Laboratory food patch exploitation in the algae-eater *(Gyrinocheilus ayomonieri)* (Tirant 1883) Pisces : Cypriniformes

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RESUME

Exploitation de zones d'alimentation par un poisson consommateur d'algues *(Gyrinocheilus ayomonieri).*

    Dans une premiere experience, les sujets ont été nourris avec des algues vertes ou bleu-vertes, tandis que dans une seconde experience, ils disposaient d'algues vertes présentées selon deux densités. Il n'apparaît pas de préférence entre les types d'algues, mais la faible densité est préférée a la forte — l'intensité de cette préférence varie avec la taille du poisson. On observe également des variations interindividuelles dans le nombre de changements entre zones d'alimentation et dans le nombre de sequences alimentaires par visite. Le taux de prises (bite rate) ne varie pas au cours des trente minutes de la periode d'alimentation. Une sequence de prises a autant de chances de se terminer n'importe quand après les premieres prises. Toutefois, tel n'est pas le cas pour l'intervalle entre séquences ou du nombre de sequences par visite d'une zone. Des intervalles courts et des visites avec une seule sequence ont été plus frequents que ne le laisserait supposer une repartition au hasard.

Mots-clés : Poisson consommateur d'algues *(Gyrinocheilus).* Préférences alimentaires. Rythme d'activité.

SUMMARY

    In Experiment I, algae-eaters fed on green and blue-green algae while in Experiment II they fed on two densities of the green alga. There were no preferences between algal types but the low density was preferred to the high, the strength of the preference varying with the size of the fish. There was also

individual variation in the number of switches between algal patches and the number of bouts per visit. Bite rate did not vary over the thirty min. feeding period. A bout of bites was equally likely to be terminated at any point after the first couple of bites. However, this was not the case with the intervals between bouts or the number of bouts per visit to a slide. Short intervals and single-bout visits were commoner than would be expected at random.

INTRODUCTION

Most of the research on fish feeding patterns has involved the study of the consumption of particulate prey items. Groups investigated include salmonids (Bryan, 1973), cyprinids (Ivlev, 1961), gasterosteids (Beukema, 1968), poeciliids (Murdoch et al., 1975), pomatomids (Olla et al., 1970), and centrarchids (Colgan, 1973; Lester, 1976). Such research has focussed on phenomena such as predator attack and success rates and the probability of accepting encountered prey. However, it is also of interest to study the manner in which fish grazing on continuous, immobile food sources pattern their behaviour, temporally and spatially, in order to exploit patches of food. Two major groups within this large ecological guild are coral reef grazers (reviewed by Ehrlich, 1975) and tropical freshwater grazers of benthic algae (Lowe-McConnell, 1975). As with grazing African ungulates (Leuthold, 1977), little is known about the feeding dynamics of members of this guild, and comparisons with other grazers [e.g. snow geese (Harwood, 1974)] for which information is available, as well as with other fishes [e.g. guppies (Dussault and Kramer, 1981)], would be valuable. The objective of the present research was to investigate the patterning of feeding in the grazing algae-eater, Gyrinocheilus ayomonieri (Tirant, 1883). Although its bionomics have not been reported in the literature, this is a suitable experimental species because it feeds with clearly observable mouth movements which can easily be recorded.

METHODS

Immature, unsexed fish obtained from local dealers were maintained under natural photoperiod at 21 ± 1° C in separate clean glass aquaria 32 x 17 x 20 cm deep with air stones, floating plants, and guppies *(Poecilia retzculata)* which were suitable as dither fish (Barlow, 1968). Green *(Chlorella)* and blue-green *(Oscillatoria) algae,* two different food sources available from axenic laboratory cultures, were grown on 2.5 x 7.5 cm. glass microscope slides in a buffered alkaline inorganic medium. The slides were placed 4 cm. apart parallel and horizontally at an end of .the aquarium which overhang the supporting bench so that feeding behaviour could be viewed via a mirror beneath the overhang by an observer who sat quietly in front of the aquarium. The times of the initiation and cessation of each bout of feeding at either slide was recorded, together with the number of bites in the bout, using a microswitch keyboard and Esterline-Angus events recorder. The fish readily became accustomed to feeding on such slides prior to the beginning of the experiment and thrived on them. Each fish was fed at a fixed time of day to allow for any possible circadian rhythms. The guppies were
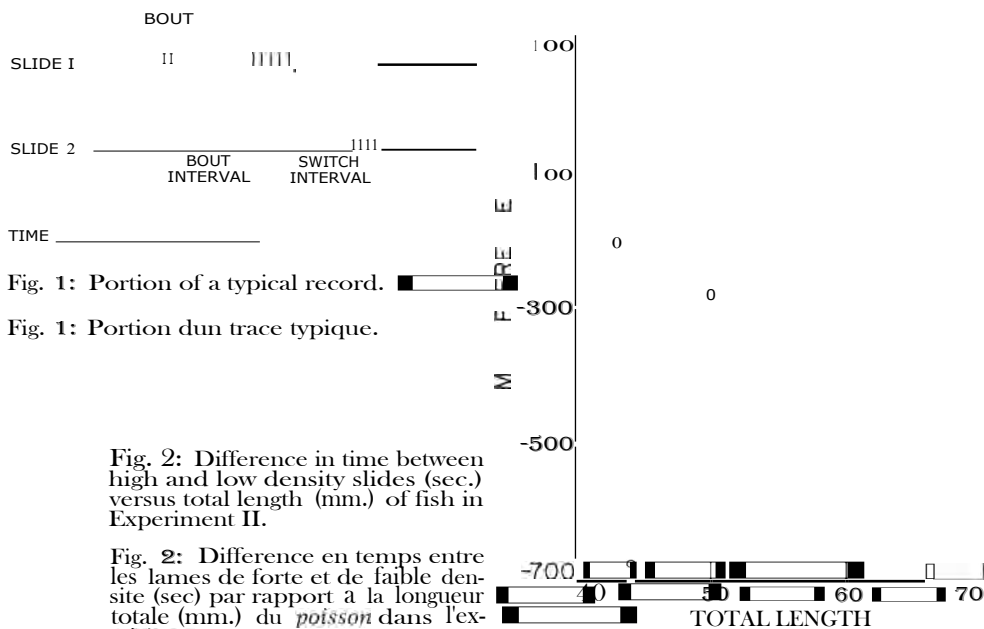
fed small amounts of floating flake food, almost none of which ever sank to reach the algae-eaters. Conversely, the algae-eaters excluded the guppies from the algal slides.

Experiment I examined feeding behaviour on the two algal species. One slide of each alga was presented in a fixed left-right manner to each of three test fish for thirty min. each day for six days.

Experiment II examined feeding behaviour on two densities of the green alga differing by a factor of 5.88 as measured colorimetrically. One slide of each density was presented in a fixed left-right manner to each of eight test fish for thirty min. each day for four days. A visual estimate of the proportion of the alga on each slide eaten was made at the conclusion of the thirty min.

RESULTS

A portion of a typical data record is presented in Fig. 1. The fish exhibited distinct bouts of biting movements separated by intervals of varying duration. Thus the common problem of identifying bouts (see Fagen and Young, 1978) is absent in this case. The total time spent feeding by the fish averaged 122 s (standard deviation = 21 s) and 146 s (s.d. = 40 s) over the thirty min. in Experiments I and II respectively. The data were scrutinized at several levels in an attempt to reveal what sorts of underlying processes could be operating to generate the observed

Fig. 1: Portion of a typical record.

Fig. 1: Portion dun trace typique.

Fig. 2: Difference in time between high and low density slides (sec.) versus total length (mm.) of fish in Experiment II.

Fig. 2: Difference en temps entre les lames de forte et de faible densite (sec) par rapport a la longueur totale (mm.) du *poisson* dans l'expérience II.

feeding behaviour.   Table I provides a summary of this analysis by giving the probabilities of the results under null hypotheses of no treatment (algal type or density) or fish effects for five behavioural measures for the two experiments. The fish showed no preference between the algal types in Experiment I but preferred the low density to high density patches in Experiment II (average : 100 and 46 s respectively, s.d. = 35 s). This is reflected in the average proportion of the alga eaten on each slide, 75 % and 41 % (s.d. = 22 %) for low and high densities respectively (p = .025).   Figure 2 shows that smaller fish spent more time at the low density patch (Spearmen rank correlation coefficient, p < .05). Returning to table I, the fish showed individual differences in both the number of switches and the number of bouts per visit. The fish averaged 6.1 (s.d. = 2.2) and 8.7 (s.d. = 3.8) switches in thirty minutes in Experiments I and II respectively. In Experiment I, fish generated fewer bouts per visit (average of 4.84 compared to 5.15, s.d. = 2.19) but more bites per bout (average of 17.2 compared to 12.0, s.d. = 3.06) at the green algal patch. The feeding rate during feeding bouts averaged 2.95 (s.d. = .38) bites per sec. and showed no significant variation with treatment, fish, or time over the thirty min. Pilot studies in which the fish were offered five slides of the green alga similarly revealed no satiation over the thirty min.

In both experiments, the fish showed no tendency to begin with either patch. Nor was there any association between the patch first encountered and either the number of bites in the first bout or the duration of the interval between the first and second bouts of feeding (Experiment I, t = 1.52, − .42, d.f. = 16, P = .14, .68).

Table I: Probabilities of the results under null hypotheses of no treatment (algal type or density) or fish effects for five behavioural measures for the two experiments. 1) Analysis of variance, 2) Chi-square, na = not applicable, ns = not significant.

Tableau I: *Probabilité* des *résultats* dans *l'hypothèse* nulle d'absence de traitement (type ou *densité algué)* ou effets *poisson* pour cinq mesures comportementales, dans les deux experiences.
1) Analyse de variance, 2) *Chi* , na = non realisable, ns = non significatif.

	Experiment	
	I = Algal type (Fish)	II = Algal density (Fish)
Total time at each patch [1]	ns (ns)	.042 (.000)
Number of switches [2]	na (.008)	na (.000)
Number of bouts/visit [1]	.021 (.010)	ns (.003)
Number of bites/bout [1]	.031 (ns)	ns (ns)
Intrabout bites/second [1]	ns (ns)	ns (ns)

Several aspects of the patterning of the feeding behaviour have been investigated more closely for the results of Experiment I. Since the fish showed individual differences in some measures, the analyses have been carried out separately for each individual. *Figure* 3 presents the log survivor plots for the number of bites per bout for each fish. (The plots show the probability of a bout with more than x bites plotted against x. The plot is linear if the bout is equally likely to terminate after any number of bites.) The data for each fish have been lumped across treatment and time over the thirty min. as they showed no significant variation with respect to these factors (x^2 tests, p > .10). The plot for the combined data is not significantly different from the linear function expected from an exponential process with dead time of 1.5 (one-sample Kolmogorov-Smirnov test, p > .10). In other words, a bout of bites is equally likely to be terminated at any point after the first couple of bites.

The next analysis considers the durations of bout intervals and switch intervals. By bout interval is meant the temporal interval between two successive feeding bouts on the same slide, and by switch interval is meant the interval between two bouts on different slides. For each fish, the overall distributions of the two types of intervals were very similar but in each case there were many more bout than switch intervals of duration one or two sec. *Figures 4 and 5* show the log
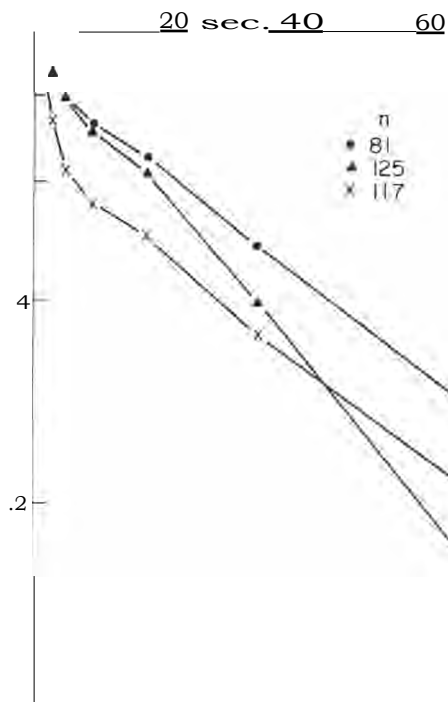

Fig. 3: *Log survivor plots for the number of bites per bout for fish 1 (•), 2 (A), and 3 (X) of Experiment I. Samples sizes are 401, 383, and 416 respectively.*

Fig. 3: *Traces de survie par rapport au nombre de morsures par attaque, pour le poisson 1 (●), 2(A), et 3 (X) de l'expérience I. La taille des échantillons est respectivement de 401, 383, et 416.*

survivor plots for bout and switch intervals respectively. The data for each fish have been lumped as before. The plots are clearly non-linear. Comparison of *figures 4 and* 5 further reveals the individual fish differences : while the plots for fish ● are very similar, those for fish ▲ are very different. There was no correlation between the number of bites in a bout and the length of the subsequent interval (r = — .024, — .018 and .085, n = 392, 367, and 397, p = .64, .73, and .08).

Finally, *table II* shows that the distribution of the number of bouts
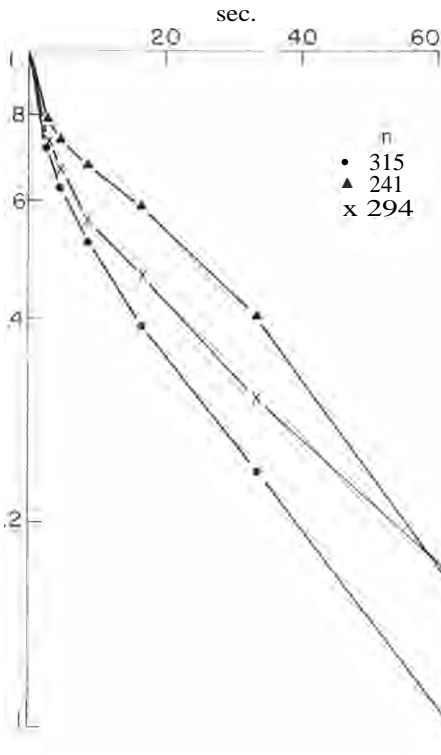

Fig. 4: *Log survivor plots for bout intervals for fish 1 (●), 2 (A), and 3 (X) of Experiment I Sample sizes are 215, 241, and 294 respectively.*

Fig. 4: *Traces de survie par rapport aux intervalles des attaques pour le poisson 1 (●), 2 (A), et 3 (X) de l'expérience I. La taille des échantillons est respectivement de 315, 241 et 294.*

Table II: *Observed and expected, by zero-truncated Poisson, distributions of the number of bouts per visit to a slide (Experiment I: Algal type).*

Tableau II: *Distribution précalculée (par le zéro-tronqué de Poisson) et observée pour le nombre d'attaque par visite à une lame (Experience I: type alginé).*

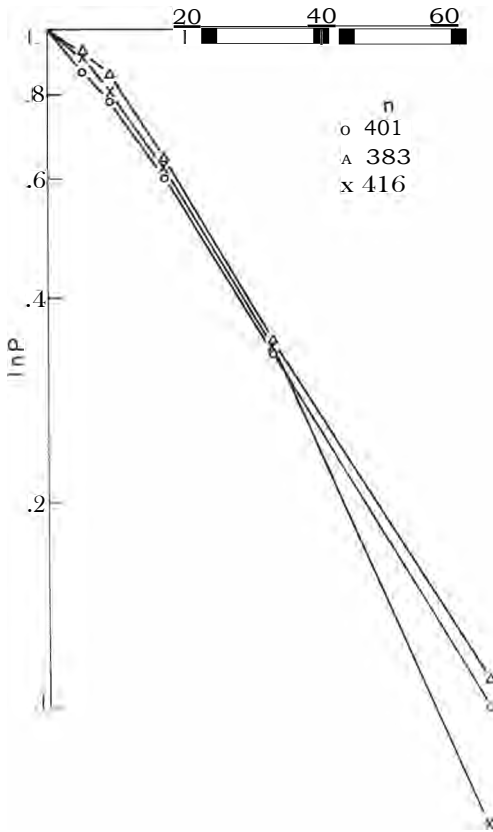|	Fish					
Number	1		2			
	Obs.	Exp.	Obs.	Exp.	Obs.	Exp.
1	21	6.4	58	25.1	48	18.5
2	22	13.2	30	33.4	34	28.4
3	15	18.3	23	29.6	21	29.0
4	13	19.0	9	19.7	11	22.3
⩾ 5	28	42.1	25	37.2	22	37.8

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Fig. 5: Log survivor plots for switch intervals for fish 1 (●), 2 (A), and 3 (X) of Experiment I. Sample sizes are 81, 125 and 117 respectively..

Fig. 5: Traces de survie par rapport aux intervalles de battement pour le *poisson 1* (●), 2 (A), et 3 (X) de *l'expérience I.* Taille des *échantillons* respectivement de 81, 125 *et* 117.

per visit to a slide is not zero-truncated Poisson (x^2 tests, $P <$ .005). In other words, the number of bouts is not generated by a simple random process. The data for each fish have been lumped as before.

DISCUSSION

The frequency with which the fish switched between the two slides indicates that the experimental environment was a fine-grained one (Levins, 1968) for them. The results of Experiment I indicate no overall preference between the two algal types. This outcome is somewhat surprising since the two algae differed in several respects [e.g. by a factor of four in their cal./g. dry weight values (Cummins and Wuycheck, 1971)] and since selectivity seems to characterize many grazers [e.g. blue geese feed selectively on higher protein sources (Harwood, 1975)]. The results of Experiment II indicate a preference for the low density patch, the strength of the preference varying with body length. This association merits further investigation for its bearing on the ontogeny of feeding

preferences. In guppies (Dussault and Kramer, 1981), feeding behaviour also varies with body length, and ingestion rate increases with algal density, but preference data have not been reported.

The temporal features of the feeding behaviour fail to indicate any satiation. We have noted a similar lack of satiation in another algae eater, Hypostomus punctatus (Valenciennes, 1840) and Dussault and Kramer (1981) give log suvivor plots similar to ours. The linearity of the log survivor plots of the number of bites per bout (fig. 3) refutes the hypothesis that each bout reflects the cropping of a fairly fixed quantity of alga (e.g. enough to fill the oral cavity) since the implications of this hypothesis is a non-linear plot. In fact, it appears that a bout of bites is equally likely to be terminated at any point in time once under way. By contrast, the non-linearity of the log survivor plots for the bout and switch intervals (fig. 4 and 5) indicates non-random termination of these intervals, with an excess of single-bout visits and paucity of multiple-bout visits relative to what would be expected under a random generation of bout number. Overall, therefore, the behaviour reflects neigher simple random processes nor dominant deterministic factors, but a complex irregularity.

The lack of preference between algal types and the lack of satiation perhaps jointly indicate that for this species food is superabundant under natural conditions and that there has been no selection for feeding mechanisms beyond a general wandering which ensures bumping into it frequently enough to meet metabolic needs. These results highlight the importance of examining a variety of feeding types within any taxonomic or ecological group before sound generalizations can be made.

REFERENCES

Barlow G.W., 1968. Dither-a way to reduce undesirable fright behaviour in ethological studies. Z. Tierpsychol., 25, 315-318.

Beukema J.J., 1968. Predation by the three-spined stickleback (Gasterosteus aculeatus L.) : The influence of hunger and experience. Behaviour, 31, 1-126.

Bryan J.E., 1973. Feeding history, parental stock, and food selection in rainbow trout. Behaviour, 45, 123-153.

Colgan P., 1973. Motivational analysis of fish feeding. Behaviour, 45, 38-66.

Cummins K.W., Wuycheck J.C., 1971. Caloric equivalents for investigations in ecological energetics. Mitt. Int. Ver. Limnol. 18, 158 pp.

Dussault G.V., Kramer D.L., 1981. Food and feeding behaviour of the guppy, Poecilia reticulata (Pisces : Poeciliidae). Can. J. Zool., 59, 684-701.

Ehrlich P.R., 1975. The population biology of coral reef fishes. Ann. Rev. Ecol. Syst., 6, 211-247.

Fagen R.M., Young D.Y., 1978. Temporal patterns of behaviours : Durations, intervals, latencies, and sequences. In: Quantitative Ethology. P.W. Colgan (ed.) Wiley Interscience, New York, N.Y.

Harwood J., 1975. The feeding strategies of blue geese, Anser caerulescens. Ph.D. thesis, Univ. of Western Ontario, 186 pp.

Ivlev V.S., 1961. Experimental Ecology of the Feeding of Fishes. Yale Univ. Pr., New Haven, Conn.

Lester N.P., 1976. Motivational implications of the temporal pattern of feeding in bluegill sunfish (Lepomis macrochirus). M.Sc. thesis, Queen's Univ. at Kingston, 160 pp.

Leuthold W., 1977. African Ungulates. Zoophysiology Ecology, 8. Springer Verlag, Berlin.

Levins R., 1968. Evolution in Changing Environments. Princeton Univ. Pr., Princeton, N.J.

Lowe-McConnell R.H., 1975. Fish Communities in Tropical Fresh-waters. Longman, London.

Murdoch W.W., Avery S., Smyth M.E.B., 1975. Switching in predatory fish. Ecology, 56, 1094-1105.

011a B.L., Katz H.M., Studholme A.L., 1970. Prey capture and feeding motivation in the bluefish Pomatomus saltatrix. Copeia, 1970, 360-362.