THE EVOLUTION AND DYNAMICS OF INTRASPECIFIC PREDATION

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INTRODUCTION

Intraspecific predation, the process of both killing and eating an individual of the same species, is a significant and widespread process that until recently has not received the attention it merits. It is a major factor in the biology of many species and may influence population structure, life history, competition for mates and resources, and behavior. It is commonly observed among many animals: For this review I read over 900 papers describing such predation in about 1300 species.

Laurel Fox's 1975 review of cannibalism (54) should be read for additional information. Here I attempt to present new or different data, references, and ideas. One of my purposes is to establish a theoretical framework for the organization and interpretation of the numerous observations of intraspecific predation. Certain topics included here are speculation intended to spark interest and indicate important problems that need further research. Because of page limitations many appropriate and important citations are not cited here but may be found elsewhere as indicated by "& incl. refs."

CHARACTERISTICS OF INTRASPECIFIC PREDATION

Size, Age, Developmental Stage, and Sex

In general larger (older) animals are more voracious cannibals than smaller (younger) animals, and smaller conspecifics are more often eaten than larger. For example, 14.2% of all prey eaten by adults of the scorpion *Paruroctonus mesaensis* are conspecifics whereas conspecifics form only 6.7% of the diet of the smallest age class; further, only 18.1% of all intraspecific prey are adults whereas 62.6% are from the smallest age class

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(109). For many species, relative rather than absolute size appears paramount. This relationship is particularly obvious in some species of fish. Conspecifics are eaten only if a threshold in the predator-to-prey size ratio exceeds 20–30% in pike (21), 60–140% in largemouth bass (37), and 80–100% for piscivorous fish in general (8, 112, 115). Size variance within a population is also one of the most significant factors in cannibalism of protozoa (57), rotifers (58), gastropods (104), and nestling birds (69).

There are exceptions to such size generalizations. Some species of fish (8, 52, 117), dragonfly larvae (48), and parasitoid larvae (5, 50, 124) are more cannibalistic when smaller (younger). Some species attack same-sized conspecifics (e.g. 34, 41, 109, 111, 121). Arthropods regularly experience cannibalistic "reversals" during development. Reversals occur when individuals are subject to predation by smaller conspecifics during vulnerable periods that accompany ecdysis and pupation. At these times, conspecifics are virtually defenseless because they are either immobile or soft. Older stages are eaten during ecdysis by younger instars in some insects and crustaceans (e.g. 7, 53, 75, 81). Smaller larvae eat larger pupae in several orders of insects (e.g. 7, 29, 75, 81). A corresponding vulnerable period occurs in some amphibian species at metamorphosis, e.g. in spadefoot toadlets (17, 111).

Large individuals may also be attacked and eaten by groups of conspecifics. Group cannibalism occurs in backswimmers (G. Polis, personal observation), other Hemiptera (130), social Hymenoptera and Isoptera (18, 149), lacewing larvae (41), *Scaphiopus* and *Bufo canorus* toad larvae [(111); R. Leong, personal communication], fish (34), social carnivores (13, 83), and primates (59, 66).

Other developmental stages are vulnerable to cannibalism. Eggs and newborn animals, rich in energy and nutrients, are relatively defenseless unless guarded by a parent. Intraspecific oophagy was reported in 118 references distributed over more than 80 families. It occurs in practically every major group of egg-laying animal: gastropods, spiders, nonsocial insects, social insects, fish, amphibians and birds (see references under "Sibling Cannibalism"). Cannibalism of newborn animals is equally widespread and common. I found over 100 references for more than 80 families. Hrdy (66) and Sherman (128) recently reviewed the evolution and significance of infanticide (but not all infanticide is cannibalistic).

In all these cases, cannibalism involves an asymmetric interaction: Cannibals are relatively invulnerable to injury and death during a predatory attack on their victims. Such decreased risk likely explains why intraspecific predation usually involves a larger size class preying on smaller conspecifics, eggs, or defenseless stages.

Sexual biases among cannibals and victims were usually neither reported nor investigated. However, in 86% of the 50 cases for which sexual differ-

ences in the predator were noted, females were more cannibalistic. Males were eaten more frequently than females in 76% of the species (n = 45) reported to differ in the sex of the prey. Both differences are highly significant (p < 0.001). In the 41 species for which biases in the sex of both predator and prey were noted, 88% involved females eating males; many (76%) were associated with courtship and mating and are discussed later.

Males are the major cannibals in a species of braconid parasitoid wasp (122), *Tribolium* on pupae (81), and several species of infanticidal primates (66); males are the only cannibals in a species of prawn (53) and in several species of hymenopteran autoparasitic wasps in the family Aphelinidae (5). In these wasps (*Encarsia* and *Coccophagus*) females are parasitoids on homopteran scale insects and males are rare. However, when males are produced, they develop not as parasitoids of scales, but as internal hyperparasitoids of larval females of their own species.

Such sexual bias may be sufficiently intense to alter the sex ratio. Differential intraspecific predation on the males of spiders (16), scorpions (109), lacewings (41), and cod (106) is reported to change the sex ratio to favor females. Cannibalism causes a decline in the sex ratio (males/total) of the scorpion *P. mesaensis* from birth (51%), to the onset of maturity (42%), to mature animals of all ages (35%). Only in one species of braconid wasp is differential cannibalism on the female known to alter significantly the sex ratio to favor males (=61%) (122).

Quality and Quantity of Diet

Reports of intraspecific predation generally lack information on the feeding history of the predator. Most data on nutritional status come from studies of animals associated with man (pests; domesticated, cultured, or laboratory animals). When diet quality is improved, cannibalism decreases in *Tribolium* (81), several species of domestic birds (67, 131), rodents (87) and pigs [(14) & incl. refs]. Further, 17 additional references attribute cannibalism to specific nutritional deficiencies—e.g. of protein, glycogen, vitamins, minerals, trace elements, and even water (e.g. 14, 63, 67, 130, 149).

Food quantity also affects rates of intraspecific predation, which increase with hunger in flatworms, predaceous insects, birds, rodents, and pigs (e.g. 4, 7, 10, 14, 70, 87). That hunger stimulates intraspecific predation is also inferred from the numerous studies in which cannibalism is found to be an inverse function of the availability of alternate prey. Fox (54) discusses the increase in cannibalism during food scarcity. Forty-three other studies provide evidence that the relationship between the availability of alternate food and intraspecific predation is a widespread and common phenomenon.

Three factors may explain why hunger or a decrease in alternate food promotes cannibalism. First, food stress generally increases foraging activity: Hunger triggers searching behavior, lowers attack threshold, increases

foraging time, and increases movement by stimulating locomotor activity, changing the location of foraging stations, and expanding the search area [(109) & incl. refs.]. Each of these behaviors increases the probability of intraspecific contact and predation. Second, this initial period of increased activity leaves animals deprived of food weak and increasingly vulnerable to cannibalism. Third, one of the well substantiated predictions of foraging theory is that consumers should expand their diet beyong the normal limits of acceptable prey during periods of hunger or low levels of food. Under these conditions the optimal diet includes items previously ignored because of their high costs or low net energy gain per unit time. The fact that cannibalism increases with hunger and low prey levels suggests that conspecifics are normally too costly or rank relatively too low in terms of net energy value. At least for some species, intraspecific predation may not be more frequent because of the attendant risks or costs of retaliation.

Cannibalistic Polyphenism

Cannibalistic polyphenism refers to phenotypic differences in behavior, morphology, growth rates, or life history between cannibal and noncannibal forms of the same population.

The most striking polyphenisms are the "giant cannibal morphs" in *Amoeba,* flagellates, several genera of ciliates [(57) & incl. refs; (36, 49, 80, 102)], *Asplancha* rotifers (58), *Scaphiopus* toad larvae (17, 110), and *Ambystoma* salamanders (108, 121) (& refs. in each). In ciliates, cannibal giants are at least twice as large as normals: e.g. *Glaucoma* cannibal = 100–250 μm, noncannibals = 30–80 μm (80); *Blepharisma* cannibals = 290 μm, noncannibals = 143 μm (57). In trimorphic populations of *Asplancha,* the noncannibal saccate morph is smallest (500–700 μm), the moderately cannibalistic cruciform morph is intermediate in size (800–1200 μm), and the highly cannibalistic campanulate morph is largest (800–1700 μm) (58). Cannibals are often the largest morph in *Scaphiopus* and *Ambystoma.* In all of these organisms cannibals possess enlarged, modified trophic structures. In ciliates, cannibals are macrostomes while normals are microstomes; in rotifers, cannibals possess disproportionately larger coronae than noncannibals; and cannibal *Scaphiopus* and *Ambystoma* have disproportionately large heads characterized by hypertrophied jaw muscles, wide mouths, and sharp predatory beaks or teeth. There are also marked dietary differences among morphs. Normal morphs feed primarily on bacteria or organic particles whereas giant morphs are facultative predators on both conspecific and interspecific prey. Giant cannibals of the ciliate *Oxytricha* are regularly observed with four to eight conspecifics in their guts (36), and cannibal *Blepharisma* may contain up to six ingested conspecifics (57). In *Ambystoma,* 100% of the cannibal morphs collected from some locations

had eaten conspecifics (121). Cannibal morphs also regularly eat large heterospecific prey. This feature expands the cannibal's resource base and thus may favor the evolution of such cannibals (58, 111).

Cannibal phenotypes morphologically similar to, but much larger than, normal phenotypes occur in the planarian *Dugesia* (4) and in several fish. There are marked differences in early growth rates between the two phenotypes of walleye (33), largemouth bass (37), striped bass (115), and *Anabis* fish (8). One to five percent of the fry are twice the size of normal fry. These "shoot fry" are voracious cannibals. For example, in an 11-day period, predation by these cannibals (=5% of the population) reduced the population of captive striped bass from 15,000 to 3000 (115). In the arctic char there are two size groups of mature fish: small adults and giant cannibals (132). Small (13–27 cm) adults remain at a relatively constant size for the three to seven years of their lives. If there is abundant food, some adults undergo a new growth phase, grow to 37–63 cm, and remature at 12–14 years of age. Conspecifics form about 50% of the diet of large cannibals but only a very small part of the diet of small adults.

Behavioral polyphenism unaccompanied by other apparent differences was found in Parsons' (105) study of intraspecific predation in breeding colonies of herring gulls. In one colony of 900 gulls, 23.3% of all eggs and chicks were eaten by conspecifics. Four individuals were the predators in over 50% of all cannibalism; each ate 2–5% of all chicks produced by the colony. These rare phenotypes were cannibalistic specialists since conspecific eggs and chicks formed their primary food. Parsons observed the same polyphenic behavior in all the herring gull colonies he investigated; he cites a similar phenomenon in black-headed gulls. Such behavioral polyphenism also occurs in arctic terns (107) and chimpanzees (59).

Most evidence indicates that the cannibal phenotype is induced by dietary factors. The presence of large heterospecific prey stimulates cannibal production in populations that normally feed on bacteria or organic particles. For example, Pomeroy (111) has found evidence that high densities of fairy shrimp may be one of the cues affecting cannibal formation in *Scaphiopus*. He produced cannibal morphs in the lab by feeding young tadpoles live fairy shrimp rather than a diet of organic particles. Likewise, Gilbert (58) produced cannibal morphs in *Asplancha* with a diet of relatively large congeneric and crustacean prey or by exposure to tocophenol (vitamin E, an indicator of the existence of large prey). Similar production of cannibalistic phenotypes occurs in the ciliates *Glaucoma* (80), *Blepharisma* (57), and *Tetrahymena* (102). The accelerated growth of cannibal phenotypes in fish is apparently due to the particularly successful feeding history of a few individuals. The absence of food may also stimulate cannibal production, e.g. in the ciliates *Oxytricha* (36) and *Climacostomum* (49). Finally, initial

differences in egg size within a clutch may increase the probability that larger newborn will become large cannibals [e.g. *Scaphiopus* (111); L. Pomeroy, personal communication].

Genetic factors are not excluded by evidence for dietary induction. However, no strong data indicate a genetic basis for cannibalistic polyphenism. Nevertheless, genetic determinants cannot be ruled out because few studies explicitly investigated their importance. Two studies on amphibians [(108, 111); B. Pierce and L. Pomeroy, personal communication] suggest that at least minor genetic differences exist between normal and cannibal phenotypes. Clearly, this is an interesting, important, and neglected area.

Genetic Basis

Several types of data indicate that, for many species, there is a strong genetic component to cannibalism. The existence of breeding strains or races with different cannibalistic tendencies constitutes some of the best evidence. Strain-specific differences were observed in rotifers (58), mites (31), *Tribolium* (46), *Heliothis* (60), turkey, duck, cockerel, pheasant, chicken (67, 131), rats, mice (62, 87), and rabbits (38) (& incl. refs. in each). For example, Hauschka (62) showed that the rate of litter cannibalism varied from 0–45% among eight strains of mice but remained constant within each strain for at least 13 generations. Gould et al (60) experimentally demonstrated significantly different cannibalistic behavior among 11 geographical strains of *Heliothis virescens.*

There is other evidence that cannibalism is genetically controlled. Heritable differences in cannibalism occur among strains of *Tribolium* and species of *Poeciliopsis* guppies [see discussion in (54)]. Further, Fox (54) argued that both differences in the sex and age of intraspecific predators and differences in the cannibalistic propensities of closely related species strongly imply a genetic basis. Finally, the widespread occurrence of various adaptations that either inhibit or promote cannibalism among relatives implies the presence of selection on genes that regulate its expression.

It is important to note that not all cannibalism need be adaptive and a product of natural selection. Obviously, some cannibalism is maladaptive resulting from stress, accidents, or unnatural conditions (54, 66, 128). Other cannibalism may occur as a by-product of the normal feeding behavior of some species. This may be the case among some facultative euryphagous predators [(86, 88, 109, 143); especially see (117)], herbivores (12, 22, 151), filter feeders [(51, 101, 114, 141, 152) & incl. refs.] and deposit feeders (73, 74, 152). However, even these types of intraspecific predation may still be regulated by natural selection and under genetic control.

SIGNIFICANCE TO POPULATION DYNAMICS

A Major Mortality Factor

Intraspecific predation is a major cause of mortality in many species. A large proportion of either the entire population or a vulnerable age class may be eaten, often in a short time: e.g. 31–50% of copepod nauplii (86, 94), > 80% of all prawn (53), 30–75% of dragonfly nymphs in eight days (48), > 50% of first instar *Notonecta* (55), 25% of perch young (138), 35% of all cod (106), 80–90% of two species of bass fry in 11–14 days (37, 115), > 90% of *Anabis* fish in 60 days (8), 23–46% of herring gull chicks and eggs [(105) & incl. refs.], 16% of barn owl nestlings (11), > 90% of crow chicks and eggs (154), and 8% of young Belding ground squirrels (128) [also see references in (54)].

A dense age class of older conspecifics may eat nearly 100% of the eggs and/or young produced by the population. Recruitment is suppressed, often for many years, until the dominant age class is substantially reduced. The elimination of entire cohorts often causes violent fluctuations in recruitment and a skewed age/size distribution. This phenomenon is common in fish, being reported for ten species [(37, 52, 64, 113); see particularly (114, 117).] It also occurs in copepods (86), eight families of insects, and several species of polychaete and molluscan filter and deposit feeders (51, 152). See Fox (54) for three detailed examples.

Populations of the animals mentioned above are large, and cannibalism is relatively easy to observe. However, it may also be important but harder to observe in animals with lower densities. For example, at least 14 species of carnivorous mammals attack and eat conspecifics: lions, tigers, leopards, cougars, lynx, spotted hyaenas, golden jackals, wolf, coyote, dingo, red fox, arctic fox, brown bear, and grasshopper mice [(13, 24, 68, 83, 92, 125, 139) & incl. refs.]. In seven cases, adults were eaten by other adults, mostly as a result of "territorial disputes". However, in 68% of the cases reported, adults preyed on immature animals and cubs. Such predation may substantially reduce the population. For example, Bertram (13) reports that about 25% of all lion cubs are eaten by older lions. Kruuk's (83) study of the spotted hyaena showed that intraspecific predation accounted for 17% of all observed deaths. Cannibalism may regulate the size of arctic fox populations (24).

Intraspecific predation may be an important cause of post-fledgling mortality in some hawks and owls [e.g. (43, 135) & incl. refs.]. As is not the case among carnivorous mammals, adult birds are prey in 67% of these reports (red tailed hawk; barn, screech, great horned, and burrowing owls). Adults were reported to eat fledged juvenile red tailed hawks, great horned

owls, and barn owls. These predations apparently occur during territorial intrusions (43). Cannibalism on adults and juveniles in combination with frequent predation among nestlings (see "Sibling Cannibalism") may pro-duce considerable mortality in some hawks and owls.

Obviously, even low absolute levels of intraspecific predation may signifi-cantly reduce population size if populations are small. Furthermore, even when cannibalism accounts for a small proportion of a species' diet, it may still account for most mortality [(54); also see (117)]. However, more data are needed before we can evaluate the speculation that cannibalism is an important source of mortality in these low-density predators.

Density Dependence/Population Regulation

Intraspecific predation is often a function of density. I found 65 reports of increased rates due to overcrowding or high densities [(54, 109); & see refs. below]. There are at least two explanations for this relationship. First, changes in the rate of cannibalism may occur for the same reasons that predators exhibit density-dependent responses to heterospecific prey. Such cannibalism is probably frequent and is best exemplified by facultative predators and species that eat conspecific eggs and young as a by-product of normal feeding activities, e.g. filter and deposit feeders and some her-bivores. Second, individuals of many species maintain inter-individual space or territory in which they are intolerant to conspecifics. Crowding increases the frequency with which conspecifics violate a critical minimum individual distance (=intraspecific space) and thus promotes the observed increase in the rate of cannibalism at high densities.

In normal predator-prey systems, "density-dependent predation" de-scribes the change in predation rate as a function of (heterospecific) prey density. In cannibalistic systems, this concept is applicable only when the entire population is composed of more or less similar individuals. However, in those species with different groups of cannibals and prey victims (e.g. age classes or morphs), the densities of the predator and the prey groups must be considered independently. Such discrimination is important in modeling cannibalism (e.g. 15, 37, 136) and in understanding fully the population dynamics of such animals as copepods (86, 88, 94), scorpions (109), *Noto-necta* (55), *Tribolium* (81, 97), and spadefoot toads (111).

Over 40 references report that cannibalism acts as a density-dependent regulator of population size [e.g. (18, 28, 37, 70, 81, 82, 86, 98, 101, 104, 109, 114, 117, 141, 142, 149, 154); also see references in (54)]. Moreover, many species gain exclusive use of an area by killing and eating encroaching conspecifics. The defended area may correspond to a territory or may simply be a discrete food resource—e.g. seeds or parasitized hosts. Thus intraspecific predation may produce more or less regular spacing among

territorial individuals. For example, territorial disputes among arctic ground squirrels often escalate into mortal battles ending in cannibalism of the loser and exclusive use of an area by the winner (65). Spacing within species of social insects often involves killing and destruction of rival colonies and queens (18, 149). "Territorial wars" accompanied by inter-colony cannibalism of the dead combatants occur frequently among many species of termites and ants. Predation on neighboring conspecifics causes overdispersion in the larvae of several insect orders (2, 29, 32, 60, 74, 100). Many benthic invertebrates are regularly spaced via the cannibalism that occurs during normal feeding activities [(73, 74, 151); & incl. refs.]. Cannibalistic defense of territories is reported to occur also in moth larvae (2, 30), tenebrionid larvae (142), owls (43), grasshopper mice (68), and hyaenas (83).

Cannibalism is also a tactic to gain exclusive use of entities that serve as both food and habitat resources. The best known example occurs among parasitoid Hymenoptera (2, 5, 50, 124). Supernumerary parasitoids are eliminated from the insect host's body initially via predation or killing by specially adapted second instar larvae and later by physiological suppression. As a result, larvae exhibit a highly significant regular distribution. An analogous case occurs among granivorous insects that eat conspecifics and thereby achieve full access to individual seeds (30, 32).

In general, intraspecific predation is a self-regulatory process whose homeostatic mechanisms are often more sensitive than those of other agents of population regulation (54, 70, 98, 104, 109, 114, 117). In many cases mortality should be a precise function of density and food because the density and feeding history of the regulatory population and the regulated population are the same (but see above). Increased (decreased) density increases (decreases) the probability of encounter and the frequency of subsequent aggressive behaviors such as cannibalism [(109); (150), p. 250].

Intraspecific predation is responsive to changes in the level of ambient prey. It increases during periods of low interspecific prey availability and decreases when the density of prey increases (see "Quality and Quantity of Diet"). It acts to adjust the population size to the existing resource base and thus functions as an adaptation to a variable food supply (54, 70, 104, 109, 144).

Three feedback loops exist between intraspecific predation and ambient food (109): First, as conspecifics are eaten, the population of intraspecific competitors declines and the per capita food level increases; second (if food is limited), as density increases, both per capita food and growth decrease producing smaller and weaker conspecifics that are more frequently eaten (101, 109, 114); third, as animals are satiated by cannibalism, there is a decrease both in feeding (effectively increasing per capita food) and in those

activities related to food stress that predispose active individuals to cannibalism.

Further, the population does not escape regulation by reaching densities that may saturate some regulatory agents (negative density dependence). Since mortality is direct and immediate, there is usually a minimal time lag effect, and subsequent population oscillations are dampened [but see (96, 97)]. Limited resources are not used by (dead) surplus animals and additional food in the form of surplus animals is available to the population. Finally, cannibalism functions in the same manner as territory and social dominance to maintain the size of the population below the carrying capacity of the environment (2, 54, 104, 109, 154).

In spite of all these characteristics, it is obvious that cannibalism is not an important strategy for all populations and is not perfectly homeostatic under all demographic and environmental conditions. Population oscillations can occur in some cannibalistic systems. The loss of entire age classes of young provides an extreme case of this phenomenon. Regulatory mechanisms that affect younger animals instead of adults produce delayed effects and thus allow the possibility of cycling population sizes (96, 97). The time lag is a function of the relative age-specific mortality rates of immature and mature animals. Cycling and negative density dependence also may occur when cannibalistic predators become saturated with conspecific prey. Such predator satiation may occur in nature (109); it was best analyzed in studies of cycling in *Tribolium* (81, 96, 97).

Finally, intraspecific predation must be both necessary and sufficient in order to be an important regulatory factor. These requisites are almost impossible to demonstrate under field conditions and are rarely satisfied. Acting separately, either density-dependent mortality rates or high levels of mortality may not be sufficient to regulate population size. It is likely that several factors (e.g. predation, starvation, and weather) contribute to the regulation of any population, but evidence suggests that cannibalism is a major mortality factor in the regulation of many populations.

Population Energetics

Intraspecific predation represents an energy loop that maintains calories within a population. Such energy recycling has two consequences. First, cannibalism decreases the ecological efficiency of secondary production and poses difficulties for an operational concept of a trophic level. Second, cannibalism may influence population energetics when young animals function as de facto "grazers" thus effectively increasing the carrying capacity of the population of reproductive animals (109). The required conditions are: (*a*) Immature animals feed on resources inaccessible to or unutilized by the adults; (*b*) adults feed on immature animals and thus indirectly

incorporate these previously unavailable resources; and (c) food is limiting to the adult population so that an increase in food intake can be converted into a higher carrying capacity.

Analysis of age-specific prey of cannibalistic species show that grazer systems may be widespread. The following are good examples of species whose young use markedly different food from adults and whose adults frequently eat younger conspecifics: scorpions (109), *Notonecta* (55), squid (47), newts (23), frogs (42), and several species of fish 113, 132). For example, in the squid *Loligo opalescens* the ratio of crustacea to fish in the diet changes from 3:1 in young to 1:3 in spawning adults; in spawning schools, 75% of all prey are young conspecifics (47). In the scorpion *P. mesaensis* adults commonly eat the youngest year class (109). The overall overlap in prey between the youngest and adult year classes is only 27% and young eat 41 species of prey uneaten by adults. Therefore, when adults eat young they expand their resource base by secondarily incorporating several prey species that are either rare or absent from their diet.

In many species of fish, young feed on small zooplankton or benthic invertebrates whereas adults eat large insects and fish species. For example, overlap in prey between young and adult yellow perch is about 20%; during certain periods young constitute 43% of the prey volume eaten by adults (26). In some extreme cases, young represent the only or the major source of food for adult fish in habitats where alternate prey suitable for adults is scarce [(64, 106, 132); see especially (101)]. In such poor environments the continued existence of a population of reproductive fish

EVOLUTION OF CANNIBALISM

If cannibalism is genetically controlled, there should be strong selection on its evolution. As discussed below, cannibalism is adaptive, offering many advantages to the individual. Individual selection, kin selection, and/or parental manipulation may operate in the evolution of cannibalism among relatives. Cannibalism also may cause differential persistence, extinction, and propagule production among populations. Therefore, I briefly evaluate the speculation that selection at the population level may also influence the evolution of cannibalism.

Selection on the Individual Level: General Benefits

Several benefits accrue to the cannibal (3, 54, 60, 66, 97, 109, 128). Most obviously, individuals gain energetically by obtaining additional food. Indeed, for many animals "cannibalism appears to be an end in itself not

clearly distinguished from predation" [(66), p. 14]. Nutritional benefits may be large. In many species, conspecifics are one of the most frequent prey items [e.g. (42, 109, 116, 143); also see species under "Population Energetics"]. When prey species are ranked by weight or volume, conspecifics may represent an important food source even when their frequency in the diet is not extraordinarily high. This is because conspecifics are usually one of the heaviest prey items. For example, in the newt *Notophthalmus,* the snake *Australeps,* and the scorpion *P. mesaensis,* conspecifics form 0.1%, 2.3%, and 9.1% of the diet by frequency, but 7.1%, 22.6%, and 28.4% by weight (23, 129, 109). Conspecifics form 19–20% of the prey volume in two species of *Rana* frogs (42). In certain human cultures cannibalism may be a major source of food (40, 61). Among the Miyanmin in New Guinea, human flesh provided as great a contribution (10%) to dietary protein as the other single major source of animal food (pig) (40). Conspecifics provide an important source of protein for other animals (82, 140, 149). In some animals protein deficiency is known to stimulate cannibalism; in at least some animals, proteinaceous food is required for egg production (140). Wilson (149) suggests that the high degree of cannibalism among termites may supplement their low-protein diet. The need to obtain protein may partially explain Fox's (54) observation that cannibalism is common among herbivores and granivores.

Under some conditions the individual cannibal is favored because conspecific prey is available when other prey is not. The energy gained from eating conspecifics may allow continued survival of individuals during periods either of ecological crisis (e.g. severe weather) (6, 18, 99, 128, 149) or when no alternate prey are available (see "Life Boat Strategy"). Consumption of its own eggs or offspring also improves survival during periods when an animal is unable to forage—e.g. while guarding nest or eggs (18, 76, 119, 149).

The energetic and nutritional benefits of eating conspecifics are manifested in some cannibals by higher developmental, growth, and survival rates, increased size, and increased reproduction as compared to conspecifics unable to cannibalize (see also 54). This is especially true when food is scarce. This is well documented for coccinellid beetles [9, 20, 39, 75, 79); & incl. refs.]. Cannibalism was shown to increase survivorship or growth rates in ciliates (36), spiders (145), and insects (18, 41, 45, 81). For example, in *Lasius* ants intraspecific oophagy can accelerate larval development from 126 to 13 days (18). Because overall reproductive potential is a function of developmental time, survivorship, and body size, cannibalism may increase fecundity. This occurs in ciliates (36), rotifers (58), lacewings (41), and *Tribolium* (81). Thus cannibalism may in part be an adaptation that, by increasing nutrient availability, promotes higher fitness in more-cannibalistic than in less-cannibalistic conspecifics (97).

By killing conspecifics, an individual also decreases potential intraspecific predation on itself (e.g. during reversals; see "Size, Age, Developmental Stage, and Sex") and offspring. For example, some cricket females that guard nests eat intruding conspecifics that might otherwise have cannibalized their broods (25). Further, a cannibalistic meal increases the probability of survival by decreasing the probability that the cannibal will itself be eaten, since an individual's risk of being eaten decreases with both the increased size and the decreased foraging activity that result from a meal.

Selection on the Individual Level: Competitive Effects

Intraspecific predation may serve as a strategy of reproductive competition by reducing the fitness of other individuals of the same sex. This may occur directly by cannibalizing sexual competitors, less directly by eating their offspring, or indirectly by eating potential mates and thus decreasing the probability that rivals will reproduce. In courtship battles for females, males may cannibalize rivals (e.g. 72), sometimes by the "hundreds" (25). Direct killing and eating of rivals commonly occurs among termites and social Hymenoptera (18, 149). Victims may be either reproductives that attempt to establish new colonies too close to existing colonies or reproductives that co-found a colony.

Reproductive competition also occurs when the progeny of rivals are eaten. In recent reviews Hrdy (66) and Sherman (128) argue that infanticide (often, but not necessarily accompanied by predation) is a highly adaptive and widespread form of post-copulatory competition favored by sexual selection (see also 1, 13). The phenomenon is well studied in primates (66), rodents (128), lions (13), and social insects [(18, 149); see also (76, 119)]. For example, in *Lasius* ants, *Polistes* wasps, and *Bombus* and other bees, the dominant nest queen eats eggs or larvae of other queens. There are four possible benefits for such cannibals. First, potential resource competitors with oneself and one's offspring are eliminated (see below). Second, such cannibals increase "their reproductive output at the expense of their rivals" [(13), p. 480] by eating their rivals' parental investment. Third (in mammals), the infanticidal male's chance to breed increases when the time to estrus of the dead infant's mother is shortened. Fourth (in social animals), the cannibal rids the group of genetically less related individuals.

Finally, under certain conditions intrasexual reproductive competition may occur through intersexual mate cannibalism (109). If the sex ratio is skewed in favor of females and males are limited to a few matings, there should be selection for females that eat their mates after insemination. Removal of males directly increases the fitness of a cannibalizing female by decreasing the probability that other females will encounter a mate. Mate cannibalism as a form of mate competition should occur if inseminations are a limited resource.

In addition to the above benefits, cannibals concurrently decrease potential intraspecific competition for physical resources by eating a competitor (54, 66, 76, 104, 109, 128). Intraspecific predation functions as an extreme form of interference competition. It often produces spacing and exclusive use of specific resources such as food, nest sites, or territory. The benefits from the removal of potential competitors may be an important selective agent that favors the evolution of the apparently frequent cannibalism observed among carnivorous mammals and raptors. The death of a conspecific also reduces potential exploitation competition by decreasing population size and increasing average access to general resources. However, benefits from a general per capita increase in resource availability are shared by all individuals in the population and not just the cannibal.

Increased access to specific (but not general) resources tends to raise the fitness of cannibals relative to less cannibalistic conspecifics. Verner (147) suggested a second way by which relative fitness could be increased as a result of interference or aggression. In proposing the "super-territorial hypothesis," he reasons that since fitness is relative to the rest of the population, it can be raised either by acting to increase one's absolute contribution to the future gene pool or by decreasing the contribution of other individuals in the population. Aggressive behavior should evolve (a) to increase reproductive capacity by ensuring access to resources, and (b) to deny resources to other individuals, thus decreasing their reproductive capacity. Thus natural selection should favor aggression merely because it excludes less aggressive conspecifics from breeding, thereby lowering population size. In terms of cannibalism, a gene for cannibalism could evolve not only because it confers the benefits outlined above but also because cannibalistic genes can reduce the frequency of less cannibalistic genes (60, 93).

In two respects Rothstein (123) criticizes Verner's hypothesis that aggression can evolve to increase the aggressor's relative fitness by reducing the population of competitors. First, using models of frequency-dependent selection, he shows that the frequency of "super-aggressors" should not normally increase in the population, especially if there is much cost to such aggression. Second, super-aggressors act spitefully because super-aggression is more costly than normal levels of aggression and all individuals in the population benefit from the population reduction. Thus the super-aggressor is relatively less fit than normal aggressors. Rothstein's arguments tend to limit the evolution of aggression for its own sake; he correctly maintains that aggression that functions solely to reduce the fitness of others is unlikely to evolve under most normal conditions. However, his objections do not fully apply to cannibalism. Although the first argument is generally correct, it is dependent on the values assigned to the benefits. Since cannibalism totally eliminates a competitor, it produces much greater benefits

than those used by Rothstein. These higher benefits may well increase the frequency with which super-cannibalistic behavior evolves in the context of Rothstein's model. His second argument does not apply because cannibalism is characterized by a net energy gain from feeding rather than the net energy loss that characterizes other forms of super-aggression for aggression's sake. "Super cannibals" do not suffer the same relative disadvantages because net benefits exceed net costs. Thus cannibalism may evolve, in part, because cannibals enjoy higher relative fitness both by contributing more genes to the next generation (energetic benefit) and by inhibiting the genetic contribution of other individuals (benefit from removing a competitor).

Selection on the Individual Level and Above: Cannibalism Between Relatives

Three hypotheses may explain the evolution of cannibalism between relatives: individual fitness, inclusive fitness, and parental manipulation (1, 45, 103, 109, 150). In all cases the cannibal benefits both phenotypically (i.e. personal and nutritional status) and genotypically (i.e. contribution to future gene pools) while the victim loses phenotypically because it dies. For individual fitness (selfishness), cost is also incurred by the victim's genotype. However, for inclusive fitness (kin selection), there is genotypic benefit for the victim: Cannibalism increases the proportion of the victim's genes in the next generation via genes shared by relatives who benefit from the victim's death. For parental manipulation, there is cost to the victim's genotype but both the cannibal and the parent benefit. Alexander (1) explains that "parental manipulation of progeny refers to parents adjusting or manipulating their parental investment, particularly by reducing the reproductive (inclusive) fitness of certain progeny in the interests of increasing their own inclusive fitness via other offspring." Note that it is operationally difficult to distinguish among these three hypotheses. Further, since the cannibal always benefits, some biologists see no necessity to invoke selection above the level of the individual.

PARENTAL CANNIBALISM OF PROGENY   In kronism (126) or filial cannibalism (119), parents eat their own eggs or newborn. This behavior is surprisingly common, and its widespread occurrence suggests a strong adaptive base, with multiple benefits to the parents (66, 76, 119, 126, 128). Filial cannibalism can increase the survival probability and fitness of either the parent or the remaining offspring. It sometimes occurs as a normal part of parental care, since a parent's eating its dying or decayed offspring can prevent infection and deterioration of the entire clutch [(76) & incl. refs.]; in some species parents also eat offspring that are deformed, weak, sick, or otherwise handicapped (66, 128).

Progeny are sometimes used as a food source during periods of food scarcity and to sustain parents during brooding or guarding of nest and eggs (see earlier references). The energy gained from filial cannibalism allows the parent to remain continually with the clutch, thereby decreasing the chance of death among the remaining offspring from predation and disease. This is a case of parental manipulation as the parent sacrifices some offspring to increase the fitness of itself and its other offspring. Rohwer (119) proposed another system that favors the evolution of filial cannibalism by males on the progeny they guard. In his model, polygynous males maximize their net reproduction by parasitizing (eating) the cytoplasmic investment that female mates put into eggs. Under certain conditions such paternal oophagy will increase overall breeding success. Rohwer's theory explains many sexual and paternal behaviors observed in fish with paternal care.

SIBLING CANNIBALISM   There are numerous reports of individuals eating eggs, embryos, or newborn from their own clutch. In many cases victims may be thought of as transitory "food caches" that store energy for their kin (109). Sibling cannibalism is thus one indirect way in which maternal tissue or high levels of ambient food are converted into offspring tissue. If an organism is unable to partition eggs with enough nutrients or to provision offspring as they develop, selection may produce well-nourished offspring via sibling cannibalism (1, 90, 109, 153). Early food abundance followed by lower levels may also favor the evolution of the tendency to use offspring as food supplies for their siblings.

An extreme case of the food-cache strategy occurs in animals that normally produce infertile "nurse" or "trophic" eggs that serve as the first food of their newborn. I found 47 references to trophic eggs in over 100 species. Most such species are predators: the practice is common in marine snails [13 species, e.g. *Murex, Thais* (91, 134)], spiders [20 species, 8 families (77, 78, 145, 146)], lacewings [11 species (41)], coccinellid beetles [16 species (9, 75, 79)], social Hymenoptera [> 50 species: 9 genera of ants, 3 genera of wasps and many bees including almost all meliponids (18, 149)], and several other orders of insects [(1, 24, 25, 120) & incl. refs. in each]. Infertile trophic eggs may form a large proportion of the clutch: 95% in *Latrodectus* (black widow spiders), 8–97% in muricid snails, 5–40% in coccinellids. Further, egg cannibalism may greatly decrease clutch size: in *Latrodectus* spp., two and five spiderlings emerged from clutches of 153 and 124 eggs, respectively (78); in *Thais emarginata,* an average of 16 eggs developed from egg capsules with >500 eggs (91).

Ingestion of trophic eggs (and/or siblings) allows newborn to survive critical early stages and accelerates their growth and development (9, 20, 41, 45, 75, 79, 145, 146). In some arthropods, a diet of only trophic eggs

allows development to second or third instar. In fact, while in the egg case, *Latrodectus* can develop to within one or two molts of full maturity solely on trophic eggs (78). Increased growth may also decrease the probability of starvation and predation. In some cases, there is the further benefit that the next generation of parasites will be reduced when nondeveloping parasitized eggs are eaten along with trophic eggs (120).

In utero sibling cannibalism [(1, 90, 153) & incl. refs.] is another extreme example of the food-cache strategy. Active embryos of salamander, sharks from several families, and Mesozoic holocephalan fish possess fetal dentition enabling them to eat other embryos and maternal tissue. For example, in the sand shark *Carcharias,* only one embryo develops in each oviduct; it eats all other embryos and egg capsules (average = 19, maximum = 77) (see 153). Embryos grow to relatively large sizes (up to 105 cm in *Carcharias*) with consequently higher probabilities of survival without placental nutrition. Such fetal maintenance beyond the yolk-absorption stage is important in the evolution of aplacental viviparity (90, 153). In utero cannibalism is the simplest method of viviparity requiring no specialized maternal structures and few fetal modifications.

Sibling cannibalism on newborn animals is widespread: I found 61 references for well over 100 species. Newborn may also serve as food caches if offspring are differentially vulnerable to cannibalism. Smaller animals are at greater risk of being eaten. Size variability may be due to asynchronous production of young, differential partitioning of embryonic material, or differential feeding of young [(1) & refs. below].

Overall, the food-cache strategy allows parents to provision developing young progressively. Parental tissue may be converted into food for offspring in a manner analogous to parental provisioning in placental animals, mammals, and those species of birds and arthropods that feed their young with regurgitated maternal tissue (1). The production of expendable offspring to be eaten by siblings could be viewed as an energetic alternative to producing fewer eggs, each containing more nutrients (109).

In many cases sibling cannibalism and the food-cache strategy can be analyzed in the context of the well-established theory of brood reduction [(1, 85, 103, 137) & incl. refs.]. Brood reduction involves adjustment of larger clutches to the best smaller size that allows maximum production of young under the current conditions of food availability. Large clutches are a bet hedge: In a good year, all offspring may survive. However, if attempts to raise all young under inadequate food conditions retards development or causes the death of the entire brood, then there is selection to destroy young with a low expectancy of survival. Selection should also favor consumption of "surplus" young, which recycles rather than wastes the energy already invested in them. In fact, cannibalism contributes to brood reduction in many species of birds (11, 69, 85, 105, 126, 137).

Sibling cannibalism is an integral part of the egg laying strategy of many species. Asynchronous hatching, "runt" production, and brood aggregation may be adaptations that regulate and time cannibalism (9, 11, 20, 39, 41, 69, 75, 91, 120, 126). Hatching asynchrony is particularly conducive to consumption of eggs and younger offspring by older siblings [e.g. in birds (69, 105, 126)]. In coccinellids, there is a direct correlation between variability of hatching time within a clutch and percent cannibalism (9, 75). Brood aggregation occurs in all the examples in this section. In coccinellids and lacewings, species lay eggs either singly or clumped (20, 41). High cannibalism rates occur only if eggs are aggregated. That many species oviposit in clumps argues that cannibalism is adaptive in these species.

Controversy has arisen about whether brood reduction and sibling cannibalism evolved by individual and inclusive fitness of the offspring (103) or by parental manipulation (1). The fact that parents produce runts and trophic eggs is evidence that certain progeny are sacrificed primarily to increase parental fitness. Alexander (1) also maintains that sibling cannibalism and consequent brood reduction are cases of parental manipulation. Lack (85) views brood reduction as a parental adaptation. However, Eickwort (45) concluded that sibling cannibalism, even at low levels, was "obviously adaptive" and should be favored by kin selection because the average fitness of the clutch increased. O'Connor's model (103) explains brood reduction in terms of inclusive fitness of the victim and individual fitness of the surviving offspring and not in terms of parental manipulation.

CANNIBALISM OF PARENTS: EXTENDED PARENTAL INVESTMENT

In nine species of spider and one species of cricket, the mother is eaten by her offspring [(19, 25, 27, 84) & incl. refs.] Spiders become a usable "food depot" when they direct digestive juices inward, liquifying their bodies, heart and respiratory system functioning to the end. This adaptive strategy of extended parental care should evolve especially in annual species such as those arthropods that die soon after giving birth.

Under some conditions selection should favor the consumption of males by their mates (35, 140). His probability of being cannibalized should be directly proportional to the male's future expectation of reproduction. A male with a low probability of future matings may best increase his fitness by providing his body as a "blood meal" for the mother of his offspring. Low probabilities may occur late in the breeding season for annual species, if males are likely to die before the next breeding season, or if males are limited in the number of possible copulations. Such a meal may increase either female survival or nutrition of eggs and embryos. Thornhill (140) suggests that since these males represent a resource, in this situation a reversal of normal sexual roles may occur, with both greater male coyness and female advertisement during courtship.

Mate cannibalism is reported in 30 species representing almost all orders of arachnids [(19, 27, 110) & incl. refs.], three orders of insects (140), and copepods (133). In spiders and scorpions mate cannibalism is frequent, and males often do not live more than one breeding season (19, 71, 110). Mate cannibalism is such an integral part of courtship in mantids that male copulatory behavior is actually facilitated by the decapitation that accompanies cannibalism (118.)

Cannibalism at the Population Level: Benefits and Possible Selection

Several de facto benefits accrue to the population of cannibals (109). An obvious group benefit is homeostatic self-regulation. Cannibalistic populations can be self-regulated below the carrying capacity of the environment; eruptions are thus damped before high densities produce overexploitation and mass starvation. Thus cannibalism may increase stability and decrease the probability of extinction. Cannibalistic populations are also more resilient because survivors of a population reduced by cannibalism are relatively more vigorous than survivors of a population reduced by exploitation (scramble) competition. Cannibalistic survivors should be better fed and capable of contributing more offspring to the next generation than those hungry survivors that competed for a limited food supply. Another group benefit occurs via "grazer systems" that effectively increase the equilibrium population of reproductives. Further, in a model of predator/prey systems Bobisud (15) showed that in some situations the equilibrium population size of the prey species should increase owing to cannibalism between prey stages (see also 136).

Cannibalism at low food levels may contribute to the continued survival of a population that might otherwise become extinct (e.g. 9, 12, 31, 39, 41, 57, 75, 109, 144, 149). Wilson [(149), p. 280] states that the brood of social Hymenoptera "functions normally as the last ditch food supply to keep the queen and workers alive." Thus cannibalism serves as a "lifeboat strategy" to decrease the probability of extinction and to increase the long-term persistence of populations that live in environments characterized by large fluctuations in food resources (109). The term "lifeboat strategy" was used by Giese (57) in describing cannibalistic morphotypes of Blepharisma. Individuals in a population of cannibals survived periods of food deprivation by eating each other whereas individuals in noncannibalistic populations starved to death. Similar results were obtained for three species of sheep blowfly (144) and different strains of mites (31). Under conditions of inadequate per capita food, the populations of the two cannibalistic blowfly species and the cannibalistic mite strains persisted while the noncannibalistic groups became extinct.

The following is speculation on the role of group selection in the evolution of cannibalism. Keeping in mind the well-known criticisms of group-selection theory (e.g. 35, 148, 150), we must nonetheless consider group selection because cannibalism can greatly benefit or harm the relative success or "fitness" of a population (as measured by differential time to extinction or differential production of successfully colonizing propagules). The existence of large group effects poses an important evolutionary question: Should they be explained parsimoniously as "statistical by-products" of individual selection [(148), p. 237] or have they themselves become the focus of selection among populations?

In some species cannibalistic genes may promote both the fitness of the individual and the population. Thus individual selection for such genes works in the same direction as potential group selection [see (136) for a model]. The individual is the unit of initial selection; if large epiphenomenal benefits to the group also accrue then group selection may occur as well. The selective advantage to the group confers a further selective advantage to individuals within the group. Conversely, cannibalistic genes may greatly reduce population fitness. In some species cannibalism produces extremely high levels of mortality, eliminates entire generations, and may even cause extinction of local populations [see above and (54)]. Such "cannibalistic suicide" is reported in *Tribolium* (81, 97) and may occur in copepods (133). It is not unreasonable to speculate that such severe mortality and lower population sizes place cannibalistic populations at a great disadvantage relative to less cannibalistic populations. In this case group selection disfavors cannibalistic genes and therefore works in the opposite direction from individual selection. In summary, I am not suggesting that cannibalism rates necessarily evolve by group selection. Rather, variation between populations in levels of cannibalism could result in the types of differences between populations in their probabilities of persistence and proliferation that are a prerequisite to evolution by group selection. Given this, it is intriguing to consider the possibility that cannibalism rates may be subject to group selection.

Limits to the Evolution of Cannibalism

Past a certain point, aggression can decrease the aggressor's fitness. Although cannibalism is not as constrained as other forms of aggression (see "Competitive Effects"), disadvantages exist that select against its evolution (35, 54, 65, 66, 71, 104, 150). There is a risk of injury and death during a predatory attack when a conspecific defends itself or retaliates (35, 65, 71). Intense cannibalistic behavior may decrease reproductive success because of the tendency to attack and eat (potential) mates (54, 104). In some cases cannibals are infected with pathogens or parasites: I have 12 references that indicate cannibalism acts as a vector for the transmission of infectious

organisms [e.g. Kuru in humans (56)]. Cannibalism may cause a net decrease in inclusive fitness if one is likely to eat progeny or close relatives (54, 71, 150). The net decrease is influenced by such factors as the relatedness of the victim and the rate of cannibalism on relatives compared to nonrelatives. Finally, in some social animals cannibalism may decrease colonial benefits, thus lowering the cannibal's fitness (66). Overall, cannibalistic behavior should evolve to a level that maximizes the difference between advantages and disadvantages as measured in units of inclusive fitness.

CONCLUSIONS

First, intraspecific predation is common and widespread in the animal kingdom. Wilson [(150), p. 246] is "impressed" with how frequently cannibalism and killing occur, especially when field studies exceed 1000 hours. Second, the notion that such predation is abnormal or unnatural should be dismissed. Sherman (128) discusses the persistence of this belief [also see (54) and below]. Perhaps this view is perpetuated because *Homo sapiens* is the only species capable of worrying about whether its food is intra- or extraspecific [although many humans do not: Shankman (127) lists 60 cultures that eat fellow humans]. Third, cannibalism is important in the ecology and evolution of many species ranging from protozoa to mammals. Fourth, much cannibalism is a result of both genetic and environmental factors. In general, it appears to be genetically based but controlled or induced by various environmental cues.

In spite of all the evidence, there is a long and continuing history of biologists who deny its importance. Ethologists in the school of Lorenz (89) and Eibl-Eibesfelt (44) were among the first to insist that intraspecific killing and predation are rare events in nature. They stressed that animal fighting is gentlemanly and universally restrained by ritual, bluff, and nonfatal violence. Eibl-Eibesfelt (44, p. 112) makes the "general observation [that] fights between individuals of the same species almost never end in death and rarely result in serious injury to either combatant." Lorenz [(89), p. 38] states that he "never found that the aim of aggression was the extermination of the fellow members of the species concerned." More recently, proponents of game theory [e.g. (35, 95) & incl. refs.] attempt to explain why dangerous tactics, lethal weapons, killing, and cannibalism "are not as common" [(35), p. 72] as one would expect. Maynard-Smith & Price [(95), p. 15] state that "intraspecific conflicts are usually of a 'limited war' type, involving inefficient weapons or ritualized tactics that seldom cause injury to either contestant." In the *Selfish Gene* [(35), p. 89], Dawkins asks the wrong question: "Why is cannibalism relatively rare?" He should have asked why cannibalism is relatively common.

Clearly there is a conflict between these theories and evidence from the real world. As discussed by Wilson (150) and Dawkins (35), the early ethologists were wrong on many points. Is game theory also incorrect? Not necessarily. At least some cases of cannibalism can be explained in terms of two aspects of game theory. First, conspecifics often wage "asymmetric contests" with large cannibals eating much smaller victims. Second, much cannibalism occurs when food is scarce, animals are hungry, and death by starvation is possible. At these times the high benefits to the winner allow an increase in the potential cost of the act. However, much cannibalism is not currently explainable by game theory. One is tempted to agree that Darwin and Tennyson were more correct: that nature is "red in tooth and claw."

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