Evolutionary attributes of headfirst prey manipulation and swallowing in piscivores

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Headfirst swallowing of fish prey is a common attribute of gape-limited predators, conferring the presumed advantage of reduced esophageal abrasion. I evaluate swallowing orientation using cutthroat trout (*Oncorhynchus clarki*) as predator and threespine stickleback (*Gasterosteus aculeatus*) as prey. Field data indicate that orientation is random when prey diameter is less than one-half the gape of the predator, but this increases to 90% headfirst orientation as prey diameter approaches and exceeds the maximum gape, consistent with the suspected reduction in abrasion. Experimental data show two additional advantages to headfirst orientation. Following capture, there is a 2- to 5-fold reduction in escape rate of the prey, and among prey that were swallowed, the manipulation period is substantially reduced (mean 29 vs. 81 s for headfirst and tailfirst orientation, respectively), the differences being most accentuated at large prey sizes.

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La consommation tête première des proies est une habitude commune chez les prédateurs piscivores à ouverture de gueule limitée, habitude qui a probablement l'avantage d'avoir un effet abrasif réduit sur l'oesophage. Je mesure ici l'orientation de la déglutition en utilisant des Truites fardées (*Oncorhynchus clarki*) comme prédateurs et des épinoches à trois épines (*Gasterosteus acul̜eatus*) comme proies. Les données recueillies sur le terrain indiquent que l'orientation se fait au hasard lorsque le diamètre de la proie mesure moins de la moitié de l'ouverture de la gueule du prédateur, mais la prédation se fait tête première dans 90% des cas lorsque le diamètre de la proie se rapproche de l'ouverture maximale de la gueule ou la dépasse, ce qui correspond à la réduction présumée de l'abrasion. Les résultats d'expériences mettent en lumière deux autres avantages d'une orientation tête première : après la capture, la fréquence des fuites est réduite par un facteur de 2-5 et la consommation des proies requiert une période de manipulation beaucoup plus courte (moyenne 29 s dans le cas d'une attaque tête première, vs. 81 s dans le cas d'une attaque queue première); cette différence s'accentue en fonction de la taille des proies.

[Traduit par la rédaction]

Introduction

A major factor influencing prey-handling efficiency of gape-limited predators is relative body size of the prey. Manipulation time (Werner 1974; Hoyle and Keast 1987, 1988) and incidence of prey escapes (Sanford and Harris 1988; Reimchen 1991) increase sharply when size of prey approaches maximum gape of the predator. Occasional reports, from both fossil fish assemblages (Grande 1984) and extant avian piscivores (Hatler 1973; Terres 1980; Septon 1989), of individuals choking to death on prey that were too large indicate a substantial cost of handling large prey. An additional attribute of prey that may be relevant to evaluating swallowing efficiency is their alignment during manipulation and swallowing. Naturalists have occasionally noted that piscivores rotate the prey into a headfirst orientation prior to swallowing (Sanford and Harris 1967; Oberholzer and Tschanz 1969; Douthwaite 1971; Reimchen and Douglas 1984). Interpretations of this behavior have not been explicitly formulated. Presumably, the primary advantage is the smooth transport of food items through the esophagus. Many structures on fish, such as opercula, scales, fin rays, and spines, would tend to lie flat during headfirst swallowing but flare outwards during tailfirst alignment and could lodge in the esophagus if the prey were large. Esophageal abrasion is most pronounced when diameter of prey is close to maximum gape (Werner 1974), and one predicts that headfirst swallowing could be most critical at these sizes if abrasion is a major component of swallowing orientation.

In this paper I present an analysis of manipulation and swallowing orientation using cutthroat trout (*Oncorhynchus clarki*) from a locality where the major prey is the threespine stickleback (*Gasterosteus aculeatus*). Results demonstrate that reduced esophageal abrasion is only one of three possible advantages to headfirst alignment of the prey.

Methods

This study is part of a longer term investigation of stickleback–predator interactions at Drizzle Lake, Queen Charlotte Islands, British Columbia. A general description of the study area and collecting methods is provided elsewhere (Reimchen 1988, 1990; Reimchen et al. 1985). For 76 trout gill-netted from 1979 to 1983, I recorded body orientation of stickleback in the anterior and central regions of the trout stomachs. Virtually all stickleback were aligned headfirst or tailfirst with respect to the longitudinal axis of the stomach. I did not record orientation in the posterior regions of the stomach, where digestion and peristaltic movement of the stomach wall obscured swallowing orientation. Standard length (SL) of the stickleback and trout was measured and values were converted to ratios of prey diameter (PD) to mouth diameter (MD) of the predator from the equations PD = $-8.74 + 0.492$ SL and MD = $-1.374 + 0.111$ SL (Reimchen 1991). PD is the maximum cross-sectional diameter of the stickleback (with spines erect) and MD is the distance between the posterior tips of the opposing maxillae of the trout with the mouth closed.

Stickleback (SL range 10–90 mm) were individually placed into a shoreline enclosure or aquarium that contained trout. Attacks often occurred as soon as the stickleback entered the water (for details see Reimchen 1991). If a stickleback was captured, I recorded the general outcome of the attack on the prey (rejected, escaped, swallowed). I also recorded, when possible, the dominant orientation of the stickleback in the buccal cavity of the trout (headfirst, sideways, tailfirst) and the manipulation period (to the nearest second) from capture to

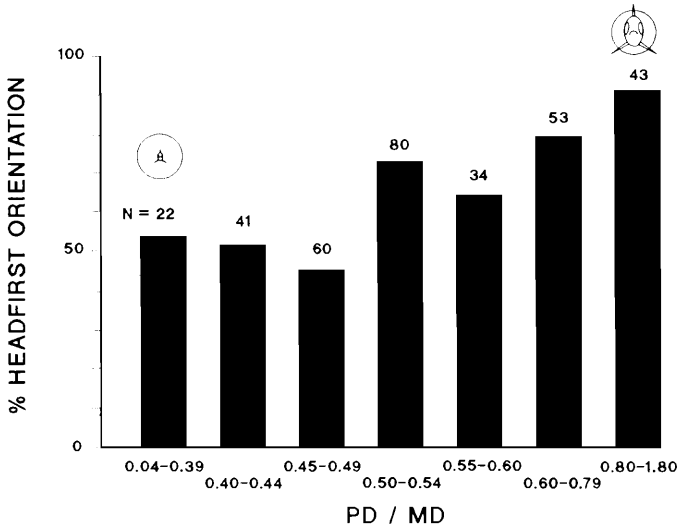

FIG. 1. Incidence of headfirst orientation of *Gasterosteus aculeatus* in stomachs of *Oncorhynchus clarki* collected from Drizzle Lake, Queen Charlotte Islands. The *x*-axis shows the ratio of prey diameter (PD) to predator mouth diameter (MD). The inset figures show schematic views of prey in the esophagus of the predator for the corresponding PD/MD ratio. Numbers above histograms are sample sizes.

swallowing. Typically, termination of "gulping" was followed by pursuit of new prey, so I have used the completion of buccal movements to define completion of swallowing. I videotaped 186 foraging events for the more detailed examination of manipulation behavior and responses of the prey. Six trout were used in the experiment (SL range 190–340 mm).

For data summary, PD/MD values were partitioned into groups (seven for field data, four for experimental data) that maintained representative sample sizes in each group. Manipulation time was log-transformed prior to analyses (*t*-tests). Log-linear models from SPSSx (Norusis 1988) were employed to test for interactions among three variables: outcome (swallowed, escaped, rejected), orientation (headfirst, mixed, tailfirst), and PD/MD. To avoid low values in cells, I collapsed the data into three PD/MD groups (<0.9, 0.9–1.2, >1.2). The relative contribution of cells to the interaction was assessed from values of Z, the ratio of λ to the standard error of the parameter (Norusis 1988). *Z* values greater than 1.96 are considered significant at $P < 0.05$.

Results

Analyses of stomachs from trout collected in the lake showed that more of the stickleback (67%, $N = 333$) were swallowed headfirst than tailfirst (23%, $P < 0.001$, binomial test). Frequency of orientation was closely associated with relative body size of the stickleback (Fig. 1). At low PD/MD ratios (<0.5) proportions of headfirst and tailfirst orientations were similar, but as PD/MD increased, headfirst swallowing increased, so that for the largest ratios (0.80–1.80), most of the stickleback (90.7%) were swallowed headfirst (Pearson $\chi^2 = 35.3$, df = 6, $P < 0.001$).

Among 480 stickleback captured by trout in predation experiments, 177 (36.9%) were manipulated headfirst, 169 (35.2%) were manipulated tailfirst, and 134 (27.9%) were mixtures of headfirst, tailfirst, and sideways manipulations; there were no significant differences among the trout (χ^2, $P = 0.22$). Of 24 mixed feedings during which rotation of the stickleback in the mouth was observed, 23 were rotated from a tailfirst to a headfirst orientation. Assuming that this was representative for all mixed handling events, about 64% of the fish would be swallowed headfirst, which is comparable to the general trend observed in the analyses of stomach contents. However, unlike the distinct pattern observed from field analyses of stomach contents, dominant handling position was not clearly associated with PD/MD. Only the largest ratios (PD/MD > 1.2) showed a marginal reduction in the incidence of tailfirst orientation (Table 1). This difference between experimental and field data is due to feeding protocol because in confinement the trout often attacked the instant the stickleback entered the water, whereas in the lake the trout would have an increased opportunity to assess prey attributes and strike positions (Reimchen 1991).

TABLE 1. Cross-tabulation of experimental data on cutthroat trout attacking threespine stickleback

		Orientation		
PD/MD	Outcome	HF	Mixed	TF
0.3–0.9	Swallowed	51	21	34
	Escaped	4	1	21
	Rejected	2	7	8
0.9–1.2	Swallowed	33	23	29
	Escaped	6	5	22
	Rejected	25	33	26
1.2–1.8	Swallowed	15	7	6
	Escaped	6	6	7
	rejected	35	31	16

NOTE: PD/MD, ratio of prey diameter to mouth diameter of predator; HF, headfirst; TF, tailfirst. Values are raw numbers.

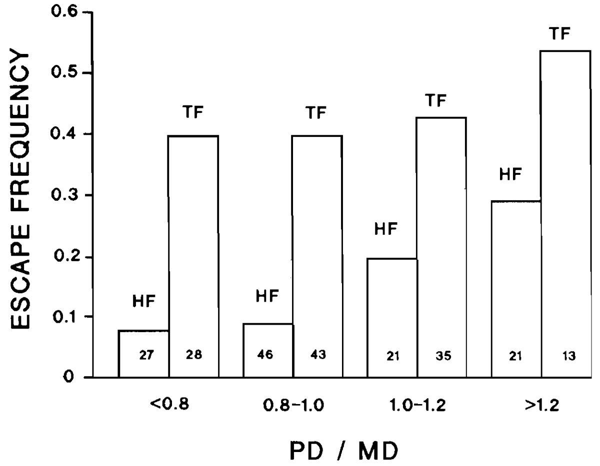

FIG. 2. Frequency of escape of *Gasterosteus aculeatus* during headfirst (HF) and tailfirst (TF) manipulation by *Oncorhynchus clarki*. The *x*-axis shows the ratio of prey diameter (PD) to predator mouth diameter (MD). Values within the histograms are sample sizes.

Outcomes (swallowed, escaped, rejected) differed among the handling orientations. Of the fish manipulated headfirst ($N = 177$), 56% were swallowed, 35% were rejected, and 9% escaped. Of those manipulated tailfirst ($N = 169$), 40% were swallowed, 30% were rejected, and 30% escaped ($\chi^2 = 46.6$, $P < 0.001$ between headfirst and tailfirst manipulations). The excess of escapes during tailfirst manipulation occurred in each of the four PD/MD groups (Fig. 2).

Backward selection from a fully saturated log-linear model (PD/MD : outcome : orientation) produces a model in which all two-way interactions are significant (Table 2). The association betweeen PD/MD and outcome is expected because there is a

TABLE 2. Log-linear analysis of experimental results (from Table 1), with the contributions of individual cells to the model

	Coeff.	SE	Z
PD/MD—outcome			
SM-SWAL	0.78	0.12	6.42*
SM-ESC	0.01	0.17	0.06
SM-REJ	−0.79	0.15	−5.22*
MED-SWAL	−0.07	0.10	−0.71
MED-ESC	−0.10	0.14	−0.76
MED-REJ	0.18	0.11	1.62
LAR-SWAL	−0.71	0.12	−5.82*
LAR-ESC	0.09	0.14	0.64
LAR-REJ	0.61	0.12	5.34*
PD/MD—orientation			
SM-HF	−0.17	0.13	−1.08
SM-MX	−0.24	0.19	−1.44
SM-TF	0.40	0.18	3.10*
MED-HF	−0.10	0.10	−0.81
MED-MX	0.04	0.18	0.35
MED-TF	0.06	0.15	0.56
LAR-HF	0.26	0.19	2.00*
LAR-MX	0.20	0.13	1.41
LAR-TF	−0.46	0.10	−3.70*
Outcome—orientation			
SWAL-HF	0.38	0.11	3.34*
SWAL-MX	−0.06	0.12	−0.47
SWAL-TF	−0.32	0.11	−2.90*
ESC-HF	−0.18	0.15	−1.22
ESC-MX	−0.39	0.17	−2.24*
ESC-TF	0.57	0.13	4.37*
REJ-HF	−0.19	0.14	−1.41
REJ-MX	0.44	0.13	3.49*
REJ-TF	−0.25	0.12	−2.19*

Best-fit log-linear model

	df	Partial χ^2	P
PD/MD × outcome	4	93.45	0.000
PD/MD × orientation	4	15.52	0.004
Outcome × orientation	4	41.14	0.000

Likelihood ratio $\chi^2 = 8.94$, df $= 8$, $P = 0.35$

NOTE: PD/MD (ratio of prey diameter to mouth diameter of predator): SM, small (<0.9); MED, medium (0.9–1.2); LAR, large (>1.2). Outcome: SWAL, swallowed; ESC, escaped; REJ, rejected. Orientation: HF, headfirst; MX, mixed; TF, tailfirst. Z = coeff./SE. A minus sign shows deficiency of individuals. Large absolute Z values have increased significance (*, $P < 0.05$).

highly significant correlation between PD/MD and the incidence of rejections (Reimchen 1991). The moderate association between PD/MD and orientation (from Fig. 2) is confirmed in this log-linear analysis, the major contribution to the association resulting from a deficiency of tailfirst orientations at higher PD/MD ratios. Of major interest is the unique association between outcome and orientation, which is independent of other interactions. The largest contribution to this interaction is an excess frequency of tailfirst orientations among fish that escaped (Z = 4.4, $P < 0.001$) and an excess frequency of headfirst orientations among prey that were swallowed ($Z = 3.3$, $P < 0.001$).

Video playback of predation events provided insight into the differential escape responses. During subjugation by the trout,

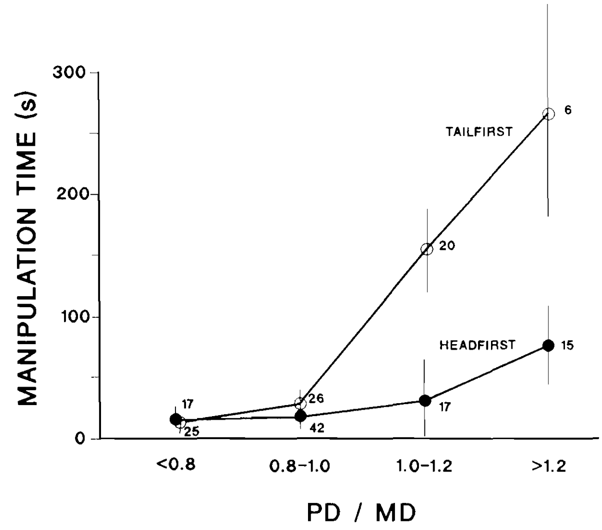

FIG. 3. Average manipulation time in seconds from capture to completion of swallowing. The prey is *Gasterosteus aculeatus* and the predator *Oncorhynchus clarki*. The *x*-axis shows the ratio of prey diameter (PD) to predator mouth diameter (MD). Numbers beside symbols are sample sizes. Vertical lines show standard error.

stickleback erected all spines, and these represented the main contact points with mouthparts of the trout. The stickleback regularly struggled to escape using strong body flexures and thrusts from the caudal fin. These escape efforts were ineffective as long as trout maintained pressure on the spines. Occasionally the trout reduced force on the spines and trunk to adjust position of the stickleback in its mouth. When stickleback were orientated headfirst, any propulsion by the sticklebacck advanced it further towards the esophagus, greatly limiting the likelihood of escape. In contrast, when stickleback were oriented tailfirst or laterally, caudal thrust propelled the stickleback out of the mouth, and escapes were frequent.

Manipulation time from capture to swallowing ranged from 2 to 960 s ($\bar{x}$ = 52.1). Headfirst orientation resulted in substantially shorter manipulation periods than tailfirst orientation ($\bar{x}$ = 28.9 and 81.0 s, respectively, t = 3.03, df = 166, $P < 0.001$). Since constraints on swallowing will be most accentuated when prey are relatively large, one predicts that differences in manipulation time will be highest at large PD/MD ratios. Partitioning data among PD/MD classes confirms this association (Fig. 3); comparisons between means (t-test) on log-transformed data give probabilities of 0.10, 0.02, 0.004, and 0.075 for successive PD/MD groups.

Discussion

General syntheses of manipulation and swallowing mechanisms in vertebrates (Lauder 1985; Bramble and Wake 1985) and manipulation efficiencies in predators (Vermeij 1982) have not specifically addressed the role of prey orientation during capture and swallowing. This may be due in large part to the paucity of quantitative data on alignment in studies of foraging behavior. It is clear from the present data that orientation can be a significant factor in at least three aspects of the handling success of the predator: escape rate of prey, manipulation time, and swallowing ability. For trout foraging on stickleback, headfirst manipulation was advantageous for each of these factors, and for the latter two, the effects were greatest when prey size approached maximum gape.

While these factors may largely account for the prevalence of headfirst attack and swallowing in predators, other proximal causes are also involved. Predatory fish such as pike (*Esox*), bass (*Micropterus*), rainbow trout (*Oncorhynchus mykiss*), and cutthroat trout (*O. clarki*) often attack prey near the center of mass, which tends to be closer to the head than the tail in most fishes. This behavior is predicted on hydrodynamic principles because the center of mass of the prey moves least during initial escape responses and should be the optimal strike position (Webb 1984). In these situations, headfirst orientation would occur as a simple correlate of the initial strike positions. However, even in these groups, prey that are attacked at midbody are generally rotated into headfirst alignment for swallowing (Hoyle and Keast 1988; this study).

Shorter manipulation time for headfirst orientation was most accentuated at higher PD/MD ratios. Both axial flexibility and distension of structures on the prey could influence manipulation time. In fishes, the head and anterior trunk are less flexible than caudal regions and appear to be more readily transported into the esophagus. Several times I observed that during tailfirst swallowing of stickleback, the caudal peduncle folded anteriorly, leaving the body in a J-shaped position lodged at the entrance of the esophagus. This prolonged the manipulation period because these prey were rejected and recaptured for another attempt at swallowing. Furthermore, the erect dorsal and pelvic spines have a posterior slant and frequently lodge against the mouth, effectively blocking further passage of the trunk into the esophagus (see also Hoogland et al. 1957). This produces frequent rejections and recaptures of the stickleback, further prolonging manipulation time. The advantages of a shorter manipulation period to the predator are numerous and have been addressed elsewhere (McCleery 1974; Werner 1974). Under conditions where the predator is vulnerable to interference and where trophic competition places a premium on minimizing the length of time for each foraging event, reduced manipulation time might confer a primary selective advantage on headfirst alignment.

The escape rate of the prey was two to five times higher during tailfirst manipulation than during headfirst manipulation. Although this association is not well documented in predator–prey studies, it occurs across unrelated taxa. Fish captured by Common Murre (*Uria aalge*) were more likely to escape if attacked near the tail than those attacked in the head region (Sanford and Harris 1967). Lycaenid butterflies attacked on the hind wings by birds had a higher escape rate than those attacked in the head region because of increased manipulation errors (Wourms and Wasserman 1985). The evolution of conspicuous tail markings and tail autotomy in some lizards (i.e., Gekkonidae, Scincidae) has probably resulted from an increased escape rate from tailfirst attacks (Cott 1940). This might also account for conspicuous caudal markings on some fishes (i.e., Pomacentridae, Chaetodontidae, Characidae). These marks are currently thought to provide misinformation on the probable direction of motion during initial pursuit (Cott 1940; Winemiller 1990), and to direct attacks from the head to a less vulnerable part of the body so that injuries resulting from an unsuccessful attack are not lethal (McPhail 1977; Owen 1980). Independent of injuries, directive marks would also be advantageous when tailfirst attacks produce more escapes than headfirst attacks as a consequence of manipulation errors rather than differential injury.

In conclusion, headfirst alignment of the prey during manipulation provides at least two additional advantages to the predator apart from the presumed reduction in esophageal abrasion. Further attention to prey orientation may be fruitful in evaluating individual differences in predator foraging behavior and efficiency.

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Burrowing behavior and soil manipulation by a tarantula, *Rhechostica hentzi* (Girard, 1853) (Araneida: Theraphosidae)

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The Texas brown tarantula, *Rhechostica hentzi*, uses silk during burrow construction to manipulate, remove, and transport soil. Soil adheres to the silk desposited on the soil surface, and the strands are pulled together to form soil–silk masses. The spiders pick up the masses in the chelicerae and carry them away from the developing burrow. We suggest that this specialized use of silk for burrowing may have evolved from a combination of existing behavior patterns.

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Durant la construction de son nid, la mygale du Texas *Rhechostica hentzi* utilise sa soie pour manipuler, enlever et transporter de la terre. La terre adhère à la soie déposée à la surface du sol et les brins sont réunis pour former des masses de terre–soie. Les araignées ramassent ces masses dans leurs chélicères et les transportent loin de leur terrier en formation. Cette utilisation spécialisée de la soie pour la construction des terriers est probablement dérivée de la combinaison de comportements déjà présents.

[Traduit par la rédaction]

Introduction

The use of silk by spiders is a characteristic that distinguishes them from most other arthropods (Savory 1928; Shear 1986*a*). Spiders use silk to (*i*) construct cases for egg masses (all spiders), (*ii*) line excavated burrows or natural cavities as retreat sites (e.g., tarantulas, Theraphosidae), (*iii*) construct silk retreats (e.g., purse-web spiders, Atypidae), (*iv*) lay out draglines to mark paths for themselves and potential mates (e.g., wolf spiders, Lycosidae), and (*v*) construct structures to capture prey, with draglines for safety and ballooning for dispersal (e.g., orb-weaving spiders, Araneidae) (Shear 1986*a*).

Most studies of silk use focus on its importance in the ''true'' (Araneomorphae) spiders, many of which employ silk constructs (sheet or orb webs) to capture prey (Eberhard 1990). Relatively little information is available concerning silk use in more primitive spider species (Mygalomorphae). This group includes 15 families (1000+ known species, including tarantulas), few of which use silk constructs to ensnare prey (Raven 1985; Coyle 1986). Mygalomorph spiders utilize silk to construct egg cases, line burrows or cavities, and construct silk retreats. They may also use silk constructs for detection of prey (Coyle 1986).

In this study, we examined the use of silk during burrow construction and the behavior patterns exhibited during burrowing by a mygalomorph spider, the Texas brown tarantula, *Rhechostica hentzi* (Girard 1853) (Theraphosidae, Theraphosinae). This species was known previously as *Dugesiella hentzi* (Girard 1853).

Methods

The burrowing behavior of nine tarantulas (five adult females, mean mass = 16.9 ± 6.7 (SE) g, and three juveniles, mass 3.8 ± 2.1 g, one of which was retested after maturing into an adult male, mass 11.3 g) was observed in the laboratory. They were collected from arid grassland habitat in north and central Texas and were maintained in the laboratory for at least 1 month prior to testing. The spiders were fed four adult crickets (*Acheta domesticus*; mass 0.35 ± 0.007 g) every 7 days, and water was available *ad libitum* prior to testing. Tarantulas were tested