and the remainder in the early to mid-rainy season. Few cicadas of any species were trapped in the late rainy season. Tropical insect seasonality will be discussed further in Chapter 3.

Predictions

In Chapter 2 of this study, I compare Malaise trapping to rearing to determine which method is more effective for collecting a diversity of Ichneumonidae at the level of subfamily, and for species of Pimplinae. Since rearing relies on hand collecting and is not likely to gather many concealed hosts, I suspect that Malaise trapping will yield a greater diversity of ichneumonids. In Chapter 3 of this study, I compare differences in ichneumonid abundance and flight phenology across a 3 site wet-dry transect. In this study, I expect the abundance of most groups of ichneumonids to be highest at the wet site and lowest at the dry site, especially during the dry season of the drier sites. The dry season of the dry sites is very hot and essentially rain free, and thus does not seem to be suitable for much activity by most insects. However, I also expect that abundances of parasitoids of Lepidoptera may be higher during the beginning of the wet season at the driest site, Santa Rosa, since the availability of hosts is very high during that time. I expect that peaks in parasitoid activity will correspond closely with peaks in host activity for all sites.

COMPARISONS OF EFFECTIVENESS OF MALAISE TRAPPING AND REARING FOR ESTIMATING INSECT DIVERSITY IN GUANACASTE, COSTA RICA[1]

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[1] Bartlett, R.P. and J. Pickering. To be submitted to Journal of Tropical Ecology.

Introduction

Much attention has been given to estimating tropical biodiversity in recent years, particularly that of insects (Erwin, 1982; Gaston, 1991; May, 1992; Stork, 1997; Bartlett et al. 1999). Several large-scale programs, such as the Smithsonian Institution /Monitoring and Assessment of Biodiversity Program (SI/MAB), have undertaken to assess species diversity at specific sites for numerous taxa, including several insect groups (Alonso and Dallmeier, 1997). However, the method of trapping is a serious consideration for any attempt to characterize tropical insect species diversity. Particularly for speciose groups of insects, the number of species collected will depend largely on which trapping method is used.

One of the largest families of insects is Ichneumonidae (Hymenoptera), with an estimated 60,000 species (Gauld and Bolton, 1988). Tropical Ichneumonidae are of particular interest due to the fact that a number of subfamilies of Ichneumonidae do not appear to show the usual trend of increasing diversity as one moves from upper latitudes towards the equator (Janzen, 1981; Gauld, 1986, 1987, 1991; Gaston and Gauld, 1993; Skillen et al., 2000). This interest has resulted in a number of attempts to characterize the species composition of tropical ichneumonid communities using a variety of different trapping methods. One commonly used method is Malaise trapping.

Malaise traps are generally considered to be a good method for collecting Ichneumonidae (Matthews and Matthews, 1970; Darling and Packer, 1988; Noyes 1989; Gauld 1991, 1997), and have been used in a number of studies of tropical Ichneumonidae (Noyes, 1989; Gauld, 1991, 1997; Janzen and Gauld, 1997; Bartlett et al., 1999). Noyes (1989) compared sweep netting, Malaise trapping, yellow pan trapping, flight intercept trapping, and canopy fogging in Indonesia, and found sweep netting and Malaise trapping to be the most efficient methods for collecting Ichneumonidae. Gauld (1991, 1997), who has been doing massive collections of Ichneumonidae in Costa Rica over the past two decades, uses Malaise traps as his primary collecting method, augmented by hand netting, light trapping, and rearing.

Another method of collecting Ichneumonidae in Costa Rica that has been used extensively by Janzen and Hallwachs (2000) over the past 22 years in the Guanacaste Conservation Area is hand collecting and rearing. In this method large numbers of hosts are hand-collected by paraecologists and then reared, noting what parasitoids (if any) emerge from them.

In this study we compare the ichneumonid parasitoids have been collected by Janzen as part of his study to what we have collected in one year of Malaise trapping (six traps) in the Guanacaste Conservation Area. We attempt to determine which method is more effective in characterizing the local community of these parasitoids, at the level of subfamily for all Ichneumonidae, and at the species level for one subfamily of ichneumonids, the Pimplinae.

Pimplinae is an appropriate subfamily to choose, as it is the most biologically diverse of all subfamilies of Ichnuemonidae (Gauld, 1991). All species of pimplines are generalist parasites (rather than specialist parasites) that are able to feed on more than one species of host, and many species feed on multiple orders of insects. Pimplines as a group parasitize a variety of hosts, including an array of insect orders, as well as adult spiders. This subfamily contains both endoparasitic and ectoparasitic members, as well as both idiobionts (which kill the host immediately upon oviposition) and koiniobionts (which allow the host to develop further). In addition, some pimplines are facultative hyperparasitoids that are able to attack other parasitoids (Gauld, 1991).

Data

We set up a total of six Townes-style (Townes, 1972) fine-mesh Malaise traps purchased from Sante Traps (Lexington, Kentucky) in the Guanacaste Conservation Area (GCA), Costa Rica. The traps were aligned along a north-south axis with the collecting head facing south. Two traps were located at 10°51.2’N, 85°36.7’W in the Bosque Humedo, Sector Santa Rosa, Guanacaste Province. These traps were in the middle of approximately 20 ha of old-growth Tropical Dry Forest at an elevation of 300 m. The mean annual rainfall for this site is approximately 1500 mm, with a six month essentially rain-free dry season from approximately December to early May. Two more traps were located at 11°02.0’N, 85°31.8’W in the Sendero Bejuquillo, Estacion Los Almendros, Sector El Hacha, Guanacaste Province. These traps were in the middle of approximately 20 ha of old secondary-growth Tropical Dry Forest at an elevation of 280 m. The mean annual rainfall for this site is approximately 1800 mm, with a five month essentially rain-free dry season during a similar period as in Santa Rosa. The final two traps were located at 10°52.4’N, 85°23.5’W by the Rio Cucaracho, Estacion San Cristobal, Sector San Cristobal, Alajuela province. These traps were in the middle of a strip of lightly logged old secondary-growth Tropical Rainforest at an elevation of 630 m. The mean annual rainfall for this site is approximately 3500 mm, with a one to two month “dry season” during which the site receives slightly less rain than the remainder of the year. This “dry season” is variable when it occurs from year to year. All six traps were run for a period of one year, from July 7, 1997 to July 6, 1998 (72 total trap-months of effort). All traps were collected on a weekly basis, and all Ichneumonidae were removed from each sample, barcoded, and identified to the level of subfamily. We then identified those ichneumonids belonging to the subfamily Pimplinae to the level of species. Specimen data are maintained in the UGCA database of the Insect Diversity Project <http://dial.pick.uga.edu>.

In Janzen and Hallwachs's (2000) sampling program, arthropods were hand collected by paraecologists in the field, then brought back to rearing barns and reared for an appropriate time, usually to adulthood. If the arthropod had been parasitized by a parasitoid such as an ichneumonid, the parasitoid that emerged was identified and recorded. Ichneumonid parasitoids were identified to a variety of end levels, ranging from family to species, although the majority was identified to at least subfamily. Most of the parasitized hosts collected were macrolepidopteran caterpillars, although a variety of other arthropod hosts were also collected, ranging sawflies to spiders. All of these records were retrieved from the publicly available database found at <http://janzen.sas.upenn.edu>. Collections were done throughout the 1200 km^2 GCA, as well as adjacent wet forest habitats (Janzen and Gauld 1997). However, the majority of the collections were done in a 50 km^2 area of Sector Santa Rosa. For more information about the study site, see Janzen (1983), Janzen (1993), and Janzen and Gauld (1997). Numerous people have done these collections over an extended period of time, from 1978 through the current time. However, not all of the year 2000 records are included in this study, as they are not yet available in the database (Janzen and Hallwachs, 2000).

Results

Table 1 gives a complete listing of how many specimens in each subfamily of Ichneumonidae found via either method were collected by our Malaise trapping and Janzen and Hallwachs's rearing. In total, 6707 Ichneumonidae were collected in the one year of Malaise trapping, while 2193 were collected in approximately 22 years of rearing. Malaise trapping found a total of 18 different subfamilies, while rearing yielded a total of 13 subfamilies. Some subfamilies, such as the Orthocentrinae and Tersilochinae, which were fairly common in the Malaise traps, were completely absent from the rearing records. Others, such as the Ophioninae, were noticeably more common in the rearing records than the Malaise trap samples.

Table 2 lists the species of Pimplinae collected by both Malaise trapping and rearing. Malaise trapping yielded a total of 28 species (375 specimens), while rearing yielded a total of 13 species (108 specimens). Of these, 7 species were using both methods, meaning that 21 were found only by Malaise trapping and 6 were found only through rearing.

Discussion

Based on the results of this study, we conclude that Malaise trapping is a more efficient way of collecting a diversity of subfamilies of Ichneumonidae quickly than rearing. Malaise trapping also fared better than rearing at collecting a large number of pimpline species quickly. These trends are easily explained. In Janzen and Hallwachs's rearing study (2000), the focus is on collecting certain groups of macrolepidopteran caterpillars, and other hosts are only collected as they are incidentally encountered in the field. Thus, it is no surprise that groups such as the Tersilochinae and Rhyssinae that attack concealed larvae of Coloeptera or the Orthocentrinae that attack fly larvae are missing from the rearing records. The higher proportion of groups such as the Ophioninae that primarily attack the larvae of Macrolepidoptera in the rearing records is also as would be expected, as Macrolepidoptera are primarily what are being collected by Janzen and Hallwachs's group. As for the Pimplinae, they attack such a variety of hosts that Malaise trapping would clearly have the advantage over a method that is limited in what hosts it would likely collect.

It is important to note that rearing does provide invaluable information about ichneumonid species biology that is absent from Malaise trapping records. Rearing records provide information about what hosts are being attacked by ichneumonid parasitoids that is especially important for a group that is significant in many biological control efforts. Malaise trapping is a good single method for determining what subfamilies and species of Ichneumonidae are present in a community, but not why they are there or what they are doing.

This study highlights the importance of using multiple collection methods to determine the fauna of a site. It is clear from comparing the two methods that neither method alone caught all of the species of Pimplinae present in the area. Other studies by Gauld (1991), Gaston and Gauld (1993), and Gauld et al. (1998) also show that more species of pimplines have been caught in other studies using Malaise trapping for a longer period of time in Guanacaste than were found in our one-year study. For example, Gauld (1991) found a total of 36 pimpline species from Santa Rosa alone. Therefore, it is possible that those species reared but not collected by Malaise traps would have been caught in time by the Malaise traps, but this is in no way guaranteed. Some aspect of the particular species biology, such as only moving on the ground or in the canopy, might always prevent that species from going into Malaise traps. Future efforts should obviously use as many trapping methods as possible for as long of a time as possible if the goal is to collect all ichneumonids in an area. However, if time and/or finances limit such an effort, and the goal is to assess the overall diversity at a site, it seems that Malaise trapping would be a good choice. Conversely, if the goal is to understand host-parasite interactions between species, then clearly rearing is better. Ideally, future studies should include both collection methods to allow for both a characterization of what species are present in an area, as well as information about what as many as possible are doing there.

Table 1. Abundances of subfamilies of Ichneumonidae collected in Guanacaste by Malaise trapping (MT) and rearing. UNKNOWN indicates that the specimens were not identified past the family level.

Subfamily	MT	Rearing
Anomaloninae	17	67
Banchinae	411	58
Campopleginae	486	650
Cremastinae	263	54
Cryptinae	1822	24
Ctenopelmatinae	28	1
Ichneumoninae	1123	183
Labeninae	61	0
Lycorininae	3	1
Mesochorinae	6	97
Metopiinae	4	28
Ophioninae	22	679
Orthocentrinae	1784	0
Oxytorinae	5	0
Pimplinae	375	108
Rhyssinae	5	0
Tersilochinae	273	0
Tryphoninae	19	11
UNKNOWN	0	232
TOTAL	6707	2193

Table 2. Species of Pimplinae collected by Malaise trapping (MT) and rearing (R) in Guanacaste, Costa Rica. The sp. 1 indicates a species that has not yet been named.

Species name	Collection Method	No. collected by MT	No. collected rearing
Acrotaphus fasciatus	MT	1	0
Acrotaphus franklini	MT	5	0
Acrotaphus tibialus	MT, R	4	1
Anastelgis garciai	MT	3	0
Apechthis zapoteca	MT	7	0
Calliephialtes sp. 1	R	0	1
Clydonium cabrerai	R	0	1
Clydonium fonsecai	MT	1	0
Dolichomitus annulicornis	MT	33	0
Iseropus barqueroi	R	0	1
Neotheronia bostrande	MT	8	0
Neotheronia brandtae	MT	1	0
Neotheronia charli	MT	3	0
Neotheronia chirquensis	MT	7	0
Neotheronia concolor	R	0	4
Neotheronia cyrusi	MT	2	0
Neotheronia donovani	R	0	5
Neotheronia lineata	MT	5	0
Neotheronia lloydi	MT, R	8	1
Neotheronia matamorosi	MT	7	0
Neotheronia mellosa	MT	104	0
Neotheronia montezuma	MT, R	11	6
Neotheronia rosai	MT	25	0
Neotheronia tacubaya	MT, R	25	77
Neotheronia tolteca	MT	4	0
Nomospecia solisi	MT, R	2	1
Pimpla azteca	MT	6	0
Pimpla caeruleata	MT	31	0
Pimpla croceiventris	MT	39	0
Pimpla sumichrasti	MT	17	0
Xanthopimpla aurita	MT, R	13	1
Zatypota petronae	R	0	1
Zonopimpla atriceps	MT, R	1	2
Zonopimpla aurae	MT	2	0

COMPARISON OF ICHNEUMONID (HYMENOPTERA) ABUNDANCE AND PHENOLOGY ACROSS THREE SITES IN GUANACASTE, COSTA RICA[2]

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[2] Bartlett, R.P. and J. Pickering. To be submitted to Biotropica.

Introduction

One of the most intensively studied groups of insects in the tropics in recent years is the family Ichneumonidae (Hymenoptera). With 37 subfamilies (Gauld 1997) and an estimated 60,000 species worldwide (Townes 1969; Gauld and Bolton 1988; Wahl and Sharkey 1993), Ichneumonidae is clearly one of the largest families of insects. The Costa Rican ichneumonid fauna is diverse, with 25 of the 37 subfamilies represented, with those not present being very small subfamilies containing about 40 or fewer species (Gauld 1991; Hanson and Gauld 1995). The vast majority of ichneumonids are parasitoids of a wide variety of holometabolous insects and spiders, with the majority attacking Coleoptera, Diptera, Lepidoptera, and Hymenoptera (Hanson and Gauld 1995, Gauld 1997). Those ichneumonids that attack insects generally parasitize the larval or pupal stages, although some oviposit into eggs, completing development in later stages.

In recent years a number of studies have considered the underlying reasons for the timing and duration of insect (and specifically parasitoid) flight activity. Attention has been given to abiotic factors as explanations for observed activity. Studies by Wolda (1988) correlated tropical insect flight activity with yearly rainfall by showing that periods of peak insect activity were more distinct in forests with pronounced dry seasons. Wolda (1989) and Smythe (1985) both demonstrated correlations between season and peaks in insect activity in Panama, with Wolda finding peaks in insect activity at either the beginning or end of the dry season and Smythe finding an early wet season peak in nocturnal insects. Most recently, Shapiro and Pickering (2000) correlated parasitoid wasp flight activity with rainfall in sites in Panama and Costa Rica. They caught over twice as many ichneumonids in wet forest traps in Costa Rica as in moist forest traps in

Pamama. Temperature has also been predicted to be an important influence on flight activity of ichneumonids. Fink and Volkl (1995) gave several examples of negative effects of high temperature and low humidity on life expectancy and reproductive success of small insects. Heinrich (1977) observed that one subfamily of ichneumonids, the Ichneumoninae, were only active in the early morning and evening hours in Florida. Gauld (1987) found that fewer ichneumonids were caught in Malaise traps in dry, sunny areas such as open fields than in nearby traps in cooler, moister areas.

Another factor that has been proposed to influence parasitoid flight activity is host phenology. Herbivorous insect populations, especially lepidopterous caterpillars, have generally been shown to greatly increase in number near the beginning of the wet season in seasonal tropical forests, usually following the first flush of leaves in deciduous trees (Buskirk and Buskirk 1976; Wolda 1978; Janzen 1993; Kato et al. 1995; Coley and Barone 1996; Janzen and Gauld 1997; Novotny and Basset 1998). Janzen and Gauld (1997) demonstrated that a number of species of ichneumonids in the subfamilies Campopleginae and Ophioninae appeared to peak in activity (based on Malaise trap catches) at the same time their hosts were most abundant. For most species, the peak lepidopteran caterpillar abundances occurred around the beginning of the wet season, although this varied in some cases based on the biology of the individual species. Gaasch et al. (1998) found that ichneumonids attacking the same orders of hosts tended to peak in abundance synchronously in Malaise traps in Georgia, U.S.A. However, as demonstrated by Janzen and Gauld (1997), the peak in host abundance usually occurs at the same time as increased rainfall, confounding whether rainfall (and thus increased moisture and lower temperatures), the abundance of hosts, or an interaction of the two is the factor responsible for the increase in parasitoid flight activity.

An additional set of factors to consider when attempting to determine the causes of parasitoid phenology are the individual life history strategies and characteristics of each parasitoid species. For example, a peak in parasitoid activity may occur due to mating activity. Such factors are difficult to determine in a large-scale study and must be dealt with on an individual species-by-species basis. This would be impossible to investigate at the current time for all ichneumonids due to the lack of any basic life history information for many species of ichneumonids. Numerous other factors such as predation (Price et al. 1980), competition (Hawkins et al. 1990), or an interaction of a myriad of factors may also affect parasitoid activity. However, abiotic factors (such as rainfall) and host phenology are the mostly commonly used explanations in the recent literature, due largely to the lack of basic life-history information on this diverse group that would allow for other explanations, such as explanations based on mating behavior or migratory patterns.

In this study we attempt to determine whether rainfall, host abundance and phenology, or other factors influence the magnitude and timing of flight activity of Ichneumonidae, as measured by Malaise trap catches. We compare across three sites with differing amounts of yearly rainfall in the Guanacaste Conservation Area, Costa Rica to determine if there is a significant difference in the abundance of the most common subfamilies among the three sites, and attempt to determine if that difference is due to rainfall, host availability, or other factors. We also look at weekly abundances in the traps to determine if peaks in activity over the year of the study coincide with peaks in rainfall or host abundance (for those groups attacking lepidopterous hosts).

Study Sites:

The Guanacaste Conservation Area (GCA) is a 104,000 ha conserved wildland in northwestern Costa Rica. It ranges from sea level to 2000 m in elevation, and from dry forest with a six-month dry season to perpetually wet cloud forest. The study was conducted at three sites within the GCA: Santa Rosa, Los Almendros, and San Cristobal. For more information about the GCA, see Janzen (1983), Janzen (1993), and Janzen and Gauld (1997).

Santa Rosa

The driest study site in Guanacaste was located in the Bosque Humedo, Sector Santa Rosa, Guanacaste Province, at 10°51.2’N, 85°36.7’W. The site was located in approximately 20 ha of old-growth Tropical Dry Forest at an elevation of 300 m. The mean annual rainfall for this site is approximately 1500 mm, with a six month essentially rain-free dry season from approximately December to early May. According to D. Janzen (personal communication), leaf flush for deciduous trees at this site generally occurs around the last week of April to about the third week of May, following closely after the beginning of the rainy season. The highest diversity and number of lepidopteran caterpillars are thus found at this site from mid-May through mid-July. The abundance of lepidopteran pupae is highly variable based on the individual biology of each species, but large numbers of pupae can usually be found during July and August, with some univoltine species remaining in the pupal stage until the beginning of the next rainy season (Janzen 1993).

Los Almendros

The second study site in Guanacaste was located in the Sendero Bejuquillo, Estacion Los Almendros, Sector El Hacha, Guanacaste Province, at 11°02.0’N, 85°31.8’W. This site was in the middle of approximately 20 ha of old secondary-growth Tropical Dry Forest at an elevation of 280 m. The mean annual rainfall for this site is approximately 1800 mm, with a five month essentially rain-free dry season during a similar period as in Santa Rosa. According to D. Janzen (personal communication), leaf flush for deciduous trees at this site generally occurs around the middle of April to about the second week of May, following closely after the beginning of the rainy season. The highest diversity and number of lepidopteran caterpillars are thus found at this site from late May through late July. Lepidopteran pupae follow a similar trend here as in Santa Rosa.

San Cristobal

Our wettest study site in Guanacaste was located by the Rio Cucaracho, Estacion San Cristobal, Sector San Cristobal, Alajuela province, at 10°52.4’N, 85°23.5’W. This site was in the middle of a strip of lightly logged old secondary-growth Tropical Rainforest at an elevation of 630 m. The mean annual rainfall for this site is approximately 3500 mm, with a one to two month “dry season” during which the site receives slightly less rain than the remainder of the year. This “dry season” is variable when it occurs from year to year. Both leaf flush and caterpillar abundance are highly variable from year to year and within each year at this site (D. Janzen, personal communication).

Methods

We set up a total of six Townes-style (Townes, 1972) fine-mesh Malaise traps purchased from Sante Traps (Lexington, Kentucky), two at each of the above sites. The traps were aligned along a north-south axis with the collecting jar of 70% ethanol facing south. All six traps were run for a period of one year, from July 7, 1997 to July 6, 1998 (72 total trap-months of effort). All traps were collected and emptied on a weekly basis, and all Ichneumonidae were removed from each sample, bar-coded and labeled, and identified to the level of subfamily. We then identified those ichneumonids belonging to the subfamily Pimplinae to the level of species. Specimen data are maintained in the UGCA database of the Insect Diversity Project <http://dial.pick.uga.edu>.

Table 1 shows the total ichneumonid catches for each of the three study sites, divided by subfamily, as well the primary hosts and life stages attacked for each of the subfamilies. We ran two repeated measures analysis of variance (RM-ANOVA) using the statistical package SAS on each of the 8 most commonly caught subfamilies of Ichneumonidae in our study. The General Linear Model procedure with a Repeated option was used. In the first of the two RM-ANOVAs for each subfamily, we log-transformed the absolute number of individuals in each subfamily that were caught per trap during each sampling period. The natural logarithm was used in this transformation since insect populations increase at an exponential rate. The second RM-ANOVA that was done for each subfamily was done using the proportion of individuals in each subfamily to the total number of Ichneumonidae caught per sample. This was done to

Table 1. Total ichneumonid catch, showing the number of individuals caught in each trap at each site for all subfamilies, also showing the proportion each subfamily comprised of the total ichneumonid catch at each site. In addition, some basic biology is given for each subfamily- whether the members are primarily egg (E), larval (L), or pupal (P) parasitoids, and the primary hosts for the parasitoid: Lepidoptera (Lep), Coleoptera (Col), Symphyta (Sym), other Hymenoptera (Hym), or Diptera (Dip).

	Santa Rosa			Los Almendros			San Cristobal				
Subfamily	Individuals caught in trap 1	Individuals caught in trap 2	% of total ichneumonid catch	Individuals caught in trap 1	Individuals caught in trap 2	% of total ichneumonid catch	Individuals caught in trap 1	Individuals caught in trap 2	% of total ichneumonid catch	E/L/P	Primary hosts
Anomaloninae	2	0	0.1	6	1	0.4	7	1	0.3	L	Lep/Col
Banchinae	68	58	5.8	68	43	5.6	90	84	6.8	L	Lep
Campopleginae	101	72	8.0	140	96	11.8	34	43	3.0	L	Lep
Cremastinae	80	27	4.9	31	14	2.3	32	79	4.4	L	Lep
Cryptinae	516	225	34.2	331	363	34.8	187	200	15.2	P	Lep
Ctenopelmatinae	1	4	0.2	4	2	0.3	6	11	0.7	L	Sym
Ichneumoninae	430	162	27.3	195	238	21.7	34	64	3.9	P	Lep
Labeninae	33	10	2.0	15	2	0.9	1	0	0.0	P	>2 host orders
Lycorininae	1	2	0.1	0	0	0.0	0	0	0.0	L(?)	Lep
Mesochorinae	1	0	0.0	0	1	0.1	1	3	0.2	L	Hym
Metopiinae	3	1	0.2	0	0	0.0	0	0	0.0	L	Lep
Ophioninae	11	9	0.9	0	2	0.1	0	0	0.0	L	Lep
Orthocentrinae	68	36	4.8	116	140	12.8	566	858	56.0	L	Dip
Oxytorinae	1	4	0.2	0	0	0.0	0	0	0.0	L	Dip
Pimplinae	135	58	8.9	38	47	4.3	29	68	3.8	E/L/P	>2 host orders
Rhyssinae	0	1	0.0	1	0	0.1	1	2	0.1	L/P	Col/Sym
Tersilochinae	24	11	1.6	66	34	5.0	63	75	5.4	L	Col
Tryphoninae	5	8	0.6	1	2	0.2	1	2	0.1	L	Sym/Lep
TOTAL	1480	688		1012	985		1052	1490			

factor out differences in between-trap efficiency, assuming that such differences would be constant across all relevant subfamilies. As is customary for such proportions, we transformed these data by taking the arcsin square root of the ratio before the analysis. The purpose of these analyses was to allow for three tests: 1) Does the collection site (whether Santa Rosa, Los Almendros, or San Cristobal) influence subfamily's abundance in Malaise trap catches? 2) Does that date on which the sample was collected influence the subfamily's abundance? and 3) Does the influence of the collection site on the abundance of the subfamily depend upon the date on which it was collected?

Results

Differences among sites

Our analysis of the 8 most common subfamilies collected at all 3 sites included the following subfamilies: Banchinae, Campopleginae, Cremastinae, Cryptinae, Ichneumoninae, Orthocentrinae, Pimplinae, and Tersilochinae. As seen in Table 2, out of these 8 subfamilies, only 2 differed statistically at a 95% confidence level (*p*-value of .05 or less) among the three sites based on the absolute number of individuals caught. The first of these 2 subfamilies was the Campopleginae (F=11.64, *d.f.*=2, *p*=0.0386), parasitoids of larval lepidopteran caterpillars. Campoplegines were most abundant in Los Almendros and least abundant in San Cristobal. The second subfamily was the Orthocentrinae (F=64.20, *d.f.*=2, *p*=0.0035), parasitoids of larval Diptera. Orthocentrines were most abundant at San Cristobal and least abundant at Santa Rosa. However, as shown in the DATE*SITE interaction, the influence of the collection site on the abundance of the subfamily did depend upon the date on which the sample was collected for all subfamilies except the Tersilochinae, parasitoids of larval beetles.

Table 2. Results of RM-ANOVAs for the 8 most common subfamilies of ichneumonids. Analyses among sites each had 2 degrees of freedom, among dates had 52 degrees of freedom, and the date*site analyses each had 104 degrees of freedom. *p*-values that are significant at the 95% confidence level are indicated by bold lettering.

(a) Total abundance

	SITE		DATE		SITE*DATE	
Subfamily	F	*p*	F	*p*	F	*p*
Banchinae	3.62	0.1584	1.22	0.1722	1.42	**0.0242**
Campopleginae	11.64	**0.0386**	5.59	**0.0001**	2.60	**0.0001**
Cremastinae	0.61	0.6004	2.47	**0.0001**	1.68	**0.0016**
Cryptinae	2.78	0.2076	1.55	**0.0210**	2.23	**0.0001**
Ichneumoninae	7.03	0.0737	2.95	**0.0001**	2.17	**0.0001**
Orthocentrinae	64.20	**0.0035**	1.73	**0.0054**	1.67	**0.0019**
Pimplinae	1.73	0.3171	1.79	**0.0032**	1.91	**0.0001**
Tersilochinae	7.67	0.0662	1.51	**0.0280**	1.30	0.0712

(b) Proportion of total ichneumonid catch

	SITE		DATE		SITE*DATE	
	F	*p*	F	*p*	F	*p*
Banchinae	0.52	0.6417	1.26	0.1378	1.13	0.2508
Campopleginae	9.12	0.0531	2.35	**0.0001**	1.55	**0.0067**
Cremastinae	2.62	0.2195	1.74	**0.0051**	1.50	**0.0106**
Cryptinae	14.09	**0.0299**	1.07	0.3750	1.80	**0.0004**
Ichneumoninae	38.20	**0.0073**	1.80	**0.0031**	2.05	**0.0001**
Orthocentrinae	355.14	**0.0003**	2.97	**0.0001**	1.64	**0.0024**
Pimplinae	6.62	0.0794	1.41	0.0567	1.66	**0.0019**
Tersilochinae	7.28	0.0706	2.63	**0.0001**	1.26	0.0957

Thus, there were significant differences among the sites for all but one group, but only for certain times of the year.

When looking at the analyses that used proportions rather than absolute trap catches, 3 subfamilies showed significant differences among the three sites. These include the Cryptinae (F=14.09, *d.f.*=2, *p*=0.0299) and Ichneumoninae (F=38.20, *d.f.*=2, *p*=0.0073), which are the two major groups of parasitoids of pupal Lepidoptera and both make up the greatest proportion of the trap catch at Santa Rosa and the lowest proportion at San Cristobal. The Orthocentrinae (F=355.14, *d.f.*=2, *p*=0.0003) are the third group, showing the same trend as in the absolute catches. When looking at the DATE*SITE interaction for the proportions, the Campopleginae (F=1.55, *d.f.*=2, *p*=0.0067), Cremastinae (F=1.50, *d.f.*=2, *p*=0.0106), and the Pimplinae (F=355.14, *d.f.*=2, *p*=0.0019) also display significant differences in their proportional catches among the sites, but only for part of the year. These subfamilies were generally more abundant at the drier sites of Santa Rosa and Los Almendros during July and August, then became more abundant at San Cristobal during March and April. This means a total of 6 of the 8 common subfamilies show significant differences among sites for part or all of the year. However, the Banchinae and Tersilochinae do not show differences among the sites at the 95% confidence level for any significant part of the year.

Seasonality within sites

Figure 1 shows the flight activity of all Ichneumonidae at each of the three sites. In general, the most flight activity seems to occur in January-March, with the exception of large peaks in trap catches in September and April in San Cristobal. These peaks were caused by large catches of Orthocentrinae (fly parasitoids) during these months.

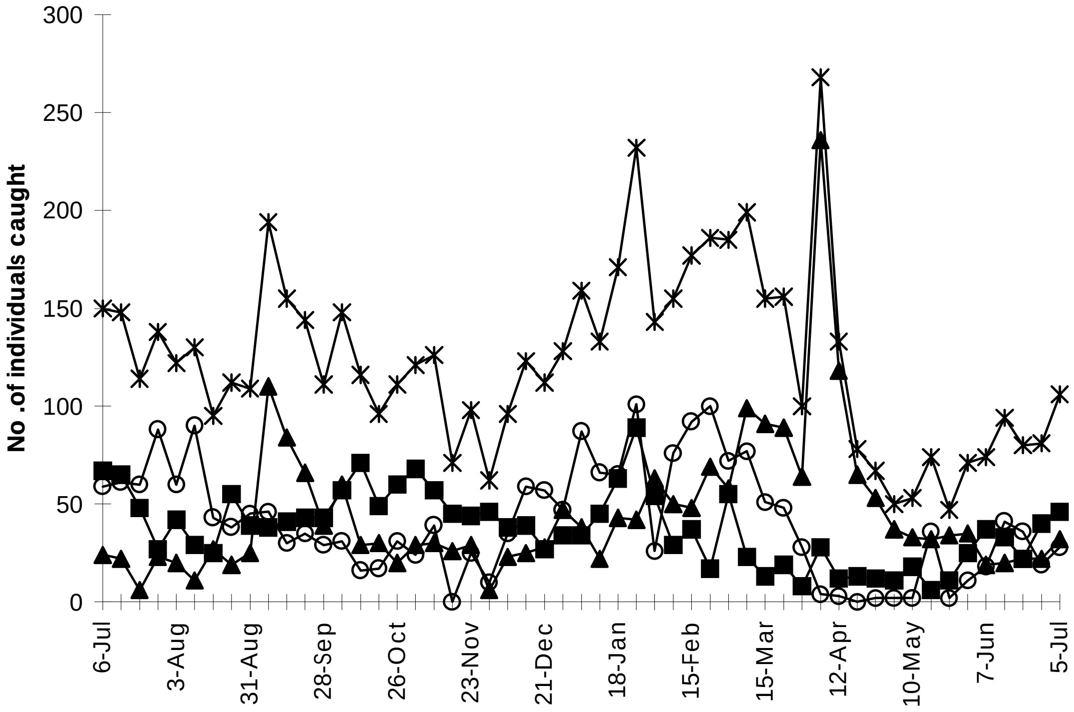


Figure 1. Flight activity of all Ichneumonidae during July 1997-July1998. The open circles represent the number of specimens caught during each sampling period at Santa Rosa, the closed squares represent the number of specimens caught during each sampling period at Los Almendros, the closed triangles represent the number of specimens caught during each sampling period at San Cristobal, and the X's represent the total number of specimens caught during each sampling period at all three sites.

However, with the exception of the orthocentrine peaks, most other groups of ichneumonids showed a lack of large differences in seasonal trends across the sites for the whole year. This is also demonstrated by the significance of date as an influence of trap catches across all of the sites, as shown in Table 2. In Table 2, it is seen that date influences abundance at a 95 % confidence level across all three sites in 7 of the 8 most common subfamilies when looking at absolute trap catches, and 5 of the 8 most common subfamilies when looking at relative proportions.

Figure 2 shows the flight activity of Ichneumonidae divided out by host taxa. We used the proportion in each sample of the total yearly catch at all traps in all sites to normalize the differences in abundance seen across ichneumonids attacking different taxonomic groups. We compared subfamilies attacking primarily Lepidoptera (Banchinae, Campopleginae, Cremastinae, Cryptinae, Metopiinae, Ophioninae, and Ichneumoninae), Diptera (Orthocentrinae), and Coleoptera (Tersilochinae). The peaks in proportional abundance did occur at different times. For those groups attacking lepidopteran hosts, the peak in proportional abundance was seen in January, with generally higher proportions in January-March than the rest of the year. For the parasitoids of Diptera, a very large peak in proportional abundance was seen in April, with a smaller secondary peak seen in September. However, both of these peaks were due to unusually large catches from only one trap at San Cristobal, with that trap catching over 90% of the total orthocentrines caught in this study. For the parasitoids of Coleoptera, the highest proportional peak was seen in early July, but over half of these specimens were caught in only one trap at Los Almendros.

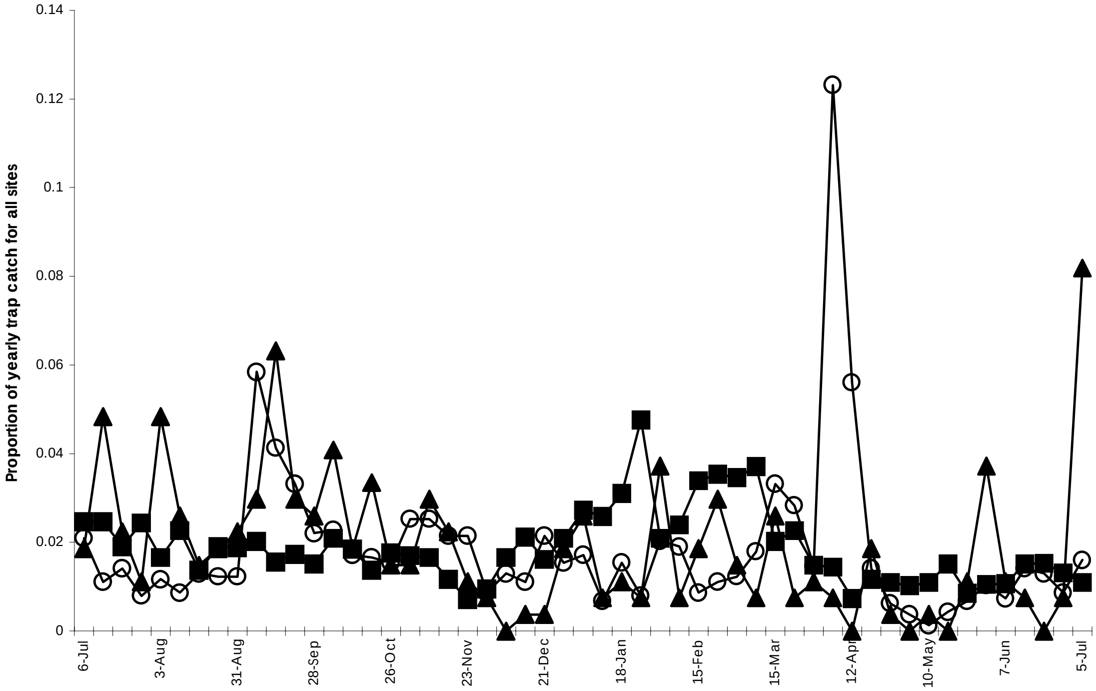


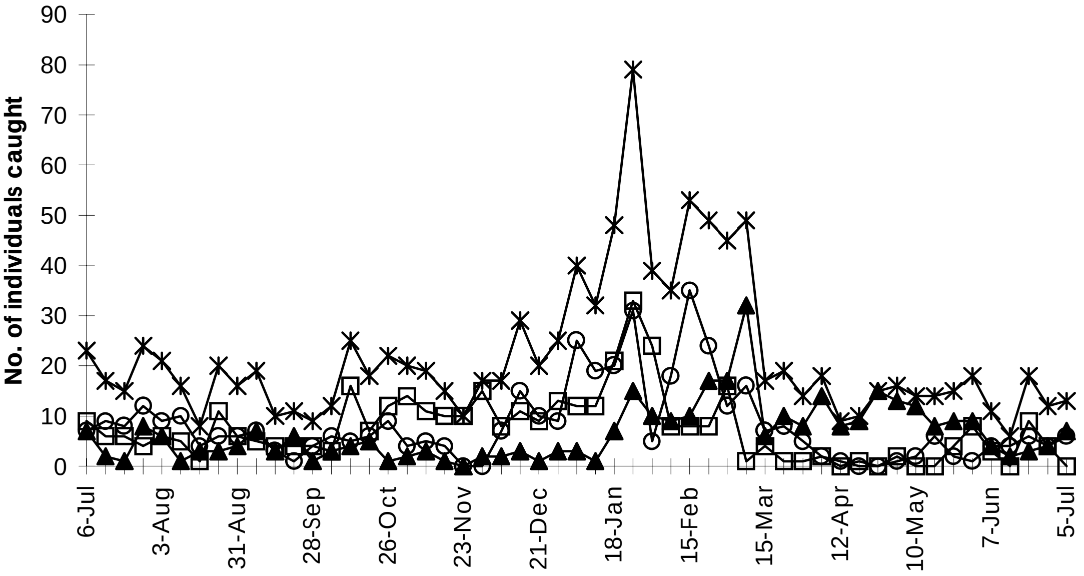
Figure 2. Flight activity of Ichneumonidae by host taxa, represented as the proportion of the total yearly catch during each sampling period at all three sites for each group during July 1997-July 1998. Parasitoid groups attacking Lepidoptera are represented by closed squares, while those attaching Coleoptera are represented by open triangles, and those attacking Diptera are represented by open circles.

Figure 3 illustrates the flight activity of parasitoids that primarily attack larvae and pupae of Lepidoptera divided by site. For parasitoids of lepidopteran larvae, peaks in abundance in trap catches were seen in January and February for Santa Rosa and Los Almendros, which is around the middle of the dry season, and is not concurrent with peak abundances of larval Lepidoptera. In San Cristobal, peaks in abundance for parasitoids of lepidopteran larvae are seen in March, later than at the drier sites. For parasitoids of lepidopteran pupae, peaks in abundance in trap catches were seen in January-March for Santa Rosa and Los Almendros, which is during the dry season, and is not concurrent with peak abundances of pupal Lepidoptera. Again, the peaks in abundance of parasitoids of lepidopteran pupae for San Cristobal are later than at the drier sites, with slightly higher abundances occurring during March and April than the rest of the year.

Discussion

Differences in abundance across sites

Based on the results of our comparisons among sites, it does not appear that moisture/rainfall alone is a significant factor in determining flight activity of most Ichneumonidae. If this were the case, we would have expected the largest number of ichneumonids to be caught for most subfamilies in the rainy site (San Cristobal), with that number decreasing at the drier site of Los Almendros, and being lowest at the driest site of the three, Santa Rosa. However, this was clearly not the case, as only the Orthocentrinae were caught in the significantly highest numbers (and proportions) in San Cristobal and the lowest in Santa Rosa. Therefore, it may be that moisture is an



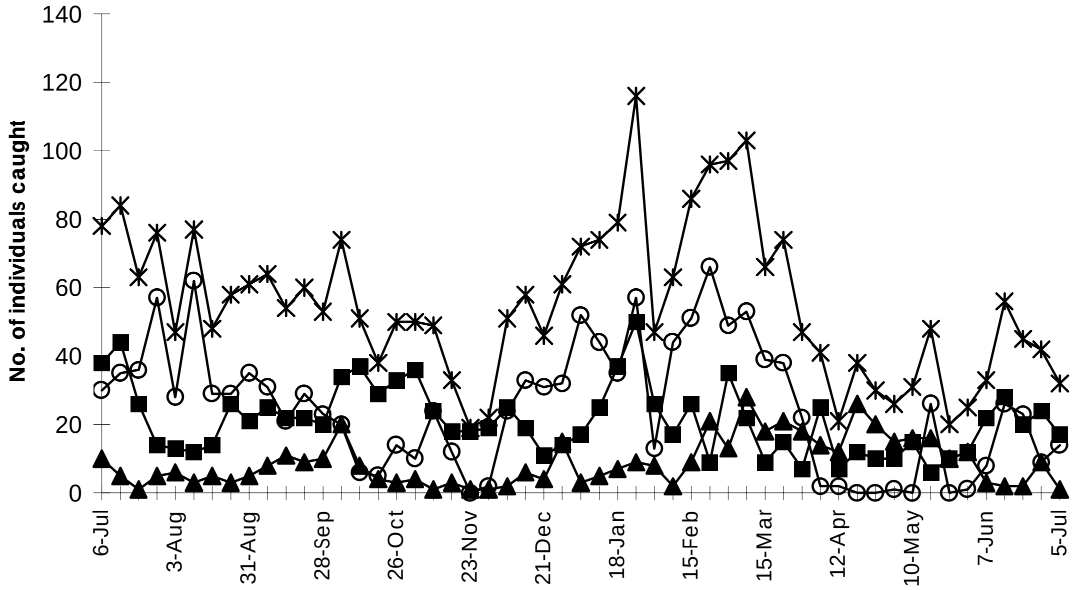


Figure 3. Flight activity of Ichneumonidae attacking larval (top graph) and pupal (bottom graph) Lepidoptera during July 1997- July 1998. The open circles represent the number of specimens caught during each sampling period at Santa Rosa, the closed squares represent the number of specimens caught during each sampling period at Los Almendros, the closed triangles represent the number of specimens caught during each sampling period at San Cristobal, and the X's represent the total number of specimens caught during each sampling period at all three sites.

important factor for parasitoids that attack Diptera, but that does not appear to be the case for parasitoids attacking Lepidoptera. In fact, the majority of the common subfamilies of ichneumonids attacking Lepidoptera were caught in higher numbers (and proportions) in the two dry sites, although most of these differences were only significant for part of the year. As for the Tersilochinae, which attack beetles, they are also most abundant in San Cristobal and lowest in abundance in Santa Rosa, although this difference is not significant at a 95% confidence level. However, the fact that the difference is significant at a 90% confidence level suggests that this may be an actual trend and not just an artifact of the data. It is also interesting to note that the largest number of species of Pimplinae, the most biologically diverse subfamily of Ichneumonidae (Gauld 1991), was found at Santa Rosa (22 species), as compared to Los Almendros (17 species), or San Cristobal (18 species). Thus, at the species level for one subfamily, we again do not see the expected trend of increasing numbers and diversity in sites with more moisture.

There does seem to be some effect of host abundance on the abundance of Ichneumonidae, at least for some of those subfamilies that parasitize Lepidoptera. Janzen (1993) states “it is much easier to find caterpillars in the Santa Rosa forest during these 3 months (referring to May-July) than in any Costa Rican rain forest.” Five of the 8 subfamilies of Ichneumonidae that attack primarily Lepidoptera, the Cremastinae, Cryptinae, Ichneumoninae, Metopiinae, and Ophioninae are also more proportionally abundant in Santa Rosa than the other two sites. This is a significant difference for 2 of the 3 subfamilies on which statistical tests were run on all dates, and the difference is significant for part of the year on the third. It is also interesting to note that the subfamilies of lepidopteran parasitoids that were significantly proportionally more abundant at Santa Rosa over the whole year are the two major subfamilies of pupal parasitoids. This agrees with the idea proposed by Shapiro and Pickering (2000) that pupal parasitoids, which tend to search closer to the ground, may fare better in drier environments than higher-flying larval parasitoids. However, the converse, that larval parasitoids would be proportionally most common at the wettest site, is not true for most of the larval parasitoids, which may be because of an interaction between the importance of host abundance and moisture levels. Unfortunately, data are not available on the abundance of beetles and flies to determine if a relationship between host abundance and parasitoid abundance holds true for those groups as well.

Factors influencing seasonality

The expected effects of moisture were also lacking in most of the seasonality data. If moisture were a controlling factor in the flight phenology of the ichneumonids, we would have expected to see much higher activity during the wet season than the dry season, especially in the drier sites. However, that was not the case. For the parasitoids of Lepidoptera, which comprised the majority of the dry site ichneumonids, more activity was observed during the dry season than the wet season. This is difficult to explain using rainfall and moisture availability. One possible moisture-based explanation for this result is that some ichneumonids may have switched behavior to deal with the dry, hot conditions present during the dry season, thus making them more likely to be caught in our traps. Thus, this trend would be an artifact of our trapping methods. For example, some ichneumonids may have flown lower to the ground (where the traps are) during the dry season to avoid desiccation. This is a reasonable scenario, since a study in Panama (Windsor, 1990) recorded relative humidity 10-15% higher near the forest floor than in the canopy. There is also some evidence that this type of behavior switching would be advantageous in the driest site (Santa Rosa). Nocturnality has been proposed to have evolved as a method of combating the daily heat (Gauld 1988). The majority of both ophionines and tryphonines found in Costa Rica are nocturnally active. As seen in Table 1, both of these subfamilies were much more common in the trap catches in Santa Rosa than either of the two other sites, with 91% of all ophionines and 68% of all tryphonines having been collected there. This suggests that nocturnality may be a way some ichneumonids are able to deal with the dryness and heat in Santa Rosa.

As shown in Figures 2 and 3, the expected trends in flight activity if host abundance was a controlling factor in such activity are not seen. For parasitoids of lepidopteran pupae, peak abundances were seen in January-March for Santa Rosa and Los Almendros, which is during the dry season. These peaks are not concurrent with expected peak abundances of pupal Lepidoptera, which are usually seen in July and August, suggesting host abundance may not be a major controlling factor in flight activity for parasitoids of lepidopteran pupae. Also, there are some secondary, slightly smaller peaks seen during the wet season in July and August, as would be expected if host abundance were a controlling factor. Also, as some univoltine Lepidoptera have pupae that are present throughout the dry season, it is possible that some of the abundance of pupal parasitoids during the dry season may have been a result of parasitoids specializing on those hosts. For parasitoids of lepidopteran larvae, peaks in abundance in trap catches were seen in January and February for Santa Rosa and Los Almendros, which is around the middle of the dry season, and again is not concurrent with peak abundances of larval Lepidoptera.

The unexpected peak in ichneumonid activity at the dry sites during the dry season might be explained if the forests in which the traps were operated are acting as a refuge. Janzen (1973) found increased activity during the dry season in areas with a milder dry season than the surrounding vegetation. Gauld (cited in Shapiro and Pickering, 2000) noted an increase in old-growth trap catches relative to those in secondary growth. Shapiro and Pickering (2000) noted a similar effect in their study in Panama. As our traps were located in one of the few areas of old-growth forest in Santa Rosa, and in old secondary growth in Los Almendros, ichneumonids may be moving into these forests from the harsher environments in surrounding cleared fields and younger successional forests. This movement could account for the increases ichneumonid abundances seen during the dry season at these sites.

Conclusions

We must also recognize that moisture levels and host availability alone are not the only differences between our three sites, and thus are not the only possible explanation for our observed results. A myriad of other differences, such as forest age or floral composition may have also played a role. We also must realize that this study only spans one year, and that the results seen, especially the unusual result of the most ichneumonid activity during the dry season at the dry sites would not necessarily be repeated. In fact, this result does not seem to agree with data from Gauld (1991) and Janzen and Gauld (1997) on a more limited number of subfamilies.

Ideally, studies of influences on tropical parasitoid abundance and phenology should be as long-term as possible and focus on species-species level interactions as much as is feasible. Long-term studies would allow yearly variation in abundance and phenology to be addressed, while species-species level studies would allow one to account for the many differences within larger-scale taxonomic groupings. However, much more basic information about the life history strategies of most tropical ichneumonid species must be gathered before such studies would be feasible, making the need for more studies such as the rearing program of D. Janzen in Costa Rica (Janzen and Hallwachs, 2000) as a basis for future ecological studies readily apparent. Until such studies are complete, however, large-scale community studies such as this one play a particularly important role. It is only through such studies that macro-trends, such as the unexpected peaks in activity at the dry sites during the dry season in this study, can be seen at the current time. This type of unexpected result is just one more small part of the complex puzzle of tropical parasitoid biology that will hopefully become clearer as similar studies are completed in the future.

CONCLUSIONS

In the first part of this study, I compared Malaise trapping to rearing as a method for collecting Ichneumonidae in Guanacaste, Costa Rica. Based on the results of this study, I concluded that Malaise trapping is a more efficient way of collecting a diversity of subfamilies of Ichneumonidae quickly than rearing. Malaise trapping also fared better than rearing at collecting a large number of pimpline species quickly. However, it is important to note that rearing does provide invaluable information about ichneumonid species biology that is absent from Malaise trapping records. Rearing records provide information about what hosts are being attacked by ichneumonid parasitoids that is especially important for a group that is significant in many biological control efforts. Malaise trapping is a good single method for determining what subfamilies and species of Ichneumonidae are present in a community, but not why they are there or what they are doing.

This study highlights the importance of using multiple trapping methods to determine the ichneumonid fauna of a site. It is clear from comparing the two methods that neither method alone caught all of the species of Pimplinae present in the area. Other studies by Gauld (1991), Gaston and Gauld (1993), and Gauld et al. (1998) also show that more species of pimplines have been caught in other studies using Malaise trapping for a longer period of time in Guanacaste than were found in my one-year study. For example, Gauld (1991) found a total of 36 pimpline species from Santa Rosa alone. Therefore, it is possible that those species reared but not collected by Malaise traps would have been caught in time by the Malaise traps, but this is in no way guaranteed. Some aspect of the particular species biology, such as only moving on the ground or in the canopy, might always prevent that species from going into Malaise traps. Future efforts should obviously use as many trapping methods as possible for as long of a time as possible if the goal is to collect all ichneumonids in an area. However, if time and/or finances limit such an effort, it seems that Malaise trapping would be a good choice.

In the second part of the study, I compared across three sites with differing amounts of yearly rainfall in the Guanacaste Conservation Area, Costa Rica to determine if there is a significant difference in the abundance of the most common subfamilies among the three sites, and attempt to determine if that difference is due to rainfall, host abundance, or other factors. I also looked at weekly abundances in the traps to determine if peaks in activity over the year of the study coincided with peaks in rainfall or host abundance (for those groups attacking lepidopterous hosts). Based on the results of my comparisons among sites, it does not appear that moisture/rainfall alone is a significant factor in determining flight activity of most Ichneumonidae. If this were the case, I would have expected the largest number of ichneumonids to be caught for most subfamilies in the rainy site (San Cristobal), with that number decreasing at the drier site of Los Almendros, and being lowest at the driest site of the three, Santa Rosa. However, this was clearly not the case, as only the Orthocentrinae were caught in the significantly highest numbers (and proportions) in San Cristobal and the lowest in Santa Rosa. Therefore, it may be that moisture is an important factor for parasitoids that attack Diptera, but that does not appear to be the case for parasitoids attacking Lepidoptera. In fact, the majority of the common subfamilies of ichneumonids attacking Lepidoptera were caught in higher numbers (and proportions) in the two dry sites, although most of these differences were only significant for part of the year. As for the Tersilochinae, which attack primarily beetles, they are also most abundant in San Cristobal and lowest in abundance in Santa Rosa.

The expected effects of moisture were also lacking in most of the seasonality data. If moisture were a controlling factor in the flight phenology of the ichneumonids, I would have expected to see much higher activity during the wet season than the dry season, especially in the drier sites. However, that was not the case. For the parasitoids of Lepidoptera, which comprised the majority of the dry site ichneumonids, more activity was observed during the dry season than the wet season. This is difficult to explain using rainfall and moisture availability. One possible moisture-based explanation for this result is that some ichneumonids may have switched behavior to deal with the dry, hot conditions present during the dry season, thus making them more likely to be caught in my traps. Thus, this trend would be an artifact of my trapping methods. For example, some ichneumonids may have flown lower to the ground (where the traps are) during the dry season to avoid desiccation. This is a reasonable scenario, since a study in Panama recorded relative humidity 10-15% higher near the forest floor than in the canopy. There is also some evidence that this type of behavior switching would be advantageous in the driest site (Santa Rosa). Nocturnality has been proposed to have evolved as a method of combating the daily heat (Gauld 1988). The majority of both ophionines and tryphonines found in Costa Rica are nocturnally active. Both of these subfamilies were much more common in the trap catches in Santa Rosa than either of the two other sites, suggesting that nocturnality may be a way some ichneumonids are able to deal with the dryness and heat in Santa Rosa. Another possible moisture-based explanation for my unusual result could be the El Niño/Southern Oscillation (ENSO) event that occurred in 1997. The ENSO event with its effects on precipitation could have caused the parasitoids to be active at a time they usually would not be.

There does seem to be some effect of host abundance on the abundance of Ichneumonidae, at least for some of those subfamilies that parasitize Lepidoptera. Janzen (1993) states "it is much easier to find caterpillars in the Santa Rosa forest during these 3 months (referring to May-July) than in any Costa Rican rain forest." Five of the 8 subfamilies of Ichneumonidae that attack primarily Lepidoptera, the Cremastinae, Cryptinae, Ichneumoninae, Metopiinae, and Ophioninae are also more proportionally abundant in Santa Rosa than the other two sites. This is a significant difference for 2 of the 3 subfamilies on which statistical tests were run on all dates, and the difference is significant for part of the year on the third. It is also interesting to note that the subfamilies of lepidopteran parasitoids that were significantly proportionally more abundant at Santa Rosa over the whole year are the two major subfamilies of pupal parasitoids. This agrees with the idea in Shapiro and Pickering (2000) that pupal parasitoids, which tend to search closer to the ground, may fare better in drier environments than higher-flying larval parasitoids. However, the converse, that larval parasitoids would be proportionally most common at the wettest site, is not true for most of the larval parasitoids, which may be because of an interaction between the importance of host abundance and moisture levels. Unfortunately, data are not available on the abundance of beetles and flies to determine if a relationship between host abundance and parasitoid abundance holds true for those groups as well.

The expected trends in flight activity if host abundance was a controlling factor in such activity were also not seen. For parasitoids of lepidopteran pupae, peak abundances were seen in January-March for Santa Rosa and Los Almendros, which is during the dry season. These peaks are not concurrent with expected peak abundances of pupal Lepidoptera, which are usually seen in July and August, suggesting host abundance may not be a major controlling factor in flight activity for parasitoids of lepidopteran pupae. Also, there are some secondary, slightly smaller peaks seen during the wet season in July and August, as would be expected if host abundance were a controlling factor. Also, as some univoltine Lepidoptera have pupae that are present throughout the dry season, it is possible that some of the abundance of pupal parasitoids during the dry season may have been a result of parasitoids specializing on those hosts. For parasitoids of lepidopteran larvae, peaks in abundance in trap catches were seen in January and February for Santa Rosa and Los Almendros, which is around the middle of the dry season, and again is not concurrent with peak abundances of larval Lepidoptera. Again, this suggests that host abundance may not be a controlling factor in flight activity. However, the flight activity during the dry season is again difficult to explain. As above, possible explanations may include trapping bias and the effects of the 1997 ENSO event.

An additional plausible explanation for the unexpected result of peak ichneumonid activity during the dry season at the dry sites might also be explained if the forests in which the traps contained are acting as a refuge. Janzen (1973) found increased activity during the dry season in areas with a milder dry season than the surrounding vegetation. Gauld (cited in Shapiro and Pickering, 2000) noted an increase in old-growth trap catches relative to those in secondary growth. Shapiro and Pickering (2000) noted a similar effect in their study in Panama. As my traps were located in one of the few areas of old-growth forest in Santa Rosa, and in old secondary growth in Los Almendros, ichneumonids may be moving into these forests from the harsher environments in surrounding cleared fields and younger successional forests. This movement could account for the increases ichneumonid abundances seen during the dry season at these sites.

Of course, I must also recognize that moisture levels and host availability alone are not the only differences between my three sites, and thus are not the only possible explanation for my observed results. The elevation of the three sites may also have played a role in the differences observed in the subfamily abundances and phenology, as there are definite differences in the composition of the ichneumonid fauna at different elevations (Gauld 1991). A myriad of other differences, such as forest age or floral composition may have also played a role. Of course, the real explanation for the differences seen in my study among the ichneumonid seasonality and abundance among the three sites would likely be a combination of numerous factors. I also must realize that this study only spans one year, and that the results seen, especially the unusual result of the most ichneumonid activity during the dry season at the dry sites would not necessarily be repeated. In fact, this result does not seem to agree with data from Gauld (1991) and Janzen and Gauld (1997) on a more limited number of subfamilies.

A further consideration that must be addressed is the bias inherent in any trapping method, including Malaise traps. As mentioned earlier, comparisons among sites and over time may be biased by species and individual behavior. Malaise trap catches can also be highly dependent on such factors as trap condition and trap location. However, Malaise traps are generally considered to be a good method for collecting Ichneumonidae (Matthews and Matthews, 1970; Darling and Packer, 1988; Noyes 1989; Gauld 1991, 1997), and have been used in a number of studies of tropical Ichneumonidae.

In conclusion, although the results of my study were not entirely as I would have predicted, they do make an important point. Ideally, studies of influences on tropical parasitoid abundance and phenology should be as long-term as possible and focus on species-species level interactions as much as is feasible. Long-term studies would allow yearly variation in abundance and phenology to be addressed, while species-species level studies would allow the many differences within larger-scale taxonomic groupings to be accounted for. However, much more basic information about the life history strategies of most tropical ichneumonid species must be gathered before such studies would be feasible, making the need for more studies such as the rearing program of D. Janzen in Costa Rica (Janzen and Hallwachs, 2000) as a basis for future ecological studies readily apparent. Until such studies are complete, however, large-scale community studies such as this one play a particularly important role. It is only through such studies that macro-trends, such as the unexpected peaks in activity at the dry sites during the dry season in this study, can be seen at the current time. This type of unexpected result is just one more small part of the complex puzzle of tropical parasitoid biology that will hopefully become clearer as similar studies are completed in the future.

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APPENDIX

The raw data from this study listing the weekly trap catches by taxon is publicly available on the World Wide Web through the following website: <http://dial.pick.uga.edu>.