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Reviewed work(s):
Source: *Behaviour*, Vol. 92, No. 1/2 (Feb., 1985), pp. 97-111
Published by: BRILL
Stable URL: http://www.jstor.org/stable/4534403
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THE ENERGETICS OF FEEDING TERRITORIALITY IN JUVENILE COHO SALMON (ONCORHYNCHUS KISUTCH)

by

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(With 7 Figures)

(Acc. 11-VI-1984)

Introduction

For animals in which rapid growth is directly linked to survival and fitness we can predict that selection will favor a net energy maximizing foraging strategy. The juvenile coho salmon (*Oncorhynchus kisutch*) is an example of an animal which should maximize net energy intake (DILL, 1978; DILL *et al.*, 1981). Coho begin defending feeding territories in streams within a week after emerging from the gravel (MASON, 1966). The coho territory system (MASON, 1966; MASON & CHAPMAN, 1965) is a relatively loose structure, sometimes shifting between a regular territorial mosaic (KALLEBERG, 1958) and a system of partial territoriality (GREENBERG, 1947). In general, the territorial coho maintains a 'station' downstream from the center of its roughly teardrop shaped territory. Prey items from the drift float past the fish and it darts out to pursue these prey or to fend off intruders. This feeding territoriality is an integral part of foraging. The fish compete for a limited number of feeding sites (CHAPMAN, 1962), and their relative success in this competition likely determines their feeding efficiency and subsequent growth and fitness. The fish must decide (*sensu* KREBS, 1978) when to be aggressive and how aggressive to be. Time and energy invested in defense are not available for other activities like prey capture, exploration, predator avoidance, etc. Therefore, on average, the benefits from territorial behavior (reduced foraging costs or increased access to prey items) must exceed the

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[1]) We thank M. V. ABRAHAMS, A. T. BECKENBACH, J. R. BRETT, R. L. DUNBRACK, T. A. MCCONNAUGHEY, P. NONACS, R. M. PETERMAN, and D. J. RANDALL for reading an earlier version of the manuscript. L. A. GIGUERE kindly provided the French summary. The research was supported by NSERC Canada Grant A6869 (to LMD).

costs of that behavior. In this regard, we can hypothesize that feeding territoriality has evolved because it increases (on average) the fitness of those fish which practice it. More specifically, territoriality increases fitness by maximizing the net energy intake rate of territorial fish relative to non-territorial fish under most environmental conditions.

Several studies provide insight into the energetics of juvenile salmonid territoriality (CARLINE, 1967; AVERETT, 1969; JENKINS, 1969; DILL, 1978; SMITH & LI, 1983), but all are limited by a paucity of data on activity costs. The purpose of the present study was twofold: 1) to determine the energetic costs of foraging and territorial defense; and 2) to investigate the mechanism by which the time and energy investment in defense activity increases foraging efficiency. To this end, fish were grouped into three categories: territorial, non-territorial, and floater. These categories were developed during field observations on fish behavior. A territorial fish spends most of its time within its defended area, and is usually found in 'glide' areas of the stream. A glide is defined by stream velocities between 5 and 20 cm/s (SOLOMON, 1979). Most of the field observations were on these fish. The nonterritorial fish, mostly found in pools, do not defend any area, but are occasionally aggressive toward other fish. The floaters are not able to defend an area or maintain a station, and they exist in the spaces between the territories (in glides) of other fish. Throughout the paper, these three types of fish will be compared. Although we refer to territorial 'fish', we do not mean to imply that individual fish adopt one feeding strategy or another permanently. It is quite possible that a given fish shifts between nonterritorial and territorial strategies on a daily or seasonal basis.

It is difficult to measure the costs of foraging and defense in a way which still reflects natural field conditions. Swimming metabolic studies are basically confined to the laboratory, but a few investigators (FELDMETH & JENKINS, 1973; FELDMETH, 1983) have attempted to link metabolic work with field conditions by measuring the tailbeat frequency associated with stream swimming activity. They argue that energy budget determinations, even those performed in laboratory streams, may not represent normal field conditions. For instance, they assert that fish handling, necessary for most energy budget determinations, is stressful for the fish and thus affects the variable to be measured. To alleviate this problem, tailbeat frequencies of free swimming fish can be measured in the field, and then tailbeat frequency can be related to both swimming speed and oxygen consumption rate measured in the laboratory (FELDMETH & JENKINS, 1973; PUCKETT, 1983).

In this paper we develop a time budget from quantitative observations of foraging behavior in a coastal stream. We then describe the tailbeat frequencies associated with stream swimming activities. Finally, we combine the time budget with metabolism and tailbeat frequency studies to develop an activity energy budget for each category of fish: territorial, nonterritorial, and floater. The differential allocation of time and energy is then evaluated with reference to fitness.

Methods

Juvenile coho were observed in the Salmon River, Langley, B.C. (sites S10-13 in HARTMAN, 1965) from June to September, 1979-1980. Most of the data (99%) were collected during 1980. Observations were made in both the main channel of the river and in a tributary, Coughlin Creek.

Six sites were chosen to represent different substrates, temperatures, and stream velocities. The sites were chosen with two main criteria in mind: 1) excellent fish visibility from shore; and 2) presence of clearly identifiable territorial, floater, or non-territorial behavior. Sites were added as located and, therefore, sample sizes for each site are not equal. Once a site was selected, it was marked off into 4-6 squares, each side a meter in length, with wooden sticks. The area was then left undisturbed for one week. Every attempt was made to visit each site at a predetermined and consistent time each day for at least ten days. In addition, fish were observed for 8-14 hours on at least one day at each site (N = 1 1979, N = 8 1980) and these data were combined with all other samples.

Each regular visit to a site lasted for about two hours. During the first 30-60 minutes the group of fish within the field of vision was watched (binoculars or naked eye) and an aggressive, visible fish chosen for observation. (In some cases, a nonterritorial or floater fish was chosen for observation.) The behavior of this fish was then monitored for the next 45-60 minutes. Three to five 4 minute quantitative 'samples' were taken during this time, usually separated by 15 minute intervals.

The inherent difficulties of viewing fish directly in the field led to certain biases. For example, fish which moved often and swam against a contrasting background (*i.e.* sand) were observed more frequently than less visible fish.

Time budget.

Territorial defense activity involves three major behavioral components: chase (an aggressive approach toward an intruder, usually continuing after the intruder flees), charge (a very rapid aggressive approach toward an intruder), and various displays. In addition, fish take feeding forays and engage in 'free swimming' (non-stationary swimming which is not associated with other defined behaviors). A six pen event recorder (Esterline Angus) was used to monitor frequency and duration of the following activities during the sample periods: feeding forays, stationary swimming (the swimming activity necessary to maintain a fixed position in running water), chase, charge, lateral and frontal displays (HARTMAN, 1965), flight, free swimming, and wigwag display (JENKINS, 1969). All aggressive activities plus flight are sometimes grouped under the heading total agonistic activity.

A micro-comparator (A. H. Thomas Co.) was used to transcribe distance on the event recorder paper tape into units of time. The number of quantitative observations, the average time of day when the observations were recorded, and the mean observation time per sample are shown in Table 1. In all, there were over 500 hours of observation, including about 25 hours of quantitative sampling.

Tailbeat frequencies.

During the observation intervals, a portable video camera was used to record the tailbeat frequency of the sample fish and other nearby fish. Whenever possible, the camera was placed directly above the sample fish (by climbing on top of fallen trees or onto bridges). Details of the activity filmed were recorded verbally, and much of the filming was done over a sand substrate to increase contrast.

In the laboratory, video tapes were viewed in slow motion (7 frames/s) and tailbeats were counted per unit time. Both the number of counts and sample times vary depending upon tailbeat visibility on the tapes. In general, slow activities (such as stationary swimming) are easy to count and fast activities are relatively difficult. A total of 1007 measurements from about 60 fish were made from the tapes.

Some of these tapes were also used to obtain more detailed time budget information by recording behaviors onto a 'DataMyte' (Electro General Corp.). Thirty-four 6.3 minute observations were made from the video tapes (3.5 hours of quantitative data). Behaviors like the wigwag display, and parallel swimming (CHAPMAN, 1962) were more easily observed on these tapes than directly in the field. Also, the information on the tapes was used to break down feeding motions into three subcategories: normal feed, slow feed, and charge feed. Charge feedings were simply counted to get a per hour rate; percent total time was recorded for normal feed, and slow feed. Slow feed and charge feed are both readily identifiable, the charge feed being exceptionally rapid and the slow feed consisting mainly of head jerk feeding, *i.e.* a rapid lateral movement of the head while the fish remains at its feeding spot.

TABLE 1. Time budget sample summary. N represents the total number of quantitative observations. Fish types include territorial (T), floater (F), and nonterritorial (NT)

Fish type	N	Sample duration (minutes)		Time of day	
		x̄	SD	x̄	Range
T	246	3.7	1.18	1358	0650-1935
F	23	3.5	0.49	1553	0910-1835
NT	30	3.1	0.28	1334	1020-1920

The field tailbeat frequencies were converted into swimming speeds using the equation of BAINBRIDGE (1958). This technique was tested and found to be appropriate for juvenile coho (PUCKETT & DILL, in press).

The energy budget.

To convert oxygen consumption rates to calories, we used an oxycalorific coefficient of 4.63 kcal/liter, or 3.24 cal/mg (BRETT & GROVES, 1979). The same regression equation ($Y = 2.24 + .12X$, where Y is the log of the oxygen consumption rate in mg O_2/kg/hr and X is swimming speed in body lengths/s) was used to calculate all the energy budgets (PUCKETT & DILL, in press). The use of this equation does not reflect variation among the fish categories due to water temperature, fish length, or fish weight, but these differences were fairly small (Table 2). This method will tend to slightly underestimate the differences between the territorial and floater fish below 1 body length/s (L/s) and to slightly overestimate the differences above 2.5 L/s. The net effect will be to slightly underestimate the total energy expenditure difference between territorial and floater fish. Just the opposite error results between territorial and nonterritorial fish: the net effect will be to overestimate the difference in energy utilization.

Some tailbeat frequency data are missing for the floater and nonterritorial fish. In these cases, an estimate was used. For example, the floater flight tailbeat frequency was used to figure floater chase costs. Also, the territorial fish wigwag cost was used to estimate the same for the floater. The nonterritorial fish's chase tailbeat frequency was used to calculate flight cost as well as chase costs. These assumptions have little impact on the final energy budgets since the time fractions are minimal in all cases. To calculate the display rate, we doubled the standard metabolic rate over the duration of the display (PUCKETT, 1983). To calculate the charge rate, we used the cost per charge (5 mg O_2/kg/charge: PUCKETT & DILL, in press) multiplied by the number of charges. This calculation was used because exact charge duration was difficult to determine in the field. Since small changes in charge duration make for large changes in metabolic rate, we felt it was better to assume a cost per charge rather than a rate.

TABLE 2. Mean values for biological and environmental variables

Variable	Territorial			Floater			Nonterritorial		
	$\bar{x}$	Min	Max	$\bar{x}$	Min	Max	$\bar{x}$	Min	Max
Temperature (C)	12	11	14	12	12	12	14	14	15
Depth (cm)	15	7	30	8	7	10	18	9	30
Velocity (cm/s)	20	10	45	14	11	15	1	0	5
Fish size (mm)	47	38	57	37	35	40	43	35	46
Fish density/m^2	6	1	10	8	6	11	8	5	10
Substrate	sand and pebble			sand			sand		

Feeding costs were divided into three groups, normal feed, slow feed, and charge feed. Charge feed costs were calculated as charges, and metabolic rates during the other feeding motions were calculated from associated tailbeat frequencies. Table 3 outlines the metabolic rates used to calculate the energy budgets for the territorial fish. Similar calculations were made for floater and nonterritorial fish.

Results

Time budget.

The complete activity time budgets, for the three fish categories, are shown in Fig. 1. The most striking difference in time allocation between the fish groups involves stationary swimming and free swimming. Figures reported below represent average percentages of total time (based on 4 minute observation samples). The territorial fish spends most of its time at the station (76%) while the floater spends most of its time free swimming (54%). Nonterritorial fish spend more time swimming stationary (50%) than free swimming (43%), but still free swim considerably more than territorial fish. The amount of time spent feeding by

TABLE 3. Hourly energy budget calculation summary for the territorial fish.

Activity	TBF	Speed (L/s)	MG/KG/HR	Time Fraction	MG/KG	cal/kg	% Total
Staswim	3.6	1.7	278	0.75	209	676	56
Swim	5.0	2.8	377	0.026	10	32	3
Chase	6.9	4.2	555	0.033	18	59	5
Flight	5.6	3.2	421	0.0047	2	6	1
Wigwag	4.6	2.5	347	0.0013	1	1	<1
Display	—	—	348	0.012	4	14	1
PSwim	6.5	3.9	511	0.0079	4	13	1
NFeed	5.8	3.4	445	0.099	44	143	12
SFeed	3.8	1.9	294	0.025	7	24	2
Unknown	—	—	278	0.041	11	37	3
			MG/KG/CHG	# CHG/HR			
Charge			5	3	15	49	4
ChgFeed			5	9	45	146	12

Legend: tailbeat frequency (TBF); oxygen consumption rate (mg O_2/kg/hr); oxygen consumption per activity (mg O_2/kg); stationary swimming (Staswim); free swimming (Swim); frontal and lateral displays (Display); parallel swimming (PSwim); normal feed (NFeed); slow feed (SFeed); charge (CHG); and charge feed (ChgFeed). Since the fish weighed about one gram, figure the true caloric cost by dividing by one thousand.

nonterritorial fish (2%) is roughly one-sixth that of territorial or floater fish (13% and 10%, respectively). All differences displayed in Fig. 1 are significant at the $P < .05$ level (Mann-Whitney U-tests), except feeding forays (territorial *vs* floater) and total agonistic activity (territorial *vs* nonterritorial).

For the territorial fish, 20% of the total time spent feeding falls into the category of slow feed and nearly 80% into normal feed; there are approximately 9 charge feedings per hour. A greater percentage of the floater's total time spent feeding can be classed as slow feed (35%) and these coho make 11 charge feedings per hour. Nonterritorial fish made approximately 5 charge feedings per hour and their feeding motions did not readily segregate as slow feed or normal feed, so all feeding motions except charge feedings were considered as normal feed.

A breakdown of agonistic behavior (Fig. 2) illustrates that time spent in chase plus display is about the same for territorial and floater fish (5%) and less for the nonterritorial fish (3%). High flight time results in the floater spending twice as much total time (10%) as the territorial fish (5%) in all agonistic activities. Charges are not shown in Fig. 1 or 2 since they are treated as discrete events (frequencies) rather than as percen-

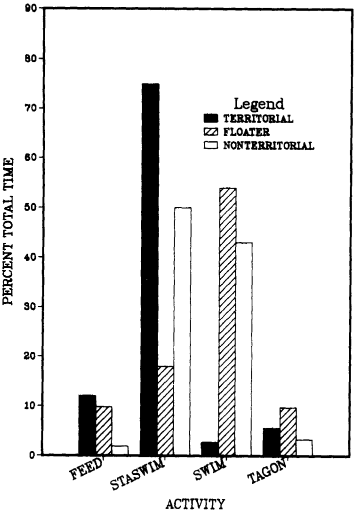

Fig. 1. Percent total time in each activity for each fish type. Behaviors include feeding forays (FEED), stationary swimming (STASWIM), free swimming (SWIM), and total agonistic activity (TAGON).

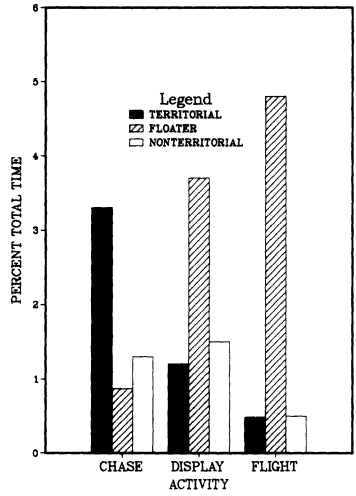

Fig. 2. Agonistic behavior as percent total time. Floaters invest the most time in agonistic activity, mainly because of elevated flight time.

tages of total time. Floater fish spend more time in flight (5%) than the territorial fish spend chasing (3%). Also, the floater's display time (3%) is roughly triple that of the territorial or nonterritorial fish (1%). The following differences illustrated in Fig. 2 are significant ($P < .05$, Mann

Whitney U-tests): territorial *vs* nonterritorial or floater (chase), territorial *vs* floater (display), floater *vs* territorial or nonterritorial (flight).

Tailbeat frequencies.

Tailbeat frequencies associated with charge motions and the most rapid feeding motions were too rapid for analysis, mainly due to a lack of contrast between the fish and the substrate. Charge speeds used in this paper were determined in the laboratory where contrast could be accentuated (PUCKETT & DILL, in press). In Fig. 3, we show the tailbeat frequencies of various activities separated into the three fish categories. The word significant is used below to represent differences between the means at the P<.05 level. Student's t-test was used if the variances were equal; otherwise a Mann Whitney U-test was used. Figures reported in parentheses represent tailbeats per second.

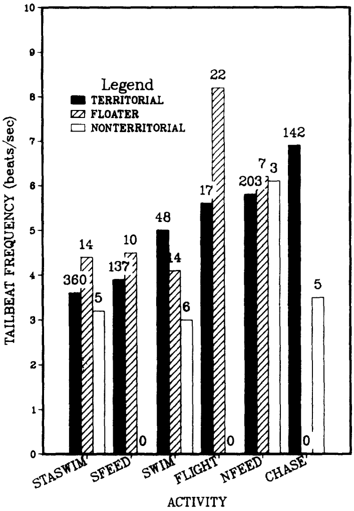

Fig. 3. Mean tailbeat frequencies for territorial, floater, and nonterritorial fish. The total number of measurements is reported above each bar. Activities include stationary swimming (STASWIM), slow feed (SFEED), free swimming (SWIM), and normal feed (NFEED).

The stationary swimming tailbeat frequency is significantly higher for the floater (4.4) than for the territorial fish (3.6). Also, the free swimming tailbeat frequency for the floater (4.1) is significantly higher than the stationary swimming tailbeat frequency for the territorial fish (3.6). Finally, the flight tailbeat frequency (floater-8.2) is significantly higher than the

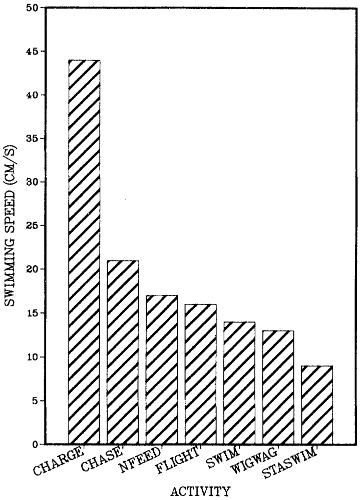

Fig. 4. Swimming speeds associated with various activities in a territorial fish. The speeds were calculated from tailbeat frequencies using Bainbridge's (1958) equation, except that for 'charge' which was measured directly.

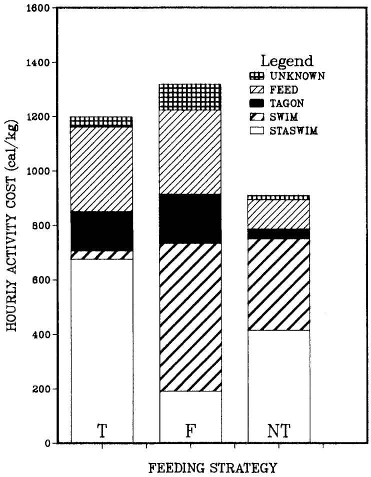

Fig. 5. Activity energy budgets for the territorial (T), floater (F), and nonterritorial (NT) fish, for one hour of normal daytime behavior.

chase tailbeat frequency (territorial-6.9). Normal feed tailbeat frequencies (territorial, floater, nonterritorial) are not significantly different but there is a significant difference between the slow feed frequencies (territorial and floater). Nonterritorial fish tailbeat frequencies are relatively low and uniform.

Tailbeat frequencies were converted to swimming speeds and average values are shown in Fig. 4 for territorial fish.

Energy budget.

The activity energy budget (Fig. 5) illustrates that the floater uses more calories than the territorial fish per hour. The floater spends more calories in stationary and free swimming combined, and more in agonistic behavior. The total activity budget for the territorial fish (1199 cal/kg) is 91% of the floater's budget (1318 cal/kg). The nonterritorial fish spends more calories on stationary and free swimming combined than the floater or territorial fish, but expends fewer calories feeding and in agonistic behavior. The activity budget of the nonterritorial fish (910 cal/kg) is 76% of the territorial fish budget. Agonistic activity is very expensive (Fig. 6). For example, total agonistic cost is 12% of the total territorial activity budget while representing only 5% of the total time budget (Fig. 1). Total agonistic cost is 14% of the total floater activity energy budget while it is 10% of the time budget. Chase and charge together represent 77% of the total agonistic activity investment for a territorial fish, while flight represents 64% of the floater's agonistic behavior investment.

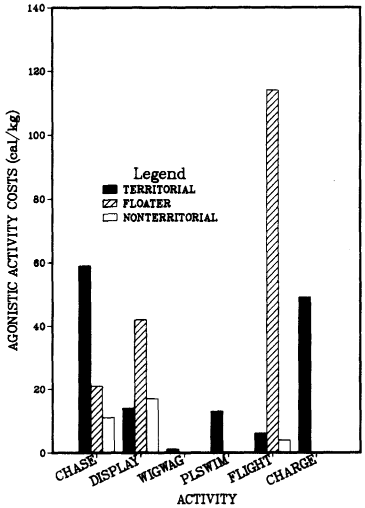

Fig. 6. Agonistic behavior costs for territorial, floater, and nonterritorial fish, for one hour of normal daytime activity. Parallel swimming is depicted as PLSWIM.

Total feeding costs are about the same for the floater and the territorial fish (Fig. 7). Each charge feed is very expensive and the slightly greater percentage of charge feedings made by the floater is significant in terms of cost.

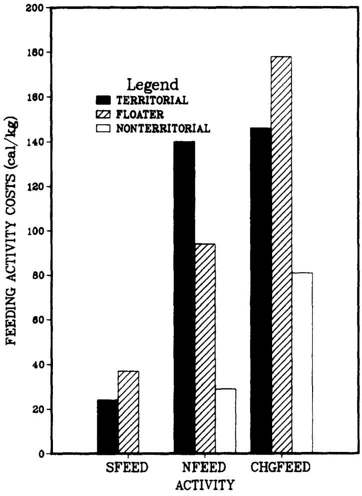

Fig. 7. Feeding costs for the territorial, floater, and nonterritorial fish, for one hour of normal daytime activity. Feeding activities include slow feed (SFEED), normal feed (NFEED), and charge feed (CHGFEED).

Discussion

These data suggest that the three fish types (territorial, floater, nonterritorial) use different feeding strategies. The territorial fish feeds mainly from the station while the floater fish feeds mainly while free swimming. The nonterritorial fish seems to shift between stationary swimming or schooling and search swimming. Differences in aggressive strategies are also apparent. The nonterritorial fish invests little time in agonistic behavior, while the floater is forced to invest much time, mostly as a result of being chased.

The energy budgets gave us a fairly clear idea of the relative cost of activity for the different feeding strategies. We then used the frequency of feeding motions (298, 268, and 90 per hour for the territorial, floater, and nonterritorial fish, respectively), to calculate the cost per prey attack for each strategy: 4.03 (territorial), 4.91 (floater), and 10.1 (nonterritorial) cal/kg. This calculation is a measure of feeding efficiency. The entire activity budget (Fig. 5) is considered in the cost of food gathering, which is quite appropriate since stationary and free swimming can be considered search costs. Juvenile coho really have only two things to accomplish in their first year of life: to grow and to avoid death. The territorial fish spends only 82% as much as the floater per feeding motion. The nonterritorial fish spends 2.5 times as much energy as the territorial fish per feeding motion. We have no data on the caloric value of prey items taken by territorial fish or floaters. However, since these fish exist side-by-side in the stream we think it is reasonable to suggest that the prey items are at least of equal value on average. It is quite probable that territorial fish actually get more calories per prey item since 1) they have more items to choose from (they are surrounded by faster flow), and 2) they can more easily 'choose' their prey items owing to the freedom from harassment conferred by the territory. In either case, the territorial fish have a growth advantage. The source of this advantage is threefold:

a. the ability to hold a station (lower search costs);
b. the ease of feeding (lower prey pursuit costs); and
c. freedom from harassment (lower prey pursuit and agonistic activity costs).

For example, if we compare stationary swimming tailbeat frequencies for the floater and territorial fish (Fig. 3), we see that the floater swims faster, even though surrounding water velocity is lower (Table 2). The territorial fish has basically found a microhabitat (eddy) which confers upon it a hydrodynamic and energetic advantage (lowered routine swimming costs). Swimming in this eddy accounts for a substantial portion of the time budget (Fig. 1). Furthermore, since the water velocity surrounding the territorial fish (but outside the microhabitat) is higher than for the floater, prey availability is also higher. Secondly, the floater is at a disadvantage in terms of directing its feeding motions since it has no territory. The territory provides a zone where one fish can feed with reduced interference and therefore feeding motions need not be so rapid. On average, the floater must charge more often to get its food since it must enter nearby territories. Finally, because the floater is forced to enter nearby territories to get food, it is often chased out and must flee at high speeds. This flight activity is not only costly, but also represents lost feeding time. These three factors represent the basis of the feeding territory advantage.

The case with the nonterritorial fish is not as easily understood. We have often observed nonterritorial fish charging (including a leap from the water into the air) after terrestrial insects. These insects, when available, may indeed provide many calories per prey item. However, the nonterritorial fish must, on average, take prey items which contain about 2.5 times more calories than those taken by territorial fish if they are to grow at the same rate. It seems unlikely that nonterritorial fish can obtain that many more calories per prey item than the territorial fish. It is now clear why a fish might choose a floater strategy over a nonterritorial strategy. The total cost per feeding motion indicates that floaters have the capacity to grow faster than nonterritorial fish, even though their total energy costs are substantially higher.

Energy efficiency is not the only important determinant of a fish's fitness. It matters little how energetically efficient an animal is if it gets eaten. There may be risks involved with the increased motion associated with territorial defense and feeding (DILL, 1983). The floater seems especially vulnerable if motion increases risk since it must flee often, move frequently from one stationary swimming spot to another, and generally make more conspicuous feeding motions. However, territorial and floater fish are mainly found in shallow glides—places which both avian and fish predators avoid. Pools, on the other hand, tend to house fish predators and provide sufficient depth for avian predator strikes, thus placing nonterritorial fish at further disadvantage.

Summary

1. A foraging time budget was developed for territorial, nonterritorial, and floater fish. Territorial fish spend 76% of total time at the station, 3% free swimming, 13% feeding, and 5% in agonistic activity. Floaters spend 18% of their time stationary swimming, 54% free swimming, 10% feeding, and 10% in agonistic activity. Nonterritorial fish spend 50% of their time stationary swimming, 43% free swimming, 2% feeding, and 3% in agonistic activity.
2. Stationary swimming tailbeat frequency for the floater (4.3) is significantly higher than for the territorial fish (3.6). The floater flight tailbeat frequency (8.2) is significantly higher than the territorial chase tailbeat frequency (6.9). Normal feed tailbeat frequencies are similar for all fish groups. Nonterritorial fish tend to move slowly (tailbeat frequency = 3.3) for all activities except normal feed.
3. The total activity budgets for territorial, floater, and nonterritorial fish are 1199, 1318, and 910 cal/kg/hr, respectively. The territorial fish uses 91% as many calories as the floater fish and the nonterritorial fish utilizes 76% of the territorial budget.
4. Total agonistic costs represent 12 and 14% of the territorial and floater fish activity budgets, respectively.
5. The costs per feeding motion for the territorial, floater, and nonterritorial fish are 4.03, 4.91, 10.1 cal/motion, respectively.
6. The territorial fish has a net energy intake advantage over the floater, and probably over the nonterritorial fish, due to 1) reduced search costs, 2) reduced prey pursuit costs, and 3) reduced agonistic activity costs.

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Résumé

1. Le budget temporel de l'activité d'alimentation des individus juvéniles du Saumon Coho a été déterminé pour ceux qui sont territoriaux (défendant un territoire, dans le courant), ou non-territoriaux (qui se trouvent dans les zones calmes), ou ''flottants'' (qui se tiennent entre les territoires des premiers). Les individus territoriaux passent 76% de leur temps à poste fixe, 3% en nage libre, 13% à s'alimenter et 5% en activité agonistique. Les individus ''flottants'' passent 18% de leur temps en station, 54% en nage libre, 10% à s'alimenter et 10% en activité agonistique. Pour des individus non-territoriaux, ces valeurs sont respectivement de 50%, 43%, 2% et 3%.

2. La fréquence des battements de queue dans la nage en station est significativement plus grande pour les individus ''flottants'' (4.3) que pour les détenteurs de territoires (3.6). Les battements de queue des individus flottants qui sont poursuivis ont une fréquence significativement plus grande (8.2) que celle des individus territoriaux en train de les poursuivre (6.9). La fréquence de battements de queue est similaire pour les trois types d'individus, lorsqu'ils s'alimentent. Les individus non-territoriaux se déplacent en général lentement (fréquence de battement de queue:3.3) dans toutes les activités, sauf l'alimentation.

3. Le budget d'activité total pour les individus territoriaux, flottants, et non-territoriaux est respectivement de 1199, 1318, et 910 cal/kg/hr. Les individus territoriaux utilisent 9% de calories en moins que les individus ''flottants''; les individus non territoriaux utilisent 24% de calories en moins que les individus territoriaux.

4. Le coût des activités agonistiques représente respectivement 12% et 14% du budget d'activité des individus territoriaux et flottants.

5. Le coût unitaire des activités d'alimentation, pour les individus territoriaux, flottants et non-territoriaux, est respectivement de 4.03, 4.91 et 10.1 calories par attaque d'une proie.

6. Les individus territoriaux ont un avantage énergétique net par rapport aux individus ''flottants'' ou non-territoriaux. Cet avantage peut être dû à une réduction des coûts de la recherche de nourriture, de la poursuite des proies, et de l'activité agonistique.