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AGONISTIC BEHAVIOUR IN *UCA (CELUCA) TRIANGULARIS BENGALI* CRANE, 1975 INHABITING THE ADYAR ESTUARY AND BACKWATER, MADRAS, INDIA.

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INTRODUCTION

In *Uca* agonistic behaviour is well developed and consists of defence and offence. The agonistic behaviour is mostly exhibited in the forms of threat and combat and the structural compenents are well developed. The mode of expression of fighting tendencies varies from species to species and a number of other factors contribute to it. Since the burrow is the cardinal point in the life fiddlers, agonistic tendencies are better seen near the vicinity of the burrows. Both male and female fiddlers exhibit aggresive behaviour, but, in males it is more conspicuous quantitatively and qualitatively. In many cases, the behaviour is more ritualized and serves the purpose of information transfer and in some it is forceful to express physical superiority over the competitiors. The maximum of aggressive activities occur during mating seasons, more precisely during courtship periods. Combat is not a prerequisite to courtship and in many situations females are not attentive to it. Crane (1975) observed that most of the aggressive behaviour but not all, whether ritualized or not is connected with reproductionand that both inter-male behaviour and courtship display serve under natural conditions as mechanisms for stimulating and synchronizing reproductive behaviour in the population as a whole.

The spectrum of agonistic activities ranges from a simple threatening posture to the physical uprooting flinging of the individual from the burrow. It is observed as inter-male behaviour (between neighbouring burrow holders between a wanderer and a burrow holder and between two wanderers) and inter-female behaviour. Christy and Salmon (1984) concluded that combat behaviour may be a tool in establishing neighbourhoods of dominance and in attainment of freedom to court the locally available females. The available literature on agonistic behaviour is meagre and mainly consists of the work of Altevogt (1955a, b: 1957), Crane (1957, 1975), Cameron (1966), Dingle (1972), Hazlett (1972), Hyatt and Salmon (1978), Christy and Salmon (1984) and Zucker, (1977). Of all the species classified under the subgenus *Celuca, triangularis* is considered to be the most lethargic exhibiting a low degree of social activity. Very little is known about the components of social behaviour in *triangularis bengali* and hence this work.

OBSERVATION

The agonistic components depend upon the physical status, size and hendedness in *triangularis* (and *lactea* also) of the Adyar estuary and backwater. Fights entangling an

aggressively wandering male and a burrow holder could be noted less frequently when compared with the males occupying neighbouring burrows since the former were more rirualistic and consisted of stronger components. A few encounters involving two aggressively wandering males could be seen in *lactea* only, while such a phenomenon does not occur in *triangularis*. In this aspect, *triangularis* is in conformity with the observations of Crane (1975) on *rapax*. More than 50% of the encounters became fierce fights in *lactea* while only 2% or less resulted in aggressive combat in *triangularis*. Combats between neighbours were more ritualistic in *lactea* but in *triangularis* agonistic activities were lesser to arrive at any tangible conclusion. In general, agonistic tendencies is could be observed more in all the four study areas (Map 1) of the Adyar estuary and backwater in the case of *lactea* only and in *triangularis* it was incomparably less. Encounters have been observed in *lactea* and *triangularis* involving a) crabs of more or less equal size range, b) smaller wanderer and large burrow holder and c) larger wanderer and smaller burrow holder.

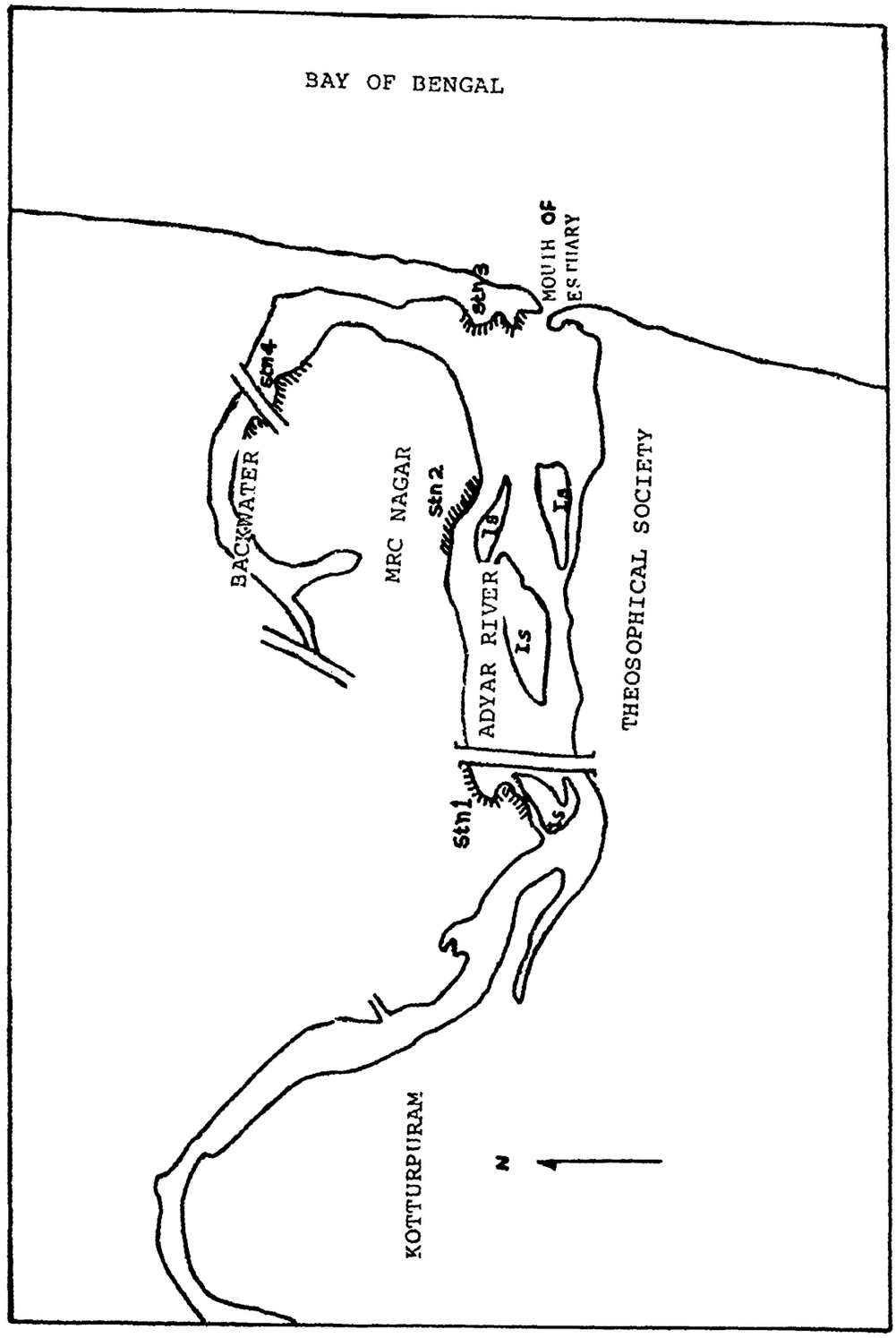
In both *lactea* and *triangularis* ritualized agonistic behaviour could be observed in crabs whose carapace width was more than 7 mm indicating the acquirement of ritualization potential at this stage. Combats between homoclawed (right and right; left and left) and heteroclawed (actor being right or left) males indicated prevalence of homoclawed (right and right) since the number of right handed animals were more.

Of the fourteen agonistic postures known in *Uca*, the male *triangularis bengali* exhibits:

1. Raised carpus - low intensity posture; 2. Forward point - moderate intensity; 3. Lunge - high intensity sudden thrust; 4. After-lunge - unpredictable and undecipherable; 5. Carpus-out - following a raised carpus; 6. Chela-out - partial withdrawal; 7. Lateral stretch - when intruder passes by (Plate 1, A); 8. Creep - after being thrown out near the burrow; 9. High-rise - more during breeding season.

Among unritualized forceful combats, manus push component (Plate 1, B) figured, more when compared with other components. Grips, fings and upsets occurred in numerically descending order. The observations are presented in Table I and II for ritualized and forceful components.

It ritualized combats, the low intensity manus rub was more a prerequisite for the other components to follow. Of the fifteen components, only five have been observed to occur with full certainly (Figure 1) and three components were overlapped. In any case, not more than eight to nine components have been observed to occur in the local populations of *triangularis bengali*. Heel and ridge component (Plate 2, A) preceded by manus rub was more, similar to the observations of Crane (1975) on *rapax* and when dactyl-slide (Plate 2, B) occurred in between manus rub and heel and ridge, ritualization terminated in 75% of the combats.



Map of Adyar River and Estuary

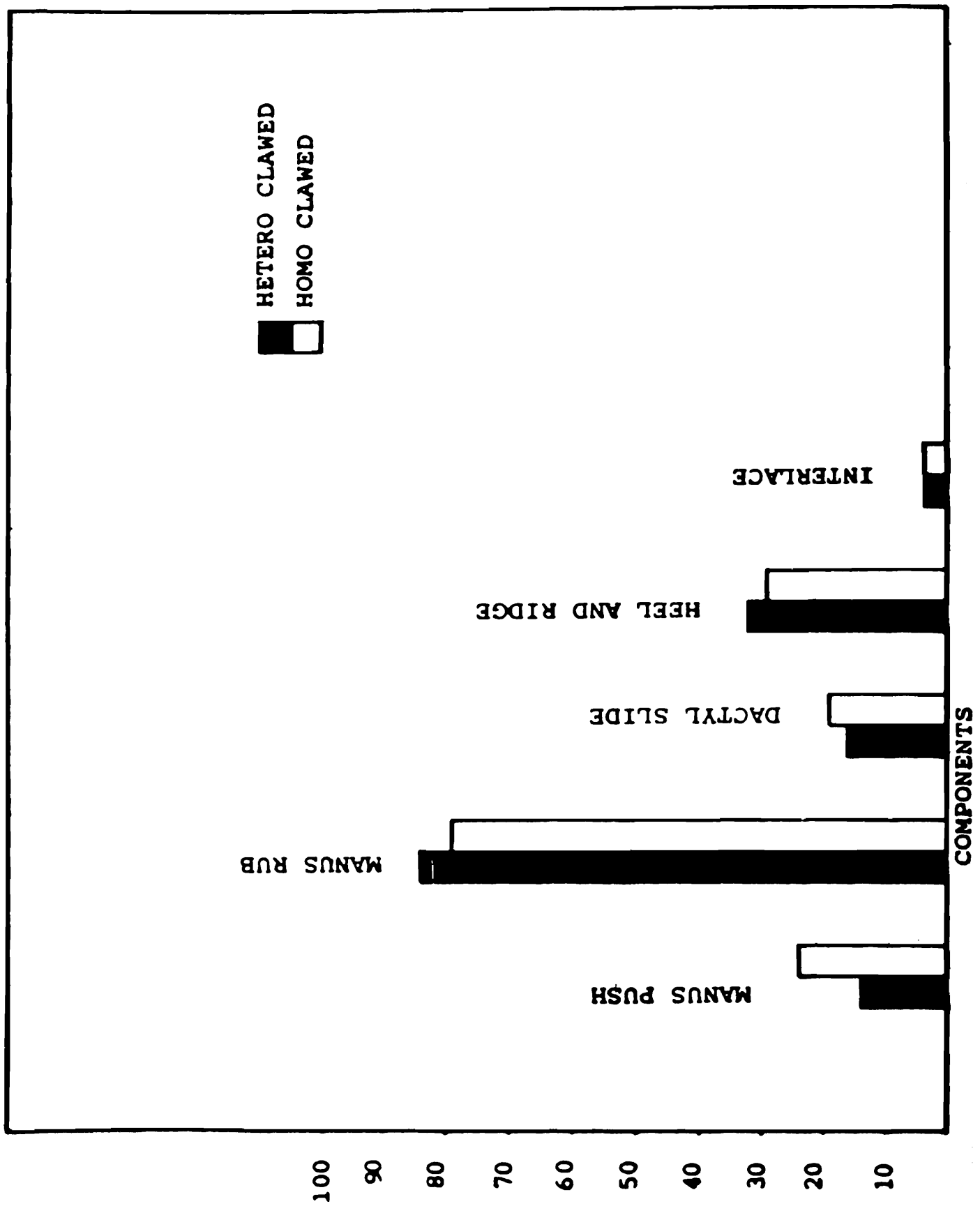


Fig. 1. Relative Frequency of Combat Components (%)

TABLE - I

Composition of 148 combats observed during 1 October - 28 November, 1984 at Adyar estuary and backwater in *Uca (Celuca) triangularis bengali.*

Sequence of components	Combats between aggresive wanderer and burrow holder		Combat between borrow holders	
	Homo Claw	Hetero Claw	Homo Claw	Hetero Claw
Manus push only	6	1	4	1
Manus push and Manus rub	4	1	9	3
Manus rub only	21	18	7	3
Manus rub + Dactylslide	7	2	6	3
Dactyl slide only	1	1	1	1
Manus rub + Dactylslide + heel and ridge	4	1	1	0
Manus push + Manus rub + heel and ridge	1	1	0	0
Manus rub + Heel and ridge	15	9	1	1
Dactylslide +	—	—	—	—
Heel and ridge only	4	1	0	1
Manus rub and Interlace	2	—	—	—
Heel and ridge + Interlace	3	2	—	—
Interlace only	—	1	—	—
Manus rub + Heel and ridge + Interlace	—	—	—	—
Dactylslide + Heel and ridge + Interlace	—	—	—	—
Manus rub + Dactylslide + Heel and ridge + Interlace	—	—	—	—
Manus rub + Dactylslide + Interlace	—	—	—	—
Dactylslide + Interlace	—	—	—	—
Total	68	38	29	13

TABLE - II

Relative percentage frequency of combats in *Uca (Celuca) triangularis bengali*

Component	Heteroclawed combats (50)	Homoclawed combats (98)	Total combats (148)
Manus push	14	24	21
Manus rub	84	79	81
Dactyl slide	16	19	18
Heel and ridge	32	29	31
Interlace	04	04	04

TABLE - III

Analysis of combat outcome in favour of burrow holders (%)

Fiddler species	When burrow holder larger	When burrow holder smaller	When more or less equal
U. (C.) triangularis bengali	95	59	100
U. (C.) lactea annulipes	100	41	74

Interlace component did not indicate any difference in hetero clawed and homoclawed fights. Heel and hollow, quite characteristic of *lactea* could not be seen to occur in *triangularis* during the entire period of observation. Tapping has not been studied due to want of facilities.

Abrupt withdrawals from ritualized and forceful fightings has been observed in 28 cases. In three combats withdrawal of the inactor into the burrow occurred due to the appearance of the lizard *Mebuya carinata* and the common crow and resumption of fight did not occur. In 7 cases abrupt withdrawal occurred for which specific reasons could not be assigned. Only in one case the actor instigated combat repeatedly even after withdrawal by the inactor and till such a time the burrow holder gave up the borrow (15 minutes approximately) the agonistic instinct did not dissipate in the aggressive wanderer. In many combats, the high intensity components were imperfect and related movements were atypical, similar to the observations of Crane (1975) in *rapax* but the dissimilarity being the delay inresumption of other activities like waving. Analysis of combat outcome presented in Table III indicates the spatial and temporal effects of competition among the wanderers and residents for the burrows. In 14 out of 216 cases of winning by the wanderers (observed over a period of one year) of larger size, the burrow was demolished immediately after evicting the residents in the case of *lactea* but such an occurrence did not happen in *triangularis*.

In interspecific fights involving *triangularis* and *lactea* most of the fights were unritualized and exhibited the presence of weak components (Plate 3A), often combats ended in manus rubs and occasionally in heel and ridge. Aggressively wandering *triangularis* tended to avoid conflicts with *lactea* when the latter were burrow holders whether smaller of larger. In the 15 interspecific combats observed between larger aggressive wanderers of *lactea* and smaller burrow holding *triangularis*, the former invariably evicted the burrow holder and demolished the burrows after eviction, in 12 cases, instantaneously.

In places where both the species occupied the neighbouring burrows, *lactea* were smaller when compared to *triangularis* (Plate 3, B). The agonistic behaviour mostly consisted of threatening postures and the few combats observed between the burrow holders indicated the benefit of size of *triangularis*.

The agonistic behaviour between females were lateral body pushes while competing for feeding places and guarding the burrows. A few fights involved the ambulatories and minor chelae and were stereotyped in components.

DISCUSSION

It is known that fighting tendencies are inbuilt in fiddlers and the extent of it varies from species to species. Agonistic expression is not for the possession of an empty burrow but to express physical superiority, more often in the presence of females. Combat behaviour is expressed more during low tide periods when both males and females are active. Reproductively active males spend more of their time in fighting and defending the site of mating, preferably breeding burrows located on the supratidal zones (Christy and Salmon 1984). The combat outcome varies from species to species and different size classes (Hyatt and Salmon, 1978; Christy, 1980). It is common occurrence that the smaller residents are ousted by the larger wanderers on the gradient where the burrows are found to be comfortable for courtship and subsequent copulation. In a number of cases, the burrow occupied by the fighting out of resident is not retained for more than a week by the winner. Hazlett (1972) inferred that in most situations, a loser in ritualized fight, particularly if the combatants have potential weapons such as large chelipeds has a better chance to reproduce, than a loser in an unritualized fight. In *triangularis*, it appears that the winner only can be the successful mate than a loser whether it be a ritualized or unritualized fight.

Christy and Salmon (1984) devised the concept of resource-defence mating systems and expressed that exhibition of agonistic tendencies is for the establishment of neighbourhoods of dominance. This holds true for both *lactea annulipes* and *triangularis bengali* of the Adyar estuary. Hyatt and Salmon (1978) indicated that the percentage outcome of combats is related to the density and size of the crabs in *pugilator*. This observation may be diluted to become a universal phenomenon, since, observations on

lactea and *triangularis* of this tripical region also confirm it. Zucker (1977) stated that the agonistic expression is the outcome of spatial intolerance. Christy and Salmon (1984) subscribed to this idea by pointing out that there exists a negative exponential relationship between inter-burrow distnces and rates of aggressive interaction between neighbouring residents. The present observation on *triangularis* also suggests that establishment of territorial rights is due to the expression of combat behaviour in addition to mating success. von Hagen (1970) expressed that combat behaviour is one of the additional modification associated with terrestrial adaptation. It indirectly may mean that the more terrestrial crabs exhibit more agonistic behaviour. The fiddler *triangularis bengali* which is more terrestrial than its counterpart *lactea annulipes* neither shows the presence of a better ritualized agonistic repertory nor the quantum of combats is more. Lack of patterns makes the agonistic encounters more efficient for survival and reproduction in dense population of *pugnax* when it occurs with *pugilator* (Aspey, 1978). Inspite of the occurence of *lactea annulipes* and *triangularis bengali* sympatrically in some areas, population density was too low to identify a similarity with the other two species of Aspey (1978), since *triangularis* lacks patterns and the intensity of combat is also low.

SUMMARY

Possession of a limited repertory of agonistic tendencies in *triangularis* has been noticed. Winner in a combat, whether ritualized or unritualized stands a better chance to copulate. The argument that a limited repertory may lead to efficient fighting does not work in *triangularis*. Inter-specific combats have been noted to be irregular in components.

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REFERENCES

Altevogt, R., 1955a. Some studies on two species of India fiddler crabs *Uca marionis nitidus* (Dana) and *Uca annulipes* (Latr.). *Jour. Bombay nat. Hist. Soc.*, **52**: 702-716.

Altevogt, R., 1955b. Beobachtungen und Untersuchungen an indischen Winkerkrabben, *Zeitschrift fur Morphologie und Okologie der Tiere*, **43**: 501-522.

Altevogt, R., 1957. Undersuchungen zur Biologie, Okologie und Physiologie indischer Winkerkrabben. *Z. Morph, Okol. Tiere*, **46**: 1-110.

Aspey, W. P., 1978. Fiddler crab behavioural ecology: burrow density in *Uca pugnax* (Smith) and *Uca pugilator* (Bosc) (Decapoda: Brachyura). *Crustaceana*, **34**(3): 235-244.

Cameron, A. M., 1966. Some aspects of the behaviour of the soldier crab, *Mictyris longicarpus. Pacific Science*, **20**: 224-234.

Christy, J. H., 1980. The mating system of the sand fiddler crab *Uca pugilator*. Ph.D. Thesis, Cornell University, Ithaca, New York (Partially seen).

Christy, J. H. & Salmon, M., 1984. Ecology and evolution of mating systems of fiddler crabs (Genus *Uca*). *Biol., Rev.*, **59**: 483-509.

Crane, J., 1957. Basic patterns of display in fiddler crabs (Ocypodidae, Genus *Uca*). *Zoologica*, **42**(2): 69-82.

Crane, J., 1975. Fiddler crabs of the world. Ocypodidae : Genus *Uca*. Princeton University Press, Princeton, New Jersey, U.S.A. pp. 736.

Dingle, H., 1972. Aggressive behaviour in stomatopods and the use of information theory in the analysis of animal communication. Behaviour of marine animals. Winn, H. E. and Olla, B. L. (Eds.), Plenum Press, New York. pp. 126-156.

Hazlett, B. A., 1972. Ritualization in marine Crustacea. Behaviour of marine animals. Winn, H. E. and Olla, B. L. (Eds.), Plenum Press, New York. pp. 97-125.

Hyatt, G. W. & Salmon, M., 1978. Combat in fiddler crabs *U. pugilator* and *U. pugnax* : A quantitative analysis. *Behaviour*, **65**(3-4): 182-211.

Schone, H., 1968. Agonistic and sexual display in aquatic and semiterrestrial brachyuran crabs. *Am. Zool.* **8**: 641-654.

von Hagen, H. O., 1970. Verwandschaftliche Gruppierung und Werbreitung der Karibischen Winkerkrabben. *Zool. Meded.*, **44**: 217-235. (Translation only seen).

Zucker, N., 1977. Neighbour dislodgement and burrow filling activities by male *Uca musica terpsichores* : a spacing mechanism. *Mar. Biol.*, **41**: 281-286.