

## A Survey of Intraspecific Predation among Reptiles and Amphibians

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**ABSTRACT.**—Numerous investigations, citing occurrences of cannibalism and/or oophagy in over 100 species of reptiles and amphibians, were reviewed with particular emphasis on predator/prey characteristics, environmental determinants, and evolutionary significance. In most species of reptiles cannibalism appears to occur opportunistically as a by-product of normal predatory behavior. Among amphibians, cannibalism is also opportunistic. However, many authors speculate that cannibalism implements particular strategies. In some cases, it is directly associated with specific behavioral, and even morphological characteristics. There is evidence that the development of cannibalistic morphotypes may be genetically and environmentally controlled.

Cannibalism was long considered an aberrant behavior (see discussion in Fox, 1975 and Polis, 1981). A growing body of evidence now indicates that cannibalism is not only common, but also important in the ecology of many species. Fox (1975) found cannibalism to be normal behavior in 147 species and Polis (1981) cites reports in approximately 1300 species. Cannibalism can strongly influence the competitive interactions, dynamics, and life histories of populations, and thus may be considered an important factor in the ecology of many species. Both authors discuss the evolution and possible significance of cannibalism and should be read for additional information.

The purpose of this article is to provide a list of references to cannibalism among the classes Reptilia and Amphibia. This report was stimulated by repeated requests for information on cannibalism by interested researchers. More than 45 papers are cited in Table 1, describing cannibalism and oophagy in 49 species from 16 families and five orders of reptiles. Table 2 lists 53 references to cannibalism and/or oophagy among 53 species of amphibians representing 18 families and two orders. This is by no means a listing of all of the literature available on this subject and additional information can be gained

from the references included in the cited articles. We hope that these tables will provide a starting place for anyone interested in cannibalism among reptiles and amphibians.

### METHODS

Ninety-eight papers were reviewed in the preparation of the accompanying tables. The factual data and the author's speculations as to their meaning when given are compiled in Tables 1 and 2.

The tables are divided into six columns: Taxon—a taxonomic breakdown of the species studied; Predator Data—size, sex, and age, when given in the article cited; Prey Characteristics—size, sex, and age, when given; Intensity—when given about cannibalism rates, percent conspecifics in diet, volume or weight of conspecifics in the diet, and the frequency of individuals that are cannibals; Comments—the author's speculation as to the function of the cannibalistic event and miscellaneous information concerning the nature of the observation (e.g., in captivity or in the laboratory—otherwise all data are from the field), number of observations, etc.; and Reference—a listing for each taxon is presented in numerical form with the numbers corresponding to those in the Literature Cited. Some species are listed without specific infor-

TABLE 1. Incidence of cannibalism among reptiles. The following symbols apply: ♂—male; ♀—female; A—adult; J—juvenile. Lab—in laboratory or captivity.

Taxa	Predator data	Prey data	Intensity	Comments	References
<b>Testudinata</b>					
<i>Sternotherus minor</i>					29
<i>Terrapene ornata</i>	A	J			29
<i>Gopherus agassizii</i>		eggs			29
<i>Trionyx sinensis</i>	A	J			29
<b>Crocodylia</b>					
<i>Crocodylus nitolicus</i>					19
<i>Caiman crocodilus crocodilus</i>	A	J		possibly major cause of hatchling mortality related to population density	87
<b>Lacertilia</b>					
<i>Hemidactylus flaviviridis</i>				due to starvation	55
<i>Anolis lineatopus</i>	A	J			73
<i>Sceloporus occidentalis</i>	A	J	0.1% (diet) 1.4% (freq.) 0.2% (diet)		45, 77
<i>S. graciosus</i>				lab	77
<i>S. undulatus hyacinthinus</i>					36
<i>S. magister</i>					36
<i>S. chrysostictus</i>	A	J			36, 82
<i>S. orcutti</i>	A	J			58, 59
<i>S. torquatus torquatus</i>	79 mm	30 mm			86
<i>S. woodi</i>					86
<i>Uta stansburiana</i>					6, 51, 81
<i>Crotaphytus wislizenii</i>					30, 62
<i>C. collaris</i>					30, 89
<i>Agama agama</i>	A	J			14
<i>Moloch horridus</i>				lab	67
<i>Eumeces laticeps</i>					24
<i>Lacerta muralis</i>					47
<i>L. lepida</i>		eggs		lab	53
<i>Varanus gouldii</i>		J			46
<b>Ophidia</b>					
<i>Elaphe guttata guttata</i>	J	sibling		lab	43
<i>E. scalaris</i>		eggs			53
<i>Thamnophis sauritus</i>	A	J		lab	25
<i>T. elegans</i>	A	J			96
<i>Lampropeltis getulus getulus</i>				lab	23
<i>Coluber constrictor</i>	A	J	1.6% (diet)		44
<i>Mehelya capensis capensis</i>					31
<i>Ptyas mucosus</i>					95
<i>Leptodeira annulata</i>					65, 66
<i>Austrelaps superbus</i>			2.3% (diet) 22.6% (weight) 3.9% (freq.) 2.2% (diet) 27% (weight) 2.4% (freq.)		80
<i>Unechis gouldii</i>					80
<i>Micrurus fulvius fulvius</i>	A	smaller			22
<i>Atractaspis bibronii bibronii</i>					31
<i>Crotalus lepidus</i>	J, A	J		lab	97
<i>C. viridis hellerii</i>	A, J	A, J		lab	72

TABLE 1. Continued.

Taxa	Predator data	Prey data	Intensity	Comments	References
<i>C. v. viridis</i>		a snake of equal size		lab	11
<i>C. cerastes laterorepens</i>	590 mm	230 mm	0.6% (diet)		33
<i>Agkistrodon contortrix</i>	A	J		lab, opportunistic	37
<i>Bitis arietans</i>					10
<i>Dispholidus typus</i>					31

mation; this reflects the absence of detail given by the cited authors.

### DISCUSSION

Few attempts have been made to explain the significance of intraspecific predation among reptiles. Most reports were found in studies that analyzed diet rather than focusing on the significance of cannibalism. From these studies, it appears that intraspecific predation generally occurs as part of normal feeding behavior. Conspecifics formed a constant, albeit low, proportion of the diet for many species. This implies that these species of reptiles treat conspecifics as just another potential prey item. In these cases, cannibalism occurs opportunistically on those animals that larger conspecifics are able to subdue. Consistent with this speculation is the observation that young animals were the prey in almost all cases of cannibalism among the reptiles. Thus, cannibalism in reptiles may simply be a product of opportunistic prey capture by euryphagous predators. Low levels of cannibalisms are characteristic of generalist predators from many taxonomically diverse groups (Polis, 1981).

Other factors that may stimulate cannibalism include environmental stress, nutritional stress, high conspecific density, and/or part of a reproductive strategy (Fox, 1975; Kaplan and Sherman, 1980; Polis, 1981). However, with the exception of nutritional stress in the form of starvation (Mahendra, 1936), we found no other explanations or even speculations of the causes of cannibal-

ism among reptiles. This lack of speculation by researchers further strengthens the notion that cannibalism in reptiles is purely opportunistic predation.

In amphibians, as in reptiles, younger animals (larvae and juveniles) are the most frequent cannibalistic prey. However in contrast to reptiles, cannibalism among the Amphibia appears to be important in the biology of many species. In some genera (e.g., *Notoophthalmus*, *Rana*) conspecifics form 7–>25% of all diet items; 3–45% of all individuals were recorded to be cannibals (see references in Table 2). Cannibalism is sometimes density related (e.g., Gehlbach, 1971; Heusser, 1971; Pomeroy, 1981; Collins and Creek, 1983), and may even contribute to population regulation (Rose and Rose, 1965; Heyer, et al., 1975; Reese, 1975). Cannibalism may be especially important for larvae inhabiting ephemeral sites, where survival is strongly influenced by the rate of developmental growth (Bragg, 1965; Pomeroy, 1981; Crump, 1983). In these habitats, the first juveniles to metamorphose and emerge include a disproportionately high frequency of the cannibal morph (see below). Blair (1976) speculates that cannibalism in ephemeral ponds is a mechanism through which some anurans concentrate food resources in times of environmental stress.

Cannibalism may also function as an extreme form of interference competition for specific biotypes (Heusser, 1970). Predation on young conspecifics further serves as a means of removing

TABLE 2. Incidence of cannibalism among amphibians. The following symbols apply: ♂—male; ♀—female; A—adult; J—juvenile; L—larvae; C.M.—cannibalistic morph. Lab—in laboratory or captivity.

Taxa	Predator data	Prey data	Intensity	Comments	References
<b>Caudata</b>					
<i>Cryptobranchus alleganiensis</i>	A	eggs		oophagy in field	49
<i>Ambystoma</i> spp.	A	J, eggs		cannibalistic polyphenism; some oophagy; density dependent; some genetic factors; in lab and field	16, 17, 18
<i>Dicamptodon ensatus</i>	large	small			3
<i>D. copei</i>	L	eggs			49
<i>Salamandra salamandra</i>			0.1% (freq.)		56
<i>Notophthalmus viridescens</i>			7.1% (diet) (July–August; 2.9%, 21.25%)		63
<i>Taricha torosa</i>		eggs			49
<i>Desmognathus fuscus fuscus</i>		eggs			4
<i>D. ochrophaeus</i>		eggs/ newborn larvae			49
<i>Plethodon dunni</i>			1.9% (freq.)		1
<i>P. glutinosus</i>	A	J			71
<i>P. cinereus</i>		eggs, J	0.6% (freq.)	in lab and field	38, 42
<i>Necturus maculosus</i>		eggs			49
<b>Anura</b>					
<i>Bombina variegata</i>	A	J			40
<i>Scaphiopus bombifrons</i>	L (cannibal morph)	L		cannibalistic polyphenism; group cannibalism; influenced by feeding history; in lab and field	7, 8, 70
<i>S. holbrookii</i>	L (cannibal morph)	L		cannibalistic polyphenism	7, 8, 9, 70
<i>S. hammondi hammondi</i>	L (cannibal morph)	L		cannibalistic polyphenism	9
<i>S. multiplicatus</i>	L (cannibal morph)	L		cannibalistic polyphenism; group cannibalism; influenced by feeding history; in lab and field	70
<i>Rana pipiens</i>	J	J			50
<i>R. cyanophlictus</i>	L	L			60
<i>R. tigrina</i>	L	L			60
<i>R. ridibunda</i>	A	J, L	45% (freq.) on L, 16% (freq.) on J, 15% (volume)		28
<i>R. esculenta</i>	A	J	20% (freq.) 17% (weight)	in lab and field	28, 48

TABLE 2. Continued.

Taxa	Predator data	Prey data	Intensity	Comments	References
<i>R. temporaria</i>	J, A	eggs, J			39, 54
<i>R. arvalis</i>	A	J			54
<i>R. catesbeiana</i>			density dependent 5.6% (freq.) on frogs, 1.3% (freq.) on eggs, 28% (diet), 26.4% (volume)		15, 79, 88
<i>R. ornatissima</i>					64
<i>Pyxicephalus adspersus</i>	A, J, L	J, L		density dependent	35, 92
<i>Hyperolius</i> (3 spp.)					92
<i>Kassina poweri</i>					92
<i>Bufo calamita</i>	A	L		density dependent, size important	40
<i>B. regularis</i>					92
<i>B. boreas halophilus</i>	48 mm	17 mm			21
<i>Lechriodus fletcheri</i>	L	eggs		facultative—if plant food is absent	57
<i>Hyla zeteki</i>	L	eggs			27
<i>H. arborea</i>					40
<i>H. brunnea</i>	L	eggs			52
<i>H. pseudopuma</i>	L (23–28 mm)	eggs, J (smaller)		in lab and field	20
<i>Ceratophrys ornata</i>	A, L				64
<i>Chacophrys pierottii</i>	A, L	all sizes		mechanism for concentrating food resources, "voracious cannibal"	5, 13
<i>Lepidobatrachus asper</i>					75
<i>Eleutherodactylus cuneatus</i>					91
<i>Leptodactylus pentadactylus</i>				"facultative carnivory"	41
<i>Rhinophrynus dorsalis</i>	L	L			85
<i>Hymenochirus boettgeri</i>	L	L (smaller)			84
<i>Hoplophryne rogersi</i>		eggs			26
<i>Dendrobates pumilio</i>	A, L			larvae fed unfertilized eggs by adult female; in lab	9

future competitors for the predator and its offspring (Kaplan and Sherman, 1980; Polis, 1981). Of course, cannibalism may be opportunistic and occur as a simple by-product of normal predatory behavior in some species of amphibians (e.g., Heusser, 1971).

Cannibalistic oophagy is also quite common among amphibians, particularly in salamanders. It may function to reduce disease when unhealthy eggs are removed from the clutch (Tilley, 1972; Kaplan and Sherman, 1980). Kaplan and Sherman (1980) suggest that oophagy

may be an important energy source for parents during mating or egg guarding (also see Rohwer, 1978 and Polis, 1981 for discussion of parental cannibalism of offspring, especially in fishes). Interestingly, Weygoldt (1980) found that adult female *Dendrobates pumilio* care for their young by feeding them unfertilized eggs. Consumption of eggs and embryos has also been observed in many invertebrate species (Polis, 1981); such prey are designated trophic or nurse eggs and represent a strong case for parental manipulation.

There is a report of in utero cannibalism among siblings. The developing embryos of *Salamandra atra* and *Salamandra salamandra* use polystichous dentation to ingest the wall of the oviduct, maternal red blood cells and even their siblings (Amoroso, 1952; Wake, 1977). Such in utero cannibalism also occurs in some species of shark and Mesozoic holocephalan fish (see Polis, 1981 for references). In utero cannibalism may be the simplest method of viviparity as it requires no specialized maternal structure and few fetal modifications.

The existence of cannibalistic polyphenism among amphibians is reviewed by Crump (1983), Polis (1981), and Pomeroy (1981). Cannibalistic polyphenism refers to phenotypic differences in behavior, morphology, growth rates, or life history between cannibal and non-cannibal forms of the same population. Cannibalistic morphotypes of *Ambystoma* (Rose and Armentrout, 1976) and *Scaphiopus* (Bragg, 1964, 1965; Pomeroy, 1981) are often larger than normal and are characterized by hypertrophied jaw musculature and enlarged mouths armed with teeth or sharp beaks. Cannibals also exhibit behavioral differences in activity, swimming and feeding (Pomeroy, 1981). Some cannibalistic morphs benefit by having a faster rate of development to metamorphosis (Heyer et al., 1975; Gehlbach, 1971; Pomeroy, 1981). They are also able to feed on large heterospe-

cific prey (crustaceans) unavailable to regular morphs (Polis, 1981; Pomeroy, 1981). This feature expands the cannibal's resource base and thus may favor the evolution of such cannibals. However, there may also be disadvantages associated with the cannibalistic morph (Pomeroy, 1981). Pomeroy showed that these animals form a disproportionately high frequency of the last *Scaphiopus* tadpoles left in many (but not all) temporary ponds. These animals are small and stunted, indicating a poor feeding history. This implies that transformation into a cannibalistic morph is not a uniformly successful strategy.

There is evidence of significant environmental and genetic influences on the development of cannibalistic morphotypes in amphibians. Collins and Creek (1983) found an environmental influence on cannibal formation in *Ambystoma*: cannibalistic morphs appeared only when larvae were reared at high densities. In *Scaphiopus*, Pomeroy (1981) also shows that environmental factors (the presence of large potential prey) can stimulate the development of cannibalistic larvae. He produced cannibal morphs in the laboratory by feeding young tadpoles live fairy shrimp rather than a diet of organic particles.

Genetic factors are not excluded by evidence for environmental induction. However, there exist only limited data that suggest a genetic basis for the development of cannibalistic morphotypes. Pierce et al. (1981) found significant differences in gene frequencies between cannibalistic and noncannibalistic morphs of *Ambystoma*. Rose and Armentrout (1976) found some genetic incompatibility between the differing morphs; they suggest that genetic factors may be involved in the maintenance of cannibalistic polymorphism in *Ambystoma*. In all probability as more work is conducted, additional evidence for a genetic basis will be found. However, it now appears that cannibalistic polyphenism is proximally produced by environmental cues that act on a geno-

type that is sufficiently plastic to produce either normal or cannibalistic morphs.

### CONCLUSION

Cannibalism is more prevalent in the classes Reptilia and Amphibia than previously believed. While broad ecological and environmental determinants have been outlined, these determinants should be viewed with caution when interpreting specific cases. Age, size, sex, density of conspecifics, available food, degree of relatedness, and other factors all may influence the occurrence and magnitude of cannibalism to various degrees (Fox, 1975; Polis, 1981).

We found reports of cannibalism and/or oophagy for over 100 species of reptiles and amphibians. Since few reptiles and amphibians are morphologically incapable of cannibalism, we expect that the number of known cannibalistic species will increase as more research is completed. As Wilson (1975) noted, there appears to be correlation between the time spent studying a species and the number of observances of intraspecific predation.

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