

foragers with high risk over similar ranges of costs for lost food items.

R. F. McMahon collected and identified the crabs.

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- FitzGerald & van Havre 1987. It would be advantageous to ripe females to identify and avoid destroying nests containing their own eggs. FitzGerald & van Havre (1987) reported kin recognition by olfaction in this species. In laboratory choice tests females directed more bites to eggs from another female than to their own eggs. Thus olfactory egg recognition could be a mechanism by which females avoid destroying their own eggs.
- At Isle Verte, Quebec, FitzGerald (1983) found a mean of 877 eggs per nest, while females laid 366 eggs per clutch on average. Thus it is probable that nests contain the clutches of three or more females. This could present a kin recognition problem to potential cannibals as the odours from a female's eggs will be diluted by the odours of the other clutches. Our study had two goals: first, to confirm the kin recognition results reported by FitzGerald & van Havre (1987); second, to determine whether a female loses the ability to recognize her own eggs when they are mixed together with the eggs of other females. We predicted that females would attack clutches that contained their own eggs less often than foreign clutches.
- Threespine sticklebacks were seined from tide pools in the Isle Verte National Wildlife Area, Quebec, during May and June 1987. In the laboratory, males and females were separated and held in large aquaria (light:dark 14:10 h photoperiod, temperature 20–22°C). We used FitzGerald & van Havre's (1987) laboratory acclimation and experimental protocols. In the week following capture, salinity was decreased from 20 ppm to 1 ppm. All tests were conducted in fresh water. On the day preceding a trial, several females were mated with different males to obtain fertilized clutches. Eggs remained in the male's nest for 1.5 h to ensure fertilization. Individual clutches were then weighed and kept in separate aerated aquaria overnight.

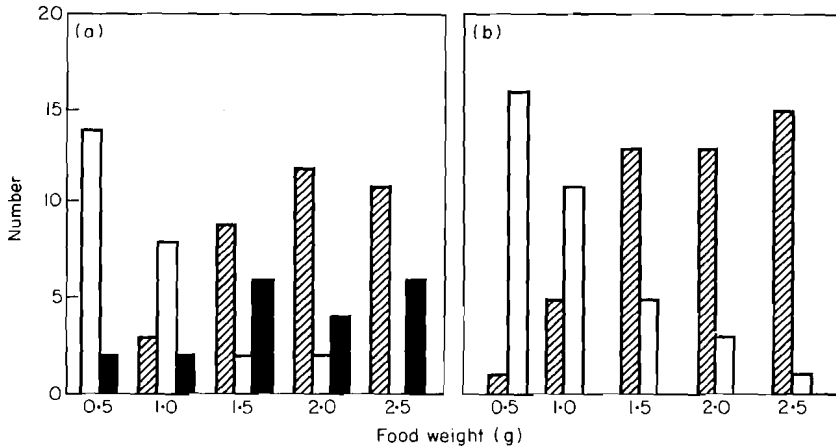
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### Multiple Clutches: Female Threespine Sticklebacks Lose the Ability to Recognize their own Eggs

Adaptive explanations for the evolution of cannibalism often require that a cannibal identify and avoid eating kin in order to maximize lifetime reproductive success (Hrdy 1979; Polis 1981; Vickery et al. 1988). The threespine stickleback, *Gasterosteus aculeatus*, has recently become a focus for research on cannibalism. Females often raid nests and cannibalize eggs (Whoriskey & FitzGerald 1985; Ridgway & McPhail 1988). Females spawn repeatedly during the breeding season, and in some instances nesting males may become a limiting resource. Ripe females will initiate attacks on males who have stopped courtship behaviour and are guarding eggs. These attacks can destroy the nest, forcing the male to rebuild and start courting again. The female initiating the raid will then be the first to spawn with the male when it

rebuilds its nest (FitzGerald & van Havre 1987). It would be advantageous to ripe females to identify and avoid destroying nests containing their own eggs. FitzGerald & van Havre (1987) reported kin recognition by olfaction in this species. In laboratory choice tests females directed more bites to eggs from another female than to their own eggs. Thus olfactory egg recognition could be a mechanism by which females avoid destroying their own eggs.

After spawning, one of the females was chosen randomly and placed in an 87-litre aquarium which served as a test arena. The following day the female participated in three trials in which she was presented with paired clutches of eggs simultaneously. The eggs were in 1-ml sacks of 0.5 mm meshed cotton that allowed the female to see and smell the eggs but not consume them. In one trial, a female was presented with a clutch of her own eggs and a clutch of one other female's eggs. In a second trial, the female was presented with one clutch containing 33% (by weight) of her own eggs mixed with equal amounts of eggs from two other females, and a second clutch of equal weights of eggs from three other females. In a third trial, the female was presented with a clutch of 20% (by weight) of her own eggs with equal contributions from four additional females, and a second clutch from five



**Figure 1.** The number of male (a) and female (b) *Uca panacea* running and carrying a food item (open bars), running and not carrying a food item (hatched bars), or staying with the food item (solid bars) when threatened by a model predator at five weights of food (minnow pieces).  $N = 18-20/\text{food weight}$  for females,  $N = 12-16/\text{food weight}$  for males.

$P < 0.05$ ). This response appeared to be defensive and involved cessation of feeding, tilting of the anterior of the body upward, and waving the enlarged chela. Females did not exhibit this behaviour. This may result from their lack of an enlarged chela with which to defend food (option 3) rather than their attempting to escape from a threat (options 1 and 2). A two-way ANOVA (Sokal & Rohlf 1981) indicated that crab running speed (cm/s) was significantly affected by the amount of weight carried ( $P < 0.001$ ) but not by sex ( $P > 0.25$ ); the interaction was not significant ( $P > 0.25$ ). Post-hoc comparisons (Student-Newman-Keuls) of running speed between weights that differed by 1 g or more were significant ( $P < 0.05$ ). The decrease in running speed is an approximation of the change in predation risk from carrying food while escaping. Data are available on the energetic cost of running in fiddler crabs (Full & Herreid 1984), but they cannot be extrapolated to our experimental system. If we assume that crabs run as fast as possible while escaping, the energetic costs of carrying food should increase monotonically, with increasing food weight. Maximum gross benefit gained from carrying food was estimated by allowing crabs to feed for 12 h. Sex and initial food weight did not significantly affect ( $P > 0.10$ ) the total weight of food eaten. The maximum amount eaten in 12 h was less ( $0.47$  g;  $\bar{X} \pm \text{SD} = 0.260 \pm 0.12$  g) than the weight of the smallest food item ( $0.5$  g). Approximately 70% of the crabs carried food when it weighed twice what could be consumed ( $1.0$  g),

indicating that increases in the energetic cost of carrying may be small relative to potential benefits.

The behavioural option employed by foragers faced with a threat is dependent on the relative costs and benefits of the options (Ydenberg & Dill 1986). Each option exhibited by fiddler crabs has an associated effect (cost) on forager survival. Escaping without the food results in loss of energy but also in relatively low predation risk. Escaping while carrying food results in increased energetic cost of escape and increased predation risk (through decreased escape speed and increased conspicuousness), but not the loss of energy in the food. Remaining with the food results in relatively high predation risk depending on the ability of the forager to defend itself and intensity of the predator threat. A food item should be carried while escaping when the cost of carrying and increased predation risk do not exceed the cost of interrupting feeding and loss of food. Remaining with the food should occur when the increased predation risk incurred does not exceed the cost of escaping with or without the food. The relative costs of the options would be sensitive to variations in predation threat severity and forager hunger level. Increases in hunger level effectively increase the cost of a lost food item. Foragers with high hunger levels would carry heavier food items when escaping than foragers with low hunger levels over similar ranges of costs for escaping while carrying. Foragers faced with low predation risk should carry heavier food items when escaping than

other females. These ratios approximate nest contents found in field studies (FitzGerald 1983). The total weights of the clutches used in each trial were equal, but differed from trial to trial due to size differences between individual females ( $\bar{X} \pm SD$  sac egg mass =  $0.43 \pm 0.16$  g, range:  $0.155-0.71$  g;  $N=13$ ). Trials were conducted in a random order. The two clutches were suspended 15 cm below the water's surface at one end of the tank, and separated by 15 cm. The side of a tank on which a clutch was placed was decided by a coin toss. The number of bites and lunges at each sack in 20 min was recorded, with a 30-min interval between presentations. Thirteen experimental females were tested, with additional eggs coming from a laboratory stock of 200 females.

Results showed that females directed significantly more attacks against 100% alien clutches ( $\bar{X} \pm SD = 6.92 \pm 6.3$ ) than against clutches of their own eggs ( $3.92 \pm 5.15$ ;  $N=11$ ,  $T=6.5$ ,  $P < 0.01$ , Wilcoxon signed-rank test; Zar 1974), confirming the results of FitzGerald & van Havre (1987). In contrast, there were no significant differences ( $P > 0.05$ , Wilcoxon signed-rank test) between the number of attacks on 100% alien clutches and either clutches of 33% of their own eggs (attacks to foreign eggs:  $\bar{X} \pm SD = 4.62 \pm 5.47$ ; attacks to own eggs:  $6.38 \pm 6.80$ ;  $N=10$ ,  $T=34.5$ ) or 20% of their own eggs (attacks to foreign eggs:  $\bar{X} \pm SD = 2.08 \pm 2.05$ ; attacks to own eggs:  $4.77 \pm 6.00$ ;  $N=11$ ,  $T=55.5$ ).

These results indicate that female threespine sticklebacks cannot detect their own eggs if they constitute 33% or less of the nest contents. Given the probability that a nest of Isle Verte contains at least three clutches (FitzGerald 1983), most likely from different females, olfaction will be of limited use for kin recognition. To make tenable the adaptive explanations of female cannibalism suggested by FitzGerald & van Havre (1987), a more reliable mechanism for recognizing kin must be found.

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## Male Mating Success in Red-sided Garter Snakes: Size is Not Important

Red-sided garter snakes, *Thamnophis sirtalis parietalis*, in Manitoba, Canada, exhibit intense mating activity on emergence from winter dormancy. This period is characterized by large aggregations in which single females are courted by a number of males; males are not overtly aggressive to other males. Since males emerge en masse while females emerge singly over a 3-week period, the effective sex ratio at the time a female mates may be 100 or more to one. Large male size is by far the most commonly reported correlate of mating success (Trivers 1972; Arak 1983; Daly & Wilson 1983; Ridley 1983). Snakes in general lack secondary sex structures and size is certainly the most notable difference between male garter snakes. In the red-sided garter snake, body length and mass are correlated ( $r=0.90$ ,  $N=876$ ,  $P < 0.0001$ ). This study examined the role of body size in determining the mating success of male red-sided garter snakes.

We studied a large population of red-sided garter snakes during the breeding season in 1983-1985 at the Narcisse Wildlife Management Area. We observed naturally occurring matings as well as conducted mating trials in controlled settings.