

DOG EAT PUPPY WORLD: A REVIEW OF JUVENILE AND FILIAL CANNIBALISM IN THE ANIMAL KINGDOM

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Cannibalism is a widespread behavioural strategy in the animal kingdom, providing many advantages to its subscribers, along with many substantial disadvantages. Most surprising are the benefits of filial cannibalism, i.e. the eating of offspring and close relatives. Here the topic of filial cannibalism is covered in detail, exploring its advantages and disadvantages to male and female parents. While it is found to be a highly beneficial and advantageous method of feeding, providing nutrition when absolutely necessary, it has many deleterious effects. Avoidance of juvenile and filial cannibalism by adults is also reviewed, along with the avoidance of becoming conspecific prey by juveniles.

Introduction

Cannibalism, or intraspecies predation (defined as the catching, killing and devouring of an animal by a conspecific), is widespread in the animal kingdom with at least 3000 species, across 900 groups subscribing at least partially to this method of feeding (Polis, 1981; Fox, 1975). What was once considered 'an aberrant and occasional' phenomenon is actually relatively common in many species (Hunte and Myers, 1984). 'Cannibalism' has been occasionally found in human history, particularly in New Guinea (Venkatachalam, 1962; Dornstreich and Morren, 1974) and often poses the same theoretical advantages to that of subscribers in the animal kingdom (though usually is in fact intraspecific necrophagy; the eating of dead conspecifics, a behaviour closely linked to

cannibalism). Many kinds of cannibalism exist in the animal kingdom and have been studied in some detail, this review explores one of the darker forms of cannibalism; filial cannibalism, the killing and eating of one's own offspring

Cannibalism in general can be very advantageous. It is an effective method of feeding, with the prey's nutrient content matching closely what is required of the predator, thus removing the danger of a nutritional mismatch (Bobisud, 1976). For example, arthropods are often limited in somatic growth by abundances of specific rare minerals such as nitrogen, and so, predating conspecifics eliminates the need to search for such substances (Denno and Fagan, 2003). Intraspecies predation ensures that these nutrients are easy to encounter.

Intraspecies predation reduces the need to search for prey, and is particularly common in colonial species, where the availability of same-species prey is high, or in areas where other species to predate on are in low densities (Polis, 1981). Cannibalism is also more likely to occur in populations that have overlapping generations in time and space, and also have notable differences in size (Wissinger, 1992). It has an indirect fitness advantage of removing potential competitors, thus increasing your potential resources. For example, female Three-spined Sticklebacks (*Gasterosteus aculeatus*) cannibalise stickleback eggs, even when alternative food is superabundant (Fitzgerald, 1992).

Cannibalism can be mediated by many other factors such as food availability, habitat type, genetics, and parasites. Females have a tendency to be more cannibalistic than males (Polis, 1981; Fox, 1975), as the majority of cannibalistic activity involves females eating males post copula (Cordoba-Aguilar and Contreras-Garduño, 2006), or mothers eating suboptimal offspring (Elwood, 1992). There is an evident genetic component to cannibalism; for example, rates of litter cannibalism in mothers remain the same for at least 13 generations in studies of laboratory mice (Hauschka, 1952). Poor quality habitats can mediate the incidence of cannibalism, with adult *Gammarus* having to turn to cannibalism due to lack of food and juveniles having to forage more widely to find food, increasing the risk of predation (MacGrath *et al*, 2007). Cannibalism can be mediated by parasitic infection., For instance, *Gammarus* infected with *Pleistophora mulleri* showed an increase in cannibalistic activity (Bunke *et al.*, 2015). Behavioural polyphenism or 'animal personality' can also mediate cannibalism (Poulin 2012). For example, in a study of a colony of 900 Herring Gulls (*Larus argentatus*), 23.3% of all eggs and chicks were eaten by conspecifics with 4 individual adults responsible for 2-5% of this figure (Parsons, 1971). Such specialist cannibalistic behaviour is also found in Smallmouth Bass (*Micropterus dolomieu*) (Clady, 1974) Californian Newts (*Taricha torosa*) (Kaplan, 1980), Chimpanzees (*Pan spp.*) (Goodall, 1977), among other species.

Why Juveniles?

In many species, smaller individuals in a population are usually cannibalized by larger individuals, known as size asymmetric cannibalism (Ebenman and Persson, 1988). Larger animals are usually the older, more fit individuals, while the smaller animals tend to be weaker or juvenile individuals. Size asymmetric cannibalism is particularly common in all species of amphipods (MacNeil *et al.*, 1997) and teleost fish (Manica, 2002), with juveniles often being prey for adults. Sexton (1928) noted in his analysis of laboratory *Gammarus* that individuals don't prey on conspecifics unless they are at some disadvantage, such as being of smaller size or weakened from a recent moult.

Studies of cannibalistic tendencies in a wide range of species indicate that there is a 'cannibalism threshold', that an individual should be a certain percentage larger than its prey to cannibalize it (Polis, 1981). For example, conspecifics are only eaten in piscivorous fish if the predator-to-prey ratio exceeds the threshold of 80-100% (Popova, 1967) i.e. predatory should be 80-100% larger than their prey. The danger of cannibalism decreases with age (Polis, 1981). By this generality, newborns are particularly vulnerable to attack and cannibalism, with predation of newborns by conspecifics found in over 80 species (Hardy, 1977). This can be a major source of juvenile mortality, for example 8% of all young Belding's Ground squirrels (*Uroditellus beldingi*) born each year are cannibalised by conspecifics (Sherman, 1980).

Infanticide is common in many species (Hardy, 1977) for example lions (*Panthera leo*) (Pusey and Packer, 1994), Belding's Ground squirrels (*Uroditellus beldingi*) (Sherman, 1980), and chimpanzees (*Pan spp.*) (Goodall, 1977), males are often found eating conspecific infants and in many, but not all cases, the infant will be eaten. In polygynous species (those in which one male receives exclusive mating rights with multiple females), an invading male will kill the progeny of the previous patriarch and the offspring will often be eaten, for instance Bertram (1975) reports that 25% of all lion cubs killed are cannibalised in this way.

Why not Cannibalise?

While cannibalism can present many advantages, and for many species may just be considered an extension of normal predation behaviours (Hardy, 1977), it can also often be disadvantageous. Cannibals and their conspecific prey (or their preys guardians (Sherman, 1981)) may be evenly matched in fighting ability, and the likelihood of injury to the cannibal may be high (Dawkins, 1976), although this is usually combated by adhering to its cannibalism threshold. Cannibalism and intraspecific necrophagy can also increase the likelihood of disease or parasite transmission (Rudolph and Antonovics, 2007). For example, cannibalistic Tiger Salamanders (*Ambystoma tigrinum*) that ate diseased conspecifics were found less

likely to survive to metamorphosis (Pfenning *et al.*, 1998) than non-cannibalistic individuals, and that the frequency of cannibalistic tiger salamanders is negatively correlated with the bacterial density in their habitat, to avoid the predation of infected conspecifics (Pfenning, 1991). Overall, cannibalism can create a net decrease in inclusive fitness if one is likely to eat close relatives, a behaviour known as filial cannibalism. Therefore, cannibalism may be highly deleterious to subscribers.

Maternal Filial Cannibalism

While some species have developed behavioural methods to avoid eating close relatives (see Avoidance of Cannibalism, below), which may be highly deleterious, many species actively partake in this method of feeding known as filial cannibalism, the purposeful catching killing and devouring of progeny, along with filial necrophagy; the eating of dead progeny. In many circumstances, it can be a highly beneficial and common behaviour. Because the investment in young is inherently different between males and females (due to energy costs of gamete production, mating and raising the clutch), the benefits of filial cannibalism vary between the sexes.

Maternal filial cannibalism occurs in species where maternal parental care is the preferred method of care (Gubernick, 1991). This is particularly common in mammals, where 90% of species are raised exclusively by their mothers (Kokko and Jennions, 2008). Mothers invest a lot of time and energy into producing their offspring and losing them may seem like an obviously deleterious event, although through filial cannibalism this loss can be advantageous. Offspring can be a beneficial food source when other food sources are in short supply, or when the survival potential of the mother is low. Cannibalism provides very high direct benefits in this instance; a mother's current survival is more beneficial than survival of the offspring, if the reproductive potential for future clutches is high (Sargent, 1992). Wholly or partially eating a current clutch increases survival and future reproductive potential, at a cost to an individual's current potential. Rowher (1978) suggests that current offspring survival is traded off against feeding, and parents use their offspring as an alternative food source. This can present as whole clutch or partial clutch cannibalism.

Whole clutch cannibalism benefits the mother, whose survival potential increases instantly through eating her nutrient rich offspring. This can be viewed as an extreme form of brood termination, where the cost of caring for the clutch is higher than the expected benefits (Clutton-Brock, 1991). By no longer providing care, the parent can save its time and energy for searching for a new mate, or increasing survival (Alexander, 1974). In species with low survival rates without parental care i.e altricial young (born in a helpless state and requiring extended parental care to survive), it is beneficial to cannibalise the offspring, as their chance of survival

is already low. This behaviour can increase the mothers' potential to successfully raise another clutch in the future, when the offspring have a higher chance of survival. It will also benefit the potential future clutches to have a fitter mother than would be the case if the current clutch had been raised to adulthood (Clutton, 1991).

Partial clutch cannibalism involves the eating of some of the offspring in the clutch, and can benefit the mothers' current and future reproduction. Partial clutch cannibalism gives the mother immediate nourishment, enough to attend to her litter without starvation. Mothers guarding their clutch are usually near starving, and for many mammals, this presents a problem. Milk cannot be produced in starving animals ("Domestic Animal Behaviour And Welfare, 2008"). Filial cannibalism eliminates the need for the mother to leave the nest to forage for food. Leaving the nest leaves the young vulnerable to predation, and to the elements. There is also a possibility of the mother dying or deserting the clutch while away from the nest, which is common in rabbits (Dennenberg *et al.*, 1959). Thus, it is beneficial for the mother to stay in the nest and seek alternative food sources- i.e. her offspring.

Partial clutch cannibalism is common, particularly in animals that produce sizeable litters. Many animals produce more young per clutch than will survive to adulthood, to maximize the chance that some will survive and reproduce (Weir and Rowlands, 1973). Large litters inherently produce some offspring that will present low survival potential, often known as the 'runt of the litter', due to lack of growth space and resources *in utero* (Lodge and Lamming, 1968). These individuals can be viewed as an energy tradeoff, wherein the energy put into creating the individual can be returned to the mother at a later stage, when she is guarding her young and starving.

Some of these offspring are likely to be weak, deformed, sick or otherwise handicapped, especially in large litters. These sub-par offspring are usually the ones cannibalised by the mother (Elwood, 1992). Diseased or infected offspring are often eaten to prevent disease spreading through the rest of the clutch. Eating of diseased offspring occurs in many species, such as Californian newts (*Taricha torosa*) (Kaplan, 1980), Belding ground squirrels (*Urocitellus beldingi*) (Sherman, 1980), and rabbits (family *Leporidae*) (Dannenberg *et al.*, 1959).

These are also benefits for the young left in the clutch, by having better care and protection from their mother. This additional care and protection helps increase the fitness and survival of the remaining offspring, along with the mother. They also receive an indirect fitness benefit from the removal of their siblings, as they are potential future competition (Clutton-Brock, 1991), but may also sustain a disadvantage, by the reduction in their inclusive fitness from the offspring of their siblings.

Paternal Filial Cannibalism

Paternal cannibalism is more common in animals where the father provides the parental care. Whole clutch cannibalism is common in male teleost fish (Manica, 2002) for example in a study of damselfish, 28.3% of males ate the entirety of their clutch. Paternal care is high in this group, and the advantages of this method of feeding are similar to those of maternal cannibalism. The father may also parasitise the female, by using her nutrient-rich eggs as food (Rohwer, 1978). The cost of parental care is the same in small and large clutches, and so it benefits the parent to brood a large clutch. An unsuitably small clutch may be fully cannibalised, so the male may mate again, and produce a larger more beneficial clutch.

Partial clutch cannibalism occurs for many of the same reasons as in maternal cannibalism; mainly that it provides nutrition without having to abandon the clutch. In many fish species, males benefit from guarding their eggs straight after fertilizing them, to prevent other males sneaking in and fertilizing some (Gross, 1996). Fathers also guard the eggs from other predators. Leaving the clutch unguarded is dangerous, and so, eating part of the clutch to avoid this benefits the fathers' fitness, and the fitness of the surviving eggs. Klug and Lindstrom (2006) suggest that partial cannibalism may be necessary to reduce egg density and increase oxygen availability to remaining eggs, thus increasing the remaining offspring's fitness, as is the case in the Sand Goby (*Pomatoschistus minutus*). Klug and Lindstrom (2006) further suggest that partial clutch cannibalism may create no net losses in reproductive success.

Avoidance of Cannibalism

While the advantages of cannibalism have been outlined above, it is in no way advantageous to the individual being eaten. As such, many behavioural mechanisms have developed to avoid being eaten by conspecifics, above and beyond the usual predation avoidance tactics (Rudolf, 2007).

In many cannibalistic species, juveniles tend not to adhere to natal philopatry; the remaining in or returning to natal territory (Pearce, 2007), and quickly expand outwards from their native zone to create a separation between the vulnerable juveniles and cannibalistic adults. Members of the genus *Gammarus*, such as *G. tigrinis*, *G. mucronatus*, and *G. lawrencianus* exhibit changes in phototactic behaviour (their movement towards or away from light) at an age that correlates to a reduction in vulnerability to predation. This movement causes a partial separation of adults and juveniles that reduces the likelihood of predation (Hunte and Myers, 1984). Smaller individuals and juveniles of *Gammarus* shift habitats to minimize the risk of predation by conspecifics. With larger conspecifics *in absentia*, juveniles of *G. pulex* will use larger pores in substrates to hide in whereas when there is predation danger, they only select smaller pores, regardless of food availability (MacGrath *et al.*, 2007). *Poeciliopsis* fish, a highly cannibalistic species, show a genetic propensity to avoid their parents from birth, with avoidance increasing as size does. (Lima and Vrijenhoek, 1996).

While juvenile and filial cannibalism presents the greatest disadvantages to juveniles, many adults have evolved behaviours to avoid filial cannibalism, to avoid the fitness costs. A temporal behavioural change occurs in relation to brood stage in female *G. pulex*, whereby the instances of cannibalism are significantly reduced concurrent to the time their own eggs are hatching, to prevent the likelihood of eating their own young (Lewis *et al.*, 2010). It is unknown if other phenotypic recognition cues are utilized in this instance, or whether males subscribe to a similar temporal avoidance of cannibalism.

Filial cannibalism can be avoided in animals where both parents confer parental care on their offspring. This is the case in approximately 90% of bird species (Kokko and Jennions, 2008). One parent may guard the clutch, while another may forage for food for itself and its offspring, and roles may alternate. As such, filial cannibalism is not common in birds.

Conclusion

Cannibalism, in general, and more specifically the instances of juvenile and filial cannibalism present a fascinating insight into the survival strategies of many species in the animal kingdom. While it may seem deleterious for parents to eat their own young, it can present many advantages, and assist in survivorship of individuals and offspring, through additional nutritional intake when it is needed the most. The behaviour, aberrant to human society and considered unnatural in most societies (Dornstreich and Morren, 1974) is in fact in some instances a highly beneficial and well evolved strategy for many species as shown. Even so, it is perhaps not the best idea to eat your own children.

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