PREY SIZE DETERMINES HANDLING AND CAPTURE TACTICS IN THE WESTERN GREBE

DAVID DORADO, Department of Biology, Division of Natural Sciences, Fullerton College, 321 East Chapman Avenue, Fullerton, California 92832-2095; ddorado@fullcoll.edu

ABSTRACT: To investigate the feeding behavior of the Western Grebe (*Aechmophorous occidentalis*), I observed the actions of one kept in a laboratory pool and fed fish of various sizes and in varying numbers during four trials per day. The grebe consumed fish under 4 cm in length underwater but brought all fish longer that 5 cm to the surface so they could be oriented for swallowing headfirst. The Western Grebe is likely gape-limited in its choice of fish and can only ingest prey that can be swallowed easily.

Grebes and other small avian divers are opportunistic predators, feeding on a variety of prey. Small fish, however, are the preferred food of the Western Grebe (*Aechmophorus occidentalis*) (Forbes and Sealy 1990). In both the field (O'Donnell 1982, Kloskowski 2004) and laboratory (Sanford and Harris 1967, Carter and Sealy 1987), piscivorous diving birds have been observed consuming fish above water after bringing them to the surface. Some reports, however, have implied that diving birds swallow fish while still submerged (Ratti 1977, Forbes 1985, Croll et al. 1992). Further investigations suggest that smaller prey fish are swallowed underwater (Ulenaers and Dhondt 1994), whereas larger prey fish are brought to the surface for consumption (Sanford and Harris 1967, Kloskowski 2004). Yet some birds discard fish too large to ingest (Sanford and Harris 1967, Forbes and Sealy 1990, Kloskowski 2004). To resolve the question of whether Western Grebes swallow fish underwater, and if so, under what conditions, I observed the capture and handling behavior of a captive grebe that was provided fish of different lengths and girths.

I used a netgun to capture Western Grebes wintering in the harbor at Santa Cruz, California (Dorado 2022). One was placed in an outdoor enclosure (5 × 5 m), with a saltwater tank (3 × 3 × 1.5 m deep). The enclosure was encircled with a chain-link fence 3 m-high in which dark plastic strips were woven to minimize visual disturbances. To ensure the grebe was hungry at the beginning of the experiment, I withheld food for 24 hours, a period long enough for previous foods to have been absorbed (Cooper et al. 1984, Winkler and Cooper 1986). The experiment consisted of four trials per day, spaced at roughly 4-hour intervals beginning at sunrise until sunset. Trials lasted for 21 days. During the first 6 days, I provided the grebe with juvenile Surf Smelt (*Hypomesus pretiosus*) 5–7 cm long and weighing 8–10 g. These were thawed completely before being tossed into the tank. On day 1 of feeding, the grebe was provided one smelt per toss and had to swallow it before another fish was presented. Fish were provided until the grebe stopped consuming them. On day 2, two smelt were delivered per toss, both had to be eaten before more were presented, and fish were provided until consumption ceased. On days 3 to 6, three fish were delivered per toss; otherwise, the protocol was the same as in previous trials. At the end of each trial, any smelt remaining in the pool after the bird stopped feeding were collected and the bird was left alone until the next feeding trial.

Beginning on day 7, through day 21, I substituted live goldfish (*Carassius auratus*) for the smelt. These fish were delivered in one of two combinations. One combination consisted of five large goldfish, 5–7 cm in length and about 10 g each. The other consisted of 10 small goldfish, about 3–4 cm in length and weighing about 3 g each (measurements after Onsoy et al. 2010). Combinations were offered sequentially but there was no set protocol for one preceding the other.

On day one of feeding, when a smelt landed in the water, the grebe dived, grabbed the sinking fish crosswise in its beak, and resurfaced. In all cases, the smelt was flipped in the air, rearranged in the beak, and swallowed headfirst. When the grebe no longer pursued a smelt, I assumed the bird was satiated. No fish were swallowed underwater.

On day 2 and beyond, when I provided two or three smelt per toss, the grebe dived and resurfaced with one fish, held crosswise in its beak. It rearranged the smelt in its beak above water and swallowed it headfirst. The bird immediately dived again in pursuit of the next fish, now typically at the bottom of the pool. Again, the grebe picked up the fish crosswise, surfaced, oriented the fish in the beak, and swallowed it headfirst, repeating the same behavior for all remaining fish from each toss, acquiring only one fish per dive. All smelt were swallowed above water.

When presented with five large goldfish, the grebe dived, chased one, captured it, and surfaced with one fish, crosswise in its beak. Above water, it was manipulated in the beak and swallowed headfirst. The grebe repeated this behavior until all five fish were caught and consumed. When the 10 smaller goldfish were placed into the tank, the grebe dived, chased, caught, and consumed either three or four of them while submerged. It resurfaced to breathe for a few seconds and then dived again, catching and swallowing three or four more while underwater. On its third and final dive, it captured and consumed the remaining goldfish before resurfacing. It swallowed these smaller fish underwater while it was either already in pursuit of the next fish or resurfacing.

This study revealed that the Western Grebe can capture and swallow multiple small fish whole while under water during a single dive. Larger fish, however, were brought to the surface for individual handling before swallowing. Although Western Grebes are opportunistic predators and feed on a variety of prey (Lawrence 1950, Forbes and Sealy 1990), their preference for smaller streamlined fish (Forbes and Sealy 1990) is likely due to the ease of swallowing prey of smaller girth. With the large goldfish or smelt, requiring handling and realignment, the grebe maintained better control of the larger fish when above water, and by keeping the prey above the surface, the grebe was also able to breathe (Mock and Mock 1980). Thus the size of the prey influenced not only the foraging behavior of the bird but also its physiological demands.

Piscivorous birds have been reported capturing prey but failing to consume them (O'Donnell 1982, Doornboss 1984, Kloskowski 2011) because the prey was either too deep-bodied to swallow (i.e., species of Centrarchidae and Percidae) or it had fins with sharp, protruding spines (Recher and Recher 1968, Forbes 1985, Glahn et al. 1995). At least two species of grebe, the Pied-billed (*Podilymbus podiceps*) and Horned (*Podiceps auratus*), appear to mitigate swallowing such prey by shaking them into consumable pieces (Storer 1969, Zusi and Storer 1969, Scholz and Hayes 2017). Such feeding behavior has not been reported for the Western Grebe, likely because its long and slender bill lacks the crushing force of the more robust bills of smaller grebe species (Lederer 1975, Lalas 1983). The prey of the Western Grebe and presumably other piscivorous birds with similar beaks, appear to be limited, instead, by the diameter of their mouth and hence the girth of the prey (Swennan and Duiven 1977, Ulenaers and Dhondt 1994). For example, Forbes (1985) reported Western Grebes foraging on black bullhead catfish (*Ictalurus melas*) and yellow perch (*Perca flavescens*), both of which have protruding fins and erectile spines, but only on extremely small individuals, all of which were brought up to the surface to be manipulated before being consumed headfirst (Forbes 1985). Birds attempting to swallow too large a spiny fish have died in the process (Holdom 1945, Behrstock 1981).

My observations of Western Grebes foraging in the wild further suggest their ability to consume piscivorous prey is limited by the prey's girth. On one occasion I watched a grebe pierce a bluegill (*Lepomis macrochirus*) but discard it because it appeared too large to swallow. I also saw another Western Grebe capture black bass (*Micropterus salmoides*) and threadfin shad (*Dorosoma petenense*) that were also discarded at the surface. The three discarded shad were at least 11 cm long, the discarded bass was 10 cm long, and the discarded bluegill was 15 cm long (pers. obs.). Despite these fish being within the length of prey the Western Grebe consumes (Forbes and Sealy 1990), they were likely abandoned because of their excessive girth. The long, narrow beak of the Western Grebe likely limits its ability to crush or shred wide-bodied prey (Lalas 1983), thereby restricting consumption to smaller, slender, and manageable items.

In studies of diving birds, detailed attention should be directed toward daily foraging behaviors and tactics. Energy acquisition and physiological ecology can more accurately be determined from prey of consumable size.

I am indebted to Kelly Koerner, trustworthy research assistant, without whom this project would not have been possible. The project was supported through funding by William T. Doyle on behalf of the Department of Marine Sciences, University of California, Santa Cruz, and by a generous grant from the Dr. Earl H. Meyers and Ethel M. Meyers Oceanographic and Marine Biology Trust. All applicable ethical guidelines for the use of birds in research have been followed (Fair et al. 2010). The subject of this experiment was captured in accordance with scientific collector's permit 7077 by the California Department of Fish and Game. I thank R. Gill, C. Handel, F. E. Hayes, and P. Unitt for their constructive criticism and guidance in the development of the manuscript.

LITERATURE CITED

Behrstock, R. A. 1981. Prey-induced mortality of a Pied-billed Grebe. W. Birds 12:183–184.

Carter, H. R., and Sealy, S. G. 1987. Fish-holding behavior of Marbled Murrelets. Wilson Bull. 99:289–291.

Cooper, S. D., Winkler, D. W., and Lenz, P.H. 1984. The effect of grebe predation on a brine shrimp population. J. Animal Ecol. 53:51–64; doi.org/10.2307/4341.

Croll, D. A., Gatson A. J., Burger, A. E., and Konnoff, D. 1992. Foraging behavior and physiological adaptations for diving in Thick-billed Murres. Ecology 73:344–356; doi.org/10.2307/1938746.

Doornboss, C. 1984. Piscivorous birds on the saline lake Grevelingen, the Netherlands: Abundance, prey selection and annual food consumption. Neth. J. Sea Res. 18:457–479; doi.org/10.1016/0077-7579(84)90015-2.

Dorado, D. 2022. Netgun capture technique for the Western Grebe *Aechmophorous occidentalis*. Waterbirds 45:367–372; doi.org/10.1675/063.045.0316.

Fair, J., Paul, E., and Jones, J. (eds.) 2010. Guidelines to the use of wild birds in research. Ornithological Council, Washington, D.C.

Forbes, L. S. 1985. The feeding ecology of Western Grebes breeding at Duck Lake. M.S. thesis, Univ. Manitoba, Winnipeg.

Forbes, L. S., and Sealy, S. G. 1990. Foraging roles of male and female Western Grebes during brood rearing. Condor 92:421–426; doi.org/10.2307/1368239.

Glahn, J. F., Dixson, P. J., Littauer, G. A., and McCoy, R. B. 1995. Food habits of Double-crested Cormorants wintering in the delta region of Mississippi. Col. Waterbirds 18:158–167; doi.org/10.2307/1521536.

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

Kloskowski, J. 2004. Food provisioning in Red-necked Grebes (*Podiceps grisegena*) at common carp (*Cyprinus carpio*) ponds. Hydrobiologia 525:131–138; doi.org/10.1023/B:HYDR.0000038860.37405.d0.

Kloskowski, J. 2011. Consequences of the size structure of fish populations for their effects on a generalist avian predator. Oecologia 166:517–530; doi.org/10.1007/s00442-010-1862-3.

Lalas, C. 1983. Comparative feeding ecology of New Zealand marine shags (Phalacrocoracidae). Ph.D. thesis, Univ. of Otago, Dunedin, New Zealand.
Lawrence, G. E. 1950. The diving and feeding activity of the Western Grebe on the breeding grounds. Condor 52:3–16; doi.org/10.2307/1364743.
Lederer, R. T. 1975. Bill size, food size, and jaw forces of insectivorous birds. Auk 92:385–387; doi.org/10.2307/4084573.
Mock, D. W., and Mock, K. C. 1980. Feeding behavior and ecology of the Goliath Heron. Auk 97:433–448; doi.org/10.1093/auk/97.3.433.
O'Donnell, C. F. J. 1982. Food and feeding behaviour of the Southern Crested Grebe on the Ashburton Lakes. Notornis 29:151–156.
Onsoy, B., Tarkan, A. S., Filiz, H., and Bilge, G. 2010. Determination of the best length measurement of fish. North-West. J. Zool. 7(1):178–180.
Ratti, J. T. 1977. Reproductive separation and isolating mechanisms between sympatric dark-and light-phase Western Grebes. Ph.D. thesis, Utah State Univ., Logan; doi.org/10.1093/auk/96.3.573.
Recher, H. F., and Recher, J. A. 1968. Comments on the escape of prey from avian predators. Ecology 49:560–562; doi.org/10.2307/1934125.
Sanford, R. C., and Harris, S. W. 1967. Feeding behavior and food-consumption rates of a captive California Murre. Condor 69:298–302; doi.org/10.2307/1366319.
Scholz, S., and Hayes, F. E. 2017. Pied-billed Grebe predation on a Common Yellowthroat. W. Birds 48:56–57; doi.org/10.21199/WB48.1.4.
Storer, R. W. 1969. The behavior of the Horned Grebe in spring. Condor 71:180–205; doi.org/10.2307/1366078.
Swennen, C., and Duiven, P. 1977. Size of food objects of three fish-eating seabird species: *Uria aalge*, *Alca torda*, and *Fratercula arctica* (Aves, Alcidae). Neth. J. Sea Res. 11:92–98; doi.org/10.1016/0077-7579(77)90022-9.
Ulenaers, P., and Dhondt, A. A. 1994. Great Crested Grebe *Podiceps cristatus* chick mortality in relation to parental fishing. Bird Study 41:211–220; doi.org/10.1080/00063659409477221.
Winkler, D. W., and Cooper, S. D. 1986. Ecology of migrant Black-necked Grebes *Podiceps nigricollis* at Mono Lake, California. Ibis 128:483–491; doi.org/10.1111/j.1474-919X.1986.tb02700.x.
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. Mich. 139.

Accepted 6 July 2023
Associate editor: Robert E. Gill Jr.