OIKOS 55: 155–158. Copenhagen 1989

Prey defences and predator handling behaviour: the dangerous prey hypothesis

L. Scott Forbes

Forbes, L. S. 1989. Prey defences and predator handling behaviour: the dangerous prey hypothesis. – Oikos 55: 155–158.

Ictalurid catfish possess locking spines which make them dangerous to gape-limited predators such as herons and grebes, but not to ospreys *(Pandion haliaetus)* which dismember prey. Herons and grebes handled ictalurids longer than prey without locking spines, but ospreys did not. As well, herons and grebes took ictalurids less frequently than ospreys. These observations are consistent with the hypothesis that prey handling is a function of the risk of injury during ingestion. Minimization of this risk may not be a constraint, but rather a foraging decision for a predator.

L. S. Forbes, Behavioural Ecology Research Group, Dept of Biol. Sci., Simon Fraser Univ., Burnaby, B.C., Canada V5A 1S6.

Introduction

Some prey are risky to eat, as defensive structures of prey (e.g., spines, thorns, claws) may injure or kill a predator during ingestion (Jordan 1907: 51, Munro 1930, Orr 1937, Holdom 1945, Mylne 1957, Wick and Rodgers 1957, Houck 1961, Tomkins 1963, Cooper 1969, Morejohn 1969, Lingle 1976, Mock and Mock 1980, Wanjala and Tash 1983). But predators may counter these defenses with a variety of handling behaviours (e.g., dismemberment, crushing, stabbing) which serve to kill or incapacitate prey (Recher and Recher 1968, Riegner 1982). How effective a predator is in disarming prey will be a function of the time invested in handling and thus is potentially variable. Within foraging theory, though, handling time if not simply viewed as a constraint, is usually considered in relation to the efficiency of resource extraction (Cook and Cockrell 1978, Sih 1980, Stephens and Krebs 1986, Cochran 1987, Valone and Lima 1987).

Spiny fish are a common problem for piscivores, but for a fish's spines to be effective they must not be easily depressed (Alexander 1965). Spines that lock mechanically are a solution, but are rare (Marshall 1965). Catfish (Pisces: Siluriformes), including the North American family Ictaluridae, are an exception. They possess dorsal and pectoral spines that lock mechanically, making them hazardous to gape-limited predators. With spines held erect, a catfish's body flexions during ingestion may injure or kill a predator which tries to swallow it whole (e.g., Jordan 1907: 51, Scott and Crossman 1973: 602, Bell-Cross 1974, Ono et al. 1983: 97, Moser 1986). However locking spines are not an effective defence against predators such as ospreys *(Pandion haliaetus)* which do not swallow prey whole, but instead dismember them.

Here I propose the dangerous prey hypothesis: handling behaviour is a function of the risk of injury to the predator, thus more dangerous prey should be handled more carefully. As a consequence of longer handling times, predators should tend to take dangerous prey less often, in accordance with the predictions of the prey model (sensu Stephens and Krebs 1986). In this paper I examine the feeding behaviour of an array of piscivorous birds in relation to the dangerous prey hypothesis. I predicted that 1) gape-limited predators should handle ictalurids longer than other prey, whereas ospreys should not, and 2) gape-limited predators should take fewer ictalurids than should ospreys.

Since locking spines may increase the effective girth

Accepted 13 December 1988

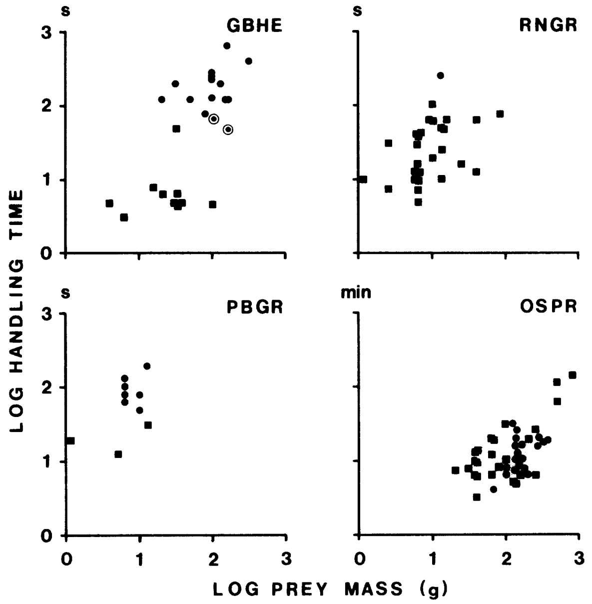

Fig. 1. Log handling time of great blue heron (GBHE), pied-billed grebe (PBGR), red-necked grebe (RNGR) and osprey (OSPR) vs log mass of prey {black bullhead (●) and other prey (■)}. (◉) indicates a bullhead swallowed rapidly when individual challenged by another heron; see text for further details. Handling times for GBHE, PBGR and RNGR are in s; handling times for OSPR are in min. Axes are logged because of wide range of handling times and prey masses; statistics were performed on untransformed data.

of a fish rendering it unavailable to some predators (Birkhead 1972, Gross 1978), I determined girth-length relationships for potential prey species.

Study area and methods

I studied the feeding behaviour of five piscivorous birds, great blue heron *(Ardea herodias)*, western *(Aechmophorus occidentalis)*, red-necked *(Podiceps grisegena)*, and pied-billed grebe *(Podilymbus podiceps)*, and osprey on the Creston Valley Wildlife Management Area (CVWMA) in southeastern British Columbia. Observations were conducted at Duck Lake and Corn Creek Marsh on the CVWMA for approximately 1050 h between May and August 1981–87. Both are shallow (<2 m), eutrophic systems where three species of fish, yellow perch *(Perca flavescens)*, pumpkinseed *(Lepomis gibbosus)*, and black bullhead *(Ictalurus melas)*, the latter an ictalurid catfish, occur in abundance. In gill-net surveys at Duck Lake, perch, pumpkinseed, and bullhead comprised 35%, 23%, and 26% of the biomass in the catch respectively; at Corn Creek Marsh, perch, pumpkinseed, and bullhead comprised 11%, 3%, and 86% of the biomass in the catch respectively (Forbes 1987).

Prey were recognized by their characteristic shapes, colours, and movements. Prey lengths were estimated as a proportion of various body parts of the bird (e.g., culmen, tarsus). Prey masses were then estimated using mass-length regressions of fish sampled from local populations.

For gape-limited predators I defined handling time as the period between prey capture and ingestion. For ospreys I defined handling time as the time taken to consume the fish (i.e., after a fish was taken to a nest or perch grasped in its talons), as this would be the only component of handling that would be affected by the presence of spines. For ospreys, the regressions of handling time and prey mass were compared for bullhead and other prey. Due to small sample sizes, binomial tests were used to compare handling times of bullhead and other prey for grebes and herons.

Tab. 1. Frequency of occurrence of black bullhead, yellow perch, pumpkinseed, and other[1] fish in the diets of great blue heron, red-necked, pied-billed and western grebe, and osprey at Corn Creek Marsh and Duck Lake in the Creston Valley of southeastern British Columbia.

Predator	Frequency of occurrence in diet (%)				
	black bullhead	yellow perch	pumpkinseed	other	n
Corn Creek Marsh					
osprey	82	8	10	0	51
great blue heron	51	34	15	0	53
pied-billed grebe	72	20	8	0	25
red-necked grebe	14	86	0	0	7
Duck Lake					
osprey	50	26	6	18	50
great blue heron	25	6	59	9	32
western grebe	0	91	9	0	678
red-necked grebe	0	72	27	1	166

[1] Includes largemouth bass and unidentified cyprinids.

Tab. 2. Girth-length regressions (girth [mm] = A × length [mm] + B [mm]) for black bullhead with spines relaxed and spines erect, yellow perch, pumpkinseed, and largemouth bass.

Prey species	A	B
black bullhead		
spines relaxed	0.54	12.2
spines erect	0.72	7.3
yellow perch	0.65	−13.9
pumpkinseed	1.06	−4.1
largemouth bass	0.60	2.7

Total lengths of netted fish were measured to the nearest mm with a steel rule; girths were determined by wrapping a thread around the fish at its greatest circumference and recording its length to the nearest mm. The girth of bullheads with the spines erect was estimated by measuring the length of the dorsal and pectoral spines with Vernier callipers, and then estimating the length of the perimeter of the triangle formed by the tips of the spines. [For more detailed descriptions of the procedures see Forbes (1982, 1985, 1987) and Flook and Forbes (1983)].

Results

Prey handling

Handling times of herons and grebes were longer for bullhead than for other prey of comparable mass (Fig. 1). In 35 of 35 cases, handling time for a bullhead was longer than that for a perch or pumpkinseed the same size or larger (binomial test, $P \ll 0.001$).

For ospreys, the regressions of handling time vs mass of fish were not significantly different for bullhead and for fish without locking spines (other prey) (Fig. 1, bullhead: handling time (min) = 0.038 × prey mass (g) + 7.74 min; other prey: handling time = 0.029 × prey mass + 8.83 min; comparison of slopes, $t_{(36)} = 0.348$, $P = 0.682$).

Prey choice

Bullhead were taken more often by ospreys than by gape-limited predators (Tab. 1, Duck Lake: osprey vs great blue heron, $\chi^2 = 5.071$, $P = 0.023$; osprey vs red-necked grebe, $\chi^2 = 93.864$, $P \ll 0.01$; osprey vs western grebe, $\chi^2 = 351.055$, $P \ll 0.001$; Corn Creek Marsh: osprey vs great blue heron, $\chi^2 = 11.484$, $P = 0.001$; osprey vs red-necked grebe, $\chi^2 = 14.873$, $P < 0.001$; osprey vs pied-billed grebe, $\chi^2 = 1.082$, $P = 0.118$).

Girth-length relationships

The girth-length relationships for the four main prey species are presented in Tab. 2. The largest fish I observed a great blue heron eat was a 24 cm largemouth bass which would correspond to a girth of 14 cm (Tab. 2). For a bullhead with its spines erect, this would correspond to a length of 19 cm. At Corn Creek Marsh, 12 of 14 (86%) of the bullhead taken were smaller than 19 cm, as were 8 of 8 taken at Duck Lake. The largest fish I observed a pied-billed grebe eat was a 14 cm yellow perch, which would correspond to a girth of 8 cm. For a bullhead with its spines erect, this would correspond to a length of 10 cm. Fifteen of 16 (94%) of the bullheads that pied-billed grebes ate were smaller than 10 cm. The largest fish I observed a red-necked grebe eat was a 19 cm yellow perch which would correspond to a girth of 11 cm. For a bullhead with its spines erect this would correspond to a length of 14 cm, which was larger than the only bullhead I observed a red-necked grebe eat.

Discussion

The observed behaviour was consistent with the dangerous prey hypothesis. Gape-limited predators, which are more vulnerable to ictalurid spines than ospreys, handled ictalurids longer and took them less frequently than did ospreys. Similarly, Mock and Mock (1980) noted that goliath herons *(Ardea goliath)* handled hard-spined clariid catfish and grunters more carefully than fish with softer spines.

Although handling costs were higher, herons and pied-billed grebes still took ictalurids. It is easy to see why. At Corn Creek Marsh and Duck Lake the feeding rates of herons ranged from 16 to 84 g h^{-1} (Forbes 1987); thus even at the longest handling time, 10 min for a 170 g bullhead (= 1020 g h^{-1}), handling bullheads was still far more profitable than searching for other prey and I suspect the same was true for pied-billed grebes but do not have comparable foraging data for this species. Elsewhere, though, long handling times made ictalurids unprofitable for grey herons *(Ardea cinerea)* and they were avoided (Moser 1986). That pied-billed grebes took bullheads more often than red-necked or western grebes is consistent with differences in morphology. With their stout bills and heavy jaw musculature, pied-bills are better able to manipulate, tear, and crush large prey than are slender billed forms such as western and red-necked grebes (Zusi and Storer 1969).

It could be argued that the locking spines of catfish increase their effective girth (Birkhead 1972, Gross 1978), thus making them too large for gape-limited predators to swallow; behaviours to overcome spines are therefore necessary. This explanation though is unsatisfactory since nearly all ictalurids the herons and grebes ate were small enough, even with spines erect, to have been swallowed without handling.

It has been suggested that predators may shorten handling time, and thereby reduce the efficiency of resource acquisition, when subject to risk of predation (e.g., Sih 1980, Valone and Lima 1987). Similar trade-offs may exist for handling dangerous prey. Twice at

Corn Creek Marsh great blue herons swallowed large bullheads rapidly (see Fig. 1) when they were challenged by other herons in apparent territorial encounters. In such cases the herons may have traded off the potential benefits of handling (i.e., a reduction in the probability of injury) against the risk of losing a large and valuable prey item, suggesting that handling time with respect to the minimization of injury is not simply a constraint but rather a foraging decision for a predator.

Similarly, Mock and Mock (1980) noted that rapid swallowing by goliath herons and white-breasted cormorants *(Phalacrocorax carbo)* was an effective defence against kleptoparasitism. Goliath herons handled fish without hard spines (but not clariid catfish and grunters with hard spines) in a leisurely manner at first, but swallowed them within 5 s when approached by African fish eagles *(Haliaeetus vocifer),* a frequent kleptoparasite. Handling time was curtailed when there was a risk of losing the prey item.

Acknowledgements – I thank L. M. Dill, P. Nonacs, and R. C. Ydenberg for providing useful comments on the manuscript.

References

Alexander, R. McN. 1965. Structure and function in the catfish. – J. Zool. 148: 88–152.

Bell-Cross, G. 1974. Observations on fish-eating birds in central Africa. – Honeyguide 77: 23–31.

Birkhead, W. S. 1972. Toxicity of stings of ariid and ictalurid catfishes. – Copeia 1972: 790–807.

Cochran, P. A. 1987. Optimal digestion in a batch-reactor gut: the analogy to partial prey consumption. – Oikos 50: 268–270.

Cook, R. M. and Cockrell, B. J. 1978. Predator ingestion rate and its bearing of the theory of optimal diets. – J. Anim. Ecol. 47: 529–549.

Cooper, A. E. 1969. Little grebe choking to death on fish. – Brit. Birds 62: 31.

Flook, D. R. and Forbes, L. S. 1983. Ospreys and water management of Creston, British Columbia. – In: Bird, D. M. (chief ed.), Biology and management of bald eagles and ospreys. Harpell Press, Ste. Anne de Bellevue Quebec, pp. 281–286.

Forbes, L. S. 1982. Prey manipulation in the great blue heron. – Murrelet 63: 89–91.

– 1985. The feeding ecology of western grebes breeding at Duck Lake, British Columbia. – M. Sc. Thesis, Univ. of Manitoba, Winnipeg, Manitoba.

– 1987. Feeding behaviour of great blue herons at Creston, British Columbia. – Can. J. Zool. 65: 3062–3067.

Gross, H. P. 1978. Natural selection by predators on the defensive apparatus of the three-spined stickleback, *Gasterosteus aculeatus* L. – Can. J. Zool. 56: 398–413.

Holdom, M. W. 1945. Strange death of a Holboell Grebe. – Murrelet 26: 28.

Houck, W. J. 1961. Notes on the Pacific striped porpoise. – J. Mammal. 42: 107.

Jordan, D. S. 1907. Fishes. – Henry Holt, New York.

Krebs, J. R. 1974. Colonial nesting and social feeding as strategies for exploiting food resources in the Great Blue Heron. – Behaviour 51: 99–134.

Lingle, G. R. 1976. Unusual mortality in gulls. – Prairie Nat. 8: 20.

Marshall, N. B. 1965. The life of fishes. – Weidenfeld and Nicolson, London.

Mock, D. C. and Mock, K. C. 1980. Feeding behavior and ecology of the Goliath Heron. – Auk 97: 433–448.

Morejohn, G. V. 1969. Brandt cormorant killed by fish. – Auk 86: 555–556.

Moser, M. E. 1986. Prey profitability for adult grey herons *Ardea cinerea* and the constraints on prey size when feeding young nestlings. – Ibis 128: 392–405.

Munro, J. A. 1930. Water fowl and sculpins. – Condor 32: 261.

Mylne, C. K. 1957. The unusual death of a late glaucous gull in Scotland. – Brit. Birds 50: 305.

Ono, R. D., Williams, J. D. and Wagner, A. 1983. Vanishing fishes of North America. – Stone Wall Press, Washington, DC.

Orr, R. T. 1937. A porpoise chokes on a shark. – J. Mamm. 18: 370.

Recher, H. F. and Recher, J. A. 1968. Comments on the escape of prey from avian predators. – Ecology 49: 560–563.

Riegner, M. F. 1982. Prey handling in yellow-crowned night herons. – Auk 99: 380–381.

Scott, W. B. and Crossman, E. J. 1973. Freshwater fishes of Canada. – Bull. Fish. Res. Bd Can. no. 184.

Sih, A. 1980. Optimal foraging: partial consumption of prey. – Am. Nat. 116: 281–290.

Stephens, D. W. and Krebs, J. R. 1986. Foraging theory. – Princeton Univ. Press, Monographs in Behaviour and Ecology, Princeton, NJ.

Tomkins, I. R. 1963. A royal tern choked by a fish. – Wilson Bull. 75: 198.

Valone, T. J. and Lima, S. L. 1987. Carrying food items to cover for consumption: the behavior of ten bird species feeding under the risk of predation. – Oecologia (Berl.) 71: 286–294.

Wanjala, B. and Tash, J. C. 1983. Largemouth bass *Micropterus salmoides* choking on prey. – Southwestern Nat. 28: 380.

Wick, W. Q. and Rodgers, H. E. 1957. An unusual merganser fatality. – Condor 59: 342–343.

Zusi, R. L. and Storer, R. W. 1969. Osteology and myology of the head and neck of the pied-billed grebes *(Podilymbus)*. – Misc. Publ. Mus. Zool. Univ. Michigan No. 139.