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MILDRED EILEEN LOWE,
*DEPARTMENT OF BIOLOGY, LOUISIANA COLLEGE,
PINEVILLE, LOUISIANA*

TULANE UNIVERSITY

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DOMINANCE-SUBORDINANCE RELATIONSHIPS IN THE CRAWFISH *CAMBARELLUS SHUFELDTII* [1]

MILDRED EILEEN LOWE,
*Department of Biology, Louisiana College,
Pineville, Louisiana*

Hierarchies based on dominance and accompanying subordination have been known among vertebrates for a number of years. Modern studies of this subject are generally dated from the 1922 paper by Schjelderup-Ebbe (from Schjelderup-Ebbe 1935). He found that individuals in small flocks of domestic chickens usually were arranged in a definite linear order of dominance based upon pecking. This was termed peck-right. Within a flock, Bird A could peck B, C, D, E; B could peck C, D, E; and so on down to E which lacked a subordinate individual on which to peck. This hierarchy was established during the first few meetings between two individuals and remained constant until a subordinate bird pecked back. If the resisting bird was successful, a new dominance order was established. Masure and Allee (1934) found a less strict type of dominance order among pigeons. In this order the dominant animal may receive some pecks from subordinates and still remain dominant. This was called peck-dominance.

Further advances have been summarized by Allee (1942, 1945, 1952), Allee et al. (1950) and Collias (1944). Hierarchies based on dominance have been reported for all vertebrate classes except Agnatha and Amphibia.

Recently Allee and Dickinson (1954) reported a dominance order based on size in the smooth dogfish, *Mustelus canis.* When two animals were swimming along paths that would meet, the smaller swerved enough to avoid contact with the larger. Only two instances were recorded in which one individual either chased or "pecked" another.

Dominance hierarchies have been found in fish; the subject has been summarized by Noble (1939). Both the peck-right and the peck-dominance types of hierarchy have been found. In some species, as in the green sunfish (Greenberg, 1947), dominance relationships were complicated further by the defending of territory by the males during breeding season. Tinbergen (1953) has published on territoriality of the three-spined stickleback in great detail. Newman (1956) found that two species of trout set up interspecific dominance orders under natural and artificial conditions.

While no hierarchies of dominance have been reported for amphibians, aggressive behavior has been shown. If two or more male wood frogs, *Rana sylvatica,* held the same female, they tried to dislodge each other by kicking with the hind legs (Banta 1914 from

[1] This work was done in partial fulfilment of the requirements for the Master of Science degree at Tulane University.

Collias 1944). Martof (1953) has recently shown territoriality in the green frog, *Rana clamitans* . Small groups of frogs tended to maintain the same spatial relation to each other for several nights even while moving from one pond to another.

The social behavior of the American chameleon, *Anolis carolinensis,* has been studied more than any other reptile (Greenberg and Noble, 1944). Usually one male dominated the individuals in a large cage with the other males equally subordinate to him. Females formed their own dominance order within the territory held by the dominant male.

More is known about social organization in domestic fowl than in any other group of vertebrates. Studies are being continued on chickens and other birds and the concept of dominance hierarchies has been extended to birds in semiferal and feral conditions (Odum, 1942; Sabine, 1949).

Uhrich (1938) was the first to study dominance relations in mice. He found one animal dominant and the others equally subordinate; in effect, a two-ranked dominance order. Carpenter (1952) reviewed the behavior of infra-human primates in natural conditions. Here dominance implied leadership and also several animals as a group might be dominant over another group. Hierarchies based on dominance have been reported for mice, rats, squirrels, cats, lions, dogs, horses, cows, monkeys, apes and men (Allee, 1945).

Pardi (1948, summarizing Italian articles of 1942 and 1946) demonstrated the existence of a dominance order among the females of the wasp *Polistes gallicus.* When two individuals met in the nest, one behaved as dominant, the other as dominated. Typically the dominant struck the head of the dominated quickly and repeatedly while the latter remained motionless. In a series of contacts between two individuals, the same individual always dominated. Occasionally two individuals appeared equivalent. They fought violently and struck one another with the prothoracic legs, the antennae and the stings.

A rigorous linear hierarchy resulted from contacts between inhabitants of the same nest, with only the reproductive females and the workers participating in the organization. All males behaved as dominated and did not establish hierarchies among themselves. The hierarchy was established initially in accordance with small ovarian differences, the female having the largest ovaries taking the dominant position. The ovaries of the other reproductives began to atrophy. Older workers dominated younger. If the queen died or was removed the oldest worker (in subdominant position) took her place and soon was able to lay fertile eggs. Deleurance (1952) confirmed Pardi's findings.

Jacobs (1955) reported the occurrence of aggressive behavior in the dragonflies *Perithemis tenera* and *Plathemis lydia.* He found that during the mating season males defended an area around oviposition sites and drove other males from this territory.

The beginning of a hierarchy based on size and strength was found in the hermit crab *Pagurus longicarpus* (Allee and Douglis, 1945). The crab lived with its soft abdomen tucked into an otherwise empty snail shell. If the shell was taken away and no vacant shell was available, the crab forcibly removed a smaller animal from its shell and immediately occupied the shell. An animal with an imperfect shell might take over a more perfect shell from its smaller companion. Hermit crabs without shells attacked others that were housed regardless of size differences. The attacker was never successful when the two were of equal size or when the housed individual was the larger.

Two-, three-, and four-ranked hierarchies have been reported by Douglis (1946a) in the lobster *Homarus americanus*. When two animals were placed together, the subordinate was kept at one end of an aquarium and attacked whenever it attempted to leave the area. In groups of three and four lobsters, signs of dominance were seldom seen when the dominant was present. The lower ranking animals became more aggressive when the animals dominating them were removed. Larger animals were dominant over smaller and males generally were dominant over females.

In another experiment Douglis (1946b) found lobsters dominant over the blue crab, *Callinectes sapidus,* the spider crab, *Libinia emarginata,* and the large hermit crab, *Pagurus polycarus*. Blue crabs dominated the spider and hermit crabs.

Bovbjerg (1953) studied dominance relations in the crawfish *Orconectes virilis*. Experimenting with groups of four equal-sized animals of the same sex, he found they established four-ranked dominance orders. An animal did not necessarily win every encounter with a subordinate crawfish. Even the lowest ranking animal won a few fights, but a definite dominance pattern could be distinguished readily by comparing the total number of encounters between individuals. Within five days a dominance order was established in each of the ten groups that Bovbjerg studied. This order remained stable for the duration of his experiment, for fifteen more days. Later Bovbjerg (1956) extended his studies to include the crawfish *Procambarus alleni* and found essentially the same relationships as in *Orconectes*. This indicated that a dominance order based upon learned recognition of individuals may occur in an invertebrate group.

Aggressive behavior has been noted in cuttlefish *Sepia officinalis* by Tinbergen (1939). While studying chromatophore changes he found that one male would fight another when certain color patterns were displayed during the mating season. Aggressive actions have been reported in common squids, *Loligo* spp. by Bovbjerg (1953) and Allee and Dickinson (1954). Allee and Dickinson (1954) stated that many invertebrates have been observed without detecting any sign of dominance behavior; fiddler crabs, termites, and ants serving as examples.

The present paper extends observations of dominance-subordinance relationships to another invertebrate species, *Cambarellus shufeldtii,* a small crawfish seldom larger than 25 mm in total length. This study again verifies the occurrence of a dominance order in invertebrate animals and, in particular, confirms Bovbjerg's finding that crawfish establish dominance hierarchies.

Materials and Methods

The experimental animals were obtained by dip-netting from a lowland pond at Crown Point, Louisiana. The pond was mud-bottomed and the water clear and exposed to direct sunlight a large part of each day. The crawfish were collected in the shallow water around the edge of the pond where the principal aquatic plant was alligator weed, *Alternanthera philoxeroides.* This habitat is typical for the species (Penn, 1950). Four collections were made.

Stock animals, maintained in two and one-half gallon aquaria, were fed on lettuce every evening and on dog food every third day. Water was changed after each meat meal. Seventy-five to 100 animals were placed in each aquarium. Except for initial mortality, probably due to injury during collection, the crawfish were maintained with very low mortality for a three-month period.

Experimental animals were maintained in shallow round plastic dishes nine centimeters in diameter. No attempt was made to simulate natural conditions but only to confine the crawfish in an environment that would induce the greatest number of encounters between individuals.

Only adult animals, 17 to 22 mm total length, were used unless otherwise indicated. Individual animals were identified by marking the carapace with various colors of fingernail polish. The four colors used were purple (P), green (G), yellow (Y), and red (R). When more than four experimental animals were placed together, a combination of colors was used to identify the additional individuals; yellow and purple (YP), yellow and green (YG), etc.

Dominance relations were manifested through tension contacts; *i.e.,* any encounter between two crawfish in which one clearly retreated following a head-on meeting. As adopted from Bovbjerg (1953) four types of tension contacts were observed; fight (F), strike (S), threat (T), avoidance (A).

The *fight* is bilateral: two crawfish meet, each striking out at the other, often locking chelae, occasionally catching the other's rostrum or a walking leg. Infrequently one animal attempts to jerk away while being held by the other, thereby losing a part of its body. The fight generally lasts less than a minute but the longest observed was eight minutes. It is terminated by the quick backward retreat of one of the animals. After this backward movement the two crawfish are no longer in contact, and the animal which retreated turns and moves to another part of the dish. The victor frequently follows the loser and hits at its tail as it departs.

The *strike* is a unilateral aggression in which one animal approaches with spread chelae which are suddenly thrust out to hit the other crawfish. The second animal retreats without defending itself.

The *threat* is merely an approach with chelae held in strike position. This is sometimes sufficient to cause retreat of the other animal before the aggressor actually strikes the other.

In *avoidance* no sign of threatening behavior is discernible yet the subservient crawfish retreats from a moving animal or gives another a wide berth in its own movements.

Only head-on encounters between individuals were included. Random crawling over one another, retreat from a rear contact, or a general movement of the whole group were not considered tension contacts.

Each group was observed for fifteen minutes every day for the duration of each experiment, five to 20 days. Observations were made between six and eight o'clock in the morning because the crawfish were most active during this period. The animals were active also in the evening. This daily rhythm of activity reflects metabolic activity as shown by Fingerman (1955). He found that respiratory rate was maximal about 6 a.m. with a secondary peak at 3-6 p.m.

A Dominance Order

A preliminary investigation was carried out to determine whether *Cambarellus shufeldtii* would establish four-ranked dominance orders. Six groups of four animals were used. Later ten additional groups were set up. Each dish contained animals of similar size ($\pm$ 0.5 mm) and sex. Only form I males and adult females were used.

The data recorded from daily observation periods were compiled into a table as adapted from Bovbjerg (1953). The data on one group are shown in Table 1. The letters heading the vertical and horizontal columns designate individuals by the first letter of the identifying color to enable comparison between any two individuals in the group. Dominance is read horizontally and subordinance vertically. In recording avoidance a dominant contact was credited to the animal avoided. This shows as subordinance for the animal doing the avoiding. Each group was observed for twenty days.

Data from 16 groups of four animals are summarized in Table 2. Each animal is listed by rank. Also given for each animal are the total "dominance contacts" indicating the number of contacts in which it was dominant. The percentage of contacts in which each was dominant, listed as "percent dominant", was obtained from the original tabulations of data (as in Table 1) by dividing the "total dominance contacts" of a particular crawfish by its total number of contacts (*i.e.,*

TABLE 1.
DOMINANCE-SUBORDINANCE RELATIONSHIPS
AMONG FOUR INDIVIDUALS
(GROUP A-1)

Code Letter	Type of Tension Contact	Code Letter of Individuals				Total Dominance Contacts		Rank
		P	G	Y	R			
P	Fight Strike Threat Avoidance		2 1	1		3 1	4	4
G	Fight Strike Threat Avoidance	8 1		2 1	1	11 2	13	3
Y	Fight Strike Threat Avoidance	12 14 3	18 6 5 1		9 1	39 21 8 1	69	2
R	Fight Strike Threat Avoidance	10 16 13 4	30 8 3	21 15 5 2		61 39 21 6	127	1
Total Subordinance Contacts		81	74	47	11		213	

"total dominance contacts" plus "total subordinance contacts"). For example, the "percent dominance" of crawfish R (Table 1) would be calculated:

$$\frac{127}{127 + 11} = \frac{127}{138} = 0.92 = 92\%$$

Groups C-9 and C-10 are not included in analyzing Table 2 as the dominant animal in each of these two groups was carrying eggs. These results are thus not comparable with the other fourteen groups as an ovigerous female reacts differently than other females in its group.

The tabulated data for the remaining fourteen groups included a total of 3326 observed tension contacts, varying from 192 to 297 contacts per group, with a mean of 237. Females were slightly more active than males with a mean of 245 and extremes of 207 and 297. The number of tension contacts among males ranged from 192 to 279 with a mean of 231.

TABLE 2.
DOMINANCE ORDER OF SIXTEEN GROUPS OF FOUR CRAWFISH ESTABLISHED OVER A PERIOD OF 20 DAYS

Social Group	Dominance Order	Dominance Contacts		Percent Dominant	Social Group	Dominance Order	Dominance Contacts		Percent Dominant
			Group Total					Group Total	
A-1	R	127		92	C-3	G	123		95
male	Y	69		59	male	Y	60		57
	G	13		15		P	37		31
	P	4	213	5		R	4	224	4
A-2	R	151		94	C-4	P	121		79
male	Y	72		55	male	G	66		55
	G	31		27		R	14		19
	P	7	261	6		Y	15	216	18
A-3	G	150		93	C-5	P	122		92
male	P	45		48	female	R	64		58
	R	17		18		Y	15		15
	Y	4	216	5		G	6	207	6
A-4	G	119		90	C-6	Y	152		96
male	P	41		55	female	R	73		57
	Y	26		27		P	48		36
	R	6	192	7		G	5	278	4
A-5	R	163		94	C-7	P	143		88
female	Y	63		57	female	G	71		50
	P	22		20		Y	55		39
	G	5	253	4		R	28	297	19
A-6	G	162		82	C-8	P	130		95
female	P	113		63	female	Y	73		57
	R	37		27		R	20		23
	Y	5	217	4		G	3	226	3
C-1	Y	144		87	C-9	R	167		77
male	R	76		59	female	G	92		60
	G	39		32		Y	48		36
	P	20	279	15		P	13	320	10
C-2	G	140		90	C-10	G	151		79
male	R	67		54	female	Y	108		48
	P	31		26		P	76		52
	Y	9	247	10		R	11	346	9

Forty-six percent of the tension contacts were fights (Table 3). The strike accounted for 31% of the total contacts; the threat, 15%; and avoidance, 8%. The percentages were not appreciably different for male and female groups. Totals for groups C-9 and C-10 were not included.

Comparison of tension contacts of any two crawfish furnished the criterion for ranking the individuals of a group. This was less reliable in determining the third- and fourth-ranking individuals where contacts between these low-ranking animals were few. Ranking by total number of dominant contacts corroborated pair-contact data with one exception (C-4). Percent dominance calculations also agreed. Rank-

TABLE 3.
TYPES OF TENSION CONTACTS TOTALS FOR TABLE 2

Type Contact	Number of Contacts	Percent of Total
F	1530	46
S	1031	31
T	499	15
A	266	8
Total	3326	

ing by total subordinate contacts always pointed out the dominant and often revealed the other three ranks, but occasionally was unreliable for the lower ranks.

Pair-contact data refers to the comparison between two animals of the same group; *i.e.,* Table 1, "G" had nine positive tension contacts over "P" (eight fights, one strike) while "P" had only three positive contacts over "G". The term positive tension contacts refers to the contacts in which an animal was dominant over another animal in the same dish.

No pattern of selective behavior toward lower-ranking animals was noted. The dominant animals had positive contacts with the second-ranking animals 621 times, with the third-ranking 640 times, and with the fourth-ranking 667. The subdominant crawfish had 156 positive contacts with the dominants and 377 and 359 positive contacts with the third- and fourth-ranking animals, respectively. The third-ranking individual had 363 contacts over the fourth, but only 42 and 87 such contacts with the dominant and subdominant. The fourth-ranking animal had 12, 36, and 73 positive contacts respectively with the three individuals above it in dominance. Higher ranking individuals often fought when attacked while lower ranking crawfish retreated at the strike or threat of a more dominant animal.

Table 4 shows the results of experiment C-1 tabulated by five-day periods. At first there were many fights in the group but as dominance patterns became established fighting gave way to strike, threat and avoidance. During the first few days an animal seldom completely avoided another or responded to a threat. The lower ranking animals were the first to retreat at signs of milder forms of aggression and then the subdominant reacted. Aggressive behavior and thus the number of tension contacts between individuals became less the longer the animals remained together.

Within the first five days a dominance order, which remained constant throughout the period of observation, was usually established. The dominant individual generally asserted its dominance during the initial period of observation; the subdominant became apparent soon afterward. The third- and fourth-ranking animals often took a little longer to establish their final positions.

This formation of dominance order corroborates the results obtained

TABLE 4.
DOMINANCE RELATIONSHIPS OF GROUP C-1 BY FIVE-DAY PERIODS

Code Letter	Type of Tension Contact	June 18-22				June 23-27				July 28-July 2				July 3-7				Total				Total	Rank
		P	G	R	Y	P	G	R	Y	P	G	R	Y	P	G	R	Y	P	G	R	Y		
P	F		4	2	1		3	1	1		2	1							9	4	2	15	4
	S		1				1	1			2								4	1		5	
	T																						
	A																						
	Total		5	2	1		4	2	1		4	1							13	5	2	20	
G	F	4		2	4	4		1	1	4		1		1				13		4	5	22	3
	S	1			2	1		1	1	2		1		4				8		2	3	13	
	T									2				1				3				3	
	A									1								1				1	
	Total	5		2	6	5		2	2	9		2		6				25		6	8	39	
R	F	5	8		6	4	4		1	8	4			2	2		1	21	18		8	47	2
	S		1			3	3		2	2	2		1	5				10	6		3	19	
	T									3				3	1			6	1			7	
	A									1				2				3				3	
	Total	5	9		6	7	7		3	14	6		1	12	3		1	40	25		11	76	
Y	F	6	5	9		4	10	6		4	3	4		1	2	2		15	20	21		56	1
	S	3	4	2		6	6	8		1	3	5		2	1	2		12	14	17		43	
	T	2	2	1		5	3	4		4	1			5	3	3		16	9	8		33	
	A					2				2				4	3	1		8	3	1		12	
	Total	11	11	12		17	19	18		11	7	9		12	7	8		51	46	47		144	

by Bovbjerg (1953) with *Orconectes virilis.* In Bovbjerg's experiment, however, the subordinate animals were less aggressive, especially the subdominant. As a consequence there was less fighting and a corresponding increase in the response to strike and threat.

As a check on the interpretation of these observations the crawfish were shifted to new dishes in a manner which Bovbjerg termed social inversion. From each of the above groups, the dominant individual was removed and isolated. Observations were continued on the behavior of the three remaining in the original dish. After a five-day period the emergent dominant was removed and placed with the isolated dominant animal. Observations were then made on the behavior of this inverted group as well as on the remaining two in the original grouping. The next emergent dominant from the original group was placed with the inverted group after five days. Finally, after another five-day period, the remaining fourth-ranking crawfish was transferred, completing the inversion.

Table 5 illustrates this procedure. These are the same animals used in group C-4, Table 2. The figures above the double lines show tension contacts before inversion. Contacts after inversion are shown below the lines. Dominance and subordinance are read in the same manner as in Table 1.

Fourteen of the 16 groups (Table 2) were inverted as described above. With one exception all of the individuals were re-established in their original positions. In two dishes the third and fourth ranks

TABLE 5.
SOCIAL INVERSION
(GROUP D-4)

Individual's Code Letter	Type of Tension Contact	1-5 days				6-10 days				11-15 days				16-20 days				Rank
		Y	R	G	P	Y	R	G	P	Y	R	G	P	Y	R	G	P	
Y	F		2	1			4								1			4
	S																	
	T																	
	A																	
R	F	2				3						1	1	6			1	3
	S	3				6								3				
	T																	
	A																	
G	F	1	5						5		5		1	1	2		1	2
	S	6	4								3		2	6	3			
	T	3	1								3		1	4	2			
	A	1																
P	F							7			2	4		4	1	1		1
	S							5			4	7		2	7	6		
	T							1			1	6		1	6	3		
	A											1			3	2		

were not confirmed due to the death of these animals. In one group the top-ranking animal dropped to second place after loss of a claw. This animal lost its claw five days before conclusion of experiment A-2 but retained its rank until inversion.

In each case, after the top-ranking crawfish was removed, the next ranking individual became more active and asserted its dominance over its remaining companions.

When the subdominant, with its five-day period of dominance, was reintroduced to the original dominant a series of fights soon established the old relationship. Frequently the subdominant repeatedly attacked the dominant, although the dominant won the fights. This behavior gradually ceased and strike and threat by the dominant often were enough to intimidate the subservient animal. To a lesser extent the same behavior was observed when the third-ranking individual was placed with the inverted group.

On the last day of this experiment a few of the animals molted. Within the next two days all except one of the animals under observation had molted and this one molted the following day. This occurred from July 27-29. Only one animal did not complete the molt successfully and none was victimized by its companions. These same animals had molted also between June 12-15. Thus in this experiment molting had little influence on the dominance order.

Four Ranked Dominance Order Among Unlike Individuals

In the previous experiments only animals of similar size and sex were used. To study the effect of size and sex on the dominance order unlike individuals were brought together. Three experiments were performed.

Two Males and Two Females of Similar Size

From eight groups of previously established dominance hierarchies the dominant individuals were removed to create two new groups of four animals, all of the same rank. Two females and two males were placed in each dish. The same procedure was followed for ranks two, three and four. Eight new groups were thus set up, each group containing two males and two females which previously held the same rank. These animals were observed for nineteen days. The results are summarized in Table 6.

In five of the eight groups a female was the dominant animal, while a male was subdominant in a majority of the groups (6 out of 8). Male and female appeared with equal frequency for the third rank, while five females and three males held lowest rank.

Additional data from five similar groups of two males, two females were included with the above in compiling Table 7. These animals were not previously ranked but animals of similar size were placed together. Table 7 shows how the sexes were distributed in each group of four as well as the total number of males and females holding each rank.

In the 13 groups, eight (61.5%) of the dominant animals were female, and five (38.5%) were male. Second-ranking position was the reverse of this; eight males to five females, as was the third rank. The lowest rank was again eight females to five males. This shows that neither sex is greatly dominant over the other. As these groups consisted of similar sized individuals, either male or female may dominate a group depending upon inherent aggressiveness.

TABLE 6.

DOMINANCE ORDER OF EIGHT GROUPS OF FOUR CRAWFISH ESTABLISHED OVER A PERIOD OF 20 DAYS. EACH GROUP CONSISTED OF TWO MALES AND TWO FEMALES OF PREVIOUSLY EQUAL RANK

Group Number	Rank	Dominance Contacts	Percent Dominant	Sex
E-1	R	99	77	♀
	G	86	53	♂
	Y	51	52	♂
	P	9	9	♀
E-2	Y	98	85	♀
	R	60	66	♂
	P	16	22	♂
	G	4	5	♀
E-3	G	93	100	♀
	P	34	44	♂
	Y	18	33	♀
	R	1	2	♂
E-4	R	121	82	♂
	P	77	56	♀
	G	35	28	♀
	Y	3	6	♂
E-5	P	105	77	♀
	R	67	56	♂
	G	52	43	♂
	Y	21	19	♀
E-6	Y	126	91	♂
	P	69	52	♂
	G	22	24	♀
	R	10	11	♀
E-7	P	83	90	♂
	G	64	71	♀
	Y	14	16	♀
	R	4	7	♂
E-8	G	72	82	♀
	P	61	71	♂
	R	30	42	♂
	Y	6	7	♀

TABLE 7.
SEX DISTRIBUTION BY RANK IN GROUPS OF FOUR INDIVIDUALS

Group Number	1	2	3	4
E-1	♀	♂	♂	♀
E-2	♀	♂	♂	♀
E-3	♀	♂	♀	♂
E-4	♂	♀	♀	♂
E-5	♀	♂	♂	♀
E-6	♂	♂	♀	♀
E-7	♂	♀	♀	♂
E-8	♀	♂	♂	♀
E-9	♀	♂	♂	♀
E-10	♂	♀	♂	♀
E-11	♀	♀	♂	♂
E-12	♀	♂	♂	♀
E-13	♂	♀	♀	♂
Totals	5♂ 8♀	8♂ 5♀	8♂ 5♀	5♂ 8♀

A curious fact is brought out by further analysis of the data in Table 7. When a female dominated the group, the other female most often was ranked last with the two males holding ranks two and three. This same phenomenon occurred under male domination. As this appeared in nine of 13 groups, the occurrence seemed rather high to be by chance alone. Only twice were first- and second-ranking animals of the same sex; once two females held these positions and once two males. Why the dominance order should be arranged in this fashion is a question that deserves further study.

Four Animals of Random Size and Sex

Animals were taken at random from the stock aquaria and placed four to a dish. No notes were taken on size or sex until the experiment was concluded. These groups were perhaps slightly closer to natural conditions in including different-sized animals of both sexes, although the groups were still abnormally small and confined to small dishes with no hiding places.

The animals were measured under a binocular microscope with dividers and a millimeter rule. The cephalothorax length was taken to the nearest 0.5 mm. In taking measurements, length of cephalothorax was more convenient to determine than total body length. Total length was twice that of the cephalothorax.

Each group was observed for twenty days except group F-8 (Table 8). As two animals died in this group, it was observed for only eleven days. The data from this group were included in the table as the dominance order had remained constant for seven days before the deaths. In general, larger animals were dominant over smaller regardless of sex (Table 8).

Table 9 shows the size difference between an animal and its next

TABLE 8.
DOMINANCE RELATIONSHIPS AMONG GROUPS OF FOUR CRAWFISH INCLUDING DIFFERENT SIZED INDIVIDUALS OF BOTH SEXES

Group Number	Rank	Dominance Contacts	Percent Dominant	Size (mm)[c] & Sex	Group Number	Rank	Dominance Contacts	Percent Dominant	Size (mm)[c] & Sex
F-1	P	150	95	10.5 ♀[a]	F-7	Y	128	86	9.0 ♂
	G	55	51	9.0 ♂		G	52	47	9.0 ♂
	Y	27	26	8.0 ♂		R	34	30	6.5 ♀
	R	9	8	9.0 ♂		P	15	17	7.0 ♂
F-2	R	125	92	10.0 ♂	F-8[b]	G	53	79	9.5 ♀
	Y	50	55	7.5 ♀		Y	33	52	9.5 ♂
	P	31	28	8.5 ♂		P	18	45	7.5 ♀
	G	17	16	8.5 ♂		R	9	16	7.5 ♀
F-3	Y	120	84	9.5 ♀	F-9	G	101	89	10.0 ♂
	G	100	68	10.0 ♀		R	51	45	7.0 ♂
	R	14	15	8.5 ♂		Y	47	42	7.5 ♀
	P	3	3	7.0 ♀		P	2	3	5.0 ♂
F-4	Y	122	94	9.5 ♀	F-10	Y	106	93	9.5 ♀
	G	58	54	6.5 ♀		R	39	44	7.0 ♀
	P	26	25	7.5 ♂		P	21	24	7.5 ♂
	R	2	5	5.5 ♂		G	12	18	6.0 ♀
F-5	G	154	97	10.5 ♀[a]	F-11	P	77	90	10.5 ♂
	R	32	39	7.0 ♀		G	36	63	8.0 ♀
	Y	27	24	7.5 ♂		Y	9	16	6.5 ♀
	P	17	16	7.5 ♂		R	1	2	5.5 ♀
F-6	R	177	95	9.5 ♀[a]	F-12	P	95	80	9.5 ♀
	Y	42	41	9.0 ♂		G	63	68	10.0 ♂
	G	26	30	8.0 ♂		R	12	16	7.5 ♀
	P	7	5	6.5 ♀		Y	4	16	7.0 ♂

[a] Females carrying eggs at beginning of experiment
[b] This group observed for 11 days only due to death of G and R.
[c] Cephalothorax length.

immediate subordinate. An asterisk indicates that the dominant animal was smaller than its immediate subordinate. This table includes all four ranks. 1.5 mm cephalothorax length, the equivalent of 3 mm total length, appeared to be the critical figure. No animal was dominated by another 3 mm smaller than itself. Of the 48 animals 11 were dominated by individuals one to two millimeters (0.5-1.0 mm cephalothorax length) smaller than themselves. In only two cases was the top-ranking animal smaller than its subordinate and then by only 0.5 mm cephalothorax length. There was no difference in size between animals of adjacent rank in five cases. These size relationships held true throughout all of the experiments.

For the June 11, 1955, collection the 50 largest females and the 50 largest males were measured (Table 10). Both sexes included two animals with a cephalothorax length of 11 mm, but the females as a group were considerably larger than the males. Thus females would dominate males in more encounters than the reverse on the basis of size alone. The observation that either male or female may dominate a group of similar sized individuals (Table 7), leads to the conclusion that females of *C. shufeldtii* may be the more dominant sex because of their larger size.

TABLE 9.
DIFFERENCE IN CEPHALOTHORAX LENGTH BETWEEN ANIMALS OF ADJACENT RANK

Cephalothorax Length (mm)	Number Of Individuals
3.5	1
3.0	2
2.5	4
2.0	2
1.5	9
1.0	3
0.5	2
0.0	5
0.5*	7
1.0*	4

From his observations on *Orconectes virilis,* Bovbjerg (1953) reported that the male appeared more dominant and that low-ranking males were seen fighting and then copulating with high-ranking females. In the present experiments only one pair was seen in copulation and these were two top-ranking animals.

Ovigerous Females with Males and Non-ovigerous Females

As noted from Table 2 (C-9 and C-10) and shown again in experiment F, females with eggs appeared more aggressive than those without eggs (note F-1, F-5, F-6, Table 8). Each of these groups included one female with eggs. This animal was dominant and very aggressive. However, these females were also the largest of their groups. In C-9, C-10, (Table 2) is seen the comparison of crawfish of similar size and sex. In both instances a female carrying eggs was dominant over females without eggs. The average number of tension contacts for the group was 333 as compared to 245 in groups of non-ovigerous females.

TABLE 10.
THE FIFTY LARGEST MALES AND THE FIFTY LARGEST FEMALES OF THE JUNE 11, 1955, COLLECTION

Cephalothorax Length in mm	Number of Males	Number of Females
11.0	2	2
10.5	7	21
10.0	11	17
9.5	15	10
9.0	10	
8.5	5	

In crawfish the eggs are attached to the female's pleopods where they hatch and where the young remain attached through the second instar (Andrews, 1904). In *C. shufeldtii* the time from hatching to the time the young leave the pleopods is about a week to ten days. As no experimental females were seen to lay eggs, the time between egg extrusion and hatching is not known.

Four groups of four animals were established in which every individual carried eggs at the beginning of the experiment. These animals were more active than non-ovigerous females. There was more active fighting among the animals and a stable dominance order was not established as quickly (Table 11). Often the number of positive tension contacts between two individuals was very nearly equal; *e.g.*, in Table 11 (observations from June 18-22) "Y" had 9 victories over "G" to eight defeats; "Y" over "R", 6 to 5; "G" over "R", 15 to 11. As the young were dropped the dominance order changed. In three of the four groups the female whose eggs hatched first was the initial dominant. Very shortly after losing the young she dropped to low rank and another ovigerous female became dominant. When this animal dropped the young it, in turn, was succeeded in the dominant position by an animal which was still carrying young. The experiment was not continued long enough to determine whether the last animal to drop its young remained in the top position or whether one of the other females again gained dominance over the group.

The total number of tension contacts varied from 334 to 417 with an average of 362 (Table 12) as compared with the non-ovigerous females' group average of 245. Fights and strikes accounted for 87% of the total tension contacts as compared to 77% for males and for females not carrying eggs (Table 3). Avoidance was elicited in only 3% of meetings between individuals (compared to 8%).

TABLE 11.
DOMINANCE RELATIONSHIPS AMONG GROUP G-1
FOUR FEMALES CARRYING EGGS

Code Letter	Type of Tension Contact	June 18-22				June 23-27				July 28-July 2				July 3-7				Total				Total	Rank
		P	Y	G	R	P	Y	G	R	P	Y	G	R	P	Y	G	R	P	Y	G	R		
P	F		5	3	3		4	2	1		6		2		1	1	3		16	6	9	31	4
	S		3				2				4				2				11			11	Eggs did
	T		1				4								1				6			6	not develop
	A																						
	Total		9	3	3		10	2	1		10		2		4	1	3		33	6	9	48	
Y	F	9		7	5	7		6	2	5		2	1	3				24		15	8	47	3
	S	6		2	1	12		7	7	5		2		2		7		25		18	8	51	Dropped
	T									2				3				5				5	young 6-27
	A									2				4				6					
	Total	15		9	6	19		13	9	14		4	1	12		7		50		33	16	109	
G	F	4	7		11	7	5		9	3	11		2		1			14	24		21	59	2
	S	3	1		4	13	5		3	4	9			9	2			29	17		7	53	Dropped
	T										3				5				8			8	young 6-30
	A																						
	Total	7	8		15	20	10		12	7	23		2	9	8			43	49		28	120	
R	F	7	4	8		5	9	5		1	8	6		3	2	6		16	23	25		64	1
	S	8	1	3		7	3	3		3	2	5		6	1	1		24	7	12		43	Dropped
	T	1					6			4	7			4	3	3		9	16	3		28	young 7-4
	A	1								1				3				5				5	
	Total	17	5	11		12	18	8		9	17	11		16	6	10		54	46	40		140	

Six groups of four similar sized (± 0.5 mm) animals were set up, each group containing one female carrying eggs. C-9 and C-10 (Table 2) were included in the data, making a total of eight groups. Three groups were all female, three consisted of two males, two females, and two groups contained one female and three males.

In all eight groups the ovigerous female asserted its dominance as soon as the groups were formed. Due mainly to this animal's greater activity the average number of tension contacts increased to 307 as compared to 237 in experiment A, C (Table 2). As they dropped the young, these females became less aggressive and soon descended in the dominance order. Three dropped from dominant to third-ranking animal and three dropped to fourth. One became subdominant and only one female retained dominance after the young left the pleopods.

TABLE 12.
TENSION CONTACTS OF OVIGEROUS FEMALES

Total Number	
Group Number	Number of Tension Contacts
G-1	417
G-2	345
G-3	344
G-4	334
Average	362

Types		
Type Contact	Number of Contacts	Percent of Total
F	775	53
S	496	34
T	145	10
A	44	3
Total	1460	

When another animal struck at its eggs or abdomen, the ovigerous female turned and fought. Males and non-ovigerous females often did not turn to defend themselves from a rear contact. If an animal turned to meet a rear contact, this was then considered a head-on encounter and credited to the victor. In all eight groups a female with eggs or young was seen to retreat only twice and no instance was recorded in which such a female avoided encounter with another animal.

One female carried eggs that did not develop (Table 11). Therefore she was carrying eggs on her pleopods during the entire time of observation, yet the animal remained in fourth rank. This is the only female observed whose eggs did not develop but this fact may indicate that it is not alone the presence of objects attached to the pleopods which stimulates aggressiveness but also that some other control mechanism may be present.

A Dominance Order of Eight Ranks

As experiments A, C (Table 2) established that *C. shufeldtii* formed stable four-ranked dominance orders, an experiment was performed to discover if larger groups also assumed a hierarchy pattern. Consequently, six groups of eight animals each were set up. Two of these groups were formed by combining groups of four in which the animals were already ranked in a dominance order (H-1, H-2, Table 13). Other crawfish were grouped from the stock aquaria. These experimental animals were maintained in shallow white enameled pans twelve centimeters in diameter. In groups H-1, H-2, and H-5 there was only 0.5 mm difference in cephalothorax length from largest to smallest animal. In the other three groups the difference was 1.5 mm.

The more dominant animals were active and often, after winning a fight, chased the loser around the dish, striking at its tail. These extra strikes were not considered additional tension contacts but only further manifestation of the original fight. Some of the lower ranking animals hardly moved but remained in the same spot until attacked by a more dominant individual.

The first three ranks were well defined in all six groups. In two hierarchies, however, there was a question as to which animal should be ranked fourth and which fifth. In group H-5 the fourth- and fifth-ranking individuals showed the same number of positive tension contacts and pair contacts but percentage of contacts which were dominant established YG in fourth place. In H-6 YP ranked over YR in pair contacts and in total number of dominance contacts but showed the same percentage dominance. In H-3 this same question arose between fifth- and sixth-ranking animals. In H-6 the sixth- and seventh-ranking crawfish had the same total number of positive tension contacts and the same percentage of dominance, but YY had one more positive pair contact over YG. In each of two groups one animal died. In the remaining four dishes the eighth-ranking individuals were subordinate to the seventh, both in number of positive tension contacts and percent of contacts which were dominant.

The relationships between individuals were not so clearly defined as in the smaller groups of four animals, especially in the lower ranks. How large a group could be assembled and still establish a definite order of dominance is not known. These groups of eight still represented communities much smaller than are found in nature and the animals were confined in a much smaller space than is available in the field. Yet this showed experimentally that *C. shufeldtii* in groups as large as eight individuals established dominance hierarchies based on tension contacts

TABLE 13.

Dominance Order of Six Groups of Eight Crawfish Established Over a Period of Sixteen Days

	Rank	Dominance Contacts	Percent Dominant	Social Group		Rank	Dominance Contacts	Percent Dominant	Social Group
	Y	152	80	♀		YY	130	88	♀
	YP	80	60	♀		P	80	73	♂
	YG	69	56	♀		G	58	59	♂
	R	61	50	♀		Y	31	38	♀
H-1	P	47	48	♀	H-4	YP	15	22	♂
	G	36	40	♀		R	13	18	♀
	YY	8	10	♀		YR	11	20	♀
	YR	3	4	♀		YG	1	2	♂
	P	145	80	♀		Y	92	88	♂
	YP	70	68	♀		YR	57	66	♀
	YY	40	45	♀		R	34	52	♂
	YR	29	31	♀		YG	10	26	♀
H-2	G	11	22	♀	H-5	YR	10	22	♂
	R	9	18	♀		YY	6	15	♀
	Y	4	9	♀		G	3	12	♀
	YG	died 7-8-55[a]		♀		P	1	4	♂
	G	125	98	♀, eggs		P	124	95	♀, eggs
	P	68	71	♀		G	48	72	♂
	YP	47	48	♂		Y	24	36	♂
	YR	32	37	♂		YP	10	21	♀
H-3	YY	12	18	♀	H-6	YR	8	21	♂
	R	9	18	♂		YY	4	9	♂
	YG	7	15	♀		YG	44	9	♂
	Y	5	13	♂		R	died 7-19-55		♂

[a] Experiment was started July 8, 1955, concluded July 23.

Changing the Dominance Order

In a previous experiment (Table 2, A-2) a crawfish which had lost a claw retained its top rank in the dominance order until the group was inverted. To study this further, twelve groups of four animals each were established and tension contacts recorded. After five days one cheliped was removed from the dominant animal in four of the dishes. In a second set of four groups a claw was removed from the dominant individual after ten days. From the remaining four groups one of the dominant's claws was removed at the end of 15 days. Each group was observed for a period of 20 days.

When a claw was removed from the dominant individual after only five days the animal did not retain its dominance but dropped to third or fourth rank. One female carrying young did maintain her position after cheliped removal but fell to fourth rank after the young were dropped.

Among animals in which claw removal took place after ten days' dominance, two retained the top-ranking position while two became subordinate to the original second-ranking animal.

Claw removal after 15 days affected the dominance order in only one group. In this group the subdominant replaced the former dominant, while the one-clawed animal retained its place over the third- and fourth-ranking individuals.

This experiment furthers the idea that crawfish can recognize each other as individuals. In groups which had been together only five days, subordinates immediately usurped the handicapped dominant's position. In groups which had been together ten days, two reversals of dominance occurred, both involving only the dominant and subdominant individuals. After the crawfish had been together 15 days only one reversal occurred and this animal was evidently weakened, for it soon died. In these latter groups very little active fighting occurred during the few days before removal of a dominant's claw. The strike and threat were sufficient to intimidate a low-ranking individual. After the claw was removed this same behavior continued, subordinates reacting to the strike and threat of the one-clawed dominant by retreating without attempting to defend themselves. When the dominant's claw was removed after only the first five days, active fighting still occurred and the handicapped dominant could no longer win over its unhindered subordinates.

From each of the above dishes the one-clawed crawfish were removed and placed with groups of three strange individuals for five days. All of these animals were strangers to each other. In this new setting the handicapped individuals ranked low; four of the twelve ranked third and the remaining eight were fourth-ranked.

After this five-day period the one-clawed individuals were placed back with their original groups. In the groups where claw removal had taken place after ten days, both individuals which had dropped to second rank before the five-day absence regained their subdominant position. The two individuals which had retained their dominance after claw removal could gain only second and third ranks in their hierarchies. In groups where claw removal had taken place after 15 days one animal died, one regained its former dominance, and the other two attained subdominance in the original groups. To this can be added group A-2 (Table 2) in which the dominant lost its claw after fifteen days and retained its dominance but dropped to second rank after inversion (after five days' isolation).

While these experiments are preliminary they indicate that crawfish may retain some recognition of individuals after a five-day absence. That these particular animals were not just superior fighters and more aggressive by nature is shown by their more subordinate position with a strange group and by the animals whose claws were removed after only five-days' dominance. These animals dropped immediately to low rank.

Dominance and Hiding Places

As there would be many hiding places available to subordinate crawfish in a natural setting, there was the question of how hiding places would modify behavior of subordinate versus dominant.

Groups of four crawfish with an already established dominance order were used and three hiding places were provided in a dish with four animals. There was some difficulty in obtaining acceptable hiding places. U-shaped pieces of thin opaque plastic were cemented to the bottom of several dishes. The crawfish ignored them. Next, the plastic was painted brown. The animals stopped momentarily under these and moved on. The plastic was then cemented tent-like to the dishes. The animals occasionally frequented the hiding places but often two crawfish were found under the same tent. Finally shells of the clam *Rangia cuneata*, 20 to 25 mm long with ventral border broken at one point, solved the problem. The crawfish readily frequented these shells and although the area under them was greater than under the tents, two animals never were observed to occupy a particular shell at the same time.

The animals faced out of the shells, body diagonally across the opening with abdomen and part of the thorax hidden. As the identifying markings on the animals were placed well forward, individuals could be distinguished without disturbing the shells or animals. Three shells were placed in a triangular pattern away from the sides of the dish. Each dish contained four animals.

Eight dishes containing shells were observed for five days. Every half hour from 7:00 A.M. to 7:00 P.M. the crawfish under shells were noted by recording which shell each was under. Also, each group was observed for 15 minutes every day during the five-day period and their behavior recorded in narrative style. Four groups were observed in the morning, two at midday, and two in the early evening. These times were for convenience only, but, as previously mentioned, the crawfish were more active in early morning and early evening. There was less movement during the midday observation period.

A five-day placement record of one group and the number of times each individual was found under each shell is shown in Table 14. Table 15 is the account of the movements of this group during the daily 15-minute observation periods.

The total amount of movement in the groups was considerably less than in dishes without hiding places. Often only two crawfish were found under shells although three shells were available (Table 14). The dominant animal often remained outside the shells. The fourth-

TABLE 14.
ANIMALS OCCUPYING HIDING PLACES
RECORDED AT HALF-HOUR INTERVALS

Time	1st Day			2nd Day			3rd Day			4th Day			5th Day		
	Shell No.			Shell No			Shell No.			Shell No.			Shell No.		
	1	2	3	1	2	3	1	2	3	1	2	3	1	2	3
7:00		Y		R	Y		G		R					Y	
7:30	Y													Y	
8:00	G	Y			G					Y					
8:30				Y	G					Y	R		G	Y	
9:00	Y						Y	R							P
9:30							Y		G	G					P
10:00	R			G						G			Y		R
10:30	Y		R	G			G			R				Y	
11:00	R			G			G							R	
11:30						G	G			R	G	Y	G	R	Y
12:00				P	R	G	G	Y			G		Y		G
12:30		Y		G	Y		G		P				G	Y	P
1:00	R	Y			R	Y	G			G	Y		G	Y	P
1:30		G		Y			G			G	P		Y		R
2:00					R	P	G				G	P			
2:30	R			G	R		G				G	P	G	Y	
3:00	R	G			G			R	G			R	Y	R	
3:30	G	R	Y	G	R	P	R			G	R	Y	G		
4:00				G		P	R		Y	G					
4:30	Y			G		R		Y	G	Y				Y	
5:00	Y	R		G	R			G	Y	Y					P
5:30	Y			G			R	G	Y				G		
6:00	Y			G					Y				G		
6:30	Y			G					G	Y					
7:00	Y		G	G			G	R	Y						

TOTALS

Dominance Order	Shell No. 1	2	3
R	11	16	6
Y	22	17	10
G	40	11	8
P	1	1	11

ranking animal also remained in the open much of the time. Its actions, however, were quite different from those of the dominant. The low-ranking animal remained in one place and moved only when another animal approached. It remained much more stationary than the fourth-ranking animals in groups not provided with hiding places, probably because some of the animals with which it would have come in contact were under shells, and it did not have to react to their movements. The dominant animal moved around quite freely. Animals occasionally entered or left different shells without apparent reason.

TABLE 15.
RECORD OF BEHAVIOR OF ONE GROUP OF FOUR CRAWFISH
PROVIDED WITH THREE HIDING PLACES
FIVE DAYS' OBSERVATION

August 10. 7:00 A.M. Y under shell #2, P stationary. R wins fight over G. G enters shell #1. R strikes out at Y in #2, Y retreats further into shell, R goes into shell #3 and out again. R wins fight over Y, R enters #2 shell. P enters #3. R comes out of #2. Y approaches #1, G comes out and fights, Y enters #1. R fights P, P defends weakly and leaves shell #3. 7:15—Y #1, R #3.
August 11. 7:00 A.M. R under #1 shell, Y under #2. R comes out, strikes P. G enters #1. R threatens P. R fights G in #1, G comes out, R does not enter. G threatens Y in #2, Y retreats into shell, G moves on. 7:15—Y #2, G #1.
August 12. 7:00 A.M. G under #1, R #3. P moves into #2. Y fights G, Y gains #1 shell. R comes out, R fights Y in #1, Y comes out, R does not enter. G enters #2. Y returns to #1. 7:15—Y #1, G #2.
August 13. 7:00 A.M. None under shells. Y under #3. R enters #1 and out again. G fights Y, G gains shell #3. Y strikes at P. R strikes Y. 7:15—G #3.
August 14. 7:00 A.M. Y under shell #2. R strikes Y, Y retreats into shell, R goes to #3. P not moving. 7:15—Y #2, G #1.

Crawfish under shells seldom gave up the hiding place to another animal without a fight. They sometimes retreated completely into the shell without fighting when another appeared and the challenger would not pursue. If a crawfish attempted to enter a shell occupied by another, the defender immediately reappeared at the entrance and engaged in the fight it had previously backed away from. As the fight continued the defender frequently was drawn completely out of the shell. As soon as the telson was no longer in contact with the shell, this animal terminated the fight by retreating; sometimes into the shell again and sometimes away from it. When this animal remained outside the shell, the challenger generally took possession, at least for a short time. If the defender retreated into the shell after a fight, sometimes another fight took place immediately, and sometimes the attacker turned away. Occasionally encounters terminated when the attacker retreated without drawing the other completely out of the shell.

Each crawfish established possession of a shell only temporarily. For nine consecutive half-hour intervals, or four hours, one crawfish was under the same shell (Table 14, third day, G). Several others were recorded under a particular shell for three and one-half hours. Whether the animals remained under these shells for the total time or whether they were out and under several times is not known.

The second- and third-ranking crawfish found shells and often remained under them until forced out by another animal. The dominant moved around freely, sometimes entered a vacant shell or evicted the occupant of another shell, but seldom remained long under any shell. Only very seldom was the dominant animal unsuccessful in obtaining a shell occupied by another animal. Movement of the fourth-ranking animal was greatly inhibited and it often remained in the open and moved only when a higher-ranking individual approached. When it had possession of a shell it remained until another crawfish attacked and then left with only feeble resistance. Except for the fourth-ranking individuals, an animal in possession of a shell never gave up the hiding place without a fight. Second- and third-ranking individuals could obtain a shell possessed by the other about as often as the defender retained possession. Occasionally a subordinate could defend its hiding place from animals higher in the dominance order. If, however, the higher-ranking animal repeatedly attacked one of these crawfish, the subordinate eventually relinquished its shell.

There appeared a tendency by all of the animals to occupy the same shell (Table 14, shell #1). This occurred in five of the eight groups and was especially evident in the second- and third-ranking individuals. This apparent choice by all the crawfish for the same shell may be explained by Bell's experiments (1906). While investigating vision of crawfish, he found that there was no response to stationary objects but there was an immediate response to moving objects. Thus the crawfish may not have been reacting to any greater advantages offered by the shell but directly to the animal occupying the shell.

When food was placed in the water the animals in hiding places often did not leave the shells. The dominant immediately came to the food. The dominant animals seemed to have no great need for places of concealment while lower ranking individuals sought them out and often remained hidden until driven out by another animal.

Discussion

Cambarellus shufeldtii established four-ranked dominance orders that remained stable for more than forty days. Usually the dominant individuals were apparent during the first observation period. After the first five days 13 of 14 groups maintained the rankings at all four levels for the entire initial series of observations.

As the crawfish remained together over a period of days the fighting diminished and the less violent forms of tension contacts became relatively more numerous. The total number of contacts also decreased with time. Lower ranking animals responded to strike and threat of the dominant and practically ceased to attack animals higher in the dominance scale.

Conditioning may occur in the relationships of *C. shufeldtii.* Dominant animals with one claw removed after active fighting had diminished generally retained their high position. Upon removal of these top-ranking animals, the second-ranking crawfish became dominant and somewhat more aggressive. Ranks three and four became further conditioned to subordinance, while the former subdominant became conditioned to dominance. When the one-clawed individuals were returned, the second-ranking crawfish fought and became dominant while the third- and fourth-ranking crawfish were bluffed by one-clawed strike and threat.

The findings in the foregoing experiments indicate the recognition of individuals by crawfish and the occurrence of true learning. Yerkes and Huggins (1903) demonstrated the ability of crawfish to learn a simple maze and to retain this learning from day to day. How long crawfish will retain a learned response is not known. They apparently continue to show some recognition of individuals over a five-day period of absence. This retention may depend on the amount of time given to learn the response before retention is tested. The upper limit of items that may be retained is still to be determined.

The problem of specific cues involved in the recognition of individuals remains to be investigated. The color markings used to identify animals were placed in the mid-dorsal line directly over the heart. While these markings may have facilitated learning, it is doubtful that one crawfish could see the marking of another in a head-on encounter.

An animal will attack another or will retreat from a threat before antennae touch. Eyestalkless animals, as observed in a different study, often blundered into each other before raising chelae to strike position. There was little fighting among these animals. When they met, chelae often were interlocked and held so without fighting. These crawfish were not seen to threaten or to avoid another individual before antennae touched.

Bovbjerg (1956) found that *P. alleni* which had had the eyes painted over with nail lacquer but with intact antennae still established dominance orders. Contact with any part of another individual or with a pencil elicited avoidance in the most subservient ranks while the dominant animals responded to any contact with immediate orientated aggressive posture and strike. Dominance order was also established in groups of four from which antennae were clipped but vision was unimpaired. The animals were able to orient, strike and fight in quite normal fashion without antennae. In absence of both vision and antennae the behavior pattern tended to disintegrate. Often no order was formed but when a dominant did emerge, this animal frequently charged around the bowl, striking indiscriminately at the others in the group and striking at the sides of the bowl.

Pearse (1909) found no evidence that crawfish possessed any power of sex discrimination. Copulation appeared to be only a matter of chance and depended largely upon the reactions of the individual with which copulation was attempted. This was also found true in the crawfishes *Cambarus bartonius bartoni* (Childester, 1908) and *Cambarus affinis* (Andrews, 1910). This apparent inability to discriminate sex would result in inability to react differentially to animals of the opposite sex in head-on encounters and may be associated with the fact that animals of either sex may be dominant over a mixed group. With *Procambarus alleni* Bovbjerg (1956) found that in adults the male was generally dominant over the female but in the juvenile stages males were dominant in only two of nine groups consisting of two males and two females. Bovbjerg (1953) remarked that males appeared to dominate females in *O. virilis.* In *Polistes* wasps, females dominated males (Pardi, 1948).

In some vertebrate species male and female do not fight but the smaller and less showy sex shows passive submission to the other and each sex establishes separate dominance hierarchies (Greenberg and Noble, 1944; Greenberg, 1947). In animals where sexual dimorphism is slight male and female tend to be more equal in aggressiveness (Allee, 1952).

By injecting the hormone testosterone proprionate Allee, Collias and Lutherman (1939) succeeded in increasing aggressiveness in low ranking hens which soon rose to higher rank in the peck-order. Such implantation into California valley quail that were allowed to remain free-ranging in their native habitat did not alter the position of either males or females in the peck-order (Allee, 1952).

The problem of hormonal control of aggressiveness in invertebrates has not been investigated. As mentioned above, eyestalkless *C. shufeldtii* seldom fought. Whether this was due solely to loss of sight or also partially to the effect caused by the accompanying sinus gland ablation is not known. Scudamore (1948) postulated the existence of sex hormones controlling the sexual activities and bodily changes connected with these activities in crawfish but as yet there is no conclusive histological or experimental evidence of secretory cells within the gonads.

Size has a definite influence on an individual's rank in a hierarchy. In these experiments 3 mm or approximately 15 percent of the total body length proved the critical measurement. No animal dominated another this much longer than itself. However, 28 percent of the crawfish tested were dominated by animals 1 to 2 mm longer than themselves. A larger animal would generally be stronger than a smaller one but because of injury, disease, lack of food, or heredity, the large animal may be weak in which case the smaller animal could dominate it.

The stage in the breeding cycle also had an important effect on the dominance order, at least among females. A female carrying eggs dominated her associates, whether male or non-ovigerous females. She usually lost this dominant status as soon as the young left the pleopods. One instance was observed in which a female carried eggs that did not develop. This female never dominated her group. This indicates that the presence of objects attached to the pleopods does not in itself stimulate aggressiveness but that some other control mechanism may be present. An idea that has not been investigated is that the developing eggs give off a substance which is absorbed by the female and which stimulates aggressiveness. Since the undeveloped eggs do not extrude this substance the female was not stimulated to fight.

Under natural conditions molting may be a factor influencing dominance order. Animals in the actual process of molting are helpless and for a short time afterwards the new exoskeleton is very soft. Bovbjerg (1953) reported that a newly molted crawfish, regardless of rank, became completely subordinate and if not removed for a few days was cannibalized. After recovery from this period the individual moved back into its previous dominance rank. In the present investigation all animals under observation molted within the same two-day period and thus all of the animals in a group were incapacitated at the same time.

Taking into consideration all of the above factors, there still seems to be some sort of innate aggressiveness, for dominance orders were established among similar-sized unisexual groups. That this aggressiveness may be controlled partially by heredity is suggested by some work done on vertebrates. Scott (from Ginsburg and Allee, 1942) and Ginsburg and Allee (1942) found differences in aggressiveness in three different laboratory strains of mice. Hall and Klien (1942) succeeded in establishing two strains of mice by selectively breeding for timidity and fearlessness from original common stock. Noble (1939) reported that a white strain of *Betta splendens* reared in the same tanks as colored varieties proved inferior to the colored in dominance, even when they greatly exceeded the colored in weight.

Extrinsic factors such as population density, population size and availability of hiding places may also influence the dominance order. *C. shufeldtii* established eight-ranked dominance orders but the time required for their establishment was longer than when only four animals were placed together. In some groups a few of the lower ranking positions remained in question throughout the experiment. Organization of larger groups appears to depend upon the number of animals a crawfish can learn to recognize and react to differentially.

When shells were provided as hiding places for a group, the movement of the animals was greatly reduced. Lower ranking animals often remained hidden until drived out by another animal. The dominant animal moved about freely and seldom remained long under any shell. If this type relationship occurs in nature the dominant freely-moving crawfish would obtain a larger share of food and would mate more frequently than the more subordinate animals. However, as *C. shufeldtii* occurs in large numbers and the contacts between any two specific individuals would be few, low ranking animals probably would not be as inhibited in their movements.

Only the most transient type of territoriality was seen. An animal defended a hiding place from attack by another but did not consistently remain in the same hiding place over long periods of time. In dishes where no hiding places were provided the animals spaced themselves about the bowl and did not aggregate but there was no consistent selection by an animal for a particular part of the dish.

To what extent the laboratory demonstration of dominance order is applicable under natural conditions is questionable. *Cambarellus shufeldtii* occurs in large numbers within small areas. Although fifteen or twenty animals may be captured in several sweeps of a dip net, this density would still be less than that used in the laboratory. Given natural conditions with hiding places and plenty of vegetation, communities of *C. shufeldtii* probably would not be organized in a hierarchy of dominance, but rather each pair contact would be essentially an initial one. The outcome of each contact would depend on the intrinsic factors of size, stage of breeding cycle in the female, and some degree of innate aggressiveness, and perhaps also upon a type of temporary possession of a desirable hiding place.

Summary

1. *Cambarellus shufeldtii* established four-ranked dominance orders under laboratory conditions. Larger groups of eight animals also established hierarchies but often the lower ranks were not diagrammatically clear as in the smaller groups.

2. These dominance orders were based on tension contacts, of which there are four types: fight, strike, threat, avoidance. As animals remained together over a period of time, fighting decreased and the subordinate animals retreated at the milder forms of tension contacts.

3. Larger animals were dominant over smaller.

4. Either male or female dominated a mixed group. As adult females were larger than males, the female might dominate males more often than not on the basis of size alone.

5. Females carrying eggs were more aggressive and dominated their groups, whether composed of males or of females without eggs. When these animals lost the young they became less active and often dropped to lower rank.

6. When a claw was removed from a dominant animal after only five days with a group the animal dropped to low rank. If a claw

was removed from the dominant after the order was well established and fighting occurred infrequently, the animal often retained its high rank.

7. When a one-clawed individual which had retained dominance was placed with a strange group, it ranked third or fourth. When replaced with its original group it often regained dominance over third- and fourth-ranking animals but only occasionally attained dominance over the former subdominant.

8. When hiding places in the form of shells were provided, the dominant often moved about actively in the open and usually obtained a hiding place any time it tried. Second- and third-ranking crawfish generally remained under a shell until forced out by another animal. Each could defend a shell from attack by the other but not from attack by the dominant. The movements of the fourth-ranking individual were greatly inhibited. It remained in one place, either in the open or under a shell, until attacked by a more dominant animal, then it defended its position only feebly or not at all.

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ABSTRACT

The crawfish *Cambarellus shufeldtii* established four-ranked and eight-ranked dominance orders under laboratory conditions. These hierarchies were based on tension contacts. As animals remained together over a period of time, active fighting decreased and the subordinate animals retreated from an attack without defending themselves.

In general, larger animals were dominant over smaller. Either males or females dominated mixed groups. Females carrying eggs were aggressive and dominated their groups, whether composed of males or of females without eggs. When these females lost the young, they became less active and often dropped to lower rank.

When a claw was removed from the dominant animal of a group which had been organized only five days this animal dropped to low rank. If a claw was removed from the dominant after the order was well established and fighting occurred infrequently, this animal often retained its high rank.

When hiding places in the form of shells were provided the dominant animal moved about actively and usually obtained a hiding place any time it tried. Lower-ranking crawfish often remained under shells until forced out by another animal. Second- and third-ranking individuals each could defend a hiding place from attack by the other but not from attack by the dominant. The movements of the lowest-ranking animal were greatly inhibited. It remained in one place until attacked, and often gave up its position without defending itself.