The Proportion of Soldiers in Termite Colonies: a List and a Bibliography (Isoptera)

by

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ABSTRACT

The percentages of soldiers found in termite colonies and the references of all known works are presented.

INTRODUCTION

Little experimental work has been done toward quantifying the caste proportions that are normal in colonies of different species of termites. However, the discovery that juvenile hormone analogs can cause the production of excess soldiers in termite colonies has recently created interest in the normal proportions of soldiers (Chu et al. 1974, French 1974, Hrdý 1972, Hrdý and Krěček 1972, Lenz 1976, Springhetti 1974, Wanyoni 1974, Wanyoni and Lüscher 1973).

Adult soldiers are seldom, perhaps never, food producers; their function is colony protection. The optimal proportion of soldiers for a species has apparently evolved through selection of the mix of castes that will minimize the energy expended in producing the maximum number of virgin males and females while maintaining adequate defense of the colony (Wilson 1971). An excess number of soldiers would burden the colony because the soldiers must be fed by food-producing members. Such a disruption might break down the social structure of a colony and could be used to control termite populations.

This paper presents data on the proportion of soldiers found in termite colonies for 112 species of termites. Data from studies dealing with incipient colonies are excluded because the proportion of soldiers in incipient colonies is not representative of that in mature ones. The proportions presented often are from observations made by scientists who were concerned with subjects other than termite population biology. For example, in studies where laboratory colonies were used, the proportions are the scientist's approximation of natural colony composition. Termite families are in evolutionary order; subfamilies and species are in alphabetical order under each family. The mean percentage of soldiers, a range, or both are given for each species and the source from

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which the information was taken is cited, except when the data are from my own observations. The status of the colony or foraging groups from which each sample was taken is indicated by the symbols ec (entire colony), fg (foraging group), lc (laboratory colony), sc (sampled colony, that is, sample taken from a mound), pg (peripheral gallery), and ? (unknown). Where percentages are from only one colony, foraging group, or sampled colony the symbols oec, ofg, or osc, are used.

The paper also presents a bibliography that is the first extensive compilation of material that deals with the proportion of soldiers in termite colonies.

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The percentage of soldiers in colonies or foraging groups of termites

Family, subfamily, and species	Percentage $\bar{X}$	Percentage Range	Status	Authority
Mastotermitidae				
Mastotermes darwininensis Froggatt	--	1.0-2.0	ec	Gay and Calaby 1970
M. darwiniensis	6.0	3.1-10.0	ec	Watson and Metcalf[2]
Kalotermitidae				
Calcaritermes parvinotus Light	2.7	--	oec	Nutting 1970
Cryptotermes brevis (Walker)	2.2	--	ec	McMahan 1966
C. cavifrons (Banks)	2.2	--	sc	Banks and Snyder 1920
C. cavifrons (Banks)	0.4	--	lc	Hrdý and Zelený 1967
C. cyanocephalus Light	1.2	--	ec	Pangga 1936
C. fatulus Light	3.8	--	oec	Nutting 1970
C. havilandi (Sjöstedt)	1.5	0.4-26.9	ec	Butterworth et al. 1966
C. havilandi (Sjöstedt)	6.3	--	?	Bouillon 1970
Glyptotermes dilatatus (Bugnion and Popoff)	3.9	--	ec	Danthanarayana and Fernando 1970
Incisitermes marginipennis (Latreille)	6.4	--	oec	Nutting 1970
I. minor (Hagen)	4.3	4.0-8.3	ec	Harvey 1934
I. minor (Hagen)	--	1.6-6.3	ec	Harvey 1942
I. minor (Hagen)	1.8	--	oec	Nutting 1970
I. platycephalus (Light)	5.5	4.2-13.3	ec	Nutting 1970
I. scharwarzi (Banks)	8.7	--	osc	Banks and Snyder 1920
Kalotermes spp.	10.0	--	ec	Hegh 1922

Family, subfamily, and species	Percentage $\bar{X}$	Range	Status	Authority
K. flavicollis (Fabr.)	5.0	--	ec	Harris 1954
K. flavicollis (Fabr.)	5.3	1.9-8.6	ec	Grassé and Noirot 1958
K. flavicollis (Fabr.)	3.0	--	ec	Lüscher 1961
K. flavicollis (Fabr.)	3.0	--	ec	Lebrun 1966
Marginitermes hubbardi (Banks)	2.9	1.4-12.7	ec	Nutting 1970
Neotermes bosei (Snyder)	--	1.3-7.8	ec	Sen-Sarma and Mishra 1972
Neotermes castaneus (Burmeister)	14.4	--	osc	Banks and Snyder 1920
N. castaneus (Burmeister)	1.3	--	lc	Hrdý and Zelený 1967
N. connexus Snyder	2.3	--	ec	Bess 1970
N. dalbergiae (Kalshoven)	1.5	--	sc	Kalshoven 1960
N. greeni (Desneux)	1.7	--	ec	Danthanarayana and Fernando 1970
N. jouteli (Banks)	--	5.0-5.4	sc	Banks and Snyder 1920
N. jouteli (Banks)	0.9	0.8-0.9	lc	Hrdý and Zelený 1967
N. jouteli (Banks)	8.1	2.6-16.7	ec	Nagin 1972
N. larseni (Light)	2.5	--	oec	Nutting 1970
N. tectonae (Dammerman)	9.1	--	ec	Miller 1942
Paraneotermes simplicicornis (Light)	11.8	4.9-22.0	fg	Nutting 1966a, 1970
P. simplicicornis (Light)	10.3	--	fg	
Postelectrotermes militaris (Desneux)	2.9	--	ec	Danthanarayana and Fernando 1970
Pterotermes occidentis (Walker)	2.2	0.0-6.3	ec	Nutting 1966b, 1970
P. occidentis (Walker)	2.3	--	ec	

Family, subfamily, and species	Percentage $\bar{X}$	Range	Status	Authority
Hodotermitidae				
Hodotermitinae				
Anacanthotermes macrocephalus (Desneux)	10.2	--	ofg	Roonwall 1975
A. ochraceus (Burmeister)	1.0	--	ec	Clément 1956
Archotermopsis wroghtoni (Desneux)	5.0	--	oec	Sen-Sarma[3]
Hodotermes mossambicus (Hagen)	1.6	0.4-3.5	lc	Hewitt et al. 1969
Stolotermitinae				
Stolotermes ruficeps Brauer	7.0	2.0-40.0	ec	Morgan 1959
Termopsinae				
Zootermopsis angusticollis (Hagen)	5.6	--	osc	Banks and Snyder 1920
Z. laticeps (Banks)	2.1	--	ec	Nutting 1965
Z. laticeps (Banks)	2.1	0.9-5.8	ec	Nutting 1970
Z. nevadensis (Hagen)	--	0.5-12.5	ec	Howse 1970
Rhinotermitidae				
Coptotermitinae				
Coptotermes formosanus Shiraki	5.0	--	ec	Nakajima et al. 1964
C. formosanus Shiraki	--	20.0-60.0	fg	Nakajima et al. 1964
C. formosanus Shiraki	10.0	--	lc	Smythe and Mauldin 1972
C. formosanus Shiraki	10.0	--	ec	King and Spink 1974
C. formosanus Shiraki	10.0	--	ec	King and Spink 1975
C. heimi (Wasmann)	33.0	--	?	Sen-Sarma 1974

Family, subfamily, and species	Percentage $\bar{X}$	Range	Status	Authority
C. lacteus (Froggatt)	2.6	1.8-2.9	ec	Gay and Greaves 1940
C. vastator Light	9.1	--	ec	Pangga 1936
Heterotermitinae				
Heterotermes aureus (Snyder)	4.0	--	fg	Nutting 1970
H. aureus (Snyder)	0.7	--	fg	Nutting et al. 1973
H. aureus (Snyder)	1.5	--	fg	
H. indicola (Wasmann)	--	3.0-5.0	?	Becker 1962
Reticulitermes flavipes (Kollar)	--	8.4-10.8	sc	Banks and Snyder 1920
R. lucifugus (Rossi)	--	0.3-1.0	ec	Hrdý and Krecek 1972
R. tibialis Banks	1.9	--	osc	Banks and Snyder 1920
Rhinotermitinae				
Prorhinotermes simplex (Hagen)	11.2	--	osc	Banks and Snyder 1920
P. simplex (Hagen)	22.2	--	lc	Miller 1942
P. simplex (Hagen)	6.9	--	lc	Hrdý and Zelený 1967
Termitidae				
Termitinae				
Amitermes emersoni Light	2.6	--	fg	
A. hastatus (Haviland)	--	0.5-0.7	?	Hegh 1922
A. hastatus (Haviland)	--	0.6-4.8	?	Bouillon 1970
A. laurensis Mjöberg	<0.1	--	?	Howse 1970

Family, subfamily, and species	Percentage $\bar{X}$	Range	Status	Authority
A. minimus Light	1.0	--	fg	
A. silvestrianus Light	33.3	--	ofg	
A. wheeleri (Desneux)	--	2.1-5.0	fg	Banks and Snyder 1920
A. wheeleri (Desneux)	1.4	--	fg	
Capritermes spp.	1.3	--	?	Hegh 1922
Cephalotermes rectangularis (Sjöstedt)	--	$\leq$0.2-0.2	ec	Grassé 1939
Cubitermes exiguus Mathot	1.2	0.6-1.2	?	Bouillon 1970
C. exiguus Mathot	--	0.7-2.9	ec	Lee and Wood 1971
C. sankurensis Wasmann	2.4	2.0-2.8	ec	Bouillon 1970
C. severus Silvestri	--	0.8-1.0	?	Bodot 1969
C. subcrenulatus Silvestri	0.9	0.4-1.4	ec	Bodot 1970
Dicuspiditermes incola (Wasmann)	1.2	--	?	Sen-Sarma 1974
D. nemorosus (Haviland)	2.4	0.9-4.5	ec	Matsumoto 1976
D. nemorosus (Haviland)	2.8	1.8-4.6	ec	Matsumoto 1976
Drepanotermes perniger (Froggatt)	--	1.0-4.4	sc	Watson and McMahan[4]
D. perniger (Froggatt)	--	12.7-13.9	fg	Watson and McMahan[4]
D. perniger (Froggatt)	--	5.6-9.4	pg	Watson and McMahan[4]
D. rubiceps (Froggatt)	8.2	--	sc	Watson and McMahan[4]
Gnathamitermes perplexus (Banks)	0.4	--	fg	Nutting et al. 1973
G. perpelxus (Banks)	1.3	--	fg	
G. tubiformans (Buckley)	1.7	--	ofg	Banks and Snyder 1920

Family, subfamily, and species	Percentage $\bar{X}$	Range	Status	Authority
G. tubiformans (Buckley)	1.3	0.0-1.8	fg	Bodine 1973
Homallotermes foraminifer (Haviland)	8.0	5.5-17.1	ec	Matsumoto 1976
Labidotermes celisi Deligne and Pasteels	1.0	0.0-4.5	ec	Bouillon and Wabo 1973
Microcerotermes spp.	2.0	--	ec	Hegh 1922
Microcerotermes beesoni Snyder	--	0.6-3.8	sc	Sen-Sarma and Mishra 1969
M. cameroni Snyder	1.5	1.0-1.9	lc	Hrdý 1970
M. fuscotibialis (Sjöstedt)	--	1.0-1.2	ec	Grassé 1939
M. parvulus (Sjöstedt)	--	0.5-1.1	ec	Lepage 1974
M. septentrionalis Light	3.5	2.2-7.8	fg	Nutting 1970
Pericapritermes heteronotus Silvestri	1.0	--	?	Bouillon 1970
Procubitermes sjöstedti (von Rosen)	--	1.0-2.0	?	Hegh 1922
P. sjostedti (von Rosen)	1.3	--	?	Bouillon 1970
Protohamitermes spp.	0.0	--	?	Emerson [5]
Tuberculitermes bycanistes (Sjöstedt)	1.0	--	?	Bouillon 1970
Macrotermitinae				
Acanthotermes acanthothorax (Sjöstedt)	2.3	--	?	Bouillon 1970
Macrotermes bellicosus (Smeathman) (as M. natalensis (Haviland))	2.4	--	ec	Grassé 1939
M. carbonarius (Hagen)	7.4	2.5-17.2	ec	Matsumoto 1976
minor soldier	5.3	1.7-11.8		
major soldier	2.3	1.0-5.5		
M. gilvus (Hagen)	8.9	--	ec	Pangga 1936

Family, subfamily, and species	Percentage $\bar{X}$	Range	Status	Authority
M. malaccensis (Haviland)	6.3	5.3-8.5	ec	Matsumoto 1976
M. natalensis (Haviland)	9.9	--	ec	Hegh 1922
M. subhyalinus (Walker)	1.3	1.3-3.5	ec	Lepage 1974
M. ukuzii Fuller	34.0	--	sc	Rohrman[6]
minor soldier	32.0			
major soldier	2.0			
M. ukuzii Fuller (all minor soldiers)	6.0	--	fg	Rohrman[6]
Odontotermes obesus (Rambur)	--	4.0-8.8	ec	Gupta, 1953
O. parvidens Holmgren	2.2	--	?	Sen-Sarma 1974
O. redemanni (Wasmann)	--	25.0-30.0	sc	Banerjee 1966
O. redemanni (Wasmann)	2.4	--	?	Sen-Sarma 1974
O. smeathmani (Fuller)	4.6	3.4-5.7	ec	Lepage 1974
Paracapritermes spp. (as Mirotermes)	1.3	--	?	Hegh 1922
Pseudacanthotermes spiniger (Sjöstedt)	2.3	--	?	Hegh 1922
minor soldier	2.0			
major soldier	0.3			
Apicotermitinae				
Anoplotermes spp.[7]	0.0	--	?	Bouillon 1970
Anoplotermes fumosus (Hagen)[8]	0.0	--	?	Emerson[5]

Family, subfamily, and species	Percentage $\bar{X}$	Range	Status	Authority
A. shillongensis Roonwall and Chhotani[8,9]	0.0	--	?	Roonwal 1970
Apicotermes desneuxi Emerson	1.3	--	ec	Bouillon 1964
A. desneuxi Emerson	0.7	--	?	Bouillon 1970
A. gurgulifex Emerson	1.3	--	ec	Bouillon 1964
A. gurgulifex Emerson	1.0	--	ec	Bouilon 1970
A. kisantuensis Sjöstedt	0.8	--	ec	Bouillon 1964
Skatitermes psammophilus Coaton	0.0	--	ec	Coaton 1971
S. watti Coaton	0.0	--	ec	Coaton 1971, Kistner 1975
Speculitermes spp.[8,10]	0.0	--	?	Emerson[5]
Speculitermes sinhalensis Roonwall and Sen-Sarma[10]	--	0.2-0.4	?	Roonwall 1970
Nasutitermitinae				
Armitermes spp.	2.0	--	?	Hegh 1922
Bulbitermes singaporensis (Haviland)	17.3	11.7-24.5	ec	Matsumoto 1976
Cornitermes spp.	5.0	--	?	Hegh 1922
Hospitalitermes hospitalis (Haviland)	9.9	--	ec	Pangga 1936
Longipeditermes longipes (Haviland)	29.6	--	ec	Matsumoto 1976
Nasutitermes costalis (Holmgren)	9.3	2.9-25.7	ec	Krečěk 1970
N. costalis (Holmgren)	29.8	--	lc	Hrdý and Zelený 1967
N. dunensis Chatt. and Thak.	--	5.2-17.1	?	Sen-Sarma[3]

Family, subfamily, and species	Percentage $\bar{X}$	Range	Status	Authority
N. exitiosus (Hill)	9.9	--	ec	Gay and Wetherly 1970
N. exitiosus (Hill)	11.1	--	ec	Holdaway et al. 1935
N. exitiosus (Hill)	17.5	--	lc	Gay et al. 1955
N. exitiosus (Hill)	6.4	6.1-6.6	sc	McMahan 1974
minor soldiers	6.3	6.0-6.6		
major soldiers	0.1	0.04-0.16		
N. exitiosus (Hill)	5.2[11]	--	sc	McMahan 1974
minor soldiers	0.8			
major soldiers	4.3			
N. exitiosus (Hill)	27.8[11]	--	fg	McMahan 1974
minor soldiers	1.4			
major soldiers	26.5			
N. exitiosus (Hill)	--	6.3-7.4	ec	McMahan 1976[12]
minor soldiers		5.3-6.0		
major soldiers		0.04-0.14		
presoldiers		0.8-1.4		
N. luzonicus (Oshima)	20.1	--	ec	Pangga 1936
N. rippertii (Rambur)	7.3	--	lc	Hrdý and Zelený 1967
N. rippertii (Rambur)	19.2	2.8-35.0	sc	Kŕeček 1970
Tenuirostritermes cinereus (Buckley)	25.0	--	sc	Banks and Snyder 1920
T. tenuirostris (Desneux)	8.0	--	sc	Banks and Snyder 1920

Family, subfamily, and species	Percentage $\bar{X}$	Range	Status	Authority
T. tenuirostris (Desneux)	25.0	--	ec	Weesner 1953
T. tenuirostris (Desneux)	41.8	20.7-71.3	fg	Nutting et al. 1974
Trinervitermes geminatus (Wasmann)	14.3	--	?	Bouillon 1970
T. trinervius (Rambur)	15.6	--	ec	Lepage 1974
minor soldier	9.9			
major soldier	5.7			

[2] Personal communication from J. A. L. Watson, on file at USDA Forest Service, Gulfport, Miss.

[3] Personal communication from P. K. Sen-Sarma, on file at USDA Forest Service, Gulfport, Miss.

[4] Personal communications from J. A. L. Watson and E. A. McMahan on file at USDA Forest Service, Gulfport, Miss.

[5] Personal communication from A. E. Emerson, on file at USDA Forest Service, Gulfport, Miss.

[6] Personal communication from G. Rohrman on file at USDA Forest Service, Gulfport, Miss.

[7] Since Bouillon's (1970) study, Sands (1972) has revised the classification of many of the soldierless termites of Africa. Many of the species which were attributed to Anoplotermes, a genus confined to the Neotropical region, were reassigned by Sands.

[8] Soldier caste has not been discovered.

[9] Because Sands (1972) confines Anoplotermes to the Neotropical region, it is probable that A. shillongensis should not be considered a member of the genus Anoplotermes.

[10] Emerson points out that the Oriental Speculitermes probably should not include New World species which are currently assigned to that genus. (Personal communication from A. E. Emerson on file at USDA Forest Service, Gulfport, Miss.)

[11] McMahan considered this colony to be aberrant. It was sawed in half and put together again and reexamined 2 years later. It had an abnormally high percentage of major soldiers. (Personal communication from E. A. McMahan on file at USDA Forest Service, Gulfport, Miss.

[12] Personal communication from E. A. McMahan on file at USDA Forest Service, Gulfport, Miss.

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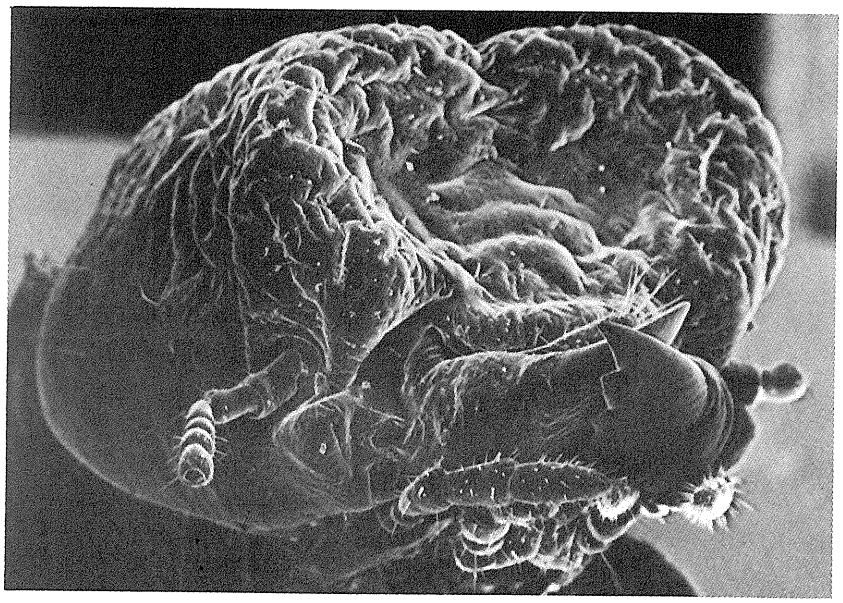

Head of a soldier of Cryptotermes brevis (Walker) (X115). This is the phragmatic soldier that protects the colony by plugging up a hole in the nest with its head. This specimen was intercepted at Gulfport, Mississippi from a stuffed chair from Hawaii. Photo by G. F. Rohrmann. Specimen from M. I. Haverty.

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