

EFFECTS OF CLEARCUTTING ON THE SPIDER COMMUNITY OF A SOUTHERN APPALACHIAN FOREST

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ABSTRACT

In order to examine the effects of clearcutting on the spider community of a southern Appalachian forest, spider populations in a mature forest, an adjacent clearcut site, and two other clearcut sites were sampled during the summer of 1976 with four techniques: pitfall trapping, Tullgren funnel extraction of litter spiders, sweep netting, and hand collecting. Clearcutting resulted in a marked reduction in spider abundance and a small decrease in the number of spider species. Spider species diversity increased, owing to a marked increase in the evenness component of diversity. While clearcutting greatly reduced the abundance and number of species of web building spiders (both ground-dwelling and aerial species), there was apparently little or no reduction in numbers of hunting spiders. In addition, the number of hunting spider species increased. It is postulated that microclimate changes resulting from removal of the forest canopy and reduced litter thickness were primarily responsible for the decline in abundance and diversity of web builders.

INTRODUCTION

Growing interest in managing forests as ecosystems which are valued for many functions has increased the need for understanding the impact of forest management practices on a wide variety of organisms (Boyce 1977), including spiders. Mounting evidence indicates that the population density, behavior, and population dynamics of spiders are such that these predators are collectively an important stabilizing agent of terrestrial arthropod populations (Brey Meyer 1966, Moulder and Reichle 1972, Turnbull 1973, Riechert 1974, Enders 1975) and thus may be an important factor in total ecosystem stability. The current study was initiated to examine how the population size, species diversity, and guild composition of the spider component of a southern Appalachian forest community are affected by clearcutting. In addition to helping understand the adaptations and response capabilities of different types of spiders, it may contribute to more informed forest management.

STUDY SITES

Four study sites were chosen, all in the Highlands Ranger District of the Nantahala National Forest in the mountains of southwestern North Carolina. The sites (Table 1)

Table 1.—General characteristics of the study sites.

	Age of clearcut in summers since clearcutting	Size in ha	Slope	Dominant aspect	Mean elevation in m
Ellicott Rock forest		8	5°-20°	100°	860
Ellicott Rock clearcut	2nd	8	5°-12°	100°	880
Buck Creek clearcut	1st	10	20°-30°	20°	975
Horse Cove clearcut	5th	16	2°-10°	130°	950

include one area of mature forest, an adjacent, topographically very similar area in its second summer following clearcutting, and two separate areas representing the first and fifth summers following clearcutting. All clearcutting was performed during the winter.

Ellicott Rock forest site.—The forest site, located near Ellicott Rock, is occupied by a mature pine-hardwood community bisected by a narrow, weakly developed cove forest community along a small stream. The dominant tree species (in order of decreasing importance values, which are based upon relative frequency and relative dominance values obtained by the point quarter method) are white pine (*Pinus strobus*), white oak (*Quercus alba*), sourwood (*Oxydendrum arboreum*), black oak (*Quercus velutina*), red maple (*Acer rubrum*), and scarlet oak (*Quercus coccinea*) in the pine-hardwood community; and red maple, Canadian hemlock (*Tsuga canadensis*), sourwood, black gum (*Nyssa sylvatica*), white pine, tulip tree (*Liriodendron tulipifera*), white oak, and holly (*Ilex opaca*) in the cove forest community. The moderately dense understory of the pine-hardwood community contained dogwood (*Cornus florida*), numerous young of canopy species, and shrubs such as huckleberry (*Gaylussacia ursina*), scattered mountain laurel (*Kalmia latifolia*), and scattered *Rhododendron maximum*. Dense stands of *R. maximum* dominated the cove forest understory. Leaf litter depth in the forest ranged from 1 to 15 cm ($n = 10$), with a mean depth of 6.5 cm.

Clearcut sites.—Vegetation at the clearcut study sites was analyzed by nested quadrat sampling (Horn 1976). The Buck Creek site was sampled the summer of the spider study, but the Ellicott Rock and Horse Cove clearcuts were sampled the previous summer. In order of decreasing importance value, the five most important species of woody plants over 0.5 m tall at each clearcut site were: Ellicott Rock — huckleberry, red maple, sourwood, greenbriar (*Smilax rotundifolia*), and pignut hickory (*Carya ovalis*); Buck Creek — American chestnut (*Castanea dentata*), huckleberry, dogwood, greenbriar, and buffalo nut (*Pyrrularia pubera*); Horse Cove — blackberry (*Rubus allegheniensis*), huckleberry, tulip tree, mountain laurel, and spicebush (*Calycanthus floridus*).

Subjective observations indicate that the foliage density and percentage of shaded ground increased significantly with the age of the clearcut sites, with the Buck Creek site having the lowest and the Horse Cove site having the greatest foliage density. Litter depth varied as follows: Ellicott Rock, range = 1-9 cm ($n = 10$), mean = 4.2 cm; Buck Creek, range = 2-10 cm ($n = 10$), mean = 4.8 cm; Horse Cove, range = 1-8 cm ($n = 10$), mean = 3.9 cm.

Comparison of both the pre-logging importance values (calculated from timber cruise curves [Horn 1976]) of tree species at the clearcut sites and the importance values of potential canopy species in the clearcut site quadrats (Horn 1976) with the Ellicott Rock forest site vegetation analysis indicates that this Ellicott Rock forest is botanically the same as the pre-clearcut forest at the adjacent clearcut site, but that the pre-clearcut

forests at the Buck Creek and Horse Cove sites are markedly different from the Ellicott Rock forest and from one another.

METHODS

Four different collecting techniques were used to sample the spider populations at these study sites during the summer of 1976. An attempt was made to distribute the samples evenly over each site and to sample from each type of microhabitat at each site. No samples were collected within 20 m of the edge of any study site. Eight 73 mm diameter sheltered pitfall traps containing an ethylene glycol-detergent mixture were set on each study site on June 25 and were then emptied and reset at three week intervals during the following 15 weeks. Ten 0.25 m² samples of leaf litter (down to the mineral soil) were collected from each study site at fairly regular intervals between June 16 and August 20 and were processed in large Tullgren funnels. Eight daytime sweep net samples of 50 sweeps apiece were obtained from vegetation between 0.2 m and 2.0 m above ground level at each site between June 29 and July 2. Four hours of intensive daytime hand collecting was performed at each site between June 22 and July 9, with an additional 30 minutes of intensive daytime hand collecting at each site on October 2. Search time was divided equally between the ground stratum and the aerial stratum (branches and leaves above the ground). Ground and aerial spiders were placed in separate collecting vials.

RESULTS

Table 2 shows the number of individuals of each spider taxon collected at each site. A total of 1729 individuals representing at least 134 species and 23 families were collected from all sites. Caution must be used in interpreting these data. The sampling was not strictly random. Temporal bias exists favoring species that are more abundant or active during the summer and the daytime. Each of the collecting techniques used collects certain kinds of spiders more effectively than others (Turnbull 1973). In addition, the forest canopy was not sampled. Because of these biases, the data cannot be expected to closely represent the real population densities or total number of species at any site. Nevertheless, since the collecting at all sites was concurrent and involved the same techniques and effort, the data should reflect with reasonable accuracy between-site differences in the spider communities.

It is very important to emphasize that, since the pre-clearcut plant communities at the Buck Creek and Horse Cove sites were different from the Ellicott Rock forest, these two clearcut sites cannot be treated as different time points of the succession one would expect to witness at the Ellicott Rock site. Consequently, the analysis of results will focus primarily on the spider data from the Ellicott Rock sites, and will be based on the assumption, supported by the vegetation analyses, that significant differences between the spider samples from these two sites are primarily the results of clearcutting.

Effects of clearcutting on species composition.—Clearcutting apparently caused a marked change in the species composition at the Ellicott Rock site. Fifty-five percent of the species in the forest sample are not present in the clearcut sample, and 50 percent of the species in the clearcut sample are not present in the forest sample. The Bray and Curtis (1957) index of similarity, $C = 2w/(a + b)$ [where a = the total number of identified individuals in one sample, b = the total number of identified individuals in the

Table 2.—Spiders collected at one mature forest site and three recently clearcut sites in the southern Appalachian mountains near Highlands, North Carolina. Stratum designations: G = all specimens collected on ground; A = all specimens collected on plants or webs above ground surface; G, A = majority of specimens collected on ground; A, G = majority of specimens collected above ground. Prey capture mode designations (based upon field observations and literature): H = hunting (cursorial, wandering) spiders; W = web building spiders. Parentheses enclose number of adults collected. Asterisk denotes any species comprising 2.5 percent or more of the total number of individuals collected at that site.

Taxon	Stratum	Prey capture mode	Ellicott Rock forest	Ellicott Rock clearcut	Buck Creek clearcut	Horse Cove clearcut
Agelenidae						
<i>Agelenopsis utahana</i> (Chamb. & Ivie)	G,A	W			8(0)	
<i>Calymmaria cavicola</i> (Banks)	G	W	1(1)	1(0)	2(2)	2(2)
<i>Circurina arcuata</i> Keyserling	G	W			1(1)	1(1)
<i>Circurina breviararia</i> Bishop & Crosby	G	W	1(1)			
<i>Circurina</i> (immature)	G	W	10(0)	2(0)	20(0)	7(0)
<i>Coras taugynus</i> Chamberlin	G	W				1(1)
<i>Coras</i> (immature)	G	W	3(0)		1(0)	2(0)
<i>Cybaeus silicis</i> Barrows	G	W	5(3)	3(2)	6(2)	9(6)
<i>Wadotes carolinus</i> Chamberlin	G	W	1(1)	1(1)		3(3)
<i>Wadotes hybridus</i> (Emerton)	G	W	14(14)	3(3)	*14(14)	*22(22)
<i>Wadotes</i> (immature)	G	W	62(0)	37(0)	48(0)	36(0)
Amaurobiidae						
<i>Callioplus armipotens</i> (Bishop & Crosby)	G	W			*40(8)	*17(1)
Antrodiaetidae						
<i>Antrodiaetus unicolor</i> (Hentz)	G	W	3(2)	2(2)	5(2)	4(4)
Anyphaenidae						
<i>Anyphaena pectorosa</i> L. Koch	A	H	1(1)	1(1)		
<i>Wulfilia alba</i> (Hentz)	A,G	H	4(3)			
<i>Wulfilia saltabunda</i> (Hentz)	A	H				1(1)
Araneidae						
<i>Acacesia hamata</i> (Hentz)	A	W		1(0)	1(0)	
<i>Araneus marmoreus</i> Clerck	A	W				1(0)
<i>Araneus nordmanni</i> (Thorell)	A	W	1(1)			
<i>Araneus</i> (immature)	A	W	1(0)			
<i>Araniella displicata</i> (Hentz)	A	W	1(1)			
<i>Cyclosa turbinata</i> (Walck.)	A	W		3(1)	5(0)	4(1)
<i>Leucauge venusta</i> (Walck.)	A	W	*17(12)	1(1)		4(4)
<i>Mangora placida</i> (Hentz)	A	W	4(2)			
<i>Mangora</i> (immature)	A	W	1(0)		1(0)	
<i>Metepeira labyrinthea</i> (Hentz)	A	W	1(0)	3(0)		1(0)
<i>Micrathena gracilis</i> (Walck.)	A	W			4(0)	
<i>Micrathena mitrata</i> (Hentz)	A	W	*15(0)			
<i>Neoscona</i> (immature)	A	W			2(0)	
<i>Nuctenea cornuta</i> (Clerck)	A	W			3(1)	
Araneidae spp. (immature)	A	W			2(0)	3(0)
Clubionidae						
<i>Castianeira cingulata</i> (C. L. Koch)	G	H				1(0)
<i>Castianeira longipalpus</i> (Hentz)	G	H		2(2)	1(1)	4(2)
<i>Castianeira variata</i> Gertsch	G	H			1(1)	

Table 2.-cont.

Taxon	Stratum	Prey capture mode	Ellicott Rock forest	Ellicott Rock clearcut	Buck Creek clearcut	Horse Cove clearcut
<i>Chiracanthium inclusum</i> (Hentz)	A	H				1(0)
<i>Clubiona</i> (immature)	G,A	H	4(0)		1(0)	3(0)
<i>Clubionoides excepta</i> (L. Koch)	G	H		2(2)		
<i>Liocranoides</i> sp.	G	H		1(1)		1(1)
<i>Phrurotimpus alarius</i> (Hentz)	G	H	*28(11)	*16(11)	*30(19)	*47(38)
<i>Phrurotimpus borealis</i> (Emerton)	G	H		6(6)	6(5)	*13(7)
<i>Scotinella redempta</i> (Gertsch)	G	H	1(1)	1(1)		4(4)
<i>Scotinella</i> sp. A	G	H	1(1)	4(4)		
<i>Scotinella</i> (immature)	G	H	4(0)	1(0)	1(0)	
Clubionidae spp. (immature)	G,A	H		1(0)	2(0)	
Ctenidae						
<i>Anahita animosa</i> (Walck.)	G	H	13(2)	*8(3)		
Dictynidae						
<i>Dictyna sublata</i> (Hentz)	A	W	1(1)		6(3)	
Gnaphosidae						
<i>Cesonia bilineata</i> (Hentz)	G	H				1(0)
<i>Drassyllus fallens</i> Chamberlin	G	H				1(1)
<i>Drassyllus</i> (immature)	G	H				2(0)
<i>Litophillus temporarius</i> Chamberlin	G	H			1(0)	
<i>Micaria aurata</i> (Hentz)	A	H				2(0)
<i>Micaria longipes</i> Emerton	G	H				1(1)
<i>Poecilochroa capulata</i> (Walck.)	G	H			1(1)	
<i>Zelotes duplex</i> Chamberlin	G	H				5(4)
<i>Zelotes hentzi</i> Barrows	G	H				1(1)
<i>Zelotes laccus</i> (Barrows)	G	H		1(1)		
<i>Gnaphosidae</i> sp. (immature)	G	H			1(0)	
Hahnidae						
<i>Neoantistea agilis</i> (Keyserling)	G	W			1(1)	1(0)
<i>Neoantistea</i> (immature)	G	W		1(0)		
Hypochilidae						
<i>Hypochilus thorelli</i> Marx	A	W	1(0)			2(0)
Leptonetidae						
<i>Leptoneta gertschi</i> Barrows	G	W	*29(29)	*7(7)		1(1)
<i>Leptoneta</i> sp. A	G	W			5(5)	
<i>Leptoneta</i> (immature)	G	W	45(0)	12(0)	5(0)	7(0)
Linyphiidae						
<i>Centromerus denticulatus</i> (Emerton)	G	W	*34(7)	*7(2)	*13(2)	
<i>Ceraticelus carinatus</i> Emerton	G	W			3(3)	
<i>Ceraticelus fissiceps</i> O. P.-Cambridge	A	W	*48(42)	*14(14)	5(5)	*10(10)
<i>Ceraticelus minutus</i> (Emerton)	G	W		2(2)	8(7)	2(2)
<i>Ceraticelus similis</i> (Banks)	A	W			1(1)	
<i>Ceratinella brunnea</i> Emerton	G	W			1(1)	
<i>Ceratinopsis formosa</i> (Banks)	G	W			1(1)	
<i>Ceratinopsis interpres</i> (O. P.-Cambridge)	A,G	W		1(1)		*12(12)
<i>Cornicularia directa</i> (O. P.-Cambridge)	A	W				1(1)
<i>Erigone autumnalis</i> Emerton	G,A	W	1(1)		*13(13)	

Table 2.—cont.

Taxon	Stratum	Prey capture mode	Ellicott Rock forest	Ellicott Rock clearcut	Buck Creek clearcut	Horse Cove clearcut
<i>Erigone brevidentata</i> Emerton	G	W	5(5)	1(1)		
<i>Florinda coccinea</i> (Hentz)	A	W		1(0)		
<i>Frontinella pyramitela</i> (Walck.)	A	W	6(3)	*12(2)	1(1)	7(2)
<i>Lepthyphantes zebra</i> (Emerton)	G,A	W	3(1)		1(0)	*16(0)
<i>Maso sundevalli</i> (Westring)	G	W			1(1)	
<i>Meioneta unimaculata</i> (Banks)	G	W	1(0)	1(1)		
<i>Meioneta</i> sp. A	G	W	2(1)			
<i>Meioneta</i> sp. B	G	W				2(2)
<i>Meioneta</i> sp. C	G	W				1(1)
<i>Meioneta</i> (immature)	G	W		1(0)		
<i>Microneta</i> (immature)	G	W	1(0)		1(0)	
<i>Pelecopsidis frontalis</i> (Banks)	G	W	1(1)			
<i>Pelecopsis moestum</i> (Banks)	G	W				1(1)
<i>Pitiohyphantes costatus</i> (Hentz)	A	W	1(0)			
<i>Scylaceus pallidus</i> (Emerton)	G	W	2(2)			
<i>Tapinoma bilineta</i> Banks	G	W			1(0)	
<i>Walkenaera spiralis</i> (Emerton)	G	W			1(1)	
Linyphiidae sp. A	A	W	1(1)			
Linyphiidae sp. B	A	W	1(1)			
Linyphiidae sp. C	A	W	1(1)			
Linyphiidae sp. D	A	W	1(1)			
Linyphiidae sp. E	G	W		3(3)		
Linyphiidae spp. (immature)	G,A	W	22(0)	6(0)	25(0)	36(0)
Lycosidae						
<i>Lycosa gulosa</i> Walck.	G	H	14(1)	*10(2)	*13(4)	3(0)
<i>Pardosa milvina</i> (Hentz)	G	H		*18(16)	1(0)	3(2)
<i>Pardosa saxatilis</i> (Hentz)	G	H		1(1)		3(3)
<i>Pardosa</i> (immature)	G	H		2(0)		
<i>Pirata minutus</i> Emerton	G	H				1(1)
<i>Pirata montanus</i> Emerton	G	H	1(1)		9(4)	*14(4)
<i>Pirata</i> (immature)	G,A	H			2(0)	1(0)
<i>Schizocosa ocreata</i> (Hentz)	G	H				1(1)
Lycosidae spp. (immature)	G	H		5(0)	3(0)	
Oxyopidae						
<i>Oxyopes salticus</i> Hentz	A	H		1(0)		
Pisauridae						
<i>Pisaurina mira</i> (Walck.)	A	H				1(0)
Salticidae						
<i>Agassa cerulea</i> (Walck.)	A	H				1(0)
<i>Eris aurantius</i> (Lucas)	A	H		1(0)	1(0)	1(0)
<i>Eris</i> sp. A	A	H				7(0)
<i>Habrocestum pulex</i> (Hentz)	G,A	H	1(1)	*13(5)	5(4)	5(2)
<i>Habronattus viridipes</i> (Hentz)	G	H		1(0)		
<i>Hentzia mitrata</i> (Hentz)	A	H		1(1)		
<i>Icius elegans</i> (Hentz)	A	H				1(0)
<i>Icius</i> sp. A	A	H	1(0)		2(0)	

Table 2.-cont.

Taxon	Stratum	Prey capture mode	Ellicott Rock forest	Ellicott Rock clearcut	Buck Creek Clearcut	Horse Cove clearcut
<i>Maevia inclemens</i> (Walck.)	A,G	H	*34(3)	*20(13)	*21(5)	8(1)
<i>Marpissa lineata</i> (C. L. Koch)	G	H		1(1)		
<i>Metaphidippus canadensis</i> (Banks)	G	H			1(0)	3(0)
<i>Metaphidippus flaviceps</i> Kaston	A	H	1(1)			
<i>Metaphidippus galathea</i> (Walck.)	A	H		2(1)		3(3)
<i>Neon nellii</i> (Peckham & Peckham)	G	H		1(1)		2(2)
<i>Onondaga lineata</i> (C. L. Koch)	A	H		1(1)		
<i>Phidippus princeps</i> (Peckham)	A	H				2(2)
<i>Phidippus</i> (immature)	G	H		1(0)		
<i>Sitticus floridanus</i> Gertsch & Mulaik	G	H				1(1)
<i>Thiodina iniquies</i> (Walck.)	A	H	4(0)	5(3)		4(3)
<i>Zygoballus bettini</i> Peckham	A,G	H	2(2)			4(3)
Salticidae sp. A	G	H	*18(11)		*33(21)	
Salticidae sp. B	A	H		6(0)		7(0)
Salticidae spp. (immature)	A	H				2(0)
Symphytognathidae						
<i>Mysmena guttata</i> (Banks)	G	W	2(1)	1(0)	1(0)	5(1)
Tetragnathidae						
<i>Tetragnatha elongata</i> Walck.	A	W		2(1)		1(1)
<i>Tetragnatha seneca</i> Seeley	A	W				2(1)
<i>Tetragnatha versicolor</i> Walck.	A	W	4(4)			
Theridiidae						
<i>Achaearanea rupicola</i> (Emerton)	G	W	1(1)		1(1)	
<i>Argyrodes trigonum</i> (Hentz)	A	W	5(5)			3(3)
<i>Dipoena nigra</i> (Emerton)	A	W		1(1)		
<i>Episinus amoenus</i> Banks	A	W				1(1)
<i>Euryopis funebris</i> (Hentz)	G	W			1(1)	
<i>Pholcomma hirsuta</i> Emerton	G,A	W	*71(21)	*16(7)	*17(5)	9(5)
<i>Robertus frontatus</i> (Banks)	G	W	14(2)	1(0)		
<i>Theridion albidum</i> Banks	A	W	1(1)	1(1)	2(2)	
<i>Theridion flavonotatum</i> Becker	A	W	2(2)			2(2)
<i>Theridion lyricum</i> Walck.	A	W	2(2)			
<i>Thymoites unimaculata</i> (Emerton)	A	W	1(1)			
Theridiosomatidae						
<i>Theridiosoma gemmosa</i> (L. Koch)	A,G	W	2(1)			2(2)
Thomisidae						
<i>Misumenoides formosipes</i> (Walck.)	A	H		2(0)	1(0)	3(1)
<i>Misumenops oblongus</i> (Keyserling)	A	H	1(0)	3(1)	1(0)	4(1)
<i>Philodromus placidus</i> Banks	A	H	1(1)			
<i>Philodromus rufus</i> Walck.	A	H	1(1)			
<i>Thanatus</i> sp. (immature)	A	H		1(0)		
<i>Xysticus pellax</i> O. P.-Cambridge	G	H				1(1)
<i>Xysticus</i> (immature)	G,A	H	4(0)	9(0)	1(0)	2(0)
Uloboridae						
<i>Hyptiotes cavatus</i> (Hentz)	A	W	4(0)		2(0)	1(0)

Table 3.—Bray and Curtis similarity indices for the spider samples from all study sites. The Bray and Curtis similarity index is defined in the text.

	(A)	(B)	(C)	(D)
Ellicott Rock forest (A)	—	.395	.407	.312
Ellicott Rock clearcut (B)		—	.414	.418
Buck Creek clearcut (C)			—	.439
Horse Cove clearcut (D)				—

other sample, and w = the sum of the lesser values for those species present in both samples] was used to assess the similarity of species composition among all four sites (Table 3). For the Ellicott Rock sites its value is 0.395, indicating low similarity. The similarity values (Table 3) also indicate that the species composition of each clearcut sample is distinctly different, a result that is consistent with the pre- and post-clearcut vegetational differences among the clearcut sites.

Effects of clearcutting on abundance.—Clearcutting reduced the total spider population at the Ellicott Rock site (Tables 2 and 4). Most of this decrease was in the form of marked declines in nine species which are common in the mature forest: *Pholcomma hirsta*, *Ceraticelus fissiceps*, *Centromerus denticulatus*, *Leptoneta gertschi*, Salticidae sp. A, *Leucauge venusta*, *Micrathena mitrata*, *Robertus frontatus*, and *Wadotes hybridus*. The only species which appear to have increased markedly as a result of clearcutting are *Pardosa milvina*, *Habrocestum pulex*, *Phrurotimpus borealis*, and Salticidae sp. B. Populations of some species which are common in the forest (*Phrurotimpus alarius*, *Anahita animosa*, *Lycosa gulosa*, and *Maevia inclemens*) and some which are less common (*Cybaeus silicis*, *Antrodiaetus unicolor*, and *Thiodina iniquies*) apparently were not strongly affected by clearcutting.

Effects of clearcutting on species diversity.—Despite its limitations (Peet 1974, 1975) and because of its use in other arachnid studies (Uetz 1975, 1976; Stanton 1979) and the absence of clearly more suitable indices, the Shannon index was used in the present study to measure the species diversity of each sample. The Shannon formula,

$$H' = \sum_{i=1}^s p_i \log_n p_i$$

[where p_i = the proportion of total individuals in species i , and s = the number of species], is a combined measure of both species richness (the number of species) and evenness (the relative equality of species abundance) of a sample. Pielou's (1966) evenness index ($H'_{\text{obs}}/H'_{\text{max}}$, where $H'_{\text{max}} = \log_n s$) was used, despite shortcomings (Peet 1974, 1975) to measure the evenness component of the diversity index for each sample. The t -test designed by Hutchesson (1970) was used to determine the significance of differences between forest and clearcut sample diversity indices.

The species diversity (Table 4) for the total Ellicott Rock forest spider sample is significantly lower than that of both the Ellicott Rock clearcut sample ($t = 2.711$, d.f. = 590, $P < 0.01$) and the Horse Cove clearcut sample ($t = 5.452$, d.f. = 701, $P < 0.001$) but not significantly lower than that of the Buck Creek clearcut sample ($t = .502$, d.f. = 654, $P > 0.5$). The higher diversity, higher equitability (evenness), though lower species richness of the Ellicott Rock clearcut total sample (Table 4) as compared to the Ellicott Rock forest total sample indicates that clearcutting of the Ellicott Rock forest decreased the number of spider species, but made population sizes of the remaining species more equitable (even).

Table 4.—Number of individuals, richness (= number of species in sample), species diversity (= Shannon's H'), and evenness (= Pielou's evenness index) of the study site spider samples compared.

		Ellicott Rock forest	Ellicott Rock clearcut	Buck Creek clearcut	Horse Cove clearcut
Total sample:	no. individuals	595	297	419	418
	richness	60	53	50	71
	diversity index	3.1667	3.4198	3.2142	3.6523
	evenness	.773	.861	.822	.857
Sweep sample:	no. individuals	134	46	38	69
	richness	22	15	7	21
	diversity index	2.1132	2.2272	1.4011	2.6735
	evenness	.684	.822	.720	.878
Aerial hand s.:	no. individuals	45	24	28	39
	richness	18	10	12	16
	diversity index	2.5421	1.8484	2.2849	2.5374
	evenness	.880	.803	.920	.915
Ground hand s.:	no individuals	30	38	37	14
	richness	9	7	13	8
	diversity index	1.9405	1.3188	2.3202	1.9351
	evenness	.883	.678	.905	.931
Pitfall sample:	no. individuals	106	111	191	159
	richness	16	18	26	28
	diversity index	2.3240	2.5952	2.5954	2.5763
	evenness	.838	.898	.797	.773
Litter sample:	no. individuals	280	78	125	137
	richness	16	16	14	16
	diversity index	1.9914	2.2754	2.0286	2.3390
	evenness	.718	.821	.769	.844

Effects of clearcutting on different spider guilds.—An examination of the responses of various guilds of spiders to clearcutting may help explain why clearcutting reduced the numbers of individuals and species yet increased the evenness and species diversity in the spider community. Clearcutting at Ellicott Rock had a significant effect upon both the relative abundance ($R \times C$ test, $P < 0.005$) and richness ($R \times C$ test, $P < 0.05$) of the three general guild categories, ground web builders, aerial web builders, and hunting spiders (ground and aerial hunters combined). The net effect of clearcutting at Ellicott Rock was to decrease the numbers and species richness of sedentary ground spiders and aerial web spiders while increasing the species richness of hunting spiders and barely affecting their numbers (Table 5). This conclusion must be tempered by the possibility that the high proportion of hunting spiders in the clearcut sample is due partly to higher pitfall and hand capture rates caused by increased activity of individual spiders in the more variable microclimate of the clearcut site.

The data summarized in Table 6 also show that web builder guilds were negatively affected by clearcutting while hunting spiders may have benefited. Eight of the nine common forest species which declined markedly after clearcutting are ground web spiders or aerial web spiders. The only four species which appeared to increase markedly after clearcutting are hunting spiders. In addition, all four of the common forest species which remained abundant after clearcutting are hunting species.

Table 5.—The guild representation of the study site samples compared.

	Ellicott Rock forest	Ellicott Rock clearcut	Buck Creek clearcut	Horse Cove clearcut
Ground web builders				
no. (and %) of individuals	334(56)	108(36)	245(59)	185(44)
no. (and %) of species	19(32)	14(26)	23(46)	17(24)
Ground hunters				
no. (and %) of individuals	89(15)	105(35)	113(27)	124(30)
no. (and %) of species	8(13)	16(30)	12(24)	21(30)
Aerial hunters				
no. (and %) of individuals	50(8)	44(15)	26(6)	52(12)
no. (and %) of species	10(17)	12(23)	5(10)	16(23)
Aerial web builders				
no. (and %) of individuals	123(21)	40(14)	35(8)	57(14)
no. (and %) of species	23(38)	11(21)	10(20)	16(23)

Horse Cove clearcut, like the Ellicott Rock clearcut, has a high proportion of species and individuals of hunting spiders and a low proportion of web building spiders (Table 5). Although the low percentage of species and individuals of hunting spiders and the high proportion of ground web spiders in the Buck Creek clearcut sample appears to weaken the hypothesis that clearcut areas support a larger proportion of hunting spiders and a lower proportion of web builders than forests, it should be pointed out that this site was sampled only a few months after clearcutting. Probably not enough time had passed for the processes of population decline, colonization, and population growth to complete initial major changes in species composition.

A comparison of the two Ellicott Rock sites by examining the abundance, richness, diversity, and evenness values of the subsamples collected by each different collecting technique (Table 4) is only marginally helpful in explaining the effects of clearcutting on the spider community, because none of these techniques collects exclusively spiders of a single guild. Although sweeping and aerial hand collecting capture primarily aerial web builders, aerial hunters are also collected. Ground hand collecting yields both ground hunters and ground web builders. Although pitfall traps collect mostly ground hunters, some ground web builders are also collected; the reverse is true for litter samples. Only the aerial hand subsample diversity indices were significantly different ($t = 2.442$, d.f. = 43, $P < 0.02$), with the forest subsample index being higher. Nevertheless, the data for the Ellicott Rock sites' sweep samples, aerial hand samples, pitfall samples, and litter samples (Table 4) suggest that clearcutting reduces aerial web spider abundance and richness, reduces ground web spider abundance, and does not negatively affect the hunting spider guild.

DISCUSSION

In summary, the reduction of species richness caused by clearcutting was primarily due to the elimination of certain species of sedentary ground spiders and aerial web spiders, but was moderated by apparent immigration of hunting spider species. Simultaneously, the evenness component of diversity increased by virtue of marked population declines in

Table 6.—Effects of clearcutting at Ellicott Rock on different guilds of spiders. Numbers in parentheses are percentages of the total number of species in each column. A = species which decreased markedly after clearcutting, B = other species present in forest but not collected in clearcut, C = species which increased markedly after clearcutting, D = other species present in clearcut but not collected in forest.

	A	B	C	D
Ground web builders	5 (56)	7 (21)		2(8)
Ground hunters	1 (11)	2 (6)	4 (100)	11 (42)
Aerial hunters		6(18)		7 (27)
Aerial web builders	3 (33)	18 (55)		6 (23)

most of the dominant forest species (most of which are ground web or aerial web spiders) and by an increase in the abundance of some hunting species. Species diversity increased on the strength of this evenness change. Similar results were obtained by Huhta (1971) in a study of the effects of clearcutting on the ground stratum spiders of spruce forests in Finland. He observed that while clearcutting reduced ground spider abundance, species diversity increased because of an increase in numbers and species of hunting spiders and a concurrent decrease in population densities of previously dominant, sedentary litter species.

It seems reasonable to postulate that the apparent decline in the abundance and diversity of ground web builders (nearly all of which live in the litter) following clearcutting at Ellicott Rock was due in large part to an increase in the frequency and amplitude of fluctuations of microclimatic factors (especially temperature and humidity) within the litter as a result of 1) the elimination of the forest canopy and its ameliorating effects on ground level microclimate, and 2) the reduction of litter thickness. McGee (1976) found that soil temperatures in a southern Appalachian site during the first summer following clearcutting occasionally exceed 60°C (140°F) at 1/16 inch below the surface and 42°C (110°F) at 1 inch below the surface. Huhta (1971) recorded greater temperature and humidity extremes in the litter of clearcut areas than in simultaneously monitored forest litter and concluded that this microclimate instability was the primary reason for the declining numbers of sedentary litter spiders. Others have demonstrated the moderating effect of sheltering vegetation and/or increased litter depth upon microclimate variation within the litter (Geiger 1950, Gill 1969, Hagstrum 1970). Stanton (1979) concluded that the greater abundance and species diversity of litter mites in forests as opposed to field communities was partly due to a more favorable litter microclimate resulting from the ameliorating effects of both the forest canopy and thicker litter. Other workers have found reduced litter thickness to be correlated with reduced ground spider abundance (Lowrie 1948, Hagstrum 1970, Berry 1967) and diversity and richness (Uetz 1975, 1979). Huhta (1971) has pointed out that a reduction of litter thickness may also reduce spider populations by decreasing the abundance and diversity of intralitter space required for web attachment, refugia, and prey. Uetz (1979) has demonstrated that, at least for ground hunting spiders, decreased litter depth reduces species richness not only because of increased microclimate instability, but also because of reduced litter complexity and reduced prey abundance.

The drastic decline in numbers and species of aerial web spiders which utilize the understory vegetation of the forest is probably due primarily to the elimination of the forest canopy and its buffering effects on light intensity, temperature, humidity, and wind (Geiger 1950). Summers (1979), in a recent study of the effects of clearcutting on

opilionids at Ellicott Rock, has reached a similar conclusion about the primary cause of the drastic reduction in abundance and diversity of opilionids which require forest understorey habitats like those used by aerial web spiders. Some studies show that shortages of appropriate spaces and attachment points for webs probably limit the abundance of some web spiders (Duffy 1962, Cherrett 1964, Judd 1965). However, in view of the abundance of shrubs and young trees in the clearcut study sites, it seems unlikely that a shortage of geometrically suitable web sites was the primary factor limiting aerial web spider success. Cannon (1965) found markedly lower numbers of aerial web spiders in two forests with relatively unstable climates than in an adjacent, climatically more stable forest, even though all three forests appeared to have similar densities of plants suitable for web attachment. Prey abundance can have an important effect on web spider abundance (Luczak 1963), but since prey population densities were not measured in the present study, the impact of this factor cannot be estimated.

The ability of hunting spiders to successfully contend with, perhaps even take advantage of, clearcutting is not surprising in view of the abundant evidence that many hunting spiders are remarkably well adapted to open and climatically harsh environments (Lowrie 1948, Herzog 1961, Turnbull 1966, Schmoller 1970a, 1970b, 1971, Almquist 1973, Riechert and Reeder 1972, Gertsch and Riechert 1976, Uetz 1976). There seem to be two important reasons for the success of hunting spiders in such environments. First, many hunting spiders live on or close to the ground where the climate is relatively stable (Geiger 1950). Secondly, their ability to move readily to patches with more favorable climate and resource values (Williams 1962, Turnbull 1966, Almquist 1973, Kronk and Reichert 1979) may be especially important in enabling them to cope with the large amount of spatial and temporal variation in microclimate that exists in a clearcut habitat.

In view of the findings of Uetz (1975, 1979) and Hagstrum (1970) that decreased litter depth is sometimes correlated with decreased species richness and abundance of ground hunting spiders, it is perhaps surprising that ground hunters could increase in richness and abundance following clearcutting. One factor that may compensate for a negative effect of decreased litter depth following clearcutting is an increase in the population densities of some prey species as a result of the high productivity of rapidly regenerating vegetation concentrated close to the ground. Enders (1975) discussed the potentially important influence on spider abundance of both high productivity at intermediate stages of succession and the number of prey per volume of habitat space as determined by the vertical distribution of this primary productivity. Another effect of clearcutting which may benefit hunting spiders is the increase of felled decomposing trees and branches which may not only increase the numbers of some decomposer chain arthropods which serve as spider food, but also increase the supply of shelters required by some hunting spiders.

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