CANNIBALISM IN NATURAL POPULATIONS

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INTRODUCTION

Cannibalism, defined as intraspecific predation, is a behavioral trait found in a wide variety of animals, although most references to this behavior are anecdotal or based on casual laboratory observations. The role of cannibalism in the dynamics of natural populations has been largely neglected; the most elegant and detailed analyses of the population consequences of cannibalism are still provided by laboratory studies of flour beetles (*Tribolium*) that describe the process, examine its interactions with other population processes, and attempt to derive generalities about its effects (60, 78, 88). Therefore, some authors have suggested that cannibalism is an artifact of laboratory systems (20, p. 324) or that it occurs only in cases of severe stress, especially when alternatives, such as dispersal, are not possible (105).

My purpose in this review is to show that cannibalism is a normal phenomenon in many natural populations, to evaluate its possible roles in influencing demographic structure and population processes, and to suggest conditions for, and constraints on, its occurrence. Cannibalism may be an interaction that reduces population size before acute resource shortage causes severe physiological stress, and in this sense its effects may be analogous to those of spacing behavior or dominance hierarchies in some social animals (104). I also discuss cannibalism as a limiting case of predator-prey interactions among potential competitors.

This review is based mainly on field experiments and direct estimates of rates of cannibalism, but I use papers describing laboratory experiments to supplement the discussion of behavioral triggers and genetic components and to fill gaps in the field evidence. I have excluded numerous references with only casual mention of cannibalistic events.

DISTRIBUTION OF CANNIBALISM

Cannibalism has been reported in many groups of animals, e.g. protozoa (54), planaria (4), rotifers (46), snails (72), copepods (3), centipedes (31), mites (24, 98,

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106), insects (63, 100), fish (66, 91), anurans (12), and birds and mammals (99, 108). Table 1 summarizes the distribution of species for which there are sufficient data to indicate that cannibalism occurs normally in the field. I have grouped these species by their predominant feeding habit as herbivores (including scavengers and a few omnivores) or predators, and by habitat. Perhaps surprisingly, a large proportion of observations of cannibalism among terrestrial animals is for species that are usually "herbivores," including butterfly larvae (14), leaf-eating beetles (35), and bark beetles (6). Several authors have noted that cannibalism may be widespread among herbivorous insects. Kirkpatrick (63, p. 194) stated that cannibalism is rare among terrestrial predatory insects, but that " . . . some plant-feeding insects are inveterate cannibals, even in the presence of an abundance of food." Strawinski (100) mentioned only one cannibalistic species among the 55 carnivorous hemipterans in Poland, but listed 6 of the 67 species (9%) of bugs usually regarded as phytophagous as eating their own species' eggs. Cannibalism is also common among granivores (88). Most species in the category of terrestrial carnivores in Table 1 are insects such as coccinellid beetles (25 species), syrphids (Diptera, 19), and chrysopids (Neuroptera, 71), but the list also includes other arthropods (e.g. 32, 71) and some vertebrates (65, 95).

The second major point of interest in Table 1 is the large proportion of known cannibalistic species that are predators living in fresh water, primarily fish and insects. This might be an artifact of the relative ease of collecting adequate samples for gut analyses in freshwater situations. In contrast, it is frequently difficult to observe or collect large numbers of individuals in terrestrial systems, and one common method for identifying prey, based on antibody reactions (27, 28), cannot detect cannibalism. Another explanation could be that the large proportion of freshwater predators among cannibalistic species might reflect basic differences in mechanisms determining population and community structure in terrestrial and aquatic systems. Freshwater habitats may be less complex faunistically or less stable than terrestrial ones, and many cannibalistic aquatic species do live in relatively ephemeral or nonstructured habitats such as rock pools or leaf axils (84, 87). However, habitats that are spatially more heterogeneous and physically more stable, such as larger ponds or lakes, also support cannibalistic populations (e.g. 66, 70).

Very few marine species are listed in Table 1. There are many anecdotal mentions of occasional cannibalistic acts by marine animals, but detailed feeding records are available for relatively few species. Apart from studies of intertidal molluscs (72, 86), most well documented examples are commercially important species of fish (85).

Table 1 Number of species for which there are sufficient data to indicate that cannibalism occurs normally in the field

	Trophic Level	
Habitat	Herbivores	Predators
Terrestrial	38	38
Freshwater	10	43
Marine	0	8

FACTORS AFFECTING CANNIBALISM

While cannibalism is frequently a response to food or density, other factors may also be important; in many species, several such factors are known to be involved.

Food

Starvation may increase cannibalistic tendencies, but it is not essential for initiating this behavior. Many animals will cannibalize as soon as all other food items are removed, but they may also respond simply to a reduction in the relative availability of alternatives. Cannibalism has been shown to be inversely related to the density of other food in intertidal opisthobranchs (86), freshwater insects (39, 43, 56), flatworms (4), and fish (16, 17, 40, 91, 97), as well as among terrestrial herbivores such as the cotton leafworm, *Spodoptera littoralis* (1), and the black cutworm, *Agrotis ipsilon* (36).

Rates of cannibalism may vary with the food resources present in different sites. Fahy (38) compared the diets of benthic insects in different parts of an oligotrophic stream in Ireland. The upper section was low in detrital content and consequently had smaller herbivore populations than a section further downstream, with higher detrital inputs. The species present were much the same at both sites but the trophic relationships differed. In the upper, poorer area, three of the predatory stoneflies and mayflies were cannibalistic and there were many predatory interactions among the predators themselves. At the more favorable lower site cannibalism did not occur and there were fewer predatory interactions. Perch, *Perca fluviatilis,* may also be more cannibalistic in lakes that are poor in nutrients than in eutrophic situations (2), and among humans, nonritual cannibalism seems to have been most common in nutritionally marginal areas supporting relatively low population densities, where it may have provided 5–10% of the annual protein requirement (30, 96). It has been suggested that cannibalism was less common in those settlements where populations were dense enough to raise their own food and produce a more predictable and adequate supply (30).

Density

The effects of crowding are often confounded with those of food shortage, but in several examples cannibalism was mainly a response to high density. Under crowded conditions survival of litters of house mice, *Mus musculus,* was low even when given excess food and nesting material (98). This mortality was attributed to improper parental care, including cannibalism, although the magnitudes of specific mortality factors were not measured. Similarly, both crowded damselfly larvae, *Lestes nympha* (39), and pike, *Esox lucius* (62), were very cannibalistic in the presence of other food, although the amount of food offered also affected cannibalism rates.

Behavior of Victims

In some situations cannibalism is initiated by particular behavioral patterns of the susceptible individuals. Laboratory experiments on fish in the *Poeciliopsis monacha–P. lucida* species complex, in which the relative densities of different age-classes

were varied, have shown that mortality may be related more to the responses of the young to density than to the density of cannibalistic adults (101). These fish are viviparous and the young were vulnerable to cannibalism for about 24 hours after birth. Below a critical density the young dispersed throughout the tank and were eaten by females as encountered, but above densities of about 10 per tank the young formed aggregations that stimulated attacks by the adult females. The adults' behavior was not affected by their degree of starvation, and the females remained unsatiated even after eating large numbers of young. In another example, differences in the rates of cannibalism of two closely related species of Lepidoptera may also be explained by differences in larval behavior patterns. Larvae of the corn ear-worm, *Heliothis armigera,* move actively and induce aggressive responses when contacted by other larvae. In contrast, larvae of *H. punctigera* do not move when encountered, and cannibalism rates are much lower than in *H. armigera* (S. Stanley, personal communication).

Stress

Physiological or psychological stress has been associated with cannibalism in only a few examples in field situations. The success of litters of Norway rats, *Rattus norvegicus,* was related to the social rank of their parents. Low ranking, scarred females that were caught in the field ate more than 60% of their young, while unscarred and presumably higher ranking females weaned all of their offspring (8). In the Australian grasshopper, *Phaulacridium vittatum,* mass emigration of older juveniles and young adults occurred if food was seriously depleted; migrating animals showed obvious signs of physiological stress, eating corpses and other migrating grasshoppers. Those remaining at the original site did not seem to be stressed and did not cannibalize (18).

Availability of Victims

In many examples initiation and control of cannibalism has not been ascribed to any obvious factor, and in these cases cannibalism may be a response primarily to the presence of vulnerable individuals. For some species, rates of cannibalism are consistent with simple encounter models in which the probability of attack is proportional to the probability of encountering a vulnerable individual. For instance, at low population densities with abundant alternative food, the freshwater backswimmer, *Notonecta hoffmanni,* cannibalized whenever vulnerable individuals were present (43). In other insects cannibalism rates on eggs and newly hatched young may be determined by the size of egg batches and the time span over which they hatch. There was no cannibalism on eggs or young larvae of coccinellid beetles if they all hatched before the oldest began to search for prey, which it did when about one hour old (59).

Herbivorous insects may cannibalize at low population densities even when their plant food seems to be abundant. For several hours after hatching, uncrowded Monarch and Queen butterfly larvae (*Danaus plexippus* and *D. gilippus berenice*) destroyed nearby eggs, although they were also eating their normal food plant (14); in both these species, as in cutworms, *Agrotis ipsilon* (36), and milkweed bugs,

Lygaeus sp. (C. A. Istock, personal communication), feeding on vulnerable young could not be prevented by satiating the herbivore with other food. Larvae of the corn ear-worm, *Heliothis armigera,* crawled from the silk to the corn husk one to two days after hatching and the first larva to reach the husk ate all subsequent arrivals, even though there was sufficient food for several animals to mature (63). On artificial diets, however, cannibalism in *H. armigera* increased with population density (102).

Refuges may reduce the chances of contact and so reduce cannibalism even in very aggressive species. Mortality of young notonectid nymphs increased as the spatial separation of the different age-classes was reduced in early summer (42), while in the wandering spider, *Pardosa lugubris,* separation of age-classes in both time and space may reduce cannibalistic interactions (34). Among crows, *Corvus corone,* the availability of eggs and nestlings as prey for intruding crows was influenced by the amount of protection provided by parents. Even within territories, parents protected their young better when food was clumped near the nest than when food was more dispersed and the adults forced to forage over a wider area (108).

CANNIBALISM AS A PREDATOR-PREY INTERACTION

Feeding Rates of the Predator

The number of cannibalized individuals in a species' diet is difficult to determine accurately. Most cannibalistic predators have very generalized feeding habits and may eat a large number of alternative food items, and among both herbivorous and predaceous species cannibalism rates may vary appreciably with time. When the annual diet of all age-classes is considered, cannibalism may account for a small part of the species' total food intake. For instance, for both the leech, *Erpodbella octoculata* (37), and the dragonfly, *Pyrrhosoma nymphula* (67), cannibalism provided less than 1% of the species' annual diet; in the backswimmer, *Notonecta hoffmanni,* it was 5% (42), and in three species of wandering spiders of the genus *Pardosa* it was 16–20% (32, 47). The annual rate, however, may fluctuate greatly: during 4 years of sampling yellow bass, *Roccus mississippiensis,* in Clear Lake, Iowa, 1–5% of bass stomachs contained other fish (64), while cannibalism accounted for 20% of the food eaten during a subsequent annual sampling period in the same lake (16). Similar variations in annual rates of cannibalism occurred in walleye, *Stizostedion vitreum* (40).

Rates of cannibalism may also be very variable over short periods of time. In the example of yellow bass mentioned above, in which 20% of the annual diet of adults was young bass, cannibalism occurred almost entirely during the summer (16). Similarly, cannibalism on young walleye usually increased in late summer (17, 40), but the smallest fish also were eaten over the winter months. Cannibalism among perch fry, *(P. fluviatilis),* usually occurred in midsummer although the intensity could vary from 0–40% of the diet within a week (97). Among rotifers (53) and backswimmers (42) cannibalism rates fluctuated between weekly and even daily sampling periods. In all of these examples changes in cannibalism rates appear to have been influenced by rapidly changing age distributions in the populations, as

well as by changes in the availability of alternative food. Rapid fluctuations in rates of cannibalism have also been reported for caddisfly larvae (76), an intertidal mollusc (86), and rock pool corixids (87), and similar changes are implicit in other studies (2, 3, 10, 13, 14, 39, 58).

Mortality of Prey

Field estimates of cannibalistic mortality among freshwater organisms range up to 95% of particular age-classes. For instance, 9% of caddisfly pupae in a stream were cannibalized by caddisfly larvae (G. Gallep, personal communication). 6% of eggs were eaten by adult water boatmen (Corixidae) in a British lake (23), while two species of corixids living in rock pools ate 20–50% of their own eggs in particular months (87). Predation by larger copepodids and adults caused about half the observed mortality of small nauplii in a freshwater cyclopoid copepod (75), and cannibalism has been invoked to explain most of the mortality of backswimmer nymphs (Notonectidae) in a lake (70) and in permanent pools of a stream (42), and also among young walleyes (17).

Data for terrestrial species are fewer and harder to evaluate. Edgar (32, 33) found 85% mortality among *Pardosa lugubris* spiderlings; he also observed that cannibalism on young spiders provided 16% of the diet, but he did not discuss any connection between these two observations. Cannibalism has been observed in some carnivorous and herbivorous coccinellid beetles in the field, and Hawkes (51) estimated 25% mortality for eggs; however, Dixon (29) argued that many of the eggs that were eaten were not viable, so that mortality attributable solely to cannibalism is difficult to estimate. Yom-Tov (108) suggested that studies in England, Germany, and Finland all have shown that 75% of crows' eggs and nestlings are eaten by other crows intruding into the parental territories.

DEMOGRAPHIC CONSEQUENCES OF CANNIBALISM

The population consequences of a behavioral trait such as cannibalism may not be immediately obvious because they may involve small changes in the population's age distribution or increases in the cannibals' survivorship or fitness, and average rates of cannibalistic mortality may bear little relationship to the importance of its role as a regulatory mechanism. It is often difficult to evaluate the importance of any mortality factor in field studies because the data frequently are inadequate for estimating population consequences. Data on cannibalism usually are given only as the numbers or percentages of members of the animals' own species found in the diets of a few, frequently large, individuals. Because most of the predatory species studied have generalized feeding habits, it is to be expected that cannibalism would contribute only a small amount to their annual diet.

To predict the consequences of cannibalism one must know at least the age structure of the population and the feeding rates of various age-classes. It is also necessary to reject alternative explanations that lead to similar predictions. For example, if food is in short supply then both cannibalism and starvation may produce similar survivorship patterns, both in descriptive studies where only popu-

lation size is monitored and in experimental work where numbers of individuals or their food supply are manipulated. Independent measurements of cannibalism are needed to distinguish between these alternatives. Arguments that conclude that cannibalism is not a major cause of mortality are often couched in terms of the "low" proportion of its own species in the cannibals' food. For example, it was concluded that cannibalism was unimportant among dragonfly (92) and damselfly (67) nymphs because of its rarity and because nymphs cannibalized only when hungry; similar arguments have been made for fish (e.g. 44, 62) even when cannibalism was relatively common (5–15%) for short periods of time (74). On the other hand, egg cannibalism was suggested as the major regulatory mechanism for the freshwater leech *E. octoculata,* even though eggs were about 0.2% of the annual diet (37).

Depending on the age composition of the population, even a very low cannibalism rate can cause significant mortality. To illustrate this point Le Cren (69) used Frost's data (44) to estimate the consequences of cannibalism on two-year-old pike. He assumed that a four-year-old pike ate about 50 fish of all species in a year, and given the age distribution (1.5 two-year-olds: 1.0 four-year-olds) in Lake Windermere, and the fact that the smaller pike were about 1% of the diet of larger fish, Le Cren calculated that cannibalism could account for all mortality among the younger class. In another example, it was suggested that less than 3% cannibalism in the diet of adult walleye was more than sufficient to explain the 88% mortality observed among the young fish (17). The effects of cannibalism may also be underestimated because encounters may be restricted to short periods of time or involve a relatively small part of the total population. Egg cannibalism among terrestrial insects might be particularly hard to detect: Brower (14) demonstrated that cannibalism by butterfly larvae occurred for several days after hatching, but that most larvae cannibalized during the first few hours.

Age Structure

Variations in cannibalistic tendencies among strains of *Tribolium castaneum* and *T. confusum* have been used to explain differences in both population size and age structure, although cannibalism is only one of a complex of processes affecting population growth. Egg cannibalism, especially by adult females and larvae, may cause cyclical fluctuations in the abundance of eggs and hence of larvae and pupae (77), while in turn, the intensity of cannibalism on eggs, and also on pupae and young adults, is influenced by the age composition. An occasional age-class of *Tribolium* will survive in large numbers when a particularly fortuitous age structure reduces the abundance of voracious beetles, and outbreak populations may result if pupae are sufficiently abundant to satiate the cannibalistic adults (77, 109).

Similar patterns of cohort dominance have been observed among other animals, and the hypothesis that cannibalism may control the age structure of some populations has been tested experimentally in the field. Alm (2) found that a single year-class could dominate European perch (*Perca fluviatilis*) populations in low nutrient (dystrophic) lakes in Sweden for many years (in one lake a single year-class was still dominant after 15 years, when the study was terminated). In more eutrophic lakes, year-classes were dominant for shorter periods of time. Alm experimentally reduced

the size of the dominant year-classes in some dystrophic lakes and found that the numbers of small perch increased in subsequent years and developed into new dominant classes. Because adult fish normally bred each year in every lake, Alm concluded that missing year-classes were eliminated from the dystrophic lakes by cannibalism and that the dominant year-class persisted until the numbers of cannibals were so reduced by other causes (e.g. senescence) that younger fish could survive. In eutrophic situations, the perch had more alternative prey and more predators, but a shorter life span possibly due to increased predation or increased intraspecific competition from the successfully developing young. Perch populations in two limnologically similar English lakes, Windermere and Ullswater, showed much the same patterns, but age-class dominance was more marked in the less dense population in Ullswater, where there were also fewer alternative fish species available as food and no predators (68, 69, 73). The absence of pike in Ullswater may have permitted a greater proportion of adults to survive and become cannibalistic (65), although intense cannibalism by adult perch occurred in Lake Windermere in some months (74).

In water striders (Gerridae), the success of the several generations of eggs that can be produced in a year depends on the presence of older individuals. In natural populations of *Gerris najas* none of the later broods survived, but when the numbers of older striders were artificially reduced the survivorship of young nymphs improved (13). One age-class dominated populations of predaceous diaptomid copepods in most of 19 Canadian lakes and ponds (3); because other predators were rare, it was suggested that the observed age distribution was caused by cannibalism on the later developing, smaller individuals. A more complicated example of cohort dominance involves the chironomid *Chironomus anthracinus,* which has different life cycles at different depths in the same lake (58). In the warmer, shallower areas where growth was rapid and predation intense, chironomids emerged every year, leaving space for the successful establishment of new egg masses dropped by the females. Both growth and predation rates were lower in the deeper water and larvae took two years to develop. The resident population of year-old larvae was dense enough to eat all eggs settling in deep water, so that a new age-class could become established only in alternate years after the two-year-old larvae had finally emerged. At intermediate depths the life cycles were variable.

Population Control

In the laboratory, cannibalistic behavior may increase population stability and persistence. One of the four species of sheep blowfly studied by Ullyett (103), *Chrysomyia albiceps,* was cannibalistic and it was the only species to persist when food was scarce because the few surviving larvae were heavy enough to produce viable pupae. The noncannibalistic species produced small individuals unable to maintain their populations successfully with intense competition. For *C. albiceps* cannibalism was a mechanism of interference competition that reduced the exploitation pressures on the food resources and maintained the physiological quality of the few surviving individuals. The predatory mite *Blattisocius tarsalis* and its lepidopteran prey *Anagasta kühniella* are both cannibalistic (106). The mites eat eggs,

larvae, and other adults of their own species, while *Anagasta* eats its own eggs. Although the details of these complex interactions have not been analyzed, the authors suggest that cannibalism increases stability in this predator-prey system by damping the magnitude of population fluctuations. Cannibalism seems to be an inherent part of the predator-prey dynamics of walleye, *Stizostedion vitreum,* and their major prey, yellow perch, *Perca flavescens* (40), in which Lotka-Volterra-type fluctuations have been observed. Reductions in predator population size, however, were caused by increased cannibalism, not starvation, following a reduction of prey. In most years, cannibalism was the major mortality factor affecting young walleye, and its action was density-dependent, with cannibalism rates increasing during years of food scarcity.

Paine's observations of growth and feeding in the opisthobranch mollusc *Navanax inermis* showed that cannibalism was density-dependent; he suggested that it may be the major factor regulating intertidal populations of *Navanax* (86). Cannibalism occurred especially when food was scarce, when the size distribution was sufficiently heterogeneous for some large individuals to engulf smaller ones, and when the population density was high enough for frequent contacts. *Navanax* was also capable of migrating to subtidal areas or to more favorable intertidal stretches, but since Paine gave no data on the magnitude of these alternatives, regulation by cannibalism was not firmly established.

It was easier to demonstrate the effects of cannibalistic behavior in populations of the freshwater backswimmer *Notonecta hoffmanni,* which were restricted to small pools in a stream with little migration between pools (42, 43). Notonectids ate each other over most of the growing season, but the period of heaviest cannibalism, two weeks in early summer, coincided with a sudden decrease in the availability of other food as well as a reduction in spatial refuges for the young nymphs. This mortality determined population sizes and age structures for the rest of the season and ensured that the first nymphs to hatch each season were the ones most likely to survive and reproduce successfully. Field and laboratory experiments demonstrated that the mortality of young nymphs was not caused by starvation, but by cannibalism as a response to reduced food supplies: nymphs survived well at low natural food densities without older notonectids, and also in the presence of older individuals provided with extra food. However, cannibalism in notonectids was not just a response to food, and occurred whenever vulnerable age-classes were present, even with abundant alternative prey. Thus cannibalism was a predictable part of the life history of this species, acting as a mechanism of population control that rapidly decreased the numbers of intraspecific competitors as food became scarce. There is evidence to suggest that a few well-fed adults would produce more young than many malnourished individuals (41).

In some species cannibalism seems to remove only those individuals that are not immune, in some way, from attack. It has been suggested, without supporting data, that all first instars of the predatory mite *Typhlodromus caudiglans* are eaten unless they have secure hiding places in tree bark (93). Perhaps the most dramatic examples are found in mosquitoes in the genera *Toxorhynchites* (22) and *Megarhinus* (57), which are cannibalistic whenever there is a sufficient size difference among

larvae. Usually one individual of a particular species is found in each tree hole, although a few individuals of equal size may occasionally be present. *Toxorhynchites* also has a "killing frenzy" for a few days before pupation, in which all other animals (of any species) are killed, but not eaten (22). This seems to be a mechanism to avoid predation when the individual becomes a vulnerable pupa, since *Toxorhynchites* larvae placed in the same container readily attacked pupae.

Finally, cannibalism is associated with complex life history patterns of some of the larger predaceous rotifers (7, 45, 46, 53). In *Asplanchna sieboldi* there are three morphological forms of asexually reproducing females that differ in their cannibalistic tendencies, as well as in their tendencies to transform directly to the sexual stage. Cannibalistic forms may be induced by high population densities, by eating large food items, or taking in vitamin E. The presence of cannibalistic morphs involves extremely complex interactions that may increase the range of food items available to the species as a whole, reduce population density, change the relative proportions of the different morphological forms present at any time, and delay sexual reproduction.

SELECTION

Tribolium strains show heritable differences in voracity (88). There may be a genetic basis for cannibalism among different morphological forms in flatworms (4), rotifers (7), and spadefoot toads (50), although the expression of these genotypes may require induction by some environmental factor. Some poeciliid fishes form interspecies hybrids that not only have expected patterns of morphological and biochemical variation, but also have cannibalistic tendencies intermediate between those of parental forms. Thibault (101) crossed two species, one cannibalistic (*Poeciliopsis monacha*) and one not (*P. lucida*), and measured cannibalism by adult females on newly hatched young. The proportion of young fish eaten by these hybrids was 0.74, while the two parental species ate 0.95 and 0.0 respectively; back-crosses of the hybrids to each parental type produced individuals with cannibalistic tendencies between those of the hybrid and the original parent species (0.88, 0.12). These differences indicate polygenic inheritance for the trait. Moore & McKay (81) suggested that overall population sizes of these poeciliid species complexes, as well as the proportions of hybrid and parental forms, are controlled by cannibalism.

In spadefoot tadpoles (*Scaphiopus*) cannibalism is also associated with different morphological forms (10, 11), and breeding experiments with *S. holbrooki* imply polygenic inheritance (50). The common form is primarily a scavenger, but a larger morph, having a notched beak and larger, more variable jaw and tooth structures, and a morphologically intermediate type, are both cannibalistic and predaceous. These aggressive morphotypes usually occur in the drier and hotter parts of the ranges of several spadefoot species, but the presence of these forms varies both spatially and temporally among adjacent pools.

The restriction of cannibalism to particular life-history stages of a single species, and the differences in cannibalistic propensities between closely related species,

provide further evidence that cannibalism is genetically determined and responsive to selection. Females of *Tribolium* primarily cannibalize eggs, while males concentrate on pupae: in *T. castaneum,* females were 19 times as voracious on eggs as males, but males were 4 times as voracious as females on pupae; in *T. confusum* the equivalent ratios were 7 and 14.5 (79). Similarly, in two species of intertidal oyster drills (*Eupleura caudata* and *Urosalpinx cinerea*), only the females (72), and, in crows, only mature birds (108), were cannibals. Particular age-classes of coccinellid beetles may be either cannibal or victim depending on species; some species, although closely related to those showing strong cannibalistic tendencies, may not cannibalize at all (51, 55, 59). The latter situation has also been demonstrated for some species of *Megarhinus* mosquito larvae (57, 84), and three species of whirligig beetle larvae display a range of responses when offered the same amount of food (56). Finally, geographical differences in cannibalism have been found: populations of the predatory mite *Typhlodromus occidentalis,* sampled from Washington and Utah, showed lower cannibalism rates than those from southern California, although there were no differences in most other life-history characteristics (24).

There are obvious advantages for the survivor of a cannibalistic encounter. The cannibal gains a meal at the same time that it eliminates a potential competitor and perhaps a potential conspecific predator as well. Because population size is reduced, more food will be available to each survivor, enhancing its chances for further survival and rapid growth. As they grow larger, individuals may themselves become less vulnerable to cannibalistic attacks. For instance, many fish grow faster on larger food items, and their own species may be the largest and most available prey (21). Larger size may also be advantageous because the smallest fish in a cohort may be those most vulnerable to mortality factors (including cannibalism by adults) over the winter (17, 62). Similar increases in growth rates are found among cannibalistic morphotypes of spadefoot toads, which develop to larger sizes and may metamophose more successfully (10–12). Cannibalism can also confer direct nutritional advantages that may be expressed in greater reproductive success: *Tribolium castaneum* that fed on eggs produced one more egg per female per day than individuals not provided with eggs, although *T. confusum* did not show a similar increase (52). In the rotifer *Asplanchna sieboldi,* the largest and most cannibalistic morphotype produces more asexual eggs than the other morphs; when these asexual females eventually transform into sexual stages they may produce twice as many resting eggs (53). Less directly, preying on the smaller individuals of its own species allows different sources of food and energy harvested by the young animals to be retained by the species, as may be the case for some fish in which the young eat small items, such as zooplankton, that the adults do not eat (85, 89).

In some species of coccinellid beetles, egg eating may more than double the survival time of instar I larvae when no further food is provided, and 2 or 3 eggs may suffice to allow molting to the next instar (5, 15). Hungry individuals become more aggressive, but larvae that have previously cannibalized may continue to attack other larvae more readily (59). Egg eating may reduce searching activity for about two days and make cannibals less successful at finding other prey (90).

However, the searching ability of these larvae is at best very limited (9), and the increased survival may improve the beetles' chances of finding other prey even at times of high food density.

Cannibalism becomes disadvantageous when individuals become too aggressive. If the cannibal destroys its own progeny or genotype, either completely or faster than those of its conspecific competitors, or if it reduces its own chances of successful reproduction by eliminating suitable mates, cannibalistic behavior will be selected against. The advantages and disadvantages of cannibalistic tendencies must be balanced against other factors that may affect survival. In some situations the disadvantages of cannibalism may be less severe than the consequences of starvation or reproductive failure caused by inadequate nutrition. For example, the growth rates of notonectids maintained at low food levels were significantly reduced by the second instar, but higher mortality did not occur until the fourth and fifth instars; a noncannibalistic population would be very slow to respond to inadequate food supplies by a reduction of its population size (43). A relatively large cohort would persist and continue to reduce resources until catastrophic mortality was caused by starvation, and even the survivors would probably be stressed physiologically (e.g. 102). By contrast, in a cannibalistic population the numbers of competitors are reduced at an early age so that per capita food supplies remain high for the survivors. Therefore, when comparing two populations reduced to the same extent, one by starvation and one by cannibalism, each individual from the cannibalistic population will make a greater contribution to future generations because it was better fed as a juvenile and is likely to grow faster, survive better, breed earlier, and/or produce more young.

Evolutionary arguments about upper limits to the severity of a socially selfish trait such as cannibalism have been based on two major points of view: interdeme selection (107) and individual selection (48, 49). Hamilton stressed that the evolutionary effect of a cannibalistic encounter depends on the degree of relationship between the individuals involved (48). As the genetic relationship between cannibal and victim becomes more distant, a smaller advantage for the cannibal is required before the frequency of this selfish trait increases in the population. If the victim were only a distant cousin, even a small advantage to the cannibal would be favored, but if the victim were a full sibling or one of its own young, then a much greater increase in fitness of the cannibal would be necessary before natural selection would favor the trait. Under some circumstances an equilibrium frequency for the selfish trait should be reached, but the existence and stability of the equilibrium and its actual value will depend on the extent to which mating and the effects of aggressive behavior are distributed nonrandomly (49). King & Dawson (61) suggested that individual preferences for feeding and egg laying in different microhabitats reduce the probability of cannibalism on close relatives in *Tribolium*. Interdeme selection, on the other hand, may oppose the increase of selfish behavior in the species as a whole because the chances of extinction of excessively cannibalistic subpopulations will be high (80, 107). The two arguments are not mutually exclusive, since nonrandom mating among very aggressive individuals could also lead to extinction. The interdeme arguments imply that local extinctions and/or migration between popula-

tions will maintain an average upper limit for the species, whereas Hamilton's model suggests that subtle selective pressures may maintain an equilibrium level for each population in response to its own environment.

Eickwort has calculated the increase in individual fitness needed to maintain egg cannibalism on full and half siblings of newly hatched chrysomelid beetle larvae, and has shown this to be surprisingly small (35). An increase in the probability of survival of an instar I beetle by 0.005, from 0.01 to 0.015, will maintain the selective advantage even if full siblings are eaten. Similarly, a decrease of two days in time required to reach maturity also will maintain the trait. The lower the original fitness, the smaller the incremental gain necessary to select for increased aggression; therefore, selection for selfish behavior might be most advantageous in the life stages with the lowest probabilities of survival, such as very young individuals. Thus, despite many of the examples described above, selection for cannibalism does not necessarily demand large increases in individual fitness.

CANNIBALISM VS PREDATION

The occurrence and intensity of cannibalism varies considerably both within and between species; because much of this variability arises from differences in the factors influencing local populations, the extent of cannibalism may not be predictable for particular situations and the proximal factors influencing the evolution of such behavior may be quite obscure. Generalizations about cannibalism must allow for at least two other aspects of individual responses that tend to complicate the picture. First, some species may respond to resource limitation by dispersal, diapause, modifications of physiological characteristics, or interference competition by other means. Second, some animals may be unable to cannibalize because they are physically incapable of handling prey as large, as aggressive, or with such effective escape mechanisms as their own species.

When several species share the same resources, interactions among individuals of competing species further complicate selection for cannibalistic behavior. There are numerous examples of species that prey on potential competitors (3, 9, 10, 25, 28, 38, 41, 59, 66, 69, 88, 94, 103), and in many cases these species are also cannibalistic; the balance between cannibalism and predation influences the coexistence patterns of the competing species. Some of the possible interactions among aggressive species are well illustrated by comparing the responses to food shortage of the larvae of three species of whirligig beetles (Gyrinidae, 56). As food supplies were reduced in laboratory experiments, the developmental rates of *Dineutes nigrior* larvae declined, but there was no cannibalism until food became particularly scarce; *D. horni* became more cannibalistic as food decreased but the larvae maintained the same developmental rates over a wide range of food regimes. *D. assimilis* was very cannibalistic at all food levels and its survivorship did not strongly reflect differences in food supply. When these species were paired in competition experiments the relative amounts of cannibalism and predation, and hence the eventual exclusion or persistence of the less aggressive one, were determined by their different aggressive tendencies at different food levels and by the initial relative abundances of the species. In

this example predation was reciprocal, but cases of unilateral predation also occur: the only cannibalistic species of the four sheep blowflies studied by Ullyett (103) was always successful in competition for food because it also was the only one that preyed on individuals of other species.

If food is in short supply for the entire assemblage of competing species, it is not surprising to find predation among both conspecific and heterospecific competitors. The selective advantages of predation upon competitors are similar to those discussed for cannibalism, and, at least in well established systems, the frequencies of cannibalism and predation will be related to the relative advantages to be gained from each type of encounter. This is particularly so if there is an evolutionary cost to being aggressive towards other aggressive individuals. Figure 1 summarizes the
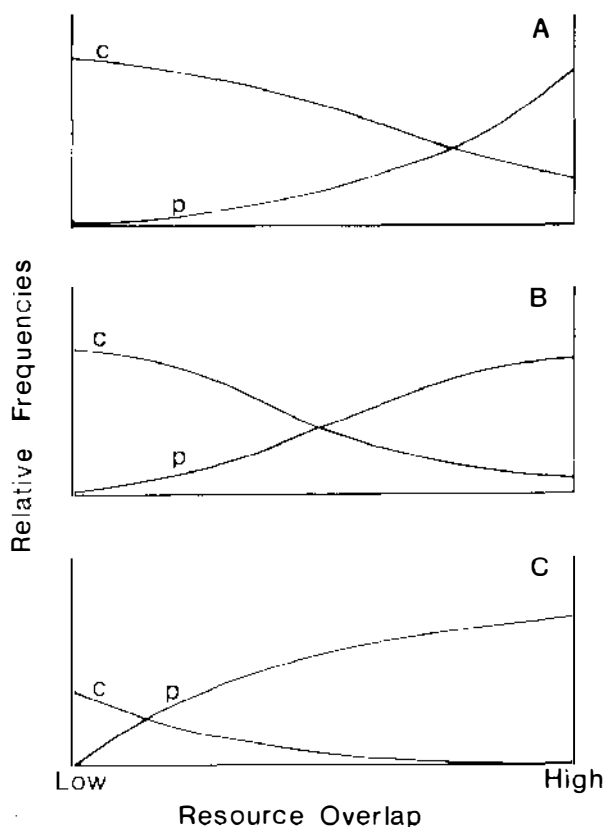

Figure 1:   Relative proportions of cannibalism (*c*) and predation on potential competitors (*p*) by an aggressive species, based on the relative abundances of the species and the degree to which the scarce resources are shared. *A,* the aggressive species is much more common than its competitors; *B,* the species are equally abundant; *C,* the aggressive species is relatively rare.

ways in which the frequencies of cannibalism and predation may change if one assumes that the advantages accruing to successful individuals depend on the relative abundances of competing species and the extent of overlap of the shared resources. Whatever their relative abundances, cannibalism rates should be highest for species without close competitors, i.e. situations where the level of resource overlap is low. In absolute terms, however, rare species may be less cannibalistic than common ones simply because fewer contacts of rare individuals are with their own species. As a larger proportion of the spectrum of a species' resources is shared, interspecific events will increase, but the relative amounts of cannibalism and predation will reflect the chances of encountering other individuals. Common species may always cannibalize to some extent even when interspecific competition is high, although the proportion of cannibalistic events in this case will be lower than if there were less overlap. On the other hand, there may be no cannibalistic events at all in the diets of rare species unless there is little overlap in the use of resources with other species.

These arguments lead to several testable predictions about the occurrence of cannibalism and predation in different situations. First, if natural selection influences a species' predatory behavior, individuals may show different feeding preferences (82) among potential competitors and the hierarchy of these preferences may directly reflect the amount of overlap between the species. For instance, individuals of rare species may have higher preferences for feeding on aggressive competitors than will individuals of dominant species, while intraspecific encounters may more often result in cannibalism in the commoner species. Unfortunately, I know of no data that test these suggestions.

A second set of predictions from Figure 1 is that predation should be particularly common among species with generalized habits and with qualitatively similar resources. These interactions have been described for several different communities including freshwater fish (66, 69), copepods (3) and insects (41, 42, 56), deep sea deposit feeders (25), and some terrestrial insects (28). Among freshwater fish, for instance, Larkin (66) noted that ". . . many species have a relatively wide tolerance of habitat type, a flexibility of feeding habits and in general share many resources of their environment with several other species of fish. Cannibalism and mutual predation are common complications of competitive relationships between species."

The heights and specific shapes of the curves in Figure 1 obviously depend on the inherent aggressiveness of the individuals and on alternative responses to limiting conditions available to the particular species. These, in turn, depend on many other aspects of the environment such as the predictability of the available resources. A fluctuating resource supply may favor the selection of individual behavior that results in a less rapid population response (83), because if there is only a short-term lack of food then species that did not cannibalize immediately, such as the larvae of *Dineutes nigrior* (56) described above, would still be abundant when food supply increased. A rapidly inducible interference mechanism, such as cannibalism, may be particularly advantageous if resource limitation is predictable: California populations of a predatory mite living in a Mediterranean-type climate with dry summers and predictable crashes of insect prey (24) are more cannibalistic than populations

from the Pacific northwest (26), and those morphs of spadefoot toads that were both cannibalistic and predaceous were more common in the drier parts of the species' range with less permanent habitats (10, 12).

CONCLUSIONS

Cannibalism is not an aberrant behavior limited to confined or highly stressed populations, but is a normal response to many environmental factors. Since cannibalistic tendencies are often sensitive to selection by local conditions, they may vary considerably among different populations or genetic strains of the same species, and among closely related species. The relative availability of alternative food, the density and behavior of both cannibal and victim, and, more rarely, extreme food deprivation or crowding may influence the intensity of this behavior. Cannibalism is an intraspecific predator-prey interaction that may also function as a means of interference competition, limiting population size before the resource itself becomes limiting. In common with some other self-regulatory mechanisms, cannibalism is a sensitive method of preserving the competitive abilities of the successful individuals while maintaining the reproductive outputs of the survivors. Cannibalism is an age-specific process frequently causing rapid changes in age distribution and population size.

Newly hatched young that eat siblings before dispersing are not sampling their own resource state before they become predators. In these cases the intensity of cannibalism is a function of the numbers of eggs laid by the previous generation, and cannibalism may act as a delayed regulatory mechanism or as a method of providing a guaranteed nutritional source to the young animals. Such situations occur especially among terrestrial insects in which the young larvae do not disperse far from egg batches before searching for food. Egg cannibalism may be inherently different from cannibalism by older individuals, but they both reduce the numbers of potential competitors that would have shared resources as the animals grew larger. Population extinctions are unlikely because cannibalism is usually a short-term event: cannibalism rates decrease as resources become relatively more available to each survivor, and, as vulnerable individuals become scarcer and harder to find, cannibals may switch to other types of prey.

The ecological consequences of predation among trophically similar species are analogous to those of cannibalism. When the same resources are in short supply for the entire assemblage of competing species, both cannibalism and predation among competitors are likely events. In this paper I have stressed examples of these behavioral traits and discussed interactions between them that may influence the populations and perhaps the community as a whole. Cannibalism may result in population self-regulation, while predation among individuals of competing species tends to "regulate" the total biomass of competing individuals. Both interactions change the system from one that might have been superficially described as exploitation competition into one of interference competition mediated through predator-prey interactions. In these systems trophic distinctions become blurred and the complexity of even the most simple food web is greatly increased.

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