

## **Ichneumonid (Hymenoptera: Ichneumonoidea) Diversity Across an Elevational Gradient on Monts Doudou in Southwestern Gabon**

Simon van Noort

*Natural History Division, South African Museum (Iziko Museums of Cape Town),  
P.O. Box 61, Cape Town, 8000, South Africa;  
e-mail: svannoort@iziko.org.za*

An analysis of the ichneumonid wasps collected during a four-week, diversity survey of Monts Doudou in southwestern Gabon revealed 112 species represented by 233 individuals. Ichneumonidae of Gabon are extremely poorly known, with 25 species in 14 genera currently recorded. This survey added a further 45 genera to the checklist of that country. The smoothed, species-accumulation curve showed no sign of reaching an asymptote, indicating that the ichneumonids were under-sampled. Abundance-based and incidence-based coverage estimators extrapolated estimated species richness to 305 and 312 species respectively, i.e., only 36–37% of the ichneumonid species estimated to be present were actually sampled. Ichneumonid species richness was similar across elevation with a 6% total variation between the 3 sampled altitudes. Species richness and abundance was highest at mid-elevation (350 m), followed by high elevation (630 m) and lastly low elevation (110 m). Species turnover was high between elevations, with 82% of the sampled species being unique to an elevation. Only 6% of the sampled species were shared across all three elevations and between 1.8% and 6% of total species richness shared between any two elevations. The Morisita-Horn index of similarity depicted that low and high elevation was more similar than mid- and high elevation or low and mid-elevation. Of the four methods deployed to collect ichneumonid wasps, sweeping was the most efficient in terms of procured species richness, followed by Malaise trapping; yellow pan trapping was inefficient, and was superseded by hand collecting. In terms of species return per individuals captured, all four methods were similarly efficient. Species complementarity between different methods was low. Malaise trapping and sweeping had the highest species overlap, although this was only 11% of the total sampled species richness and hence none of the sampling methods were redundant.

### RÉSUMÉ

Une analyse des Ichneumons collectés pendant une période de 4 semaines au Mont Doudou a révélé 112 espèces représentées par 233 individus.

Les Ichneumonides de Gabon sont extrêmement mal connus avec, au jour d'aujourd'hui et avant cette étude, 25 espèces incluses dans 14 genres. Le présent inventaire a ajouté 45 autres genres à la liste des Ichneumonides du pays. La courbe d'accumulation régularisée d'espèces, qui n'atteint aucune asymptote, montre que les Ichneumonides sont encore insuffisamment inventoriés. Les estimateurs de richesse d'espèces basées sur l'abondance (ACE) et l'incidence (ICE) ont respectivement estimé le nombre d'espèces extrapolées à 305 et 312 et montre ainsi que seulement 36–37% des espèces supposées être présentes ont réellement été récoltées. La richesse en espèces d'Ichneumons était similaire

le long du gradient avec seulement une variation totale de 6% entre les trois altitudes échantillonnées. Le site à mi-élévation (350 m) est le plus riche en espèces et en spécimens, suivi par celui à haute élévation (630 m) et finalement par celui à basse altitude (110 m). La succession d'espèces est élevée entre différentes élévations avec 82% des espèces collectées sur une élévation étant uniques à cette élévation. Seulement 6% des espèces peuvent être trouvées sur les trois élévations et entre 1.8% à 6% peuvent être partagées par n'importe quel des deux sites choisis. L'index de similarité Morisita-Horn a présenté que les sites à basse et haute altitudes sont plus similaires entre eux que les sites à haute et mi-élévation ou les sites à basse et mi-élévation. Sur les quatre méthodes déployées pour récolter les ichneumons, le filet fauchoir est le plus effectif en termes de richesse en espèces, suivi par le piège malaise. Le piège bac est inefficace et est supplanté par la récolte manuelle. En termes de nombre d'espèces accumulées par individus capturés, les quatre méthodes sont aussi efficaces les unes que les autres.

La complémentarité d'espèces entre les différentes méthodes est faible. Même si le piège malaise et le filet fauchoir ont le plus d'espèces similaires capturées, ceci ne représente que 11% des totaux, montrant ainsi qu'aucune des méthodes n'est superflue.

#### INTRODUCTION

The order Hymenoptera is second only to the Coleoptera and Lepidoptera, in terms of number of described species (Arnett 1985). There are an estimated 115,000 described species of Hymenoptera (Gaston 1993; Grissell 1999; LaSalle and Gauld 1993), while the number of described species of Coleoptera ranges from 290,000 (Wilson 1992) to 400,000 (Hammond 1992), and that of Lepidoptera from 112,000 (Wilson 1992) to 150,000 (Hammond 1992). The current lower species richness of the Hymenoptera may be a function of unequal taxonomic attention, since investigations of local species richness have shown that the Hymenoptera are the most species rich of the insect orders in both temperate and tropical areas (Gaston 1991; Stork 1991). The estimated richness of extant Hymenoptera ranges between 300,000 and 2.5 million species (Grissell 1999). Whichever figure is more accurate it is clear that the Hymenoptera are taxonomically poorly known at species level. This predicament is slowly being addressed through rigorous quantified inventory surveys such as the Sulawesi Indonesia "Project Wallace" (Noyes 1989a; 1989b) and the INBio program in Costa Rica (Gauld 1991; Hanson and Gauld 1995; Gaston et al. 1996). Recently a number of structured hymenopteran inventories have been conducted in Tanzania, Namibia and South Africa. As part of an ecological inventory survey of Mkomazi Game Reserve in northeastern Tanzania (Coe et al. 1999), an assessment of hymenopteran species richness of this semi-arid east African savanna region was carried out (Robertson 1999; van Noort and Compton 1999; van Noort in prep.). An elevational assessment of hymenopteran species richness was assessed on the Brandberg Massif in Namibia (van Noort et al. 2000), and a comparative assessment of formicid and ichneumonid species richness between Afrotropical forest and the adjoining upland grassland was conducted in Kwazulu-Natal in South Africa (Fisher and van Noort, in prep.). These studies, together with the current inventory survey of Monts Doudou, form part of a program of rigorously quantified inventory surveys targeting Afrotropical Hymenoptera, thereby allowing for repeatable and comparative assessments of species richness (Longino and Colwell 1997).

The Ichneumonidae are one of the most species-rich families of all organisms with an estimated 60,000 species in the world (Townes, 1969). According to Gauld (1991) many

authorities regard this figure as an underestimate. An estimated 12,100 species of Ichneumonidae occur in the Afrotropical region, of which only 1,815 had been described by 1973 (Townes and Townes 1973). Subsequently the single major revision of Afrotropical ichneumonids added a further 70 species of Ophioninae (Gauld and Mitchell 1978), with the result that only an estimated 15% of the Afrotropical ichneumonids are known to science. The ichneumonid fauna of Gabon is extremely poorly known, with a paltry 25 species in 14 genera having been recorded from the country (Yu 1998). Quantitative studies of ichneumonid species richness are scarce in Africa. The limited number of assessments have been conducted in Sierra Leone and Uganda (Owen and Owen 1974); Namibia (van Noort et al. 2000); Tanzania (van Noort in prep.) and South Africa (van Noort and Fisher, in prep.). The Ichneumonidae, along with other groups of parasitic Hymenoptera, are purported to be no more species rich in the tropics than in the Northern Hemisphere temperate regions (Owen and Owen 1974; Janzen 1981; Janzen and Pond 1975), although a number of hymenopteran families, for example the Chalcididae (Hespenheide 1979) and Encyrtidae (Noyes 1989b) exhibit an increase in species richness with a decrease in latitude. Other hymenopteran taxa such as sawflies (Symphyta), gall-forming Cynipidae, and bees (Apoidea) peak in species richness at mid- or high latitudes (Michener 1979; Noyes 1989b; Kouki et al. 1994). Considerable debate has centered on the apparent species richness anomaly exhibited by a number of hymenopteran parasitoid taxa in the tropics (e.g., Morrison et al. 1978; Gauld 1991; Gauld and Gaston 1994).

The family Ichneumonidae is currently split into 37 subfamilies, of which 24 have been recorded from the Afrotropical region (Yu 1998). Ichneumonids utilise a diverse array of insects and arachnids as their hosts and play an essential role in the normal functioning of most ecosystems, underlining the need to inventory their diversity. Comprehensive, quantitative, biodiversity surveys will enable the identification of hotspots of species richness and endemism. This essential base line data will enable informed conservation management decisions.

In this paper a baseline inventory assessment of ichneumonid species richness and diversity on Monts Doudou is provided and placed in the context of contemporary knowledge of world ichneumonid species richness. Patterns of species richness across an elevational gradient of 550 m, from the base to the peak of Monts Doudou, are assessed. The known biogeographical affinities and biology of the sampled genera are reported.

## MATERIALS AND METHODS

### Study site

Three localities representing different elevations were sampled on Monts Doudou, which is situated in Province Ogoové-Maritime in southwestern Gabon. The first locality was situated in the Réserve de la Moukalaba-Dougoua at an elevation of 110 m, 12.2 km 305° NW Doussala, 2°17.00'S, 10°29.83'E. The second and third localities were situated in the Réserve des Monts Doudou. The second locality was 24.3 km 307° NW Doussala, 12.2 km 309° NW of the first locality, 2°13.35'S, 10°24.35'E, at an elevation of 350 m. The third locality was 25.2 km 304° NW Doussala, 1.36 km 253° WSW of the second locality, 2°13.63'S, 10°23.67'E, at an elevation of 630 m, 35 m below the highest peak of Monts Doudou. Sampling was carried out between 600 and 660 m. The habitat of all three localities comprised coastal lowland rain forest (White 1983). The first locality had been selectively logged up to 1992.

### Sampling methods

The Ichneumonidae were sampled using Malaise traps, yellow pan traps, sweep netting and hand collecting at each of the sampled elevations (110 m, 350 m and 630 m) on Monts Doudou. A transect consisting of 25 stations, spaced at 5 m intervals was laid out at each sampled elevation. At each station a yellow plastic bowl (165 mm diameter  $\times$  40 mm depth) was placed on the forest floor and charged with propylene glycol. These yellow pan traps were left for seven days and serviced at the end of this period, with each station being retained as a separate sample. Four Malaise traps were deployed at each elevation and serviced each day for a period of seven days. The Malaise traps were constructed to the specifications of the Townes design (Townes 1972), and made with a fine-meshed netting (grid size 0.2 mm), with black walls and a white roof. Fifty samples, each sample comprising 20 net sweeps (each sweep encompassing an arc of 180°), i.e., 1000 sweeps, were carried out at each elevation. The collection of these samples was spaced over a period of seven days at each elevation. Each sweep was conducted in previously unsampled vegetation. The sweep net used for sampling was based on the design of Noyes (1982), with an opening area of ca. 1300 cm<sup>2</sup>, and a collecting bag constructed from fine-meshed netting with a grid size of 0.2 mm. Sampling effort is portrayed in Table 1.

TABLE 1. Sampling effort for ichneumonid wasps across elevation on Monts Doudou (24 February to 21 March 2000).

	110 m	370 m	630 m
Malaise trap	28 trap days	28 trap days	28 trap days
Yellow pan trap	175 trap days	175 trap days	175 trap days
Sweeping	1000 sweeps	1000sweeps	1000 sweeps
Hand collecting	8 days	8 days	8 days

### Identification and analyses

Specimens were identified to subfamily and to genus and in a few cases to species level. The majority of the specimens, however, were only sorted to morpho-species. Comparative species richness of the Ichneumonidae across elevation and between sampling methods was assessed by plotting smoothed, species-accumulation curves, also known as rarefaction curves (Gotelli and Colwell 2001), using the program EstimateS (Colwell 1997). An estimate of ichneumonid species richness present at the sampled localities, using the methods that were deployed during the survey and within the particular sampled season, was interpreted from the results of the abundance-based coverage estimator and incidence-based coverage estimator options within the program EstimateS. These estimators function on the principle that “. . . all the useful information about undiscovered classes lies in the rarer discovered classes” (Chazdon et al. 1998), and hence the abundance-based coverage estimator extrapolates estimates based on species with fewer than ten specimens in a sample and the incidence-based coverage estimator extrapolates estimates based on species that are present in ten or fewer sampling units (Colwell 1997). EstimateS was also used to compute the Shannon diversity index, which is based on the proportional abundance of species and combines richness with evenness (i.e., how equally abundant the species are) (Magurran 1988). Specimens resulting from all the deployed collection methods were included in the analyses. The collected material is deposited in the South African Museum, Cape Town. Representative specimens will be returned to Libreville, Gabon.

## RESULTS

Two hundred and thirty-three specimens representing 112 species were collected on Monts Doudou. Forty-five of the 50 sampled genera were new records for Gabon. Thirteen subfamilies were represented in the collected material, only six of which had previously been recorded from Gabon. Table 2 lists the sampled species and their abundance at each of the sampled elevations. The smoothed, species-accumulation curves for total observed ichneumonid richness showed no indication of reaching an asymptote, when either plotted against sampling effort or against abundance (Figs. 1 and 2). Species richness estimates indicated that between 305 (ACE) and 312 (ICE) species should be expected on Monts Doudou using the same sampling methods during the same season (Fig. 1). From an abundance perspective the ichneumonids comprised 6.4% of the ca. 3650 hymenopteran specimens (excluding ants and reared fig wasps) that were sampled on Monts Doudou.

In terms of overall sampling effort, the mid-elevation site produced the highest species richness and abundance, followed by the high elevation site and lastly the low elevation site (Table 3, Fig. 3). Conversely, by plotting cumulative species against abundance rather than against sampling effort, and by assessing the shape (species return per individuals captured) of the smoothed, species-accumulation curve, a different pattern emerged. This approach indicated that, with increased sampling, the peak of Monts Doudou, followed by the mid- and low elevation sites, would be the most species rich of the three sampled sites, and was also the most diverse (richness in relation to abundance) site of the survey (Fig. 4). None of the smoothed, species-accumulation curves for the three sampled elevations on Monts Doudou approach an asymptote (Figs. 3 and 4). Estimates of species richness expected at these three elevations indicate an expected doubling to tripling of species richness (Table 3, Figs. 5 and 6).

Species turnover was high between elevations (Fig. 7). Eighty-two percent of the sampled species were unique to an elevation, with only 6% shared across all three elevations and between 1.8% and 6% of total species richness shared between any two elevations (Fig. 7). Strict complementarity across elevation, where species that are shared across all three elevations are included in the shared tally between any two elevations still showed a low complementarity between elevations, with between 8% and 12.5% of the total sampled species richness shared between any two given elevations (Table 4). The Morisita-Horn index of similarity depicted that low and high elevation was more similar than mid- and high elevation or low and mid-elevation (Table 4).

Of the four methods deployed to collect ichneumonid wasps, sweeping was the most efficient in terms of procured species richness and abundance, followed by Malaise trapping; yellow pan trapping was extremely inefficient, and was superseded by hand collecting (Table 5). Smoothed, species-accumulation curves showed that sweeping was the most efficient method in procuring species per sampling effort followed by hand collecting, Malaise trapping and lastly yellow pan trapping (Fig. 8). Conversely, plotting cumulative species against abundance showed that all four methods were similarly efficient in returning species per number of specimens captured (Fig. 9). Malaise trapping and hand collecting slightly superseded sweeping and yellow pan trapping. Species richness estimators indicated that the deployed sampling methods procured between 19 and 38 % of expected species richness (Table 5, Figs. 10 and 11).

TABLE 2. Ichneumonids sampled on Monts Doudou and their presence and abundance across the three elevations that were sampled.

Subfamily	Genus	Species	110 m	350 m	630 m	Total
Acaenitinae	<i>Paracollyria</i>	sp. 1	0	0	1	1
	<i>Phorotrophus</i>	sp. 1	0	1	0	1
	<i>Phorotrophus</i>	sp. 2	0	0	1	1
Anomalinae	<i>Bimentum</i>	sp. 1	2	0	0	2
Banchinae	<i>Apophua</i>	sp. 1	0	0	1	1
	<i>Spilopimpla</i>	sp. 1	0	0	1	1
Brachycertinae	Genus 1	sp. 1	0	0	1	1
Campopleginae	<i>Campoplex</i>	sp. 1	1	0	0	1
	<i>Casinaria</i>	sp. 1	0	4	0	4
	<i>Casinaria</i>	sp. 2	1	0	0	1
	<i>Charops</i>	sp. 1	3	1	0	4
	<i>Chriodes</i>	sp. 1	1	0	0	1
	<i>Hyposoter</i>	sp. 1	1	0	2	3
	<i>Klutiana</i>	sp. 1	1	0	0	1
	<i>Olesicampe</i>	sp. 1	0	0	1	1
	<i>Xanthocampoplex</i>	sp. 1	0	0	2	2
	Genus 1	sp. 1	1	0	0	1
Cremastinae	<i>Pristomerus</i>	sp. 1	1	0	0	1
	<i>Pristomerus</i>	sp. 2	1	0	0	1
	<i>Pristomerus</i>	sp. 3	1	0	0	1
	<i>Trathala</i>	sp. 1	2	0	0	2
Cryptinae	<i>Ateleute</i>	sp. 1	2	0	5	7
	<i>Bodedia</i>	sp. 1	0	1	2	3
	cf. <i>Bodedia</i>	sp. 1	1	0	0	1
	<i>Bozakites</i>	sp. 1	0	2	0	2
	<i>Bozakites</i>	sp. 2	1	0	0	1
	<i>Chirotica</i>	sp. 1	0	1	0	1
	<i>Fitatsia</i>	sp. 1	0	2	0	2
	<i>Fitatsia</i>	sp. 2	3	0	0	3
	cf. <i>Gabunia</i>	sp. 1	0	0	1	1
	<i>Handaioa</i>	sp. 1	0	1	0	1
	<i>Handaioa</i>	sp. 2	1	0	0	1
	<i>Hoeocryptus</i>	sp. 1	0	1	0	1
	<i>Lienella</i>	sp. 1	1	0	0	1
	<i>Lienella</i>	sp. 2	0	0	1	1
	<i>Lienella</i>	sp. 3	0	1	0	1
<i>Lienella</i>	sp. 4	1	0	0	1	
<i>Lienella</i>	sp. 5	0	0	1	1	
cf. <i>Mamelia</i>	sp. 1	0	1	0	1	
cf. <i>Mamelia</i>	sp. 2	0	0	1	1	

ICHNEUMONID DIVERSITY OF MONTS DOUDOU

TABLE 2. continued.

Subfamily	Genus	Species	110 m	350 m	650 m	Total
	<i>cf. Mamelia</i>	sp. 3	0	3	0	3
	<i>Mansa</i>	sp. 1	0	0	1	1
	<i>Nematocryptus</i>	sp. 1	2	0	0	2
	<i>Nematocryptus</i>	sp. 2	1	0	0	1
	<i>Nematocryptus</i>	sp. 3	1	0	0	1
	<i>Nematocryptus</i>	sp. 4	1	0	0	1
	<i>Nematocryptus</i>	sp. 5	1	0	0	1
	<i>cf. Nematocryptus</i>	sp. 1	0	0	1	1
	<i>cf. Nematocryptus</i>	sp. 2	1	0	0	1
	<i>Paraphylax</i>	sp. 1	0	0	2	2
	<i>Paraphylax</i>	sp. 2	1	0	0	1
	<i>Paraphylax</i>	sp. 3	5	1	2	8
	<i>Paraphylax</i>	sp. 4	5	10	3	18
	<i>Paraphylax</i>	sp. 5	0	0	2	2
	<i>Paraphylax</i>	sp. 6	0	1	0	1
	<i>Paraphylax</i>	sp. 7	0	2	1	3
	<i>Platymystax</i>	sp. 1	1	0	0	1
	<i>Platymystax</i>	sp. 2	0	1	1	2
	<i>Platymystax</i>	sp. 3	0	0	1	1
	<i>Platymystax</i>	sp. 4	1	1	3	5
	<i>Stenarella</i>	sp. 1	1	0	0	1
	<i>Tanyloncha</i>	sp. 1	2	6	1	9
	<i>Tanyloncha</i>	sp. 2	0	0	2	2
	<i>Tanyloncha</i>	sp. 3	12	1	2	15
	<i>Tanyloncha</i>	sp. 4	1	0	0	1
	Genus 1	sp. 1	0	1	0	1
Ichneumoninae	<i>Aethioplitops</i>	<i>fulvator</i>	0	1	0	1
	<i>Afrolongichneumon</i>	sp. 1	0	0	1	1
	<i>Afrolongichneumon</i>	sp. 2	0	1	0	1
	<i>Afrolongichneumon</i>	sp. 3	0	1	0	1
	<i>Afrolongichneumon</i>	sp. 4	2	0	0	2
	<i>Depressopyga</i>	<i>cf. tanzanica</i>	0	0	1	1
	<i>Foveosculum</i>	<i>striatiferops</i>	1	0	0	1
	<i>Gibbosoplites</i>	<i>guineensis</i>	0	0	1	1
	<i>Hemibystra</i>	sp. 1	0	1	0	1
	<i>Hemibystraps</i>	<i>cf. vallatus</i>	1	0	0	1
	<i>Oriphatnus</i>	sp. 1	0	1	1	2
	<i>Pseudotogea</i>	<i>albidora</i>	0	1	0	1
	<i>cf. Rhadinodontops</i>	sp. 1	0	1	0	1
	<i>Serratosculum</i>	sp. 1	0	0	1	1
	<i>Spinellamblys</i>	sp. 1	0	0	1	1

TABLE 2. continued.

Subfamily	Genus	Species	110 m	350 m	650 m	Total
Ichneumoninae	Genus 1	sp. 1	0	0	1	1
	Genus 2	sp. 1	0	1	0	1
Mesochorinae	<i>Mesochorus</i>	sp. 1	1	1	0	2
	<i>Mesochorus</i>	sp. 2	0	1	1	2
	<i>Mesochorus</i>	sp. 3	0	2	0	2
	<i>Mesochorus</i>	sp. 4	0	2	0	2
	<i>Mesochorus</i>	sp. 5	0	1	0	1
	<i>Mesochorus</i>	sp. 6	0	2	0	2
	<i>Mesochorus</i>	sp. 7	0	2	0	2
Ophioninae	<i>Enicospilus</i>	<i>expeditus</i>	0	0	1	1
	<i>Enicospilus</i>	<i>senescens</i>	0	0	1	1
Orthocentrinae	<i>Chilocyrtus</i>	sp. 1	0	0	1	1
	<i>Orthocentrus</i>	sp. 1	0	1	0	1
	<i>Orthocentrus</i>	sp. 2	0	1	0	1
	<i>Orthocentrus</i>	sp. 3	0	1	0	1
	<i>Orthocentrus</i>	sp. 4	3	0	2	5
	<i>Orthocentrus</i>	sp. 5	2	9	2	13
Pimplinae	<i>Orthocentrus</i>	sp. 6	0	1	0	1
	<i>Xanthopimpla</i>	sp. 1	0	1	0	1
	<i>Xanthopimpla</i>	sp. 2	0	1	0	1
Tersilochinae	<i>Xanthopimpla</i>	sp. 3	1	0	1	2
	<i>Diaparsis</i>	sp. 1	0	1	0	1
	<i>Diaparsis</i>	sp. 2	0	3	1	4
	<i>Diaparsis</i>	sp. 3	1	0	0	1
	<i>Diaparsis</i>	sp. 4	3	2	1	6
	<i>Diaparsis</i>	sp. 5	0	0	2	2
	<i>Diaparsis</i>	sp. 6	0	1	0	1
	<i>Diaparsis</i>	sp. 7	0	1	0	1
Subfamily undet.	<i>Diaparsis</i>	sp. 8	0	1	0	1
	<i>Sathropterus</i>	sp. 1	0	5	1	6
Total abundance			77	91	65	133

Species complementarity between different methods was low. Malaise trapping and sweeping had the highest species overlap, although this was still only 11% of the total sampled species richness and hence none of the methods made any other method redundant (Table 6, Fig. 12).

An ichneumonid species richness comparison with studies conducted elsewhere in the tropics and at increased latitude in the northern and southern hemisphere temperate regions is portrayed in Table 7.



DISTRIBUTION AND BIOLOGY OF ICHNEUMONIDAE FROM MONTS DOUDOU

Subfamily Acaenitinae: Tribe Acaenitini

*Paracollyria* Cameron

A single species of *Paracollyria* was collected at the top (660 m) of Monts Doudou. Nine species have been described from the Afrotropical region, two of which, *P. fenestrata* Kriechbaumer and *P. terebrator* Szépligeti, are known from Gabon (Townes and Townes 1973; Yu 1998). *Paracollyria* is confined to the Afrotropical region where species have also been recorded from Sierra Leone, Democratic Republic of the Congo (Zaire), Zimbabwe, and South Africa (Yu 1998). Biology of the genus is unknown, although hosts of other Acaenitini are wood-boring Coleoptera (Townes 1971).

*Phorotrophus* Saussure

Two species of this genus were collected on Monts Doudou, one from the peak (660 m) and the other from mid-elevation (350 m). Thirty-three described species of this Afrotropical genus are known from the region, none of which have been recorded from Gabon (Townes and Townes 1973; Yu 1998). The biology of *Phorotrophus* species is unknown.

Subfamily Anomalinae: Tribe Gravenhorstiini

*Bimentum* Townes

A single species of *Bimentum* was collected at low elevation (110 m) on Monts Doudou. This monotypical Afrotropical genus is only known from Sierra Leone (Yu 1998). Biology is unknown.

Subfamily Banchinae: Tribe Glyptini

*Apophua* Morley

A single species was trapped at the peak (660 m) of Monts Doudou. *Apophua* is a large genus present in the Nearctic, Palaearctic, Oriental, Australian and Afrotropical regions; thirteen species are known from the Afrotropical region, none of which have been recorded from Gabon (Townes and Townes 1973; Yu 1998). Members of the tribe Glyptini are parasitoids of lepidopteran larvae living in concealed situations, such as leaf rolls, cases, or tunnels in plant stems.

Tribe Atrophini

*Spilopimpla* Cameron

A single species of this genus was trapped on top (660 m) of Monts Doudou. Twenty described species are present in this Afrotropical genus, none of which have been recorded from Gabon (Townes and Townes 1973; Yu 1998). Members of the tribe Atrophini are parasitoids of lepidopteran larva.

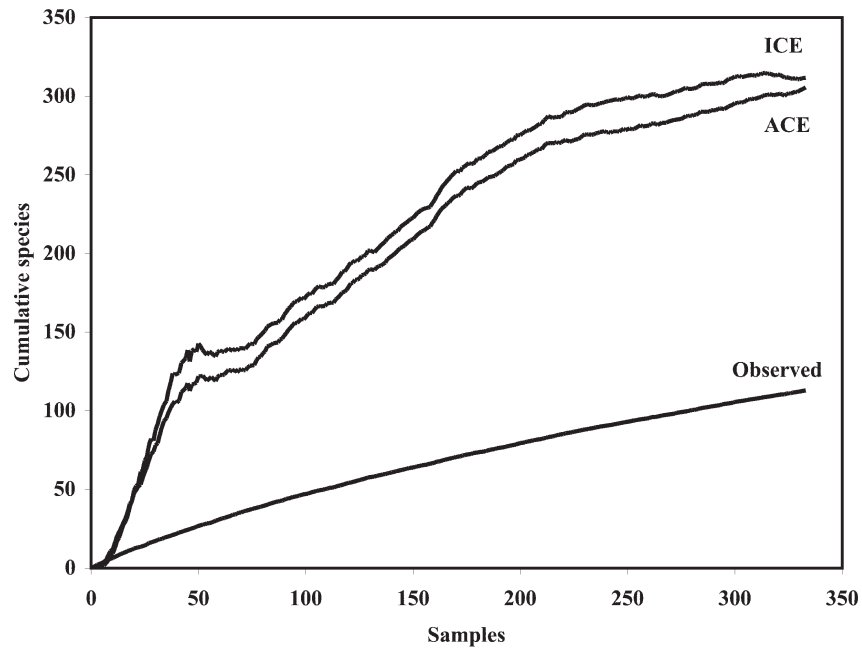


FIGURE 1. Observed and estimated cumulative ichneumonid species richness plotted against sampling effort on Monts Doudou. ACE = Abundance based coverage estimator. ICE = Incidence based coverage estimator.

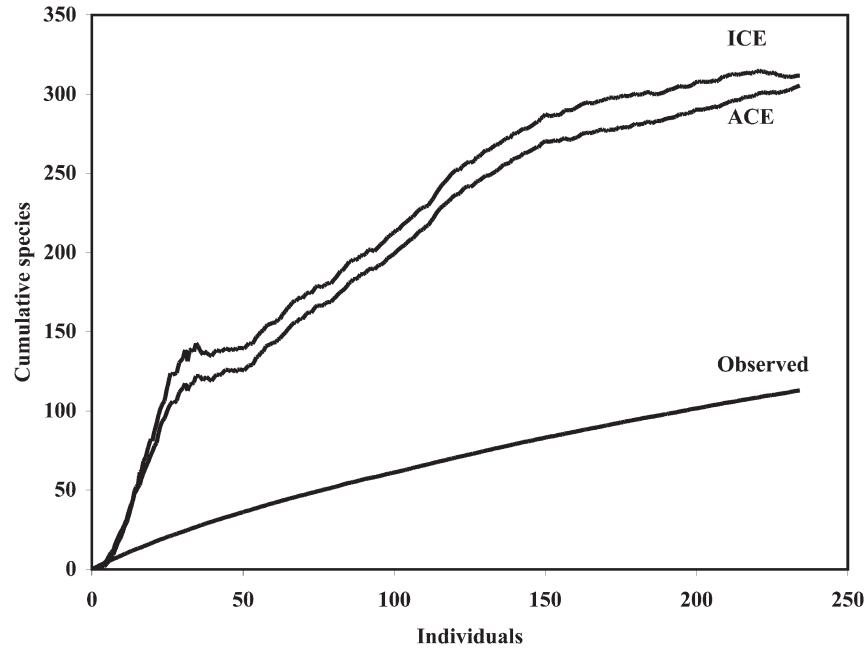


FIGURE 2. Observed and estimated cumulative ichneumonid species richness plotted against abundance on Monts Doudou. ACE = Abundance based coverage estimator. ICE = Incidence based coverage estimator.

ICHNEUMONID DIVERSITY OF MONTS DOUDOU

TABLE 3. Observed species richness and abundance of ichneumonid wasps across elevation on Monts Doudou. Estimated expected species richness [ICE-ACE] in brackets.

Altitude	Species	Individuals	Shannon index
110 m	43 [96-99]	77	3.45
350 m	50 [157-167]	91	3.60
630 m	46 [101-134]	65	3.74

TABLE 4. Species complementarity of ichneumonid wasps across elevation. Numbers above the asterisk denote shared species; numbers below the asterisk denote the Morisita-Horn similarity index.

Altitude	110 m	350 m	630 m
110 m	*	9	11
350 m	0.34	*	14
630 m	0.42	0.38	*

TABLE 5. Efficiency of sampling method in collecting ichneumonid wasps on Monts Doudou. Estimated species richness [ICE-ACE]

Method	Species	Individuals	% of total sampled richness
Malaise trap	36 [98-108]	51	32
Yellow pan trap	8 [21-22]	11	7
Sweeping	75 [286-297]	152	67
Hand collecting	16 [72-84]	19	14

TABLE 6. Species complementarity of ichneumonid wasps between different sampling methods. Numbers above the asterisk denote shared species; numbers below the asterisk denote the Morisita-Horn similarity index.

	Malaise trap	Sweeping	Yellow pan trap	Hand collecting
Malaise trap	*	12	3	1
Sweeping	0.27	*	4	6
Yellow pan trap	0.11	0.19	*	1
Hand collecting	0.02	0.15	0.04	*

Subfamily Brachycyrtinae

Genus undet.

A single female was swept near the top of Monts Doudou (600 m). This does not fit any of the described world genera of this subfamily. The only genus recorded from the Afrotropical region is *Brachycyrtus* Kriechbaumer (Townes and Townes 1973).

Subfamily Campopleginae

*Campoplex* Gravenhorst

A single species of *Campoplex* was collected at low elevation (110 m). This is a cosmopolitan genus with two species recorded from the Afrotropical region (South Africa) (Townes and Townes 1973; Yu 1998). *Campoplex* species attack lepidopteran larvae.

*Casinaria* Holmgren

Two species of this genus were collected on Monts Doudou, one at low elevation (110 m) and the other at mid-elevation (350 m). *Casinaria* is cosmopolitan, with two described species present in the Afrotropical region, neither recorded from Gabon (Townes and Townes 1973; Yu 1998). Species of *Casinaria* are parasitoids of lepidopteran larvae.

*Charops* Holmgren

A single species of this genus was collected at low (110 m) and mid-elevation (350 m). *Charops* is a cosmopolitan genus centered in the tropics with 11 species recorded from the Afrotropical region, none of which are known from Gabon (Townes and Townes 1973; Yu 1998). *Charops* species are parasitoids of lepidopteran larvae.

*Chriodes* Foerster

A single species of *Chriodes* was trapped at low elevation (110 m). Three species of this Old World tropical genus are known from the Afrotropical region, none of which have been recorded from Gabon (Townes and Townes 1973; Yu 1998). Biology of the species is unknown.

*Hyposoter* Foerster

One species of this genus was collected at both low (110 m) and high (660 m) elevation. *Hyposoter* is a cosmopolitan genus with three described species present in the Afrotropical region, none of which have yet been recorded from Gabon (Townes and Townes 1973; Yu 1998). Species of *Hyposoter* are parasitoids of lepidopteran larva.

*Klutiana* Betram

A single species was swept at low elevation (110 m). A single species of this Old World tropical genus is known from the Afrotropical region (Kenya) (Townes and Townes 1973; Yu 1998). Host relationships of *Klutiana* species are unknown.

*Olesicampe* Foerster

A species of this genus was trapped on the peak (660 m) of Monts Doudou. *Olesicampe* is a predominantly Holarctic genus with representatives in the Oriental and Afrotropical regions; no species have yet been described from the Afrotropical region

ICHNEUMONID DIVERSITY OF MONTS DOUDOU

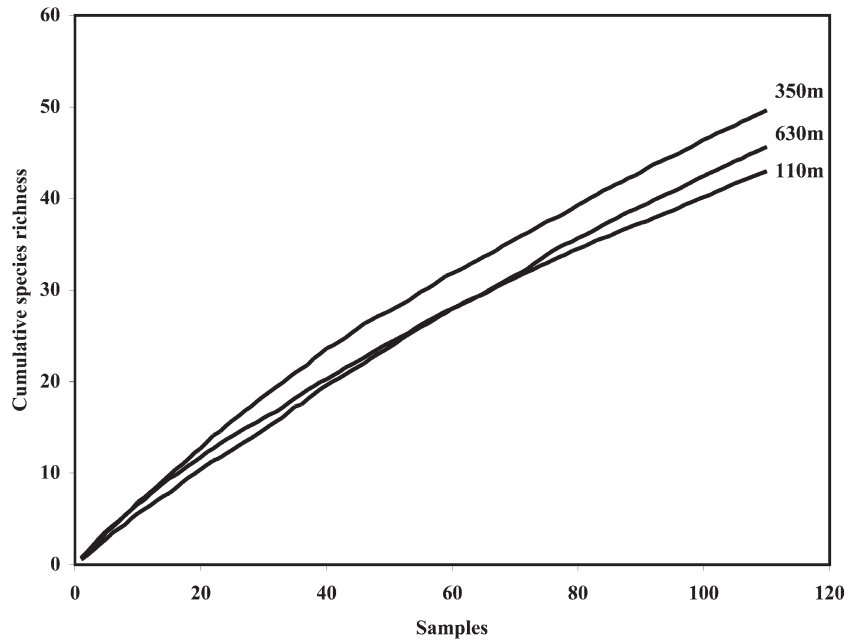


FIGURE 3. Observed spatial species richness patterns, plotted as cumulative species richness against sampling effort, of Ichneumonidae on Monts Doudou as determined by elevation.

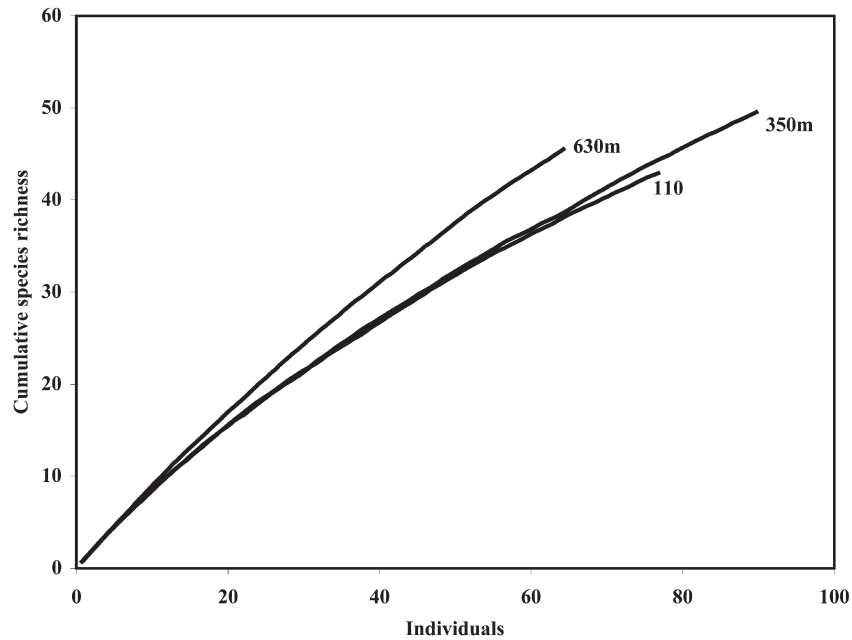


FIGURE 4. Observed spatial species richness patterns, plotted as cumulative species richness against individuals, of Ichneumonidae on Monts Doudou as determined by elevation.

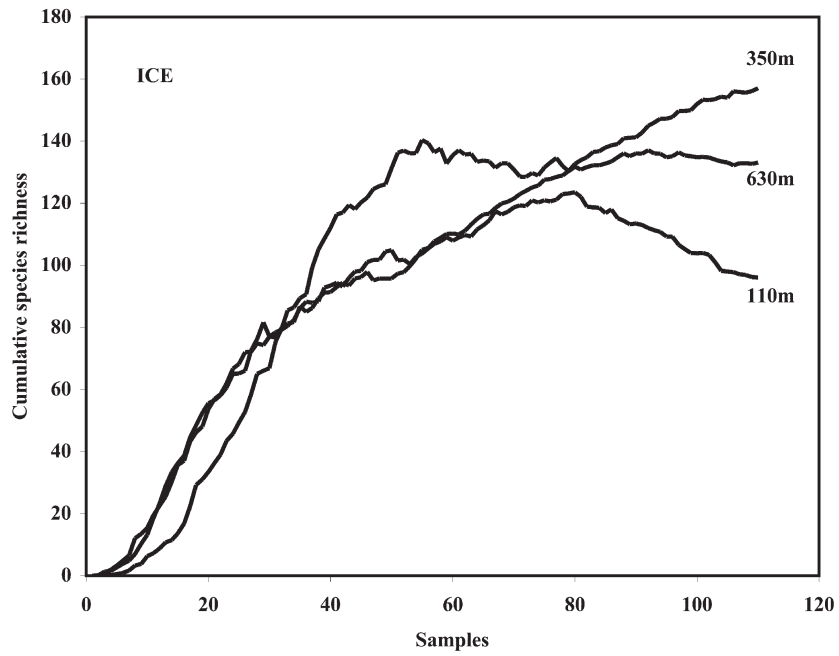


FIGURE 5. Incidence based coverage species richness estimates (ICE) of the Ichneumonidae for the three sampled elevations on Monts Doudou.

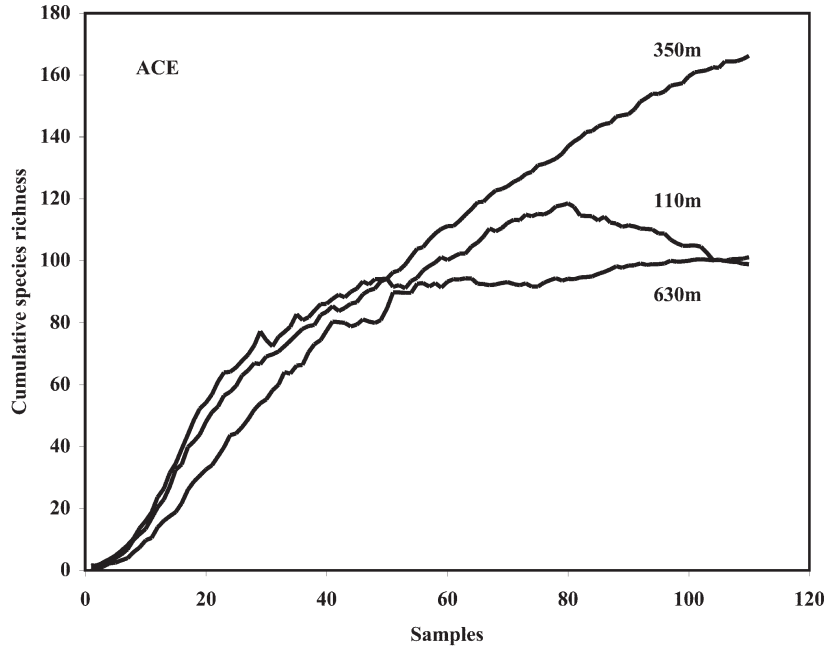


FIGURE 6. Abundance based coverage species richness estimates (ACE) of the Ichneumonidae for the three sampled elevations on Monts Doudou.

ICHNEUMONID DIVERSITY OF MONTS DOUDOU

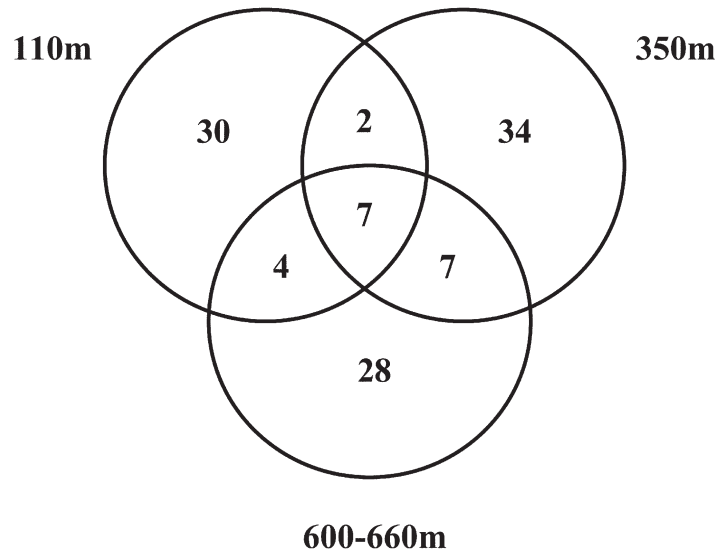


FIGURE 7. Venn diagram illustrating ichneumonid species richness across elevation on Monts Doudou: number of species unique to elevation, number of species shared between elevation pairs and number of species shared between all three elevations.

(Townes and Townes 1973; Yu 1998). Hosts of species of this genus are sawflies (Tenthredinidae, Hymenoptera).

*Xanthocampoplex* Morley

A single species was collected on the top of Monts Doudou (660 m). *Xanthocampoplex* is a cosmopolitan genus, with a single species described from the Afrotropical region (Kenya, South Africa) (Townes and Townes 1973; Yu 1998). Hosts of this genus are lepidopteran larva.

Genus undet.

A male of an unidentified campoplegine genus was swept at low elevation (110 m).

Subfamily Cremastinae

*Pristomerus* Curtis

Three species of *Pristomerus* were collected at low elevation (110 m). *Pristomerus* is another large, cosmopolitan, mostly tropical genus, with eight described species known from the Afrotropical region, none of which have been recorded from Gabon (Yu 1998). Species of *Pristomerus* are endoparasitoids of concealed lepidopteran larvae living in tunnels, leaf rolls, or buds (Townes 1971).

*Trathala* Cameron

A single species of *Trathala* was collected at low elevation (110 m). This is a large cosmopolitan genus with eight species recorded from the Afrotropical region, none of which are known from Gabon (Townes and Townes 1973; Yu 1998). Species of *Trathala* are endoparasitoids of lepidopteran (usually Pyraloidea) larva (Townes 1971).

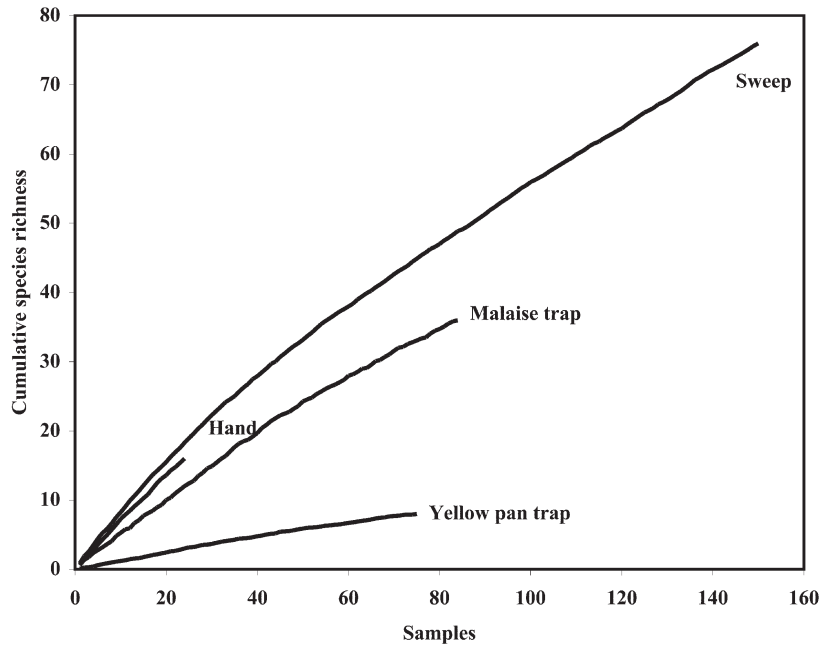


FIGURE 8. Observed hymenopteran species richness patterns between the different sampling methods deployed on Monts Doudou per unit sampling effort.

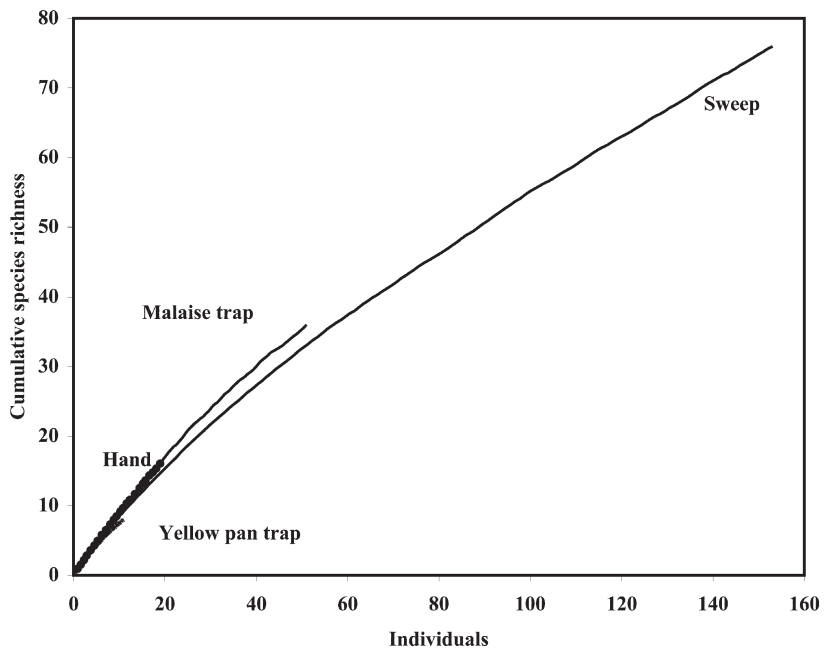


FIGURE 9. Observed hymenopteran species richness patterns between the different sampling methods deployed on Monts Doudou per sampled specimens.



ICHNEUMONID DIVERSITY OF MONTS DOUDOU

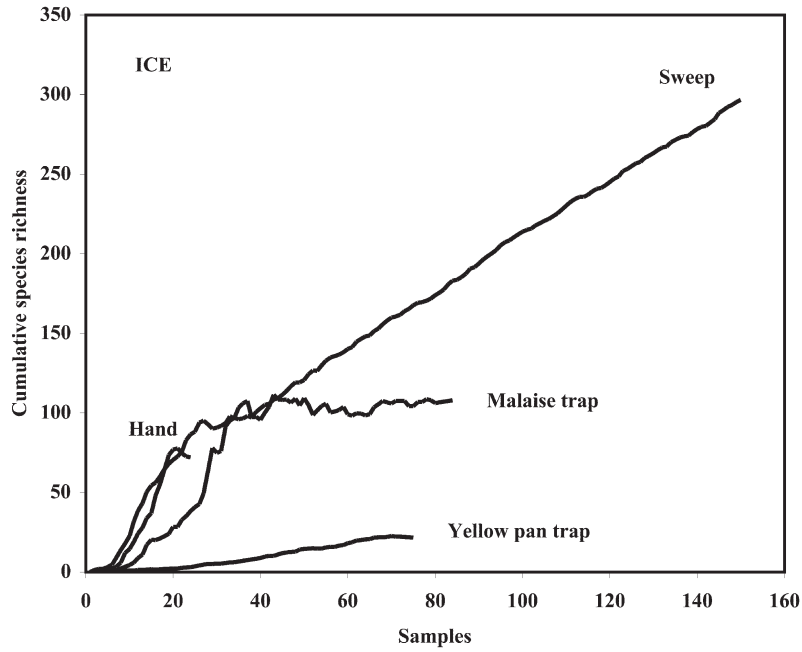


FIGURE 10. Incidence based coverage species richness estimates (ICE) for the different methods deployed to sample ichneumonids on Monts Doudou.

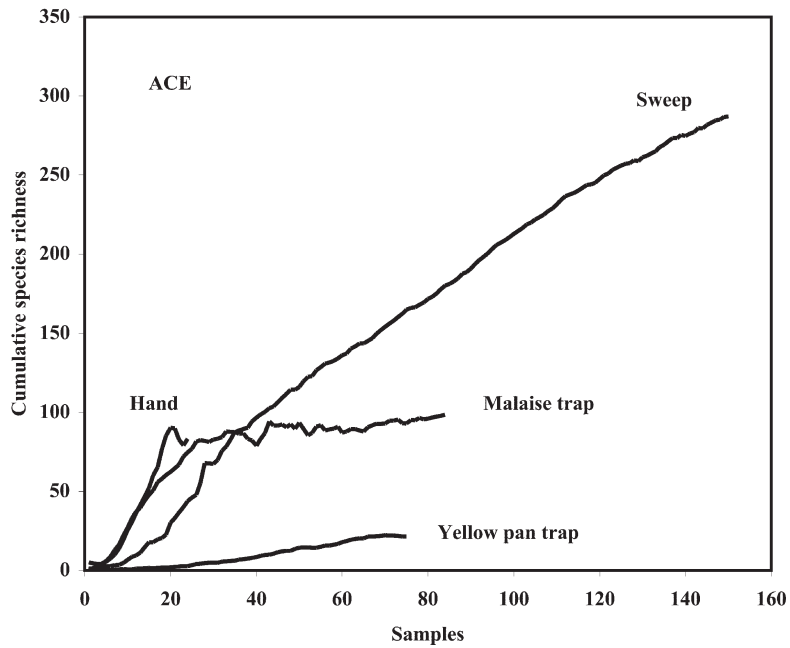


FIGURE 11. Abundance based coverage species richness estimates (ACE) for the different methods deployed to sample ichneumonids on Monts Doudou.

Subfamily Cryptinae: Tribe Cryptini

*Ateleute* Foerster

A single species of *Ateleute* was collected at both low (110 m) and high (600-660 m) elevation. This cosmopolitan genus is centered in the Old World tropics, with 24 species known from the Afrotropical region, all of these except for one recorded from Madagascar (Townes and Townes 1973; Yu 1998). None are known from Gabon. The only recorded hosts are Psychidae (Lepidoptera).

*Bozakites* Seyrig

Two species of *Bozakites* were hand collected or swept at low and mid-elevation. Seven described species of this Afrotropical genus are known from Madagascar, Tanzania, Guinea, Liberia, and South Africa (Townes and Townes 1973; Yu 1998), although there are at least 41 species present in museum collections (Townes 1969). Biology is unknown.

*Fitatsia* Seyrig

This genus was represented by two species on Monts Doudou. Four of the five specimens were hand collected, the other swept. *Fitatsia* is an Afrotropical and Oriental genus with only a single Afrotropical species described from Madagascar (Townes 1969; Yu 1998). Biology is unknown.

cf. *Gabunia* Kriechbaumer

A single female belonging to a probably undescribed genus that is near to *Gabunia* Kriechbaumer was collected by hand at the top of Monts Doudou (660 m). The new genus shares characters, in part, with three related described genera: *Gabunia* Kriechbaumer 1895 (6 species from central and east Africa, 3 of which have been recorded from Gabon), *Anepomias* Seyrig 1952 (monotypic, Madagascar) and *Schreineria* Schreiner 1905 (2 species, South Africa and Madagascar) (Townes and Townes 1973; Yu 1998). Species of *Schreineria* are distributed through the Palaearctic, Oriental and Afrotropical regions and are parasitoids of cossid, aegeriid and cerambycid larvae that bore in trees; biology of *Anepomias* and *Gabunia* (both genera are restricted to the Afrotropical region) is unknown (Townes 1969), but they are also likely to attack larvae concealed in wood, a feeding behavior that is characteristic of related genera (Gupta and Gupta 1983).

*Hoeocryptus* Habermehl

A single species was swept at mid-elevation (370 m). *Hoeocryptus* is an Afrotropical genus, with 7 described species occurring in Madagascar, east and west Africa, with none known from Gabon (Yu 1998). Biology is unknown.

*Nematocryptus* Roman

Five species of *Nematocryptus* were collected at the base of Monts Doudou (110 m). Eight species have been described from the Afrotropical region, with a widespread species, *N. pallidus* Kriechbaumer, recorded from Gabon (Townes and Townes 1973; Yu 1998). This is a predominantly Afrotropical genus with an additional two species described from India; biology of the genus is unknown (Townes 1969).

ICHNEUMONID DIVERSITY OF MONTS DOUDOU

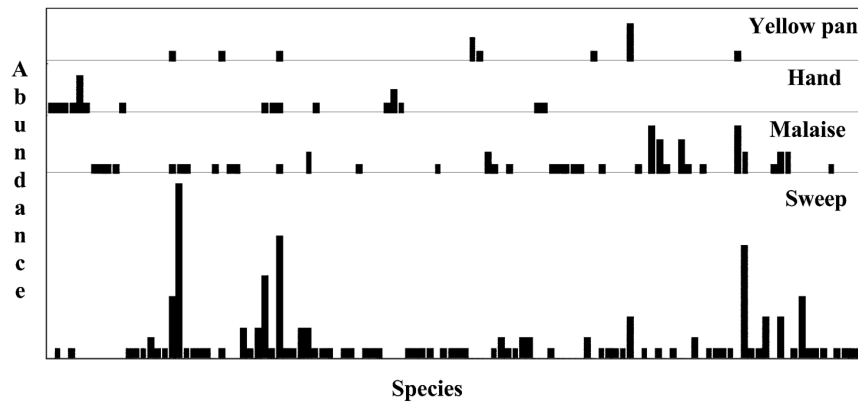


FIGURE 12. Histograms illustrating complementarity of ichneumonid species between the four deployed collecting methods.

cf. *Nematocryptus* Roman

Two species that may represent an undescribed genus, close to *Nematocryptus* were collected at 110 m and 600 m, respectively.

*Stenarella* Szépligeti

A single species of *Stenarella* was collected at the base of Monts Doudou (110 m). The genus is known from three described species in the Afrotropical region, none of which have been recorded from Gabon (Townes and Townes 1973; Yu 1998). *Stenarella* is distributed throughout the tropics and subtropics in the Old World, but is centered in the Afrotropical region; biology of the genus is unknown (Townes 1969).

*Tanyloncha* Townes

Four species of this genus were collected across all three sampled elevations, mostly by sweeping, but several specimens were collected by hand, in Malaise traps or yellow pan traps; one was taken at UV light. *Tanyloncha* is a monotypical genus recorded from Congo and the Democratic Republic of the Congo (Townes and Townes 1973; Yu 1998). Biology of the genus is unknown.

Tribe Aptesini

*Mansa* Tosquinet

A single male of this genus was collected in a Malaise trap at 600 m. *Mansa* is a large Old World tropical genus, with 7 described species from the Afrotropical region (Democratic Republic of the Congo, Equatorial Guinea, Cameroon, Rwanda, and Tanzania) (Townes and Townes 1973; Yu 1998). Biology is unknown.

*Platymystax* Townes

Four species of *Platymystax* were collected on Monts Doudou. The genus was represented across all three sampled elevations. Two described species are known from the Afrotropical region (Togo and Guinea) (Townes and Townes 1973; Yu 1998). This is a large pantropical genus; biology is unknown (Townes 1969).

TABLE 7. Recorded global ichneumonid species richness. Figures in square brackets represent the estimated species richness (using EstimateS). Data from Owen and Owen (1974)<sup>1</sup>, Owen et al. (1981)<sup>2</sup>, Sawoniewicz (1979)<sup>3</sup>, 1986<sup>4</sup>, Noyes (1989b)<sup>5</sup>, van Noort et al. (2000)<sup>6</sup>, van Noort (in prep.)<sup>7</sup> and van Noort and Fisher (in prep.)<sup>8</sup>. MT = Malaise trap, SW = sweeping, YP = yellow pan trap, WL = Winkler bag extraction of leaf litter, PT = pitfall trap, FI = flight intercept trap, LT = UV light trap, CF = tree canopy fogging, CM = tree canopy misting.

COUNTRY	LATITUDE	METHODS	SAMPLING PERIOD	NUMBER OF SPECIES	NUMBER OF SPECIMENS	MARGALEF'S DIVERSITY INDEX
Gabon	2°S	MT, YP, SW	4 weeks	112 [312]	233	20.36
Sierra Leone <sup>1</sup>	8°N	MT	15 months	319	1979	41.90
Uganda <sup>1</sup>	19°N	MT	18 months	293	2268	37.79
Tanzania <sup>7</sup>	4°S	MT, YP, SW, LT, CM, WL, PT	6 weeks, 1MT 5 months	183 [419]	563	28.89
Namibia <sup>6</sup>	21°S	MT, YP, SW, WL	6 weeks	28	53	7.05
South Africa <sup>8</sup>	30°S	MT, YP, SW, WL, PT	5 days	88 [175]	1849	11.53
Sulawesi <sup>5</sup>	1°N	MT, YP, SW, FI, CF	2 months	420	4373	49.98
England <sup>2</sup>	52°N	MT	28 months	326	2495	41.55
England <sup>1</sup>	52°N	MT	9 months	529	9666	57.54
Poland <sup>3</sup>	52°N	SW, YP	14 months	680	12203	72.16
Poland <sup>4</sup>	52°N	YP	4 seasons	392	7920	43.55
Sweden <sup>1</sup>	59°N	MT	6 months	758	10994	81.35

Tribe Phygadeuontini: Subtribe Chiroticina

*Bodedia* Seyrig

This genus was represented by a single species, swept at mid- and high elevation. *Bodedia* was known previously only from Madagascar, represented by 13 described species (Townes and Townes 1973; Yu 1998). Biology is unknown.

cf. *Bodedia* Seyrig

A species representing an undescribed genus close to *Bodedia* was swept at low elevation (110 m).

*Chirotica* Foerster

A single species of this genus was collected in a Malaise trap at mid-elevation (350 m). This cosmopolitan genus is represented by a single species in the Afrotropical region (Madagascar) (Townes and Townes 1973; Yu 1998). Species of *Chirotica* are parasitoids of Psychidae (Lepidoptera).

*Handaoia* Seyrig

This genus was represented by two species, collected at low and mid-elevation respectively. *Handaoia* has a fragmented distribution (South Africa, Tanzania, Madagascar, Philippines, Japan, and Peru) (Townes 1969). Only the Madagascan (seven species) and Tanzanian (one species) species are described (Townes and Townes 1973; Yu 1998). Biology is unknown.

*Lienella* Cameron

*Lienella* was represented by five species, all singletons that were mostly swept, except for one that was hand collected. This large, Old World, tropical genus contains 17 described Afrotropical species, mostly from Madagascar, but also South Africa and Tanzania (Townes and Townes 1973; Yu 1998). Biology is unknown.

cf. *Mamelia* Seyrig

Three species of a genus close to *Mamelia* were swept or collected in a Malaise trap. *Mamelia* contains a single described species from Madagascar (Townes and Townes 1973; Yu 1998). Biology is unknown.

*Paraphylax* Foerster

Seven species of this large, mostly Old World, tropical genus were collected across all elevations. Sweeping collected most specimens, but Malaise traps and yellow pan traps also produced material. From an abundance perspective this was the most common genus on Monts Doudou (representing 14% of total abundance), and was also one of the more species rich genera. Thirty-three species have been described, mostly from Madagascar, but also South Africa, Burundi and Tanzania (Townes and Townes 1973; Yu 1998). *Paraphylax* species are mostly parasitoids of cocoons (such as other ichneumonids and spider egg cocoons); some species are parasitoids of Psychidae (Lepidoptera) (Townes 1969).

Genus undet.

A single male of an unidentified cryptine genus was swept at low elevation.

Subfamily Ichneumoninae

*Aethioplitops* Heinrich

A female of *Aethioplitops fulvator* (Morley) was collected at mid-elevation (350 m). This species is known from Uganda, Kenya, Angola, and Guinea (Heinrich 1968a). *Aethioplitops* is an African genus that occurs from South Africa to Guinea, and contains four described species (Townes and Townes 1973; Yu 1998). Biology is unknown.

*Afrolongichneumon* Heinrich

Four undescribed species of *Afrolongichneumon* were collected on Monts Doudou, all represented by females. One species was swept at 600 m, another at 370m; the third species was collected in a Malaise trap at 350m and the last in yellow pan traps at 110 m. This is an Afrotropical genus represented by 6 described species, with a generic distribution covering Madagascar, and east, central and west Africa (Townes and Townes 1973; Yu 1998). The genus has not previously been recorded from Gabon. Biology is unknown.

*Depressopyga* Heinrich

A female of an undescribed species close to *Depressopyga tanzanica* Heinrich was swept on the peak of Monts Doudou (660 m). Only three specimens, each representing a species of *Depressopyga*, are known from Zambia, Tanzania, and Uganda respectively (Heinrich 1968b; Yu 1998). Biology is unknown.

*Foveosculum* Heinrich

A female of *Foveosculum striatiferops* Heinrich was hand collected at the base of Monts Doudou (110 m). The species is known only from the female holotype collected in Equatorial Guinea. *Foveosculum* is Afrotropical in distribution and is one of the characteristic genera of the region (Heinrich 1967c), containing 24 described species, none of which have previously been recorded from Gabon (Townes and Townes 1973; Yu 1998). Biology is unknown.

*Gibbosoplites* Heinrich

A single female of *Gibbosoplites guineensis* Heinrich was hand collected at the peak of Monts Doudou (660 m). The species is known only from the holotype collected in Equatorial Guinea (Heinrich 1968a; Townes and Townes 1973). *Gibbosoplites* is a tropical African genus with 3 species recorded from Togo, Equatorial Guinea, Democratic Republic of Congo (Zaire), and Uganda (Heinrich 1968a; Yu 1998). Biology is unknown.

*Hemibystra* Heinrich

An undescribed species of *Hemibystra* was swept at mid-elevation (370 m). *Hemibystra* is an Afrotropical genus with 24 described species recorded mostly from east and southern Africa (Townes and Townes 1973; Yu 1998). This is the first record of the genus from Gabon. Biology is unknown.

*Hemibystrops* Heinrich

A female of an undescribed species of *Hemibystrops*, close to *H. vallatus* (Morley), was swept at the base of Monts Doudou (110 m). This is a monotypical genus recorded from South Africa, Tanzania, and Uganda (Townes and Townes 1973; Yu 1998). Biology is unknown.

*Pseudotogea* Heinrich

A female of *Pseudotogea albidora* Heinrich was swept at mid-elevation (370 m). This species was described from a single specimen collected in northwestern Angola (Heinrich, 1968a). *Pseudotogea* is a rain forest genus with five described species that occur in lowland rain forest in Central Africa (Angola) and Afromontane forest in east and southern Africa (Uganda, Tanzania, and South Africa). Biology is unknown.

cf. *Rhadinodontops* Heinrich

A female of an undescribed genus that shares some characters with *Rhadinodontops* was swept at mid-elevation. *Rhadinodontops* is a monotypical genus recorded from Uganda and South Africa (Heinrich 1968b; Yu 1998).

*Serratosculum* Heinrich

A female of an undescribed species was swept on the peak of Monts Doudou (660 m). *Serratosculum* is only known from the holotype male of *S. flavonigrum* Heinrich that was collected in Equatorial Guinea (Heinrich 1968b). Biology is unknown.

*Spinellamblys* Heinrich

An undescribed species, represented by a single female, was collected in a Malaise trap at 600 m. *Spinellamblys* is a monotypical genus previously only recorded from Uganda (Heinrich 1968b; Yu 1998). Biology is unknown.

*Oriphatnus* Heinrich

Two females, representing a single species, were hand collected at 350 m and 660 m on Monts Doudou. *Oriphatnus* is represented by two species, so far only found in Equatorial Guinea, Cameroon, Uganda, and Angola (Heinrich 1967c; Yu 1998). Biology is unknown.

Genera undet.

Two females, each representing an unidentified ichneumonine genus, were collected on Monts Doudou.

Subfamily Mesochorinae

*Mesochorus* Gravenhorst

Seven species of *Mesochorus* were collected on Monts Doudou. One species was present across all three sampled elevations; another species at mid-and top elevation, and the remaining five species were only collected at mid-elevation. Twenty-five described species are known from the Afrotropical region with none yet recorded from Gabon (Yu 1998). This is a large cosmopolitan genus. The subfamily includes nine genera, three of which are present in the Afrotropical region (Yu 1998). Mesochorine species are hyperparasitoids, most commonly of Ichneumonoidea, but a few attack Tachinidae (Diptera).

Subfamily Ophioninae: Tribe Enicospilini

*Enicospilus* Stephens

Two species of *Enicospilus*, *E. senescens* (Tosquinet), and *E. expeditus* (Tosquinet), were collected on top of Monts Doudou (at 600 m and 660 m respectively). *Enicospilus*

*senescens* is a widely distributed species in the Afrotropical region, but most common in central and east Africa and has previously been recorded from Gabon (Mvoung, Mt. Sable); a recorded host is *Anomis leona* Schaus (Lepidoptera: Noctuidae) (Gauld and Mitchell 1978). *Enicospilus expeditus* is also a widely distributed species from equatorial Africa to Yemen and Madagascar, but not yet recorded from Gabon; the species has been reared from an unidentified lepidopteran pupa (Gauld and Mitchell 1978). There are 152 described species of *Enicospilus* in the Afrotropical region, 7 of which have been recorded from Gabon (Yu 1998).

#### Subfamily Orthocentrinae

##### *Chilocyrtus* Townes

A single species of this genus was sampled at the peak (660 m) of Monts Doudou. One species has been described from the Afrotropical region (Madagascar) (Townes and Townes 1973; Yu 1998). Biology is unknown.

##### *Orthocentrus* Gravenhorst

Six species of *Orthocentrus* were collected on Monts Doudou, of which four were sampled at mid-elevation (350 m), one at low (110 m) and high (660 m) elevation and the last species across all three elevations. This is a large cosmopolitan genus, with 14 described species known from the Afrotropical region, none of which have been recorded from Gabon (Townes and Townes 1973; Yu 1998). There are very few rearing records, but the Mycetophilidae and Sciaridae (Diptera) have been recorded as hosts.

#### Subfamily Pimplinae: Tribe Pimplini

##### *Xanthopimpla* Saussure

Three species of *Xanthopimpla* were recorded from Monts Doudou, two from mid-elevation (350 m) and one from both low (110 m) and high (600 m) elevation. Forty-three species have been described from the Afrotropical region, three of which have been recorded from Gabon: *X. occidentalis* Krieger, *X. octonotata* Krieger, and *X. ogovensis* (Dalla Torre) (Townes and Townes 1973; Yu 1998). This cosmopolitan genus is centered in the Old World tropics; biology of the genus is unknown.

#### Subfamily Tersilochinae

##### *Diaparsis* Foerster

Eight species of *Diaparsis* were collected, four at mid-elevation (350 m), one each at low and high elevation, one at mid- and high elevation and one across all three elevations. This is a large genus that has an almost worldwide distribution with the exception of the Neotropical and Australian regions. *Diaparsis* is centered in the Afrotropical region, but only two of the many species have been described from there (Townes and Townes 1973; Yu 1998). Species of *Diaparsis* are parasitoids of coleopteran larvae, particularly Curculionidae.

##### *Sathropterus* Foerster

A single species of this genus was collected at mid- and high elevation. This is a monotypical genus with the single, widespread, Old World species recorded from South



Africa in the Afrotropical region (Townes and Townes 1973, Yu 1998). Biology is unknown.

Subfamily undet.

A single male that could not be placed at subfamily level was collected in a Malaise trap on the peak of Monts Doudou.

#### DISCUSSION

In the context of global ichneumonid species richness and abundance, based on the observed species richness during this survey, the Ichneumonidae is fairly depauperate on Monts Doudou (Table 7). There is a dramatic disparity in richness compared with surveys conducted in the Northern Hemisphere temperate regions (Owen and Owen 1974; Owen et al. 1981; Sawoniewicz 1979, 1986), and in the Indo-Australasian tropics (Noyes 1989b). In an Afrotropical context, Monts Doudou is richer than two southern temperate localities in Africa (van Noort et al. 2000, van Noort and Fisher in prep.), and with increased sampling effort would probably approach or supersede the species richness recorded from the other three tropical African localities (Uganda, Sierra Leone and Tanzania) that have been far more comprehensively surveyed for Ichneumonidae (Owen and Owen 1974; van Noort in prep.). The Gabon inventory was a short-term survey and the shape of the species-accumulation curve and the species richness estimators illustrated that the Ichneumonidae had not been sampled sufficiently. The sampling effort of a summed total of only three Malaise trap months at three sites on Monts Doudou is clearly inadequate in assessing species richness of the ichneumonid fauna at this locality. Ichneumonid taxa can be rare and localised in distribution, as exemplified by two Costa Rican genera: 1473 Malaise trap months collected only 106 specimens representing six species of *Cryptophion* Viereck, the majority of the specimens being collected at a few of the many sites sampled in Costa Rica (Gauld and Janzen 1994) and 15 years of Malaise trapping produced only 4 specimens of *Arotes pammae* Gauld (Gaston et al. 1996). The thousand sweeps conducted at each elevation during this survey were expected to be sufficient to sample the ichneumonid fauna associated with the forest undergrowth and low canopy using this method. In a sweep survey of foliage inhabiting beetles and bugs in Costa Rica, 800 sweeps were usually sufficient to produce a levelling off of the species-accumulation curves (Janzen 1973a). However, in this study the accumulation curve for sweep sampling was still steadily rising, both as a function of samples and individuals, indicating that a thousand sweeps were inadequate in sampling ichneumonids in this habitat. The collecting methods that were deployed on Monts Doudou restricted sampling to the forest undergrowth and low forest canopy that was accessible in clearings and along paths. Hence, the forest canopy at a height of 40-50m (Sosef, this volume) was not sampled. The proportion of the ichneumonid faunal assemblage that resides in the canopy in Afrotropical rain forest habitats is simply not known, but it is likely that the use of tree canopy fogging, or misting with a knockdown pyrethroid insecticide, to sample this component of the forest would increase the species richness total for Monts Doudou. The forest canopy has been shown to harbor a high diversity of vascular epiphytes and arthropods (Wolda 1979; Erwin 1982; Stork 1991; Nadkarni 1994), and Basset and colleagues (2001) showed that density and abundance of many arthropod taxa was higher in the canopy than in the understory. However, Gauld and Gaston (1995) suggest that, based on species emanating from limited samples taken from the forest canopy in comparison to species assemblages from extensive Malaise trapping at

ground level during the INBio program in Costa Rica, there is not a large unsampled hymenopteran canopy fauna. Whether or not the canopy fauna was under sampled in this survey, a baseline inventory assessment of a local ichneumonid faunal assemblage has been provided for a country that has been extremely poorly surveyed for Hymenoptera. Only 25 ichneumonid species in 14 genera were previously recorded from Gabon (Yu 1998). The survey of Monts Doudou added a further 45 genera to the ichneumonid checklist for Gabon. Given the poor taxonomic resources for identifying ichneumonids, it was generally not feasible to identify the collected specimens to species level. The Ichneumonidae is one of the most species rich families of all organisms, but with only an estimated 15% of more than 12,000 species in the Afrotropical region known to science, existing species level identification keys are largely useless. For many taxa identification keys do not exist or where they do they are outdated and poorly backed up with pertinent illustrations. For this reason the examination of type specimens is necessary for reliable identity. Due to the logistic constraints the majority of species were only sorted to morpho-species, with the result that it is difficult to predict the number of undescribed species that were collected or the number of new species records for the country. Even so it was established that a number of undescribed species and genera were produced during this survey, and no doubt the majority of sampled species were new records for Gabon.

As a general rule species richness towards the tropics increases for many invertebrate taxa. In contrast, species richness of the Ichneumonidae is fairly constant across latitude. Three hypotheses, which probably work in conjunction, have been forwarded to explain this apparent anomaly. The resource fragmentation hypothesis maintains that tropical lepidopteran species may be too rare for utilization by specialist parasitoids (Janzen and Pond 1975; Janzen 1981). The predation hypothesis predicts that predation of parasitized hosts is more severe in the tropics (Rathcke and Price 1976), whereas, the nasty-host hypothesis is based on the fact that tropical tree species are in general richer in toxic compounds than temperate species. Caterpillars sequester toxins from their food-plants and therefore tropical species are likely to be better chemically defended against parasitoids than those in temperate regions (Gauld et al. 1992; Gauld and Gaston 1994). The results emanating from Monts Doudou support the tenet of a relatively depauperate, tropical, ichneumonid fauna in comparison to the increased tropical diversity of many other invertebrate taxa, including those that are hosts to parasitic ichneumonid wasps.

Assessments of species richness parameters can vary, depending on whether these are interpreted from sample-based or individual-based rarefaction analyses (Gotelli and Colwell 2001). This is clear from the comparative elevation results presented in this paper with the shape of the rarefaction curves changing, depending on whether cumulative species are plotted as a function of samples or individuals. Although strictly speaking the validity of species richness comparisons depends on the rarefaction curve reaching an asymptote, this is never achieved in invertebrate sampling (Fisher 1999). Hence, it is critical that appropriate scaling of the curves is implemented for comparative, species richness assessments (Gotelli and Colwell 2001). Sample-based data accounts for natural levels of taxon patchiness in the samples, but this preferred data set should still be plotted as a function of the accumulated number of individuals, because of the disparity in the mean number of individuals per sample (Gotelli and Colwell 2001).

Different sampling methods target different species, and hence are biased and non-random (Boulinier et al. 1998), and therefore not strictly comparable. However, it is possible to compare method efficiency in terms of species return per number of individuals that need to be processed (Longino and Colwell 1997). In this case the rarefaction curve

needs to be plotted as a function of individuals. Sampling units are temporally and spatially disparate between the different methods and hence comparison of methods based on this parameter leads to erroneous conclusions. This is clear when comparing Figures 8 and 9. Conversely to the results presented in Figure 8, Malaise trapping and hand collecting are more efficient than sweeping in terms of returning species per number of captured individuals. Malaise trapping, however, would require a dramatic increase in replication to return a species richness similar to sweeping over the same period of time. Fisher (1999) showed that a doubling of sampling effort with respect to a 25-station Winkler bag extraction of leaf litter transect would only produce a 11–20% increase in ant species richness. Assuming that a 20% increase would hold for Malaise trap sampling as well, to return a similar species richness to sweeping, each sampled locality would require an exponential increase in deployed Malaise traps from four to 64. Thus, in terms of maximizing species return from a logistic perspective, sweeping is more efficient than Malaise trapping in lowland rain forest. However, it needs to be born in mind that the type of habitat that is being sampled can influence method efficiency. Sweeping is practically redundant in many arid habitats, where the vegetation is sparse and thorny, as shown in a survey of the Brandberg massif in Namibia (van Noort et al. 2000).

The ichneumonids in the Gabon survey comprised 6.4% of the total hymenopteran abundance that was sampled by Malaise traps, Yellow pan traps, and sweeping, excluding the ants. This is in stark contrast to the situation in the Northern Hemisphere, where ichneumonids comprise around 15–20% of the hymenopteran fauna in temperate samples, for example 19.4% in a study in Spain (Segade et al. 1997). The Gabon ichneumonid component is more in line with other tropical rain forest studies, such as the 7.4% recorded in Sulawesi (Noyes 1989a). In contrast, tropical and subtropical African savannas appear to support lower ichneumonid abundance. Ichneumonidae comprised 2.4% of the total hymenopteran abundance (excluding ants) in a five-week survey of Mkomazi Game Reserve in northeastern Tanzania where a 183 ichneumonid species represented by 563 individuals were collected (S. van Noort in prep.). A six-week hymenopteran inventory survey on the Brandberg Massif situated in the arid Namib Desert Biome in northwestern Namibia produced 28 species represented by 53 specimens of Ichneumonidae, which from an abundance point of view comprised between 1.6–1.7% of the total hymenopteran specimens that were collected (van Noort et al. 2000). In an inventory survey of a temperate Southern Hemisphere locality that comprised fragmented Afromontane forest and adjoining moist upland grassland in Kwazulu-Natal (South Africa), the Ichneumonidae comprised 32.5% of the total hymenopteran abundance (excluding ants), but had a low species richness—88 species represented by 1848 individuals (Fisher and van Noort in prep.). This may be a consequence of the inventory having been carried out along a river course in the dry season, when there is a concentration effect in moist refugia (Janzen 1973b). However, this concentration effect should equally affect all the hymenopteran families, and the comparatively high ichneumonid proportion may be more feasibly attributed to high levels of parasitism by a few species of a common host in this habitat. Five species accounted for 71% of the ichneumonid abundance and 23% of the total hymenopteran abundance (van Noort, unpub.).

The lack of an evident elevational effect on ichneumonid species richness and abundance can probably be ascribed to homogeneity of the habitat across the limited altitudinal range on Monts Doudou (Sosef, this volume). Altitudinal gradients of species richness are well correlated with energy (temperature) (Rohde 1992; Rahbek 1995). Although there is climatic disparity across the sampled elevational range (Goodman, this volume) the re-

corded temperature gradient from 110 to 625 m (22.0–20.1°C daily minimum average and 28.2–24.9°C daily maximum average) is probably not sufficient to affect ichneumonid species richness. The high species turnover across elevation is likely to be a function of under sampling. The species-accumulation curves show that none of the elevations were sufficiently sampled; with the result that further sampling may increase the number of shared species between elevations.

## ACKNOWLEDGMENTS

I would like to thank Brian Fisher for organizing this expedition, and all of the staff, in particular Olivier Langrand, Prosper Obame Ondo, and Andre Kamdem Toham of WWF-Gabon in Libreville for logistical support. The late Faustin Oyono, and Jean-Jacques Tanga provided assistance in the field. Collecting and export permits were kindly granted by Emile Mamfoumbi Kombila, Directeur de la Faune et de la Chasse, Libreville. The manuscript was improved by the comments of a referee. Fieldwork was funded by the World Bank through WWF-US, and the processing and identification of the samples by the National Research Foundation (South Africa).

## LITERATURE CITED

- ARNETT, R. H. 1985. American insects: a handbook of the insects of America north of Mexico. Van Nostrand Reinhold Company, New York. 850 pp.
- BASSET, Y., H. P. ABERLENC, H. BARRIOS, G. CURLETTI, J. M. BÉRENGER, J. P. VESCO, P. CAUSSE, A. HAUG, A. S. HENNION, L. LESOBRE, F. MARQUÈS, AND R. O'MEARA. 2001. Stratification and diel activity of arthropods in a lowland rain forest in Gabon. *Biol. J. Linn. Soc.* 72:585–607.
- BOULINIER, T., J. D. NICHOLS, J. R. SAUER, J. E. HINES, AND K. H. POLLOCK. 1998. Estimating species richness: the importance of heterogeneity in species detectability. *Ecology* 79:1018–1028.
- CHAZDON, R. L., R. K. COLWELL, J. S. DENSLOW, AND M. R. GUARIGUATA. 1998. Statistical methods for estimating species richness of woody regeneration in primary and secondary rain forest of NE Costa Rica. Pp. 285–309 *in* Forest biodiversity research, monitoring and modelling: conceptual background and Old World case studies, F. Dallmeier and J. A. Comiskey, eds. Parthenon Publishing, Paris.
- COE, M., N. MCWILLIAM, G. STONE, AND M. PACKER, eds. 1999. Mkomazi: the ecology, biodiversity and conservation of a Tanzanian savanna. Royal Geographical Society (with The Institute of British Geographers), London. 608 pp.
- COLWELL, R. K. 1997. EstimateS: Statistical estimation of species richness and shared species from samples. Version 5.1. User's Guide and application published at: <http://vice-roy.eeb.uconn.edu/estimates>.
- ERWIN, T. 1982. Tropical forests: their richness in Coleoptera and other arthropod species. *Coleopt. Bull.* 36:74–75.
- FISHER, B. L. 1999. Improving inventory efficiency: a case study of leaf-litter ant diversity in Madagascar. *Ecol. Applic.* 9:714–731.
- GASTON, K. J. 1991. The magnitude of global insect species richness. *Cons. Biol.* 5:283–296.
- . 1993. Spatial patterns in the description and richness of the Hymenoptera. Pp. 277–293 *in* Hymenoptera and biodiversity, J. Lasalle and I. D. Gauld, eds. CAB International, Wallingford. 348 pp.
- GASTON, K. J., I. D. GAULD, AND P. HANSON. 1996. The size and composition of the hymenopteran fauna of Costa Rica. *J. Biogeog.* 23:105–113.
- GAULD, I. D. 1986. Latitudinal gradients in ichneumonid species-richness in Australia. *Ecol. Ent.* 11:155–161.
- . 1991. The Ichneumonidae of Costa Rica, 1. Introductions, keys to subfamilies, and keys to the species of the lower pimpliform subfamilies Rhyssinae, Pimplinae, Poemeniinae, Acaenitinae and Cyllocerinae. *Mem. Amer. Ent. Inst.* 47:1–577.
- GAULD, I. D. AND K. J. GASTON. 1995. The Costa Rican Hymenoptera fauna. Pp. 13–19 *in* The Hymenoptera of Costa Rica, P. Hanson and I. D. Gauld, eds. Oxford University Press, Oxford.

- GAULD, I. D. AND D. H. JANZEN. 1994. The classification, evolution and biology of the Costa Rican species of *Cryptophion* (Hymenoptera: Ichneumonidae). *Zool. J. Linn. Soc.* 110:297–324.
- GAULD, I. D. AND P. A. MITCHELL. 1978. The taxonomy, distribution and host preferences of African parasitic wasps of the subfamily Ophioninae (Hymenoptera: Ichneumonidae). Commonwealth Agricultural Bureau, Slough. 287 pp.
- GRISSELL, E. E. 1999. Hymenopteran biodiversity: some alien notions. *Amer. Ent.* 45:235–244.
- GUPTA, S. AND V. GUPTA. 1983. *Ichneumonologia Orientalis*, 9. The tribe Gabuniini (Hymenoptera: Ichneumonidae). *Orient. Insects Monog.* 10:1–313.
- GOTELLI, N. J. AND R. K. COLWELL. 2001. Quantifying biodiversity: procedures and pitfalls in the measurement and comparison of species richness. *Ecology Letters* 4:379–391.
- HAMMOND, P. M. 1992. Species inventory. Pp. 17–39 in *Global Biodiversity, Status of the Earth's Living Resources*, B. Groombridge, ed. Chapman and Hall, London. 585 pp.
- HANSON, P. AND I. D. GAULD, eds. 1995. *The Hymenoptera of Costa Rica*. Oxford University Press, Oxford. 893 pp.
- HEINRICH, G. H. 1968. Synopsis and Reclassification of the Ichneumoninae Stenopneusticae of Africa South of the Sahara (Hymenoptera). Farmington State College Press 4:695–941.
- HESPENHEIDE, H. A. 1979. Are there fewer parasitoids in the tropics? *Amer. Natur.* 113:766–769.
- JANZEN, D. H. 1973a. Sweep samples of tropical foliage insects: description of study sites, with data on species abundances and size distributions. *Ecology* 54:659–686.
- . 1973b. Sweep samples of tropical foliage insects: effects of seasons, vegetation types, elevation, time of day, and insularity. *Ecology* 54:687–708.
- . 1981. The peak in North American ichneumonid richness lies between 38° and 42°N. *Ecology* 62:532–537.
- JANZEN, D. H. AND C. M. POND. 1975. A comparison, by sweep sampling, of the arthropod fauna of secondary vegetation in Michigan, England and Costa Rica. *Trans. R. Ent. Soc. Lond.* 127:33–50.
- KOUKI, J. P. NIEMELÄ AND M. VIITASAARI. 1994. Reversed latitudinal gradient in species richness of sawflies (Hymenoptera, Symphyta). *Ann. Zool. Fenn.* 31:83–88.
- LASALLE, J. AND I. D. GAULD, eds. 1993. *Hymenoptera and biodiversity*. CAB International, Wallingford. 348 pp.
- LONGINO, J. T. AND R. K. COLWELL. 1997. Biodiversity assessment using structured inventory: capturing the ant fauna of a tropical rain forest. *Ecol. Applic.* 7:1263–1277.
- MICHENER, C. D. 1979. Biogeography of the bees. *Ann. Miss. Bot. Gard.* 66:277–347.
- MORRISON, G., M. AUERBACH, AND E. D. MCCOY. 1978. Anomalous diversity of tropical parasitoids: a general phenomenon? *Amer. Natur.* 114:303–307.
- MAGURRAN, A. E. 1988. *Ecological diversity and its measurement*. Croom Helm, London. 179 pp.
- NADKARNI, N. M. 1994. Diversity of species and interactions in the upper tree canopy of forest ecosystems. *Amer. Zool.* 34:70–78.
- NOYES, J. S. 1989a. A study of five methods of sampling Hymenoptera (Insecta) in a tropical rain forest, with special reference to the Parasitica. *J. Nat. Hist.* 23:285–298.
- . 1989b. The diversity of Hymenoptera in the tropics with special reference to Parasitica in Sulawesi. *Ecol. Ent.* 14:197–207.
- OWEN, D. F. AND J. OWEN. 1974. Species diversity in temperate and tropical Ichneumonidae. *Nature* 249:583–584.
- OWEN, J., H. TOWNES, AND M. TOWNES. 1981. Species diversity of Ichneumonidae and Serphidae (Hymenoptera) in an English suburban garden. *Biol. J. Linn. Soc.* 16:315–336.
- RAHBEK, C. 1995. The elevational gradient of species richness: a uniform pattern? *Ecography* 18:200–205.
- RATHCKE, B. J. AND P. W. PRICE. 1976. Anomalous diversity of tropical ichneumonid parasitoids: a predation hypothesis. *Amer. Natur.* 110:889–893.
- ROBERTSON, H. G. 1999. Ants (Hymenoptera: Formicidae) of Mkomazi. Pp. 321–336 in *Mkomazi: the ecology, biodiversity and conservation of a Tanzanian Savanna*, M. J. Coe, N. C. McWilliam, G. N. Stone, and M. Packer, eds. Royal Geographical Society (with The Institute of British Geographers), London. 608 pp.
- ROHDE, K. 1992. Latitudinal gradients in species diversity: the search for the primary cause. *Oikos* 65:514–527.
- SAWONIEWICZ, J. 1979. The effect of scrub layer on the occurrence of the Ichneumonidae (Hymenoptera) in pine stands on different sites. *Mem. Zool.* 30:89–130.

SIMON VAN NOORT

- . 1986. Structure of Ichneumonidae (Hymenoptera) communities in urban green areas of Warsaw. *Mem. Zool.* 41:255–271.
- SEGADE, C., P. ROS-FARRÉ A. ALGARRA, D. VENTURA, AND J. PUJADE-VILLAR. 1997. Estudio comparativo de las capturas realizadas con trampa Malaise en Andorra con especial atención a los Himenópteros (Hymenoptera). *Zapateri Revta. Aragon. Ent.* 7:71–82.
- STORK, N. E. 1991. The composition of the arthropod fauna of Bornean lowland rain forest trees. *J. Trop. Ecol.* 7:161–180.
- TOWNES, H. 1969. The genera of Ichneumonidae, Part 1. *Mem. Amer. Ent. Inst.* 11:1–300.
- . 1972. A light-weight Malaise trap. *Ent. News* 83:239–247.
- TOWNES, H. AND M. TOWNES. 1973. A catalogue and reclassification of the Ethiopian Ichneumonidae. *Mem. Amer. Ent. Inst.* 19:1–416.
- VAN NOORT, S. AND S. G. COMPTON. 1999. Fig wasps (Agaonidae, Hymenoptera) and fig trees (Moraceae) of Mkomazi. Pp. 299–320 *in* Mkomazi: the ecology, biodiversity and conservation of a Tanzanian Savanna, M. J. Coe, N. C. McWilliam, G. N. Stone, and M. Packer, eds. Royal Geographical Society (with The Institute of British Geographers), London. 608 pp.
- VAN NOORT, S., G. L. PRINSLOO, AND S. G. COMPTON. 2000. Hymenoptera excluding Apoidea (Apiformes) and Formicidae (Insecta). Pp. 289–364 *in* Dâures—biodiversity of the Brandberg Massif, Namibia, A. H. Kirk-Spriggs, and E. Marais, eds. Cimbebasia Memoir 9, National Museum of Namibia, Windhoek. 389 pp.
- WHITE, F. 1983. The vegetation of Africa. A descriptive memoir to accompany the Unesco/AETFAT/UNSO vegetation map of Africa. Unesco. Paris.
- WILSON, E. O. 1992. The diversity of life. Belknap Press, Cambridge, Massachusetts. 424 pp.
- WOLDA, H. 1979. Abundance and diversity of Homoptera in the canopy of a tropical forest. *Ecol. Ent.* 4:181–190.
- YU, D. S. 1998. Interactive Catalogue of World Ichneumonidae 1998. CD-ROM. Taxapad. Vancouver, Canada.