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Chafing in fishes: occurrence, ontogeny, function and evolution

Richard L. Wyman & Marilyn F. Walters-Wyman
Department of Biology, Hartwick College, Oneonta, NY 13820, U.S.A.

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Synopsis

Modal action patterns used in maintenance behavior have often been included in animals' communication repertoires during evolution, yet for fish neither the occurrence nor subsequent ritualization of maintenance behavior has been demonstrated. We review the literature and show that one maintenance behavior, the chafe, occurs in at least 30 families of fish. The chafe thus appears to offer a fruitful tool for the phylogenetic analysis of behavior of fish. We show that chafing in *Etroplus maculatus* and *Xiphophorus helleri* functions to remove sources of irritation from their skin. We also show that during ontogeny and when in social groups the frequency of chafing does not change with age in *E. maculatus* and *E. suratensis*. *Etroplus suratensis* have about twice the body surface and chafe twice as often as *E. maculatus*. Chafe-like behavior in *Etroplus* is observed during ontogeny when young glance on their parents' body. Young *E. maculatus* without parents present chafe more frequently than young with parents present suggesting that chafing on the substrate may substitute for parent contacting. Chafing is also included in adult behavior where it occurs during pair-formation, nest relief behavior and as an interspecific signal performed by the cleaner *E. maculatus* upon the host *E. suratensis*. The maintenance chafe and glance upon the parent both occur rapidly while the chafe performed during pair-formation is slow suggesting a degree of ritualization.

Introduction

A primary goal of ethology is the elucidation of phylogeny. Modal action patterns (Barlow 1977) used during locomotion and maintenance have been especially useful in determining the probable phylogeny of behavior in some birds and mammals (Kortland 1940, Lorenz 1941, Daanje 1959). The utility of using maintenance behavior of fish to construct phylogenetic relationships has been questioned by Noakes (1978), who believes that fish lack much of the ongoing maintenance behavior that has been so useful in birds and mammals. However, fish do possess a few modal action patterns that appear to function as maintenance activities such as the chafe, quiver, fin-flicker (Baerends & Baerends-van Roon 1950) and yawn (Rasa 1971a). With the exception of Rasa's work on yawning, little experimental evidence is available to prove that these behaviors serve a maintenance function.

Below we list characteristics which maintenance behavior ought to possess: (1) They should be useful in maintaining the body, such as by the removal of parasites or other foreign material from the body surface; (2) They should occur rapidly especially where predation pressure is high and when during the maintenance act the animal is not ready to respond to attack; (3) They should not change with age except for changes in frequency that may accrue with change in body size or when body morphology of the adult is dramatically different from young; (4) They may show diel changes in frequency especially after prolonged periods of inactivity; (5) Differences among species may occur where one species is more prone to external infections and where body size differs between species; (6) They may be used as a redirected behavior when the normal releasing situation is unavailable (Rasa 1971b); (7) They may be used in communication where we might find some form of ritualization to have occurred.

To be of maximum use in establishing phylogenetic relationships and in increasing our understanding of the ways natural selection may work on behavior, the maintenance behavior should occur in many species.

We examine the exogenous causation, function and distribution of chafing among fishes and we present an example of the probable ritualization of the chafe into a signal. When chafing, fish swim toward an inanimate object and when close curve their body; contact is usually made with the convex portion of the body. Chafing may occur as a single act or in bouts of 10 or more chafes within a few seconds. During a bout fish may continue moving forward in a circular path as dictated by their curved body, and thus circle around to chafe again. Or they may move forward to chafe and then back up to be ready to chafe again. Any area of the body may be contacted. We have seen fish turn completely upside down so as to touch the dorsal surface of the head on the bottom. Fins may be held partially open in *Etroplus* (Wyman & Ward 1973) or in close to the body as in *Badis badis* (Barlow 1962) when chafing.

Materials and methods

Literature was reviewed for the occurrence of chafe-like behavior in fishes with heavy emphasis since 1965, as good descriptive documentation of fish movements before that time are scanty. In addition we present data from personal observations on many species made in laboratories at Illinois State University and Hartwick College and while snorkeling or with SCUBA in Lake Ontario, the Hudson River, other lakes and rivers of New York, on the coral reefs around the island of San Salvador (the Bahamas) and in Negombo Lagoon (Sri Lanka).

Ontogeny of chafing was studied by observing 5 groups of 5 fish of *E. maculatus* and 6 groups of 5 fish of *E. suratensis* from 21 days after young began to swim to 101 days. In both cases young fish were removed from their parents on the 19th day; were fed ground Tetramin flakes and frozen brine shrimp to satiation twice per day (food remaining after 15 min.). Fish were reared in 39 l aquaria containing a centrally located plant, heater, airfilter and 2 cm of gravel (diameter 2 mm) and covered on 3 sides with ruled, yellow paper and with a viewport on the fourth side. Water temperature was 28° C (± 2° C), salinity 1 ppt, photoperiod of 13 h light, 11 h dark and 1/2 h of dimmed lights simulating dusk and dawn. Lighting was provided by 40 W incandescent bulbs over each tank.

In a second set, 4 groups of 15 young *E. maculatus* were reared with their parents to 101 days. In order to maintain parental motivation at least 15 young were required, as fewer young were ignored or eaten after a few days.

Observations of chafing rates were made every fifth day on each of the 3 types of groups of young fish between 1200 and 1700 h. Fish total length and depth at the first dorsal spine to the nearest millimeter were determined at the end of the experiment. For comparison between the species we assumed their surface area equal to that of twice a parallelogram. Although not accurate estimation of surface area, it is sufficient for relative comparisons between these two species.

Frequency of chafing versus age was analyzed with a one-way analysis of variance and frequency comparisons of *E. maculatus* with and without parents or between the species were made with the two-way analysis of variance and follow-up t-tests (Hays 1963).

The causation of chafing was examined in experiments on one-year old *E. maculatus* (mean S.L. = 5.3 cm) imported directly from Sri Lanka and sexually mature *Xiphophorus helleri* (mean SL = 4.2 cm) obtained from a local aquarium shop. Observations were conducted in 39 l aquaria as described above between 1300 and 1600 h over a period of 5 weeks. A scale located on the lateral body surface below the lateral line and posterior to insertion of the dorsal fin was loosened by grasping it with a pair of fine forceps and twisting slightly. Frequently several scales would thus become loosened and data included herein are for fish with from 1 to 3 scales affected. The technique was perfected and fish remained out of water for less than 1 min. A single fish was then placed in the aquaria and observed for 1 h. Controls were netted and held for 45 sec and placed in aquaria and observed.

A second experiment was performed on *E. maculatus* only. A scale located in the same region as described above was lifted and a small piece of charcoal was inserted under the raised epidermis and scale. These fish were then observed for 1 h. Observations were also made on fish which had either a fungal growth on the tail or paired fins or individuals with 'red-line' (a red-line below the dorsal fin is indicative of an internal bacteria infection, Lewis 1963). A Mann-Whitney U test was used to compare chafing rates for experimental fish and controls (Siegel 1956).

Three forms of chafing were analyzed for speed of occurrence. First, time required for adult *E. maculatus* to chafe was determined by analyzing videotapes made of fish chafing. Videotapes were made with a 1.27 cm reel-to-reel Sony videotape recorder (1/30 sec resolution). Secondly, young *E. maculatus* also make frequent physical contact with the side of their parents during the first five to six weeks after they begin to swim (Ward & Barlow 1967, Quertermus & Ward 1969). This contacting is composed of two discrete acts: glancing a chafe-like movement and micronipping a foraging movement whereby mucus produced by the parents is ingested by the young fish (Quetermus & Ward 1969). Ward (1976) published a motion picture film of this behavior and we analyzed portions of this film to determine the time required for the performance of a glance. Thirdly, the exaggerated type of chafe that occurs during pair-formation and courtship of *E. suratensis* was analyzed in another published film (Ward & Klaper 1976). All movies were made with a Bolex, M-16 Reflex movie camera on Kodak 4X film at 24 frames per sec and analyzed with stop action using a Lafayette Analytical projector.

Results

We found references to chafing in nine orders of fish and even a reference to chafe-like behavior of the killer whale (*Orcinus orca*, Table 1). We mention the latter as an example of convergent evolution due to selection of a body shape needed for efficient locomotion in water. Chafing is represented in 30 families of fish and data are presented for 81 species. Fin-flickering and quivering are often associated with chafing. The dorsal, ventral and pelvic fins may all be moved in and then away from the body immediately before or after a chafe. Baerends & Baerends-van Roon (1950) first placed fin-flickering and chafing in the category of maintenance activities, although they presented no data to support this contention. Other authors have also included fin-flickering as a maintenance activity (Barlow 1962).

When chafing, fish are usually located out of the normal orientation and must perform a twisting type reorientation movement that appears in slow motion to be an exaggerated form of undulatory swimming. At regular speed it looks as if the fish is quivering (Wyman & Ward 1973).

Chafing rate was similar for young *E. maculatus* with and without parents from 21 to 36 days; after this time young with their parents chafed less than those without parents ($F = 8.78$, $P<0.05$, $df = 1, 16$). The rate of chafing for young *E. maculatus* both with and without parents remained relatively constant from 41 to 101 days. *E. suratensis* chafed about twice as often as *E. maculatus* without parents ($F = 10.33$, $P<0.05$, $df = 1, 16$) and *E. maculatus* without parents chafed about twice as often as young with parents ($F = 15.11$, $P<0.05$, $df = 1, 16$, Fig. 1). *E. suratensis* at 101 days had a surface area of 14 cm^2 and *E. maculatus* one of 6.6 cm^2 (Fig. 2).

Table 1. Fish and a mammal for which the modal action pattern chafe has been reported in the literature or observed by the authors.

Order	Family	Species	Reference
Cetaceae	Delphinidae	*Orcinus orca*	Thomas 1970
Clupeiformes	Clupeidae	*Alosa pseudoharengus*	
		Dorosoma cepedianum	
Salmoniformes	Salmonidae	*Salmo trutta*	
	Esocidae	*Esox niger*	
Cypriniformes	Cyprinidae	*Rhodeus amarus*	Wiepkema 1961
		Carassius auratus	
		Barbus partipentazona	
		Brachydanio rerio	Eaton personal communication
		Pimephales notatus	
		Semotilus atromaculatus	
		Tanichthys albonubes	
	Characidae	*Cheirodon axelrodi*	
		Hemigrammus rhodostomus	
		Paracheirodon innesi	
	Cobitidae	*Acanthophthalmus semicinctus*	
	Callichthyidae	*Corydoras aeneus*	
	Ictaluridae	*Ictalurus nebulosus*	
Cyprinodontiformes	Cyprinodontidae	*Cyprinodon variegatus*	Raney et al. 1953, Able 1976
		Fundulus heteroclitus	
		Fundulus majalis	Able 1976
		Oryzias latipes	
	Poeciliidae	*Poecilia reticulata*	
		Mollienisia latipinna	
		Xiphophorus helleri	
		Xiphophorus variatus	
		Xiphophorus maculatus	
		Gambusia manni	
Gasterosteiformes	Gasterosteidae	*Gasterosteus aculeatus*	
		Culaea inconstans	
Beloniformes	Belonidae	*Strongylura timucu*	Böhlke & Chaplin 1968
Beryciformes	Holocentridae	*Holocentrus rufus*	
Perciformes	Serranidae	*Morone americana*	
		Morone chrysops	
	Centrarchidae	*Lepomis gibbosus*	Brown personal communication
		Lepomis macrochirus	Brown personal communication
		Micropterus salmoides	
		Micropterus dolomieui	
		Ambloplites rupestris	
	Percidae	*Perca flavescens*	Abel 1971
		Etheostoma nigrum	
	Mullidae	*Mulloidichthys martinicus*	
		Pseudopeneus maculatus	
	Pomadasyidae	*Haemulon flavolineatum*	
		Haemulon sciurus	
	Embiotocidae	*Hypsurus caryi*	Edwards 1970
	Badidae	*Badis badis*	Barlow 1962
	Blenniidae	*Meiacanthus nigrolineatus*	Fishelson 1975
	Labridae	*Thalassoma bifasciatum*	
		Halichoeres radiatus	
	Scaridae	*Sparisoma vettula*	
		Scarus inserti	

Table 1. Continued.

Order	Family	Species	Reference
	Acanthuridae	*Acanthurus coeruleus*	
		Acanthurus chirurgus	
	Pomacentridae	*Eupomacentrus leucostictus*	
		Abudefduf saxatilis	
		Microspathodon chrysurus	Rasa 1971b
	Lutjanidae	*Ocyurus chrysurus*	
	Cichlidae	*Etroplus maculatus*	Wyman & Ward 1973 Ward & Wyman 1977 Rasa 1968 Rechten 1980
		Etroplus suratensis	Barlow 1962 Ward & Samarakoon 1981
		Cichlasoma citrinellum	Noakes & Barlow 1973
		Cichlasoma nigrofasciatum	
		Cichlasoma cyanoguttatum	
		Cichlasoma biocellatum	Baerends & Baerends-van Roon 1950
		Astronotus ocellatus	Baerends & Baerends-van Roon 1950
		Aequidens portalegrensis	Greenburg et al. 1965
		Aequidens latifrons	Baerends & Baerends-van Roon 1950
		Chromidotilapia guentheri	
		Haplochromis burtoni	Fernald 1977
		Hemichromis bimaculatus	
		Geophagus jurupari	
		Nannacara anomala	
		Pelmatochromis kribensis	
		Pterophyllum scalare	
		Symphysodon discus	
		Sarotherodon mossambicus	
		Tilapia melanotheron	Oppenheimer & Barlow 1968, Barlow & Green 1970
	Anabantidae	*Trichogaster leeri*	
		Helostoma temmincki	
		Betta splendens	
Tetrodontiformes	Tetrodontidae	*Canthigaster rostrata*	
	Ostraciidae	*Lactophrys triqueter*	

In both *X. helleri* and *E. maculatus* the loosening of one or more scales resulted in a significant increase in chafing (Table 2). Furthermore the addition of a piece of charcoal under a scale increased chafing in *E. maculatus*. *E. maculatus* with an internal bacterial infection did not show an increase in chafing while those with an external fungal infection did.

Chafing by *E. maculatus* with either a loosened scale or embedded charcoal had a mean duration of 0.95 sec (s.d. = 0.8 sec). Chafing by young *E. maculatus* on their parents is composed of an approach to the parent (of variable duration), a contact portion wherein the body of the juvenile is tightly curved and is followed by a rebound away from the parent. In the laboratory the mean value for 8 contacts was 69 msec (s.d. = 24 msec).

Chafing during pair formation and courtship of *E. suratensis* is more elaborate. The fish positions itself in a head down posture and appears to visu-

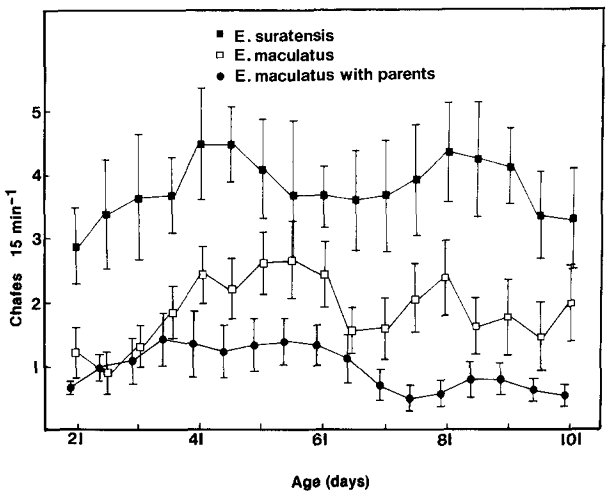

Fig. 1. The frequency of chafing during ontogeny of *Etroplus maculatus* and *E. suratensis* reared in groups of 5 fish from 21 days after the young began to swim to 101 days. The frequency of chafing for *E. maculatus* reared in groups of 15 fish with their parents over the same time period. The plot shows means for each day of observation and vertical bars are standard errors.

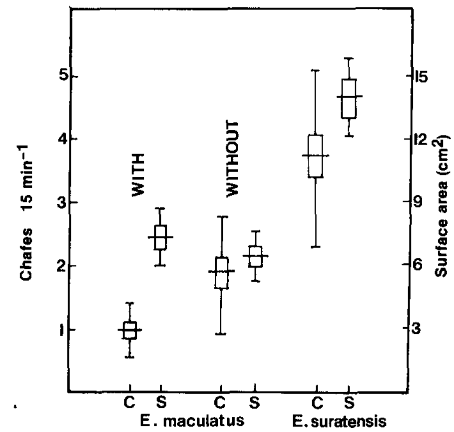

Fig. 2. Comparison of chafing rate per fish (C) and body surface area (S) for *E. maculatus* reared in groups of 15 fish with their parents and groups of 5 fish without their parents. Chafing rate and body surface area for *E. suratensis* reared in groups of 5 fish without their parents. Plotted are means for individual per 15 min of observation, standard errors (boxes) and standard deviations (vertical bars). Surface areas are from fish 101 days after they began to swim.

ally inspect the substrate. Slowly it curves its body while swimming toward the bottom and then rubs the ventral lateral surface beginning anteriorly and proceeding posteriorly along the substrate. At one point the fish may lie flat against the substrate. It then rebounds with an obvious quiver and the act ends with the fish appearing to stand on its tail. The mean duration for 12 chafes of this sort was 3.3 sec (s.d. = 0.75 sec). The focal point during chafing by *E. suratensis* was usually a large depression in the substrate previously constructed by the fish.

Discussion

Care must be exercised when assessing the literature as regards the causal or functional significance or distribution of modal action patterns (Barlow 1977). Information exists on only some 700 species (3.5%) of the 20 000 extant fish species. Second, there is a lack of precise definitions of movement patterns particularly evident in older literature (see Breder & Rosen 1966 for many examples). Third, more modal action patterns are reported for frequently studied species, and fourth, peculiar modal action patterns (such as circling or carouseling and clasping) are more often described than common

Table 2. Chafing rates for fishes with loosened scale, embedded charcoal, fungal infection, bacterial infection and controls.

Treatment	Species	Mean chafe rate h^{-1}	S.D.	N	P
Control	*X helleri*	1.6	1.2	5	
Loosened scale	*X. helleri*	5.8	3.1	5	0.008
Control	*E. maculatus*	3.3	3.1	5	
Loosened scale	*E. maculatus*	12.6	7.6	5	0.008
Red nares	*E. maculatus*	2.8	2.5	6	0.286
Fungus	*E. maculatus*	15.3	14.3	4	0.032
Embedded charcoal	*E. maculatus*	12.0	6.6	6	0.002

behaviors such as chafing. Barlow (1977) suggested that there should be a positive correlation between the amount of time devoted to a species and the number of modal action patterns reported (see also Schleidt 1974, Fagen 1978). Fifth, a real difficulty is that some MAPs occur with great speed (20 msec) and high speed cinematographic techniques are needed. These techniques are not readily adaptable to the field situation and few investigators use them even in the laboratory. The speed of an act or its duration may be critical in determining its functional significance (discussed below).

These limitations lead us to suggest that chafing is probably more widespread among fishes than the literature reveals (Table 1). This supposition is supported by the fact that for those species with a large number of references, chafing is usually reported. Also we were able to add significantly to the list of fish that chafe even though the behavior of many of our 'new' species has already been described.

The most frequently reported function of chafing is as a maintenance activity (Baerends & Baerends-van Roon 1950, Barlow 1962, 1968, 1970, Greenberg et al. 1965, Böhlke & Chaplin 1968, Oppenheimer & Barlow 1968, Rasa 1971b, Wyman & Ward 1973, Fishelson 1975). To our knowledge the significance of chafing as a maintenance activity or its proximate causation has not been rigorously demonstrated. Fishelson (1975) found that *Meiacanthus nigrolineatus* which chafed often had external infections of ciliates, and Able (1976) reported that *Fundulus majalis* infected with external parasites often chafed and occasionally during 'excited periods' of chafing the fish would bury itself in the sand.

In our experiments loosened scales, embedded charcoal and external fungal infections all elicited an increase in chafing. Therefore, we conclude that chafing may at times be used as a maintenance activity by fish in an attempt to remove externally located objects and sources of irritation.

Parent-contacting occurs in four families of fish and is most widespread in the cichlids (Noakes 1979). Young *E. maculatus* touch their parents by micronipping and glancing (Quertermus & Ward 1969). The glance appears identical to high-speed chafes against the substrate except the parent substitutes for the substrate. Chafing rate was greater in young *E. maculatus* without parents present than for those with their parents. This may be due to the young focusing their chafe-like behavior on their parents (recorded as glancing) and the higher rate for young without parents present then may be a result of fish redirecting their glances to the substrate.

We predicted that chafing rates for healthy fish should not change over time. Chafing rates did not change for young *E. maculatus* and *E. suratensis* after 41 days. The 101 days *E. maculatus* with parents chafed at about the same rate as the parents themselves and other adult *E. maculatus*. We also predicted that larger fish should chafe more often than smaller fish. The larger *E. suratensis* chafed about twice as often as the smaller *E. maculatus* without their parents present. It may also be that *E. suratensis* glance on their parents more often than *E. maculatus* and what we observed in *E. suratensis* was in part a result of their redirecting glancing toward the substrate. We need more data on parent contacting by *E. suratensis* to be able to determine which hypothesis is correct.

We also predicted that chafing when used as a maintenance behavior should occur rapidly, and it did. It would be important for fish to chafe rapidly for they would be more vulnerable to attack by predators if they moved slowly (Moynihan 1970). We have the impression that chafing in the laboratory is slower than when observed in the field but our field data are from visual observations. Clearly we need high-speed cinematographic data from the field.

Chafing on the mate and on the substrate occurs during courtship and pair-formation in *E. suratensis* (Ward & Klaper 1976) and *E. maculatus* (Stafford & Ward 1983). Chafing on the substrate or the mate does not appear to be involved in the courtship of other species; although its occurrence has been mentioned frequently, it is not well integrated into courtship patterns of other species (e.g. Wiepkema 1961, Greenberg et al. 1965, Barlow & Green 1970, Fernald 1977). In *E. maculatus* chafing, nipping the substrate and digging all increase in frequency as spawning approaches (Stafford & Ward 1983). Chafing on the mate is also used as a pair-relief ceremony in *E. maculatus* (Rechten 1980). In *E. suratensis* chafing on the substrate and on the mate becomes frequent as spawning approaches (Ward & Klaper 1976, Samarakoon 1981). Chafing on the substrate in *E. suratensis* is slower than when used as a maintenance behavior (3 sec versus 1 sec). Maintenance behavior is frequently incorporated into courtship behavior of birds and mammals (Morris 1956, 1970, Barlow 1977). Morris (1956) and Barlow (1977) say that the perfection of signals nearly always involves some sort of modification or ritualization. For *E. suratensis* that ritualization appears to be the reduction in speed with which the act is performed.

Chafing may also be of significance during ontogeny of behavior in other contexts than with the parent and maintenance. In *E. maculatus* young fish interact with one another following desertion by parents. During this period of interaction they glance on one another (Wyman & Ward 1973). From the glance, the charge, lateral display, carousel and tail beat all appear to be derived during development. The basic foundation (in Lorenz's 1980 sense) for these modal action patterns is the curved body of the fish as observed during chafing. Lastly, young *E. maculatus*, when behaving as a cleaner, chafe on their host *E. suratensis* (Wyman & Ward 1972).

Since chafing is widespread among fishes it probably represents an ancestral modal action pattern. Chafing has subsequently been incorporated into ontogeny, courtship, pair-formation, nest-relief behavior, parental care and interspecific communication in *Etroplus*. The wide occurrence of chafing among fishes may provide fruitful grounds for further study of the evolution of behavior.

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