Aggressive distance in juvenile coho salmon (*Oncorhynchus kisutch*)

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The distances from which resident coho salmon approached, charged, or gave lateral displays to intruders were recorded, as were the approach and charge velocities. Each of five residents was tested while under three feeding regimes, and in response to three sizes of intruder (20 mm smaller, 10 mm smaller, and of the same size as the resident). Larger intruders were approached and displayed to from greater distances, and charge distance also tended to increase with intruder size. Feeding regime had no effects on aggressive distance. Neither approach nor charge velocity was influenced by intruder size, but charge velocity was highest in the least well fed fish. These results are discussed with reference to the economic defendability theory of territoriality.

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On trouvera ici une étude des réactions de saumons argentés à l'approche d'un intrus; les distances d'approche, d'attaque ou de manifestations latérales ont été enregistrées et les vitesses d'approche et d'attaque ont été mesurées. Cinq saumons 'résidents' ont été soumis à trois diètes différentes et à l'arrivée d'intrus de trois tailles différentes (20 mm ou moins, 10 mm ou moins, taille identique à celle du résident). Les comportements d'approche ou les manifestations latérales se font à des distances plus éloignées de l'envahisseur lorsque celui-ci est de grande taille; le poisson attaque également de plus loin si l'intrus est de taille importante. La diète n'influe pas sur la distance de l'agression. La taille de l'intrus n'affecte pas la vitesse d'approche; cependant, la vitesse d'attaque est moins grande chez les poissons les moins bien nourris. Les résultats sont considérés à la lumière de la théorie économique de défense de territoire.

[Traduit par le journal]

Introduction

The distance between an animal and a biologically relevant stimulus is an important factor in determining whether a response will occur, i.e. many behaviours are distance contingent. Animals appear to have critical or threshold distances for various stimuli. If this distance is not penetrated the response will not occur, even if other stimulus qualities (such as colour, form, and size) are adequate. In the most trivial case, animals cannot respond to objects beyond the maximum range of their sensory apparatus. However, well within this maximum range there appear to exist other, equally important, threshold distances.

A wide variety of visual predators, for example, will only orient to or attack prey when these are within the predator's so-called reactive distance (reviewed in Dill 1975). Similarly, in intraspecific interactions, threshold distances for various aggressive behaviours have been recorded in rainbow trout (Cole 1976), damselfish (Myrberg and Thresher 1974; Thresher 1976), spiders (Buskirk 1975), various crabs (Jachowski 1974; Zucker 1974; Hazlett 1975, 1976), anolis lizards (Hover and Jenssen 1976), chaffinches (Marler 1956*a*, 1956*b*), and gulls (Hutson 1977). One purpose of the present paper is to demonstrate the existence of reactive distances for aggression (or more simply, aggressive distances) in juvenile coho salmon (*Oncorhynchus kisutch*), a species of territorial stream-dwelling salmonid.

The effects of feeding regime and of stimulus (intruder) size on aggressive distance are also examined. Feeding regime was varied because reports of the effects of food supply on aggression in salmonids are contradictory, probably due to the variety of experimental techniques used (see Discussion). It was hoped that by concentrating only on the behaviour and feeding rate of individual fish, hypotheses concerning the extent to which salmonid aggression is food linked could be more readily tested.

Relative size has been shown repeatedly to be of great importance in determining the outcome of aggressive interactions between individuals, including fishes (Chapman 1962; Barlow and Ballin 1976; Gibson 1968). Gibson (1968) attempted to explain his observations by hypothesizing the existence of aggressive distances which vary with relative size, but provided no data. Effects of intruder size on aggressive distance have been observed in spiders (Buskirk 1975), but not in damselfish (Myrberg and Thresher 1974) or hermit crabs (Hazlett 1975).

In addition to aggressive distances, velocities of resident approach and charge were measured to determine whether feeding regime and intruder size affect these parameters, which may be considered measures of the intensity of aggression.

Materials and Methods

The coho salmon used in this study were of two origins. The five residents were captured in Widgeon Creek, B.C., and averaged 79.9 mm fork length (range 79.0–82.2 mm). Intruders, obtained from the Capilano Hatchery, North Vancouver, B.C., were separated into three size groups, nominally designated 60, 70, and 80 mm, of 15 fish each. Means and ranges were 60.1 (58.0–62.0), 69.7 (68.0–72.5), and 79.7 (78.0–82.5) mm, respectively.

Between tests, residents were held individually in 9.2-ℓ Plexiglas aquaria (of the same colour as the test tank) and fed live brine shrimp. Intruders were maintained in identical aquaria in groups of three fish of equal length and fed commercial fish food (Tetramin). Each intruder was used on only one test day but was always replaced in the holding tank by a fish of equivalent size, thus maintaining constant density. On the test day, intruders were held in aerated 3.8-ℓ glass jars between exposures to the resident.

All tests were carried out in a large Plexiglas arena filled to a depth of 15 cm (Fig. 1). The arena was painted with green epoxy paint and surrounded by curtains hiding the experimenter from the fish. At one end, a pair of tubes connected to a peristaltic pump provided a water current (21 cm/s at the outflow) over a few pieces of gravel. The residents spent most of their time oriented into this current. Fish behaviour was filmed with a Sanyo video camera (equipped with a Fujinon lens of 25 mm focal length) located 1.6 m above the water surface, and recorded on video tape for later analysis. Cool white fluorescent bulbs over the arena provided 204 lx of illumination at the water surface. Water temperature in the test arena and holding tanks was maintained at 14–15°C.

The resident was introduced to the test arena at 0900 hours on the day preceding testing. It was fed live brine shrimp at the origin of the water current by injecting these into the delivery system at a point outside the curtains (Fig. 1). The resident was fed in this way 12 times prior to testing, at hourly intervals from 1000 to 1700 hours on the pretest day and from 0900 to 1200 hours on the test day. Testing began at 1300 hours, and nine trials per resident were conducted and filmed. Each of three intruders (one per size class) was presented to the resident three times in random order. Each trial lasted a minimum of 5 min, or until one charge and one lateral display initiated by the resident was observed (trials were terminated after 15 min if these behaviours did not occur). The average trial lasted 7.6 min. Intruders were allowed into one end of the arena, by raising the sliding door with a string, only when the resident had assumed position in the current (occasionally, intruders had to be gently pushed into the test arena with a net). Following each trial the intruder was removed and returned to the holding jar. At the end of each test day the resident was returned to its holding tank, the intruders measured, and the arena water replaced. The above procedure was repeated under three different feeding regimes for each resident.

The three feeding regimes were 8, 16, and 24 shrimp per feeding, or 96, 192, and 288 per acclimation period (12 feedings). All prey were consumed. Preliminary experiments on four of the residents showed that they could eat an average of 189 (range 164–204) live brine shrimp following a 24-h deprivation period. The amounts fed thus represented approximately 0.5, 1.0, and 1.5 times the assumed maximum gut capacity of the fish.

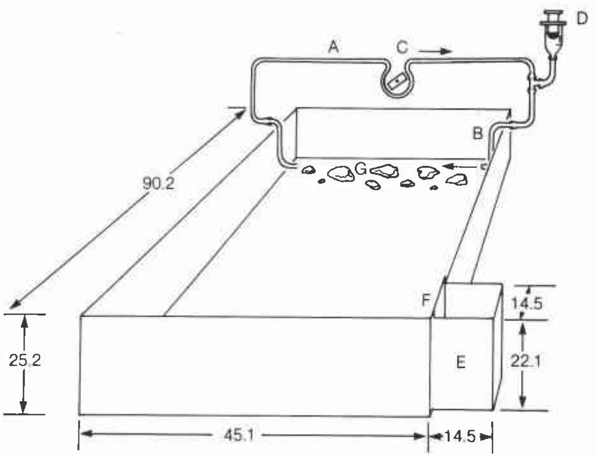

FIG. 1. Test arena. A current was produced by driving water through a tygon tube (A) and out through 6-mm inside diameter glass tubing (B) with a peristaltic pump (C). Food was added through the syringe (D). The intruder was released from the small chamber (E) by raising the sliding door (F) with a string. The resident usually maintained position in the water current over the gravel (G). All distances are inside measurements (centimetres).

Each of the five residents was tested under each of the three feeding regimes, the 15 combinations being run in predetermined random order (the only constraint being that no resident was used on two consecutive test days). Nine trials were conducted on each of the 15 test days; thus a total of 135 trials were filmed. Residents were measured at the onset and at the end of their experimental series. These lengths were averaged to provide the best estimate of resident size. Residents grew an average of 2.0 mm between measurements.

Video tapes were examined on a Conrac 58-cm monitor (image size 0.51 times actual size) and fish positions traced onto plastic sheets wrapped around the slightly curved screen surface. Positions of the two fish were traced when the resident first approached the intruder, first charged the intruder, and first displayed laterally to the intruder. Distances from the tip of the resident's nose to the tip of the intruder's nose (approach and charge) or to the nearest part of the intruder's body excluding the nearly transparent caudal fins (lateral display) were later measured from these tracings.

Approach behaviour has not previously been described in coho salmon but has been well described in Atlantic salmon, *Salmo salar* (Kalleberg 1958). It was invariably the first response to the intruder, when it occurred at all, but was only observed in about one-half of the interactions. The charge of the coho is very similar to that described by Keenleyside and Yamamoto (1962) in Atlantic salmon, and has been called "drive toward" in coho (Mason 1966). In practice an approach was distinguished from a charge by its lower velocity; mean approach velocity (n = 63) was 115.5 cm/s, and mean charge velocity (n = 109) was 199.4 cm/s. Approach and charge velocities were measured in the first 15 frames (0.25 s) of the resident's straight-line path towards the intruder. Lateral display in coho is very similar to that described by Keenleyside and be noted that approach and charge distances are behaviour initiation distances, whereas lateral display distance is that at which the display was complete in form, not that at which it was initiated by the resident. The point of initiation was virtually impossible to detect in the films, as the behaviour did not begin abruptly.

TABLE 1. Mean approach, charge, and lateral display distances (millimeters) for each of the nine treatments (three intruder sizes × three feeding regimes). Sample sizes in parentheses

Shrimp per hour	Approach distance when intruder size (mm): 60	70	80	Charge distance when intruder size (mm): 60	70	80	Lateral distance when intruder size (mm): 60	70	80
8	503.7 (5)	565.6 (10)	666.4 (4)	184.7 (15)	141.3 (13)	183.1 (12)	71.4 (15)	85.7 (11)	121.3 (10)
16	518.2 (8)	660.4 (9)	647.7 (10)	183.8 (14)	243.4 (15)	177.3 (11)	72.5 (13)	78.3 (13)	129.7 (12)
24	474.6 (7)	584.3 (7)	636.8 (6)	160.6 (13)	190.7 (15)	180.0 (14)	82.3 (14)	82.1 (14)	110.1 (14)
Pooled	499.3 (20)	603.4 (26)	648.1 (20)	176.9 (42)	194.1 (43)	180.2 (37)	75.4 (42)	81.9 (38)	119.7 (36)

There was considerable interresident variability in aggressive distance. Consequently, data for each fish were scaled as follows. The largest approach distance exhibited by a particular resident was given a value of 1.0 and all other approach distances for that resident were expressed as a proportion of this value. This was done separately for approach, charge, and lateral display for each resident. These relative aggressive distances were transformed (arcsine square root) prior to conducting analyses of variance. Resident number could not be used as a covariate in the analyses because all residents were not equally represented in all treatment blocks. This resulted from the fact that approaches, charges, and lateral displays were observed in only 66, 122, and 116 of the 135 trials, respectively. An identical procedure was followed in the analysis of velocities.

Results

Means of the raw data for the various aggressive distances are shown in Table 1. Both approach and lateral display distances tend to increase with increasing intruder size; the effects of intruder size on charge distance are less clear. There are no apparent trends due to feeding regime.

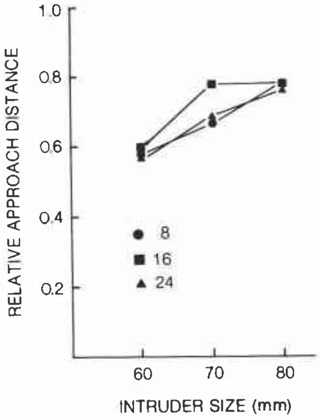

FIG. 2. Mean relative approach distance (see Materials and Methods) as a function of intruder size (millimetres) and resident feeding regime (8, 16, 24 brine shrimp per hour).

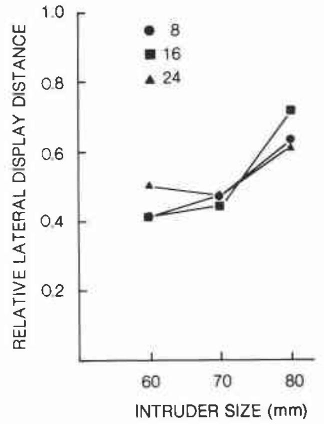

FIG. 3. Mean relative lateral display distance (see Materials and Methods) as a function of intruder size (millimetres) and resident feeding regime (8, 16, or 24 brine shrimp per hour).

The effects of intruder size on approach distance (Fig. 2) and lateral display distance (Fig. 3) are more evident when the data are transformed as described above. These effects are both significant ($p < 0.05$ for approach; $p < 0.001$ for lateral display). There were no significant effects of feeding regime, nor any evidence of a feeding regime – intruder size interaction. There were no significant effects of feeding regime, intruder size, or their interaction on relative charge distance.

Further examination of the relative charge distance data (pooled over all feeding regimes) revealed an effect of intruder size that was concealed in the statistical analysis owing to the considerable degree of variability. In particular, the distribution of relative charge distances in response to 80-mm intruders was characterized by many large values not seen when the intruder was smaller (Table 2). Application of the median test to the data (Siegel 1956) indicates that this difference is significant

TABLE 2. Distribution (number and percent frequency) of relative charge distances to intruders of three sizes (all feeding regimes combined). The median and mean relative charge distance are also shown for each intruder size

Categories of relative charge distance	Intruder size, mm					
	60		70		80	
	n	%	*n*	%	*n*	%
0.01–0.20	13	31	8	19	6	16
0.21–0.40	18	43	22	51	12	32
0.41–0.60	6	14	5	12	6	16
0.61–0.80	2	5	3	7	10	27
0.81–1.00	3	7	5	12	3	8
Median	0.33		0.31		0.43	
Mean	0.34		0.41		0.38	

TABLE 3. Effect of feeding regime on relative approach and relative charge velocities of the residents (pooled over all intruder sizes)

	Feeding level, shrimp/h			Significance level
	8	16	24	
Approach	0.52	0.64	0.49	NS
Charge	0.60	0.47	0.48	<0.01

NOTE: NS, not significant.

($p < 0.05$). However, since the samples were not strictly independent (i.e. the same residents were used in each treatment) this evidence must be regarded as suggestive but not conclusive.

There were no significant effects of intruder size on either approach or charge velocity. However, feeding regime significantly influenced relative charge velocity but not approach velocity (Table 3).

Discussion

Juvenile coho salmon defend feeding territories in the field, at least under certain circumstances (Chapman 1962; Hartman 1965), and the present experiments were designed to take advantage of this fact. Stream-dwelling salmonids are more likely to hold territories in currents than in still water (Kalleberg 1958; Hartman 1965). Coho in the present experiments tended to hold station in a current over the only few pieces of gravel present in an otherwise featureless tank. They received food in the current and resided in the tank 28 h prior to introduction of the first intruder. The resident may therefore be considered a territory holder defending its feeding station against intruders, and the approach and (or) charge distances observed may well be measures of territory size. (Even if approach behaviour is investigative and not aggressive, it decreases the distance between resident and intruder and thereby increases the probability that a charge will subsequently occur.) If this assumption is correct, then the data may be used to test certain hypotheses derived from current ecological theory.

According to Brown's (1964) economic defendability theory an animal should only defend a feeding territory if the energetic benefits thus obtained outweigh the costs (time, energy, risk of injury) of defense. It may therefore be predicted that the size of the feeding territory defended will be a function of the diet overlap between resident and intruder. This has been demonstrated in the damselfish *Eupomacentrus planifrons* (Thresher 1976). These fish defend 'serial territories,' driving off intruders of different species from different maximum distances, and the area defended is largest when the intruding species eats the same benthic algae as the resident.

Because diet overlap between two conspecifics is likely to be a function of their relative sizes (Wilson 1975), intraspecific serial territoriality should also occur; i.e. attack distance should decrease with increasing size difference between resident and intruder. Myrberg and Thresher (1974) and Hazlett (1975) were unable to demonstrate such an effect. However, Buskirk's (1975) data for spiders clearly indicate that intruder size is a major determinant of the distance at which agonistic behaviours are shown by a resident. Unfortunately, Buskirk apparently pooled data over several resident size classes, making interpretation of relative size effects impossible. In the present experiments the approach distances, and possibly charge distances, of resident coho towards intruders decreased as the intruder became increasingly smaller than the resident, supporting the intraspecific serial territory hypothesis. Charges may be initiated more readily against smaller intruders (either because they are less intimidating or easier to chase away), and this might account for the fact that charge distance is less dependent on intruder size than is approach distance.

These distances should also decrease as the intruder becomes increasingly larger than the resident; i.e. aggressive distance should be maximal for intruders about the same size as the resident, where diet overlap is expected to be maximal. However, preliminary experiments (Dill, unpublished data) indicate that coho approach and charge distances both continue to increase with increasing intruder size, even for intruder:resident size ratios greater than 1.0. Although further studies are required, this may indicate either that (*a*) the intraspecific serial territoriality hypothesis is incorrect, (*b*) niche overlap does not decrease for fish larger than the resident (perhaps coho diet does not change markedly with size, and increased potential food consumption by increasingly larger intruders therefore causes overlap to rise continuously with increasing intruder:resident size ratio), or (*c*) some other measure of aggression, such as persistence or intensity, is maximal for intruders about the same size as the resident, as shown by Stamps (1977) for females of the territorial lizard *Anolis aeneus*. Data to test these alternatives are not presently available, but no effect of intruder size on velocity (a measure of intensity) was observed in the present study.

Territory size should also vary with food availability according to the economic defendability hypothesis, and this has been observed in several species of birds (Stenger 1958; Gass *et al.* 1976; Cody and Cody 1972), wolves (Haber *et al.* 1976), and rainbow trout (Slaney and Northcote 1974). Symons (1971), however, observed no such effect in high-density laboratory populations of Atlantic salmon. There is no unequivocal evidence for food-linked territory size in coho salmon (contrary to Chapman's (1962) conclusion), but Mason's (1976) data are suggestive. If approach and charge distances are measures of territory size, then the present study suggests that juvenile coho do not alter territory size in response to short-term changes in food availability. Similarly, Marler (1956*a*,1956*b*) could find no effect of hunger on individual distance in chaffinches.

In general the effects of food supply on salmonid aggression are poorly understood. Newman (1956), Keenleyside and Yamamoto (1962), and Mason (1966) observed increased aggression following feeding to satiation, but Symons (1968) found aggression to be highest during periods of starvation. Slaney and Northcote (1974) found the frequency of aggressive encounters to decrease with increased food supply and ascribed contradictory results to the unnatural feeding regimes used in other studies. The effect of food availability on aggression is confounded by its effects on general activity (Andrew 1957; Keenleyside and Yamamoto 1962), because more active, feeding animals are likely to encounter one another more frequently. In addition, the mere presence of food in some experiments may cause general arousal (Kalleberg 1958), or its sudden removal cause redirection of attack behaviour (Newman 1956). The present experiments were designed to avoid these problems: resident fish were fed in a seminatural manner for 1 day before testing; the last feeding period occurred 1 h prior to introduction of the first intruder; and the feeding regime, and presumably the activity level, of the intruders was constant. Under these conditions no effect of feeding regime on any of the three aggressive distances was observed. Charge velocity was greatest for the least well fed coho in these experiments, suggesting that intensity of aggression is food supply dependent, but further studies are obviously required.

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ANDREW, R. J. 1957. Influence of hunger on aggressive behavior in certain buntings of the genus *Emberiza*. Physiol. Zool. **30**: 177–185.

BARLOW, G. W., and P. J. BALLIN. 1976. Predicting and assessing dominance from size and coloration in the polychromatic midas cichlid. Anim. Behav. **24**: 793–813.

BROWN, J. L. 1964. The evolution of diversity in avian territorial systems. Wilson Bull. **76**: 160–169.

BUSKIRK, R. E. 1975. Aggressive display and orb defense in a colonial spider, *Metabus gravidus*. Anim. Behav. **23**: 560–567.

CHAPMAN, D. W. 1962. Aggressive behavior in juvenile coho salmon as a cause of emigration. J. Fish. Res. Board Can. **19**: 1047–1080.

CODY, M. L., and C. B. J. CODY. 1972. Territory size, clutch size, and food in populations of wrens. Condor, **74**: 473–477.

COLE, K. S. 1976. Social behaviour and social organization of young rainbow trout, *Salmo gairdneri*, of hatchery origin. M.Sc. Thesis, University of Guelph, Guelph, Ont.

DILL, L. M. 1975. Predatory behavior of the zebra spider, *Salticus scenicus* (Araneae: Salticidae). Can. J. Zool. **53**: 1284–1289.

GASS, C. L., G. ANGEHR, and J. CENTA. 1976. Regulation of food supply by feeding territoriality in the rufous hummingbird. Can. J. Zool. **54**: 2046–2054.

GIBSON, R. N. 1968. The agonistic behaviour of juvenile *Blennius pholis* L. (Teleostei). Behaviour, **30**: 192–217.

HABER, G. C., C. J. WALTERS, and I. MCT. COWAN. 1976. Stability properties of a wolf–ungulate system in Alaska and management implications. Univ. B.C. Inst. Anim. Res. Ecol. Rep. R-5-R.

HARTMAN, G. F. 1965. The role of behavior in the ecology and interaction of underyearling coho salmon (*Oncorhynchus* *kisutch*) and steelhead trout (*Salmo gairdneri*). J. Fish. Res. Board Can. **22**: 1035–1081.

HAZLETT, B. A. 1975. Individual distance in the hermit crabs *Clibanarius tricolor* and *C. antillensis*. Behaviour, **52**: 253–265.

——— 1976. Agonistic behavior of two sympatric species of xanthid crabs, *Leptodius floridanus* and *Hexapanopus angustifrons*. Mar. Behav. Physiol. **4**: 107–119.

HOVER, E. L., and T. A. JENSSEN. 1976. Descriptive analysis and social correlates of agonistic displays of *Anolis limifrons* (Sauria, Iguanidae). Behaviour, **58**: 173–191.

HUTSON, G. D. 1977. Agonistic display and spacing in the black-headed gull, *Larus ridibundus*. Anim. Behav. **25**: 765–773.

JACHOWSKI, R. L. 1974. Agonistic behavior of the blue crab, *Callinectus sapidus* Rathbun. Behaviour, **50**: 232–253.

KALLEBERG, H. 1958. Observations in a stream tank of territoriality and competition in juvenile salmon and trout (*Salmo salar* L. and *S. trutta* L.). Inst. Freshwater Res., Drottningholm, Rep. **39**: 55–98.

KEENLEYSIDE, M. H. A., and F. T. YAMAMOTO. 1962. Territorial behaviour of juvenile Atlantic salmon (*Salmo salar* L.). Behaviour, **19**: 139–169.

MARLER, P. 1956*a*. Territory and individual distance in the chaffinch *Fringilla coelebs*. Ibis, **98**: 496–501.

——— 1956*b*. Studies of fighting in chaffinches. 3. Proximity as a cause of aggression. Br. J. Anim. Behav. **4**: 23–30.

MASON, J. C. 1966. Behavioral ecology of juvenile coho salmon (*Oncorhynchus kisutch*) in stream aquaria with particular reference to competition and aggressive behavior. Ph.D. Thesis, Oregon State Univ., Corvallis.

——— 1976. Response of underyearling coho salmon to supplemental feeding in a natural stream. J. Wildl. Manage. **40**: 775–788.

MYRBERG, A. A., JR., and R. E. THRESHER. 1974. Interspecific aggression and its relevance to the concept of territoriality in reef fishes. Am. Zool. **14**: 81–96.

NEWMAN, M. A. 1956. Social behavior and interspecific competition in two trout species. Physiol. Zool. **29**: 64–81.

SIEGEL, S. 1956. Nonparametric statistics for the behavioral sciences. McGraw-Hill, Toronto.

SLANEY, P. A., and T. G. NORTHCOTE. 1974. Effects of prey abundance on density and territorial behavior of young rainbow trout (*Salmo gairdneri*) in laboratory stream channels. J. Fish. Res. Board Can. **31**: 1201–1209.

STAMPS, J. A. 1977. The relationship between resource competition, risk, and aggression in a tropical territorial lizard. Ecology, **58**: 349–358.

STENGER, J. 1958. Food habits and available food of ovenbirds in relation to territory size. Auk, **75**: 335–346.

SYMONS, P. E. K. 1968. Increase in aggression and in strength of the social hierarchy among juvenile Atlantic salmon deprived of food. J. Fish. Res. Board Can. **25**: 2387–2401.

——— 1971. Behavioural adjustment of population density to available food by juvenile Atlantic salmon. J. Anim. Ecol. **40**: 569–587.

THRESHER, R. E. 1976. Field analysis of territoriality of the threespot damselfish, *Eupomacentrus planifrons* (Pomacentridae). Copeia, 1976: 266–276.

WILSON, D. S. 1975. The adequacy of body size as a niche difference. Am. Nat. **109**: 769–784.

ZUCKER, N. 1974. Shelter building as a means of reducing territory size in the fiddler crab *Uca terpischores* (Crustacea: Ocypodidae). Am. Midl. Nat. **91**: 224–236.