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Kleptoparasitism and Cannibalism

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Introduction

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Animals acquire resources in many ways, and this diversity allows for many types of interactions between individuals. Students of behavior commonly use the idea of resource ownership to classify these. When, for example, a group of feeding animals contests a limited amount of ownerless resources, we call this interaction ‘exploitative competition.’ In many situations, however, animals obtain exclusive control of resources in a manner analogous to human ownership. These acquired and defended resources present an opportunity for thieves. Kleptoparasitism is an interaction in which one individual takes a resource from its owner by stealth or aggressive conflict. The Greek word *kleptes* literally means ‘thief,’ so kleptoparasitism means ‘parasitism by theft.’ In the end, the food resources that animals acquire are assimilated into their bodies, so killing and eating another animal is, in a way, the ultimate theft.

p0010

Cannibalism is one form of this ultimate theft. To the more squeamish human readers, cannibalism – killing and eating a member of your own species – makes the ‘theft’ implicit in kleptoparasitism seem neighborly. The word ‘cannibalism’ comes from the Spanish word *Canibales*, which is the variant of the English word *Caribes*, the name of a West Indian people reputed to eat humans.

p0015

Figure 1 shows kleptoparasitism and cannibalism in a schematic space of the biological interaction of resource exploitation. Cannibalism is exploitation of the resource with full ownership, that is, the body, in which the resources are already assimilated and stored. Thus, the act is lethal to the victim. Kleptoparasitism is in the wide spectrum of varieties of parasitism. The victims of kleptoparasitism may be members of the same or different species, but the act of the kleptoparasite does not kill the victim. The resources ‘stolen’ in an act of kleptoparasitism may be food or objects such as nest material.

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Kleptoparasitism

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Kleptoparasitism takes many forms and occurs in many situations. Reports of kleptoparasitism have often used words with anthropomorphic connotations, such as ‘usurpation,’ ‘robbing,’ ‘stealing,’ ‘pilfering,’ and ‘sponging,’ and even phrases, such as ‘using others as truffle pigs.’ In their authoritative book, Giraldeau and Caraco recognized three distinct forms of kleptoparasitism: overt aggression,

competitive scramble, and stealth. An aggressive kleptoparasite uses force or the threat of force to gain exclusive access to resource. In scramble kleptoparasitism, one or a few individuals actively hunt for resource, but nonhunters can exploit discovered resources in an open scramble. A stealthy kleptoparasite takes the resource, but avoids interaction with the host.

Distribution Among Animal Groups

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A recent review by Iyengar found that most reports of kleptoparasitism involve birds. The preponderance of records from birds probably reflected research effort and visibility more than a true pattern in nature. Investigators have reported kleptoparasitism in insects, spiders, mollusks, fishes, birds, and mammals. The following paragraphs give several concrete examples of kleptoparasitism.

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Spotted hyenas are masters of piracy in African savanna. Group of hyenas steal kills made by wild dogs, cheetah, and lions. Kleptoparasitism by spotted hyenas profoundly affects the energy acquisition of wild dogs and cheetah. Chipmunks take seeds from their neighbors by entering the burrows of absent conspecifics and pilfering seeds from the larders.

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Observers frequently see intra- and interspecific kleptoparasitism in sea birds colonies. Jaegers and skuas rely exclusively on kleptoparasitizing other seabirds, such as terns, kittiwakes, and gulls. These birds take food from others in the air, during courtship feeding, and when adults regurgitate food to their chicks. Ornithologists have also reported kleptoparasitism in several species of waterfowl, passerines, egrets, and bird of prey. In feeding flocks of passerine species, we often see some individuals actively searching for food, while others search for opportunities to exploit the food discoveries of the others (see the discussion of producer–scrounger systems in chapter **Group Foraging** (00215) – by Giraldeau).

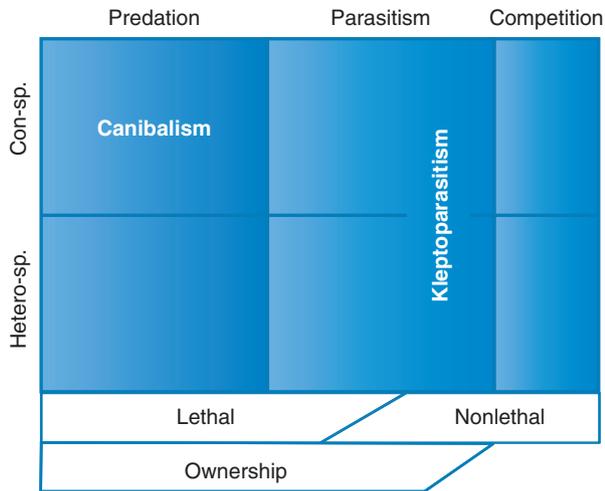
p0035

In fishes, there are a few reports of kleptoparasitism. Among territorial reef fishes that gather food algae at a fixed site (termed as ‘garden’), theft from gardens occurs, and theft is not only when the territory holder is absent. Blue tang surgeonfish and striped parrotfish forage in large roving groups, feeding from the algal turf defended by damselfish.

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Thrips and flies create shelters (galls) on host plants. Invading individuals sometimes actively evict occupants from their galls. Some parasitic wasps steal hosts that another wasp has located previously. In some water striders, males, which are usually smaller than females, ride

p0045

f0005 **Figure 1**

on their mate's back for long periods; during this time, they often take food items that their mate catches.

Kleptoparasitism among mates is common in spiders when males live on or near the female's web for extended periods. These 'cohabiting' males will feed on prey caught in the female's web. Several spiders of genus *Argyrodes* steal prey from other spiders. They can move on the webs of their hosts without being detected, yet they can detect the position of prey trapped in the web. Some spiders engage in a unique form of kleptoparasitism called 'silk stealing.' Silk thieves cut silk out of the hosts' orb webs and eat it.

We have a few records of kleptoparasitism of terrestrial and marine gastropods. Carnivorous plants capture large quantities of high-quality food. A slug species is known to take over the food resource. Some species of conches (a marine snail) steal food from tube-dwelling polychaete worms.

s0020 **Extension of the Concept of Kleptoparasitism**

p0060 Outright expropriation of a food resource from its owner is the fundamental phenomenon we call kleptoparasitism. Kleptoparasites, however, also take inanimate objects. Several warbler species engage in nest material stealing, and each of these species can act both a perpetrator and a victim.

p0065 Furthermore, kleptoparasites can also exploit intangible quantities. A kleptoparasite may exploit the searching behavior of another individual and usurp food discoveries before the discoverer can consume them. This type of parasitism has significance for the value of group living, because within a group some members may produce information for themselves while others scrounge information from the producers. Little brown bats, for example, eavesdrop on echolocation calls of others to find prey and other resources.

Brood parasitism occurs in some birds, fishes, and, rarely, insects, and some authors interpret this to be a type of kleptoparasitism in which the parasite uses several services, including nest-building labor and parental care. In mating situations, peripheral males may obtain matings by parasitizing the displays and other female-attracting activities of dominant males. One can view this well-known stealthy mating tactic as a form of kleptoparasitism, and investigators sometimes call it 'kleptogamy.' Thus, we realize that kleptoparasites can exploit a wide range of nonfood resources such as nest materials, domicile, parental care, mating partners, and information.

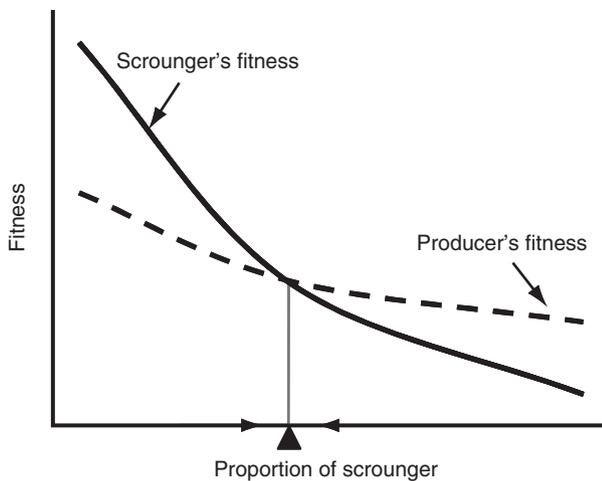
s0025 **Evolutionary Ecology of Kleptoparasitism**

Kleptoparasitism represents an adaptive strategy that may pay off in some situations but not in others. Taking resources from another eliminates the need to search for and handle food items, and it may therefore save time and energy. The fitness value of kleptoparasitism depends on the relative cost obtaining resources on your own, and the ease with which the kleptoparasite can steal food from others.

In some cases, kleptoparasites work in groups, and we predict that this will only happen if the resource in question can be divided. Of course, in a world composed entirely of kleptoparasites, no one would eat. The value of kleptoparasitism hinges on the presence of individuals who find and capture their own food. In the language of behavioral game theory, kleptoparasites are 'scroungers' who depend on the presence of 'producers.' Therefore, the mix of producers and scroungers in a population determines the relative payoffs of the two strategies.

The producer–scrounger game, a model proposed by Barnard and Sibly in 1981, addresses this question. **Figure 2** demonstrates an envisaged fitness change of producer individual and scrounger individual in the population of a given proportion of scroungers. When proportion of scroungers is low, scroungers do well because there are many producers to exploit. As scroungers become more common, encounters with producers become less common and the fitness of scrounger ultimately falls below the fitness of producers. These fitness relationships stabilize a mixture composition of producer/scrounger in population.

The producer–scrounger framework helps us to understand how and why kleptoparasitism can evolve and be maintained in a population. As with most adaptive arguments, however, one needs to consider other factors to achieve a deep understanding of kleptoparasitism. Internal state, growth and developmental history of the individual, and genetic and epigenetic constraints probably all play a role in kleptoparasitism. Iyengar reviewed a wide range of distribution patterns of kleptoparasitism among animal kingdom and argued some explanations of the distribution pattern among taxonomic groups. Morand-Ferron et al.



0010 **Figure 2**

also review the distribution pattern of food-stealing in birds and offer some explanations of this phenomenon.

s0030 **Kleptoparasitism and Ecology**

p0095 Kleptoparasitism has some implications that go beyond its effects on perpetrators and their victims. For example, large groups of African wild dogs have higher rate of food intake, because large groups can defend carcasses against kleptoparasitic hyenas. So 'defense against kleptoparasites' may play an important role in animal group size. To take another example, in Zeus bugs, male Zeus bugs ride on the backs of their mates and steal food secured by females. In response, females produce a glandular secretion that males feed on, which reduces the extent to which the males kleptoparasitize the female's food.

p0100 Kleptoparasites exploit various types of resources including food, inanimate objects, domicile, parental care, mating partner, and information. Perpetrator and victims may be solitary or in groups, and they may be conspecifics or heterospecifics. The amount of damage that kleptoparasites cause also varies. This diversity makes it difficult to draw general conclusions about implications of the ecological consequences of kleptoparasitism. However, we do often find that interspecific kleptoparasites are often fairly close phylogenetic relatives of their victims, which in turns suggests that kleptoparasitism will often have important implications for dynamics of guilds within ecological communities.

s0035 **Cannibalism**

p0105 In earlier discussions, investigators dismissed cannibalistic behavior as an anomaly. Zoos and animal-rearing facilities commonly observed cannibalism in captive situations, but

it was dismissed as an artifact of crowding and stress. In addition, animals sometimes eat their relatives. Parents eat their babies, juveniles eat their siblings, and so on. This odd behavior seemed to preclude an evolutionary explanation, and further suggested some type of mistake or behavior out of context.

Notwithstanding this preconception, comprehensive surveys by several authors show that cannibalism occurs in nature in many groups of including: protozoa, planaria, rotifers, gastropods (snails and slugs), ciliates, copepods, centipedes, mites, insects, fish, amphibians, birds, and mammals. In short, cannibalism seems nearly ubiquitous, so much so that it is not even restricted to carnivorous species; we commonly find cannibalism in herbivores and detritivores.

Variety of Cannibalism

Relative size and vulnerability dependence

As noted earlier, cannibalism can take many forms. The relative sizes, ages, and developmental stages of the consumed and the consumer can vary. Crudely speaking, however, the consumers tend to be larger and more aggressive, while the consumed are small and vulnerable.

In many situations, differences in relative size create opportunities for cannibalism. Predators that swallow their prey whole – like many species of fish – can only open their mouths so much, so for these animals, cannibalism can only occur when large individuals attack victims small enough to fit in their mouths.

Animal can vary in size for many reasons. An individual may be smaller because it is younger or because it is a different gender. Yet, we find size variation even within cohorts of the same age and sex. This can occur because of differences in resource allocation during development or it may be due to random variation during an individual's development. Size variation, regardless of its source, sets the stage for cannibalism, even within cohorts of the same age and sex.

In addition, developing animals often pass through vulnerable life-history stages such as ecdysis and pupation. Cannibalism often occurs during these vulnerable periods. Indeed, younger and smaller individuals may cannibalize older and larger individuals during these vulnerable stages. We find situations where smaller individuals cannibalize larger individual in some insects, crustaceans, and amphibians.

Parental cannibalism of progeny

Filial cannibalism, where parents eat their own eggs or infants, is widely observed in mammals (e.g., chimpanzees, lions, hyenas, and baboons), birds (e.g., several bird of prey, house finches, and house sparrows), amphibians (e.g., salamanders), reptiles (e.g., skink and boas), insects (e.g., assassin bug and burying beetles), and spiders (e.g., wolf spiders).

Studies of teleost fish suggest that filial cannibalism is especially prevalent in this group (e.g., bullheads, damselfish, cichlid, flagfish, goby, and stickleback). Filial cannibalism occurs most frequently while parents are caring for their eggs and young.

p0140 Filial cannibalism presents an evolutionary conundrum, because consuming your own offspring surely decreases your current net reproductive success. One explanation is that filial cannibalism represents a ‘decision’ to redirect resource away from current reproductive output and toward survival and future reproduction. Cannibalism by fathers occurs more frequently than cannibalism by mothers. Presumably, this pattern arises because males typically have less invested in offspring than females.

p0145 Another explanation of filial cannibalism is that cannibalism removes failed offspring. Parents eat diseased or parasitized eggs from their clutches. We can view this as a form of parental care that prevents diseases and parasites from spreading to the entire clutch.

s0055 **Sibling cannibalism**

p0150 Cannibalism among siblings occurs when sibling groups aggregate. This may be important for some species in which juvenile commonly pass through an aggregating developmental stage. Investigators have observed sibling cannibalism in birds (e.g., several birds of prey, several sea birds and house sparrows), teleost fishes (e.g., pike, perch and cods), selachian fishes (sharks), reptiles (snakes), amphibians (salamanders), mites (predatory mites), insects (e.g., ant lions, lady beetles and water bugs), gastropods (snails and slugs), Spionidae (segment worms), and echinoderms (viviparous sea stars). In this form of sibling cannibalism, the developmentally advanced individuals in a clutch consume eggs, embryos, or newborn siblings within their clutch. Asymmetric development among sibs makes differential vulnerability among offspring and facilitates sibling cannibalism. Small or stunted offspring experience a greater risk of cannibalism. In many bird species, asynchronous hatching which creates a size and age difference within the next sets the stage for sibling cannibalism.

p0155 In some amphibians, insects, spiders, and gastropods, newborns eat eggs from their clutch as the first food of their life. In some cases, these eggs are ‘nurse’ or ‘trophic’ eggs that are sterile or have stopped developing at any early stage. In some live-bearing sharks, embryonic offspring eat their embryonic siblings while they are still within their mother’s body.

s0060 **Cannibalism of parents (matriphagy) and mate cannibalism**

p0160 In some species of spiders, scorpions, and insects, offspring eat their mother. We interpret this behavior as a form of parental care, because the mother’s body provides resources that promote growth and development of her

offspring. In one species of earwig, the mother-eating (or matriphagy) delays offspring dispersal and increases their survival. From an evolutionary perspective, offspring cannibalizing parents is less surprising than parents cannibalizing young, because the consumed parents are typically postreproductive and decrepit.

Sexual cannibalism occurs when one sexual partner eats another. Sexual cannibalism frequently occurs as part of courtship and mating, and we see it in mantids, scorpions, and spiders. In most situations, females eat their male partners, and not the other way around. People often think of courtship and mating as a harmonious and cooperative reproductive partnership, so sexual cannibalism reminds us that mating can be fraught with conflict. In cases where the female consumes the male after copulation, we can interpret the male’s ‘sacrifice’ as parental investment. Yet, females sometimes consume males before insemination, and this suggests sexual conflict.

Cannibalism and Ecology

s0065 Cannibalism is synonymous with ‘intraspecific predation’. p0170 It has implications for population and community ecology that go beyond its importance in behavior, physiology, and life history.

Cannibalism directly eliminates conspecific individuals, so it inevitably lowers population density. In some cases, we have evidence that high densities lead to increased cannibalism and hence to greater reductions in population size via cannibalism. The relationship between cannibalism and conspecific density is direct and immediate. Thus, cannibalism can help regulate population size.

Classical models of predator-prey dynamics suggest that predator and prey population may exhibit couple oscillations. Allowing cannibalism with the predator can reduce or eliminate these oscillations and stabilize predator-prey dynamics in the following way. When the prey population is low, predators cannot obtain enough energy from prey, and they will engage in some cannibalism. This quickly reduces the predator numbers and hence the effect of predators on prey. The net effect is that when predators increase their rate of cannibalism, this stabilizes predator and prey population densities.

On the contrary, cannibalism can also destabilize population dynamics. Consider a situation, for example, in which older individuals cannibalize younger and more vulnerable age classes. If cannibalism eliminates a high proportion of a given cohort, this age class will be a small group throughout its life history. The resulting group of cannibalistic adults will, because they are small in number, have a smaller effect on cohorts that follow them. This ‘less cannibalized’ cohort will in turn have a larger effect on the cohorts younger than themselves, and so on. This multistep chain inference implies that the intercohort cannibalism may cause violent population fluctuations.

Cannibalism can have various implications for ecological communities. For example, cannibalistic species often have complex food habits, where young animals feed on resources that adults do not eat, and adults cannibalize the young. Thus, a single cannibalistic species can connect multiple trophic levels, and it can influence a community's food web in a complex manner.

s0070 Evolutionary Arguments

p0190 As with other traits, we would like to understand the evolution and adaptive significance of cannibalism. As this review shows, cannibalism takes many forms and we cannot offer a single comprehensive explanation for all cannibalistic phenomena. The following paragraphs outline current thinking about the evolution of cannibalism.

s0075 *The basic principles of adaptation*

s0080 *Individual fitness*

p0195 Among free-living animals, cannibalism is usually facultative (meaning that it only occurs in some conditions). Cannibalism should occur when populations are crowded or alternative preys are rare or difficult to obtain. This, of course, broadly agrees with observed facts: crowding and poor access to alternatives do increase cannibalism. We can apply foraging theory's diet model (see chapter **Optimal Foraging Theory – Introduction** (00210) by Pyke) to further understand the conditions that favor cannibalism. The diet model assumes that the forager makes choices that maximize its own energy acquisition or probability of survival under fear of death from hunger.

p0200 Typically, we would expect that conspecific prey would have a lower rank as potential diet items than other food types, because attacking and handling conspecifics (who have similar size and defensive abilities) will be costly in line for potential menu items. The diet model predicts that when the abundance of relatively high-ranking food types decreases, the lower-ranked prey should be included in the diet menu, and thus, cannibalism occurs. The widespread observation that cannibalism increases when the availability of alternative foods declines is consistent with this argument.

p0205 We could explain facultative parental cannibalism of offspring as a conditional decision to give up the current reproductive output in order to increase future reproduction. We would expect to observe parental cannibalism, therefore, in harsh environmental conditions where a parent must choose between eating its offspring and starvation.

s0085 *Parental manipulation*

p0210 As explained earlier, differences in size and development can set the stage for sibling cannibalism. In some cases, however, parents may pull the strings behind the scene. For example, parents may produce embryos asynchronously, differentially partition resources among their

embryos, or simply feed some offspring more than others. All the mechanisms can generate asymmetries among offspring and create the potential of sibling cannibalism.

One rather surprising interpretation of sibling cannibalism is that it represents a parental food storage strategy. According to this view, we see the bodies of vulnerable offspring as food stores for larger, older, or more viable offspring. And, of course, the larger offspring must cannibalize the smaller to exploit this 'stored food'. This may seem fanciful to some readers, but it clearly happens in some cases, where parents produce trophic eggs (eggs that others eat) that offspring need for survival. In cases like these, sibling cannibalism may be an integral part of a parent's reproductive strategy. p0215

Evolutionary game theoretical view

Consider the question 'why is cannibalism relatively rare?' or even the reverse 'why is cannibalism relatively common?' How can the energy-based optimization argument answer these questions? Explaining this variation via simple optimization requires pre-existing differences in size or vulnerability and treats victims as merely food item. s0090 p0220

Suppose, however, that all individuals are the same, and there is no energetic advantage to including conspecifics in the diet. Can cannibalism occur? Can we imagine conditions where some individuals act as cannibals while others do not? To answer this question, we turn to evolutionary game theory. According to this body of theory, we need to ask how the frequency of individuals 'playing' the cannibal and noncannibal strategies influences the fitness value of the two strategies. p0225

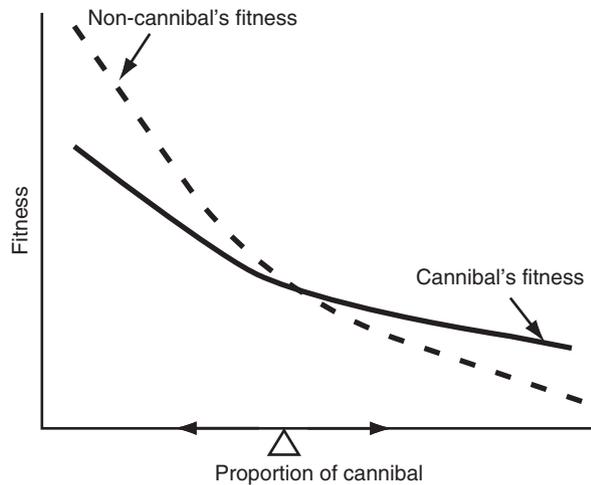
In a mixed population of cannibals and noncannibals, each individual is threatened by not only starvation but also by cannibalism. Cannibal types are more likely to survive attacks from others than noncannibals. Fitness of both cannibals and noncannibals depends on relative encounter rate to cannibal-type individuals in the population. p0230

Figure 3 shows a hypothetical example of the fitness curves for the two types. When the proportion of cannibals is low, the risk of death via cannibalism is low for both cannibals and noncannibals, and so, noncannibals have higher fitness. As cannibals become more common, encounters with cannibals become more common and the fitness of noncannibal falls below the cannibal's fitness. As the figure shows, a critical proportion of cannibals exists; below this we expect a population of noncannibals to evolve, and above this we expect a pure cannibal population of cannibals. This argument shows how evolutionary game theory can help us understand the evolutionary origins and maintenance of cannibalism. p0235

Evolutionary implications

Disease transmission

Evidence from several species (including several mammals, reptiles, amphibian, insects, crustaceans, and fishes) s0095 s0100 p0240

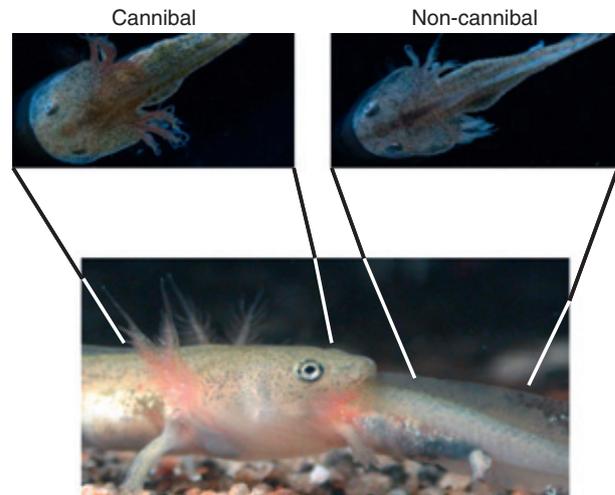
f0015 **Figure 3**

shows that cannibalism can transmit diseases such as viral, bacterial, and parasitic infections. So a possible answer to the question ‘why is cannibalism relatively uncommon?’ is that cannibalism incurs a potential cost of pathogen transmission from conspecifics. Cannibals experience a greater risk than other predators because they are genetically similar to their prey, and hence susceptible to the same kinds of pathogens. Studies by Pfennig document the enhanced risk cannibals experience. Using tiger salamanders, these studies showed that eating diseased conspecifics (cannibalism) caused infections more frequently than eating heterospecifics (normal predation).

s0105 **Cannibalistic polyphenism**

p0245 Cannibalistic polyphenism is an intriguing phenomenon known in some flagellates, ciliates, rotifers, and amphibians. In cannibalistic polyphenisms, some individuals in a population are cannibalistic, while others are not even though both types have the same genetic background. Cannibals commonly have modifications to their eating machinery (bigger jaws, sharper teeth) that make them more efficient cannibals. Cannibalistic polyphenism is an instance of developmental plasticity, because cannibalistic morphs develop their enlarged jaws in response to environmental conditions – primarily crowding.

p0250 Early developmental stage larvae of the salamander, *Hynobius retardatus*, can become cannibals. In crowded conditions, some individuals become cannibal morphs that prey on noncannibals and have distinct morphological structures such as a broad head and a large jaw and a large body (**Figure 4**). We can observe either of dimorphic or monomorphic local population in natural ponds depending on larval density during the sensitive phase

**Figure 4**

f0020

of development. The facultative cannibalism involves important evolutionary questions, such as what conditions maintain this developmental phenotypic plasticity and what allows the coexistence of both morphs within a given population.

See also: Propagule behavior and parasite transmission (00130); Avoidance of parasites (00131); Foraging Modes (00209); Optimal Foraging Theory – Introduction (00210); Defense Against Predation (00213); Group Foraging (00215); Optimal Foraging & Plant-Pollinator Co-Evolution (00278); Decision-Making (00280).

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Non-Print Items

Au3 Glossary:

Evolutionary game theory – Evolutionary game theory is an application of the mathematical theory of games to evolutionary biology contexts, arising from the realization that frequency-dependent fitness introduces a strategic aspect. A game defines fitness of players, which reflects not only strategy of the protagonist player but also strategy of other ones. Evolutionary game theory analyzes transition of strategists' frequency in the population according to the expected fitness of each strategist, which reflects the current relative frequencies of the strategists and the game rule. The transition process is an analogy of evolutionary change of population members driven by natural selection.

Abstract:

Kleptoparasitism, literally meaning parasitism by theft, is a form of resource acquisition where one animal takes resources from another. Although kleptoparasitism of food (i.e., kleptoparasitic foraging) is the best known example, the stolen resources may be food or another resource such as nesting materials. As with theft in human society, kleptoparasitism may be stealthy or aggressive. Cannibalism occurs when one individual of a given species kills and consumes all or part of another individual of the same species. Cannibalism is within-species predation that occurs because individuals vary in vulnerability and aggressiveness. Cannibalism occurs when alternative foods are scarce and populations are crowded.

Keywords: Anticannibal; Brood parasitism; Cannibal; Filial cannibalism; Foraging theory; Intraspecific predation; Matriphagy; Nurse eggs; Parental care; Parental manipulation; Producer–scrounger game; Sexual cannibalism; Trophic eggs

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Biographical Sketch for Online Version



When Kinya Nishimura was an undergraduate, he was introduced to the active age of behavioral and evolutionary ecology. Immediately, foraging theory attracted him and brought him to a study of foraging behavior of Ural owls. He conducted experimental studies explaining prey and patch utilization patterns of Ural owls, and mathematical model analysis of foraging theory of sit-and-wait forager, in Ph.D. course at the University of Tsukuba. After receiving his Ph.D., Kinya did postdoctoral studies on mathematical models of sex allocation, foraging behavior, and cooperative behavior considering stochasticity of several environmental and behavioral factors

ANBV: 00279

at the University of Tsukuba and partly at the University of Nebraska. He accepted a faculty position at Hokkaido University, where he has remained since 1994. The author is currently an Associate professor in the Graduate School of Fishers Sciences where he teaches courses in ecology and mathematical biology. Kinya studies early life-history traits evolution of fish species, and evolution of inducible phenotype plasticity, particularly, inducible cannibalistic polyphenism experimentally and theoretically.