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DEVELOPMENT OF ASYMMETRY AND HANDEDNESS IN THE FIDDLER CRAB *UCA (CELUCA) TRIANGULARIS BENGALI* CRANE, 1975 INHABITING THE ADYAR ESTUARY AND BACKWATER

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INTRODUCTION

The male fiddler commands instantaneous recognition due to its enlarged cheliped of one side (Plate 1). The allometrically enlarged cheliped which arises due to inequality of growth rate (Gould, 1966) at times accounts for 48% of the body weight of the fiddler. Handedness and development of handedness had always been attracting scientific workers to the male fiddlers (Haseman, 1907 ; Morgan, 1923, 1924 ; Vernberg and Costlow, 1966 ; Yamaguchi, 1977 ; Ahmed, 1978 ; Jones and Georges, 1982). Cheliped asymmetry is useful in sexual discrimination (Salmon and Stout, 1962), agonistic encounters and waving display (Crane. 1975) while percentage of handedness is considered to be tool in taxonomy (Jones and George, 1982).

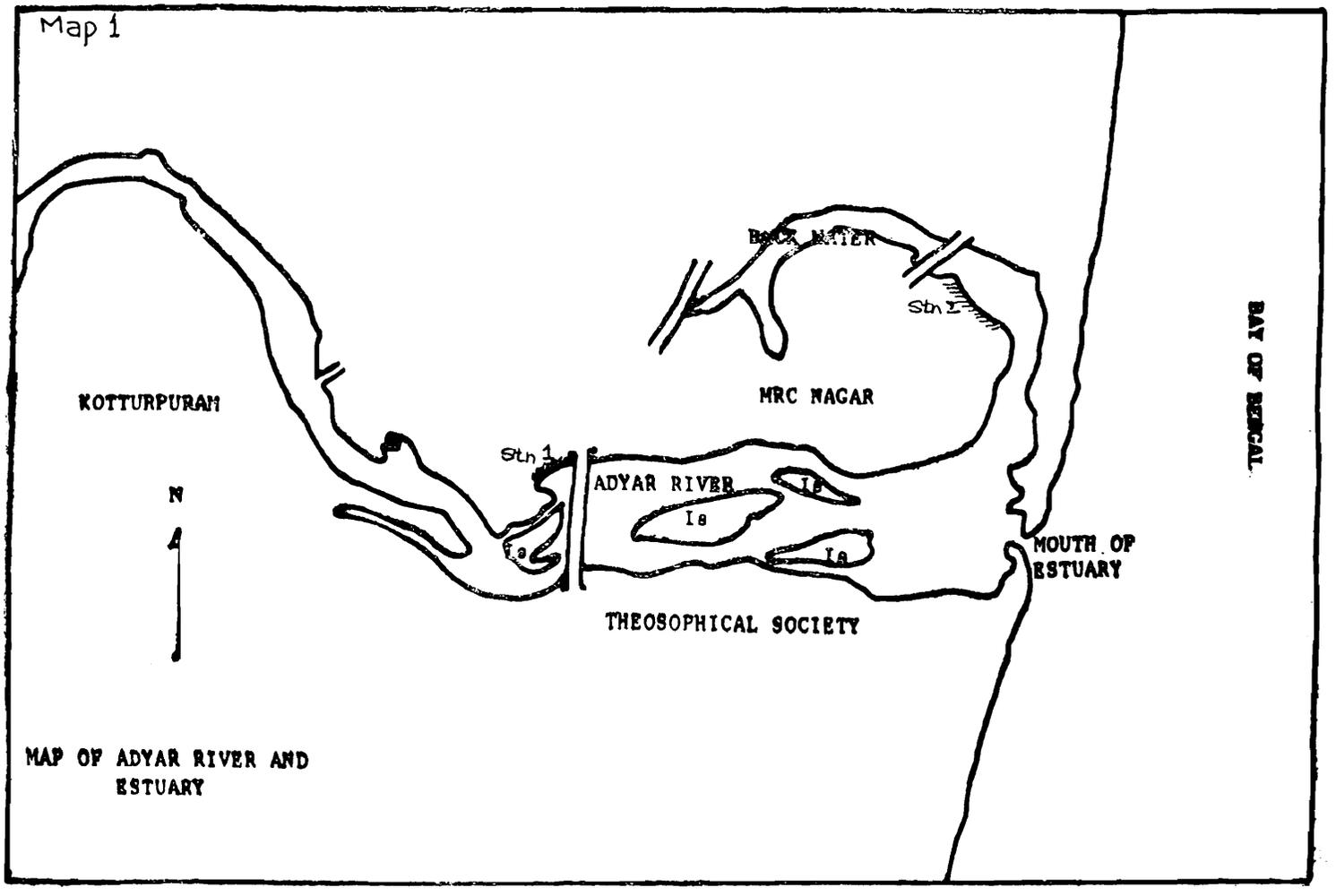
Work done so far at the macrolevel in the East and West still leaves our understanding incomplete. Little is known about handedness and development of handedness of the fiddlers in the Indian subcontinent. Fiddlers from the western parts of the world, especially *Uca pugilator*, *U. pugnax*, *U. minax* and *U, cumulanta* start exhibiting sexual differentiation from 1·7 to 3 mm carapace width while no difference could be noticed in the structure of cheliped of *U. (C.) triangularis* occurring in the Adyar backwater of Madras, India below 3·6 mm carapace width. Only after this stage, a slight enlargement in the size of the right or left cheliped could be noticed. Males with two large claws could not be located at all over the period of three years while those with two small chelipeds were seen rarely.

On handedness in *Uca*, Morgan (1923) and Vernberg and Costlow (1966) have observed that if the enlarged claw is amputated a new large claw develops at the same

locus and the other small claw does not enlarge so that asymmetry is not shifted to the other side. Further observations of Morgan (1923) indicate that if the left cheliped is removed from the fiddlers with 2·0 to 3·5 mm carapace widths, 57% of the fiddlers regenerated small claws only so that symmetry results; the rest had enlarged right cheliped. None developed enlarged left claws. The present study is to compare the development of handedness with other species of *Uca* studied by Morgan (1923), Vernberg and Costlow (1966) and Ahmed (1978) and to analyse the influence of asymmetry on the carapace.

Materials and methods

Random collection of the study material *U.* (*C.*) *triangularis bengali* was done from the resident populations of the Adyar estuary and backwater from two stations (Map 1). The occurrence of fiddlers could be seen throughout the year. Juveniles could be located only



MAP 1

seasonally, more during January-February. The number of right handed males was more at any point of time in the resident populations of the MRC Nagar area. Symmetrical stage crabs of less than 4 mm carapace width and asymmetrical juvenile males of 4 to 7 mm carapace width were captured at the waterline and upper burrow areas by bare hands. These were immediately transported to the laboratory and kept as such for one day. The dead ones were removed and the survivors were measured for carapace width and cheliped length on a Mitu-Toyo dial calipers (0·05 mm accuracy). The fiddlers were divided into two sets, one consisting of symmetrical stage crabs of less than 4 mm carapace width and the other asymmetrical, more than 4 mm but less than 7 mm carapace width. The sets were again divided into subsets according to carapace width and the claws were pinched with a stainless steel forceps. Crabs whose left, right and both chelipeds pinched were maintained separately in polypropylene troughs of 10 litre capacity. The crabs were fed on Kheema (mashed mutton meal) or mashed trash fish. Fresh supply of brine was maintained from the collection spot atleast twice a week. In the smaller class of fiddlers occasional presence of juveniles of *lactea annulipes* could not be ruled out. In some cases moulting occurred twice within the experimental period. On a few occasions discontinuity of the experiment could not be avoided and hence those were repeated. The entire laboratory and field work lasted for a year (June, 1983—May, 1984).

For the statistical analysis, 106 crabs of varying sizes were collected at random and measurements of carapace width, length and cheliped length were taken after preserving them in a 5% formaldehyde solution.

Results

The results are presented in Tables I and II. Set I : (a) Slightly enlarged right claw pinched (4-7 mm).

Regeneration of the lost limb was noticeable from the 4th day and the process of formation of the limb was completed on 12th day. Considerable increase in size of the regenerated right cheliped could be observed from the 18th day. None of the animal showed any increase in the size of the left cheliped worth recording. When moulting occurred just after pinching regeneration was found to be accelerated. Of the 132 crabs pinched 75 survived till the 28th day. The animals were maintained in the laboratory till the 78th day and during this period mortality was very limited.

(b) Slightly enlarged left claw pinched (4-7 mm).

Of the 131 crabs subjected to extirpation, 78 survived till the 28th day. No enlargement of the right cheliped could be observed. After 78 days of maintenance in the laboratory,

Table I

HANDEDNESS IN CELUCA TRANGULARIS AFTER REMOVAL OF CHELIPED AND SURVIVORSHIP (SET I)

SIZE	AMPUTATION	Day 1	Day 4	Day 8	Day 12	Day 18	Day 28	Enlarged Left	Enlarged Right
4-4·9 mm	Left	42	37	31	27	27	21	21	×
	Right	39	30	27	24	21	20	×	20
	Both	55	31	26	21	21	21	7	14
5-5·9 mm	Left	36	31	29	25	23	20	20	×
	Right	31	27	23	19	19	17	×	17
	Both	78	59	46	41	41	37	12	25
6-7 mm	Left	53	47	45	40	37	37	37	×
	Right	62	53	49	42	40	38	×	38
	Both	89	69	61	56	49	41	11	30
Total		**485**	**364**	**340**	**295**	**278**	**252**	108	**144**

Table II

HANDEDNESS IN CELUCA TRIANGULARIS AFTER REMOVAL OF CHELIPED AND SURVIVORSHIP (SET II)

SIZE	AMPUTATION	Day 1	Day 4	Day 8	Day 12	Day 18	Day 28	Females Enlarged Left	Females Enlarged Right
Less than 2 mm	Left	33	24	19	17	16	14	4	4	6
	Right	29	21	18	16	12	11	4	2	5
	Both	63	30	23	21	17	16	×	4	12
2 to 2·9 mm	Left	39	29	28	26	25	23	4	6	13
	Right	42	31	30	30	24	21	7	7	7
	Both	74	46	30	22	22	16	×	7	9
3 to 3·9 mm	Left	54	47	41	38	36	31	9	6	16
	Right	46	40	37	35	31	27	3	11	13
	Both	81	32	28	21	17	14	×	5	9
Total		**461**	**300**	**254**	**226**	**200**	173	**31**	**52**	**90**

the morphometric characters of the carapace and cheliped were compared with the natural resident populations and no significant variation could be seen.

(c) Both claws pinched (4-7 mm).

Of the 222 crabs amputated only 99 survived till the end of the experiment. 30 turned out to be left handed, the right handed ones being the rest and all of them developed a new enlarged cheliped only at the locus of amputation. Percentage survival was very low due to excess trauma of pinching when compared to the other subsets.

Set II : (a) Symmetrical stage right claw pinched (less than 4 mm).

Of the 117 crabs amputated 59 survived. 14 turned out to be females, 20 males with left enlarged claw and 25 with right enlarged cheliped,

(d) Symmetrical stage left claw pinched (less than 4 mm).

Of the 126 crabs pinched 68 survived and the end product constituted of 17 females, 16 left handed and 35 right handed males. Percentage survival was comparable to (a).

(c) Both claws pinched (less than 4 mm).

Of the 238 fiddlers subjected to experimentation only 46 survived indicating a mortality of nearly 80% while in the 4-7 mm group it was only 55%, the visible effect being the inability to withstand the trauma.

Interestingly in Set II (c) where both the claws were amputated, no female survived ; indicating the probable physiologically frail condition. The number of males with right handedness was nearly two times when compared to left handed ones.

When regenerated chelipeds were cut off again on the 28th day, only 15 survived (6 left handed and 9 right handed) till the end of the 5'st day. But the survivors did not indicate any shift in the direction of asymmetry.

In statistical analysis, the estimated relationship was

$$Y = \underset{(2\cdot6700)}{-5\cdot4188} + \underset{(1\cdot1918)}{0\cdot1440} \times 2i + \underset{(0\cdot4475)}{0\cdot8385} \times 3i + \underset{(0\cdot2609)}{1\cdot1917} \times 4i$$

based on the model

$Y = B_1 + B_2 \times 2_i + B_3 \times 3_i + B_4 \times 4_i + e_i$ where

Y_i = the male propodus length of ith sampled crab.

2_i = 0 if the ith sampled crab is left handed.
1 if the ith sampled crab is right handed.

3_i = the ccrapace length.

4_1 = the carapace width on the assumption that ei's are random residuals which are independently normally distributed with the same mean 0 and (unknown) variance. The analysis of variance using ordinary least square method and t test is presented in Table III.

Table III

ANALYSIS OF VARIANCE BY ORDINARY LEAST SQUARES & t TEST

Source	d. f.	Sum of squares	Mean sum of squares	F. ratio
Due to regression	3	3352·3	1117·4	31·2534
Residual	102	3646·9	35·753	
	105	6999·2		

The F statistic indicates that the above model significantly explains the relation between the male propodus length on the other three study variables. The value of $R^2 = 0{\cdot}4790$ indicates that about 48% of the variation found in the male propodus length is explained by these three variables. On a closer examination of the beta coefficients it is revealed that the average (expected) length is not significantly more for a right handed crab than a left handed crab (B_2 having a t value of 0·1208). The t value corresponding to coefficient of carapace width is 1·874 which also is not significant. Hence it is evident that the male propodus length is not dependent on carapace length. However, the coefficient corresponding to carapace width with a t value of 4·5675 is highly significant. The result indicates that the variation in the propodus length is mainly dependent on carapace width among the study variables. A further analysis of the effect of right or left handedness on the mean carapace width indicates non-interference of handedness (t value of carapace width being 1·56 and the handedness being 0·99).

Discussion

Fritsch (1968) while discussion the philosophy of right and left in Science and life remarked that asymmetry is the mark of the organic in general, life and argued that,

right is no better than left either functionally or physically. Ethological information on the fiddlers does not indicate any superiority of right handedness over left. In addition, both right and left handed fiddlers occur in the same population, their ratio being different for different species (Takeda and Yamaguchi, 1973 ; Frith and Frith, 1977 ; Williams and Heng, 1981 ; Jones and George, 1982), It is still a matter of different opinions whether right handedness is determined genetically or is the result of an interplay of the environmental conditions and the genetic constitution or differential expression of hormonal activity. Again, shifting of asymmetry from one side to another in the life of the fiddlers during early stages poses a problem in some species.

Morgan (1923, 1924) could locate occasionally the presence of males with two enlarged chelipeds while others (Vernberg and Costlow, 1966 ; Yamaguchi, 1977) could rear such individuals in the laboratory. In *U. (C.) triangularis bengali* under natural conditions and in the laboratory, not a single individual with two enlarged chelipeds could be noted. As opined by Ahmed (1978) such occurrence may be species specific or production of specific environmental conditions.

Shifting of asymmetry from one side to another has been noted in *U. rapax* (Vernberg and Costlow, 1966) and *U. cumulanta* (Ahmed, 1978), Yamaguchi (1977) stated that at the symmetrical stage, if *U. lactea*-male loses one cheliped, the other becomes enlarged and that if in the very young stages both the chelipeds are extirpated the crab does not develop enlarged cheliped at all. In the present study, no shifting of asymmetry occurred in *triangularis bengali* providing evidence in favour of genetic determination of handedness. In contrast to the observations of Yamaguchi (1977) the young crabs which suffered simultaneous extirpation of both the chelipeds developed either right or left handedness. In the larger stages also enlargement of cheliped occurred only at the locus of extirpation and the remaining claw did not derive the potential to enlarge in the absence of the extirpated enlarged claw indicating the validity of Huxley's (1932) hypothesis that the center for development of asymmetry in *Uca* lies somewhere near the base of the claws. It is possible that handedness being a secondary sexual character may be maintained by the androgenic hormone (Adiyodi and Adiyodi, 1970) supplementing the genetic constitution. The regenerated enlarged cheliped (Plate 1) does not appreciably vary from the one possessed by the fiddler under natural conditions. This is in contrast to the observation of Yamaguchi and Takeda (1973) in some cases of *U. marionis* where the regenerated larger chela was toothless. Successive loss of cheliped does not lead to shift in handedness.

Yerkes (1901) and Yamaguchi (1977) stated that handedness in the fiddlers is determined by chance but the latter tends to deviate from his own view that it is reasonable to consider handedness to be a genetic expression in some species. The autotomy or loss of cheliped at a particular stage marks the beginning of development

of asymmetry. Yamaguchi (1977) indicated that differences in temperature may be leading to the loss of cheliped. It my be considered that the genetically pre-programmed event is triggered by the temperature factor. Shedding of one of the cheliped may be of some physiological advantage (osmoregulation ?) during terrestrialization of young crabs.

The morphometric studies in relation to handedness indicate that the male propodus length is not significantly dependent on right or left handedness or carapace length. The male propodus length is dependent on the carapace width. The propodus length of the left and right handed crabs do not vary significantly. Even though it is concluded that male propodus length is dependent on carapace width, while predicting the propodus length one has to take cognisance of carapace length as well due to the presence of multicolinearity ($r=0{\cdot}49$) which is explained through the significant linear correlation between carapace wldth and length. Left or right handedness does not affect the carapace morphology to noticeable extent.

Summary

Extirpation expriments indicate that asymmetry in *triangularis* may be the expression of genetic constitution rather than an interplay of genetic and environmental factors. No shifting of asymmetry could be noticed. Handedness does not appear to influence the carapace morphology. Right handedness though prevalent does not appear to be better than left. Shedding of one claw at a particular stage seems to be a programmed event than by chance. The regenerated claw does not appear to be different from the one lost. A question has been raised whether the loss of cheliped may be considered as a means of terrestrialization.

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