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FORAGING ROLES OF MALE AND FEMALE WESTERN GREBES DURING BROOD REARING[1]

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Abstract. The foraging roles during brood rearing of males and females of the sexually dimorphic Western Grebe (*Aechmophorus occidentalis*) were examined during a 2-year study in southeastern British Columbia. The larger males fed larger fish to the young than females. Females foraged more when young were small and could eat only small fish, whereas males increased their foraging effort when the young were larger. In 1982 when the primary prey, year-class-one yellow perch (*Perca flavescens*), were scarce, both males and females fed smaller fish, primarily young-of-the year perch, to the brood. As well, parents fed pumpkinseed (*Lepomis gibbosus*) to the chicks in 1982, whereas none were eaten in 1983. Parents foraged longer in 1982 than in 1983, and caught more but smaller fish. Such behavioral flexibility by parents may be important in buffering offspring from the inimical effects of environmental variation in resource yield.

Key words: *Western Grebe;* Aechmophorus occidentalis; *foraging roles; parental behavior.*

INTRODUCTION

Differences in size imply differences in foraging performance. All else being equal, larger predators should have larger prey-size-optima (Wilson 1975). Fjeldså (1981) has suggested that dimorphism may be advantageous in monogamous species of grebes since it allows parents to exploit a broader range of prey when provisioning their offspring. Where food supplies are variable, such flexibility in diet choice may be valuable in buffering offspring from the effects of environmental uncertainty. Western Grebes (*Aechmophorus occidentalis*) are fish-specialists that exhibit biparental care, the males having larger bodies and bills than females (Palmer 1962, Herman 1973). Foraging is a major component of reproductive effort, and success in this activity will strongly influence offspring survival. Thus, we should expect strong selection for parental foraging efficiency.

In this paper we examine the foraging roles of male and female Western Grebes during brood rearing. Our questions were twofold. First, do males and females exploit different species and/or sizes of prey when feeding young, and does this covary with body size? Second, how do males and females allocate foraging effort during brood rearing, and does this reflect differences in prey taken? As answers to these questions may be affected by variability in the abundance of prey, we also measured fish abundance.

STUDY AREA

Western Grebes were observed on Duck Lake (49°15'N; 116.40°W) in the Creston Valley of southeastern British Columbia. Duck Lake is eutrophic and is uniformly shallow (less than 2 m deep) over most of its 1,200-ha area. Its southern, western, and northern sides are dyked and water levels are controlled. Fish are abundant and are preyed upon by large numbers of fish-eating birds including Western Grebes. Further information about Duck Lake and its bird and fish fauna can be found in Butler et al. (1986) and Forbes (1988). In 1982 and 1983, 90 and 75 pairs of Western Grebes, respectively, nested amid *Typha latifolia* in the southeastern corner of Duck Lake. Eggs were laid in early June and hatched in late June and early July.

METHODS

Western Grebes were observed for 195 hr from 28 June to 24 August 1982 and from 30 June to 17 August 1983. Grebes were observed from several sites on shore through spotting telescopes at distances usually less than 400 m but occasionally up to 1 km. At the beginning of the study,

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TABLE 1. Time budgets of male and female Western Grebes during back-brooding (BB) and free-swimming (FS) periods in 1982 and 1983. Percentage of time is shown.

	1982				1983			
	BB		FS		BB		FS	
Behavior	Male	Female	Male	Female	Male	Female	Male	Female
Diving	29	27	28	33	26	40	32	40
Swimming	23	28	27	38	1	3	8	10
Other[1]	48	45	45	29	73	57	60	50
Observation time (min)	405	812	704	591	3,226	3,226	835	858

[1] Other behavior included brooding, preening, bathing, and sleeping.

observations made from a blind were compared with those made where the observer was unconcealed. The grebes appeared oblivious to the observer in the open, thus most observations subsequently were made without a blind. The males were easily distinguished from the females by their larger bodies and bills (Palmer 1962). Only pairs with broods were observed. Observation effort was distributed evenly among three blocks of time: 04:00 to 10:00, 10:00 to 16:00, and 16:00 to 22:00. Individual watches of grebes ranged from 20–120 min: recorded were sex of adult, size and age class of brood, the size and species of prey (which were always fish) and whether the bird during each minute was diving, swimming, sleeping, sitting, preening, fighting, courting, or prey handling.

Fish were identified according to their diagnostic shapes, colors, and movements; yellow perch (*Perca flavescens*) and pumpkinseed (*Lepomis gibbosus*) were easily distinguished by differences in body form; the former is shallow-bodied, whereas the latter is deep-bodied. At greater distances (>250–500 m depending upon light conditions) small fish could not be identified confidently. When grebes were closer and small fish were identified with certainty, >95% were yellow perch, the remainder being pumpkinseed. Therefore we considered any unidentified fish (about 10% of the total number and <2% of the total biomass) to be yellow perch. Prey lengths were estimated as a proportion of the length of the exposed culmen of the grebe (1/8 culmen increments), using 75 and 65 mm for the lengths of the male and female bills, respectively (Palmer 1962, Godfrey 1986). We assessed the accuracy of this method of estimating fish length in a double-blind test using a Western Grebe skull and model fish; each fish was presented in profile against the grebe skull for 2 sec under conditions imitating the field situation. In 36 of 50 cases (72%) the estimated length of the model fish was within 1 cm of the actual length. In all cases the estimated length was within 2 cm of the actual length. Prey masses were estimated from mass-length regressions of prey species netted in Duck Lake.

The size distribution of yellow perch and pumpkinseed in Duck Lake was estimated from seine-net (20 × 2.5 m with a 6-mm mesh) surveys. Total lengths of the fish were measured to the nearest millimeter. Fish were weighed with hand-held spring balances, those <100 g to the nearest 1 g, those >100 g to the nearest 5 g. Most

TABLE 2. Statistical comparisons of time budget data (time males and females spent diving and swimming during back-brooding [BB] and free-swimming [FS] periods in 1982 and 1983). *G*-statistic (*G*) and probability value (*P*) are shown.

	Diving		Swimming	
Comparison	*G*	*P*	*G*	*P*
Male vs. female				
BB 1982	0.6	>0.5	3.5	>0.05
FS 1982	3.8	>0.05	18.1	<0.01
BB 1983	143.4	<0.001	35.0	<0.01
FS 1983	11.8	<0.01	2.1	>0.05
Male, BB vs. FS				
1982	0.2	>0.5	2.2	>0.1
1983	11.6	<0.01	105.5	<0.001
Female, BB vs. FS				
1982	5.9	<0.05	15.9	<0.01
1983	0.0	>0.5	64.6	<0.01
Male, 1982 vs. 1983				
BB	1.8	>0.1	292.5	<0.001
FS	2.9	>0.1	100.8	<0.001
Female, 1982 vs. 1983				
BB	48.7	<0.01	422.9	<0.001
FS	7.4	<0.01	163.0	<0.001

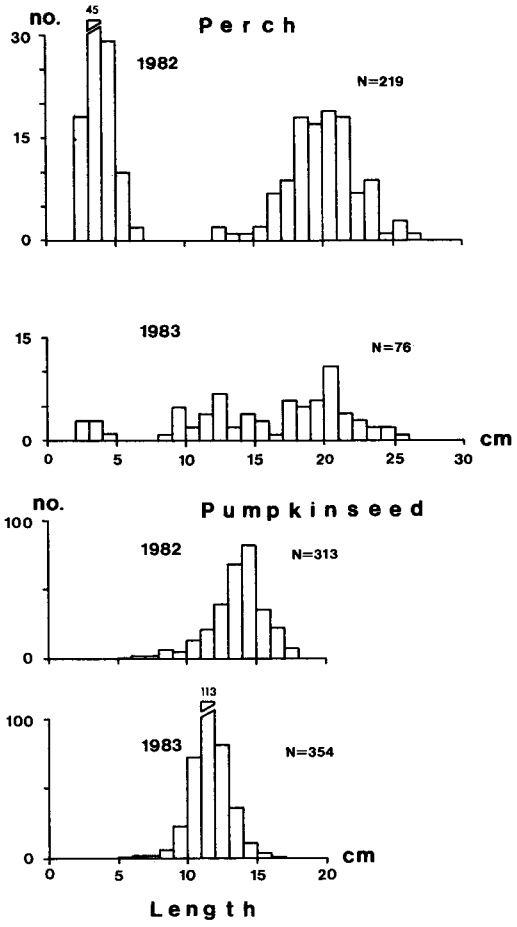

FIGURE 1. Frequency distributions of total length (length) of yellow perch and pumpkinseed in the seine catch at Duck Lake in 1982 and 1983.

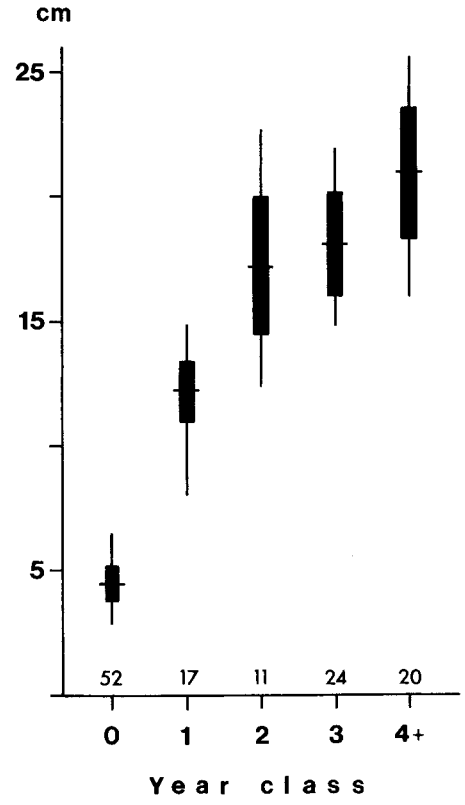

FIGURE 2. Age-length relationship for yellow perch at Duck Lake in August 1982. Mean total length (horizontal line), range (vertical line), and ±1 SD (vertical bar) are shown for year-class-0 (=young-of-the-year) to year-class-4+ perch.

fish were released after capture, but some were collected and aged. Ages of yellow perch were determined by counting scale annuli under a microscope, a method validated for this species by Jobes (1952) and Joeris (1956).

RESULTS

ABUNDANCE OF PREY

Significant interyear differences occurred in the abundance of perch and pumpkinseed, the only fish fed to chicks during brood rearing; the total biomass of fish did not differ significantly between years, but the sizes of fish did. The mean biomass of perch and pumpkinseed per seine haul, an index of abundance in biomass, did not differ significantly between 1982 and 1983 (perch: $t = 0.35$, $P > 0.5$; pumpkinseed: $t = 0.67$, $P > 0.5$). However the length-frequency distributions of perch and pumpkinseed (Fig. 1) differed between years (perch: $G = 52.4$, $P < 0.001$; pumpkinseed: $G = 91.3$, $P \ll 0.001$). In 1982, perch 8–15 cm in length (=year-class-one; the age-length relationship for yellow perch is presented in Fig. 2) were much less abundant than in 1983 (Fig. 1), indicating a year-class failure in 1981. Year-class failures are common in yellow perch, recruitment being depressed by low summer water temperatures (Hokansen and Kleiner 1974, Clady 1976, Craig and Kipling 1983). Fewer pumpkinseeds in 1983 were greater than 16 cm but more were 8–12 cm (Fig. 1). Since the maximum size of pumpkinseed that parents can ingest is approximately 13–15 cm (parent and offspring grebes swallow prey whole: males and females released pumpkinseed of that size after attempt-

TABLE 3. Fate of fish brought to the surface by male and female Western Grebes during brood rearing at Duck Lake in 1982 and 1983. *G*-tests used for all comparisons.

Number of fish	Perch		Pumpkinseed	
	1982	1983	1982	1983
Male				
Brought to surface	92	268	6	0
Fed to young	79	213	2	0
Eaten by male	6	46	4	0
Eaten by female	7	9	0	0
Female				
Brought to surface	87	376	12	0
Fed to young	80	332	11	0
Eaten by male	3	35	0	0
Eaten by female	4	9	1	0

Proportion of fish fed to the young, 1982 vs. 1983: $G = 0.75$, $P > 0.1$.
Proportion of fish eaten by males and females, 1982 vs. 1983: $G = 9.5$, $P < 0.01$.

TABLE 4. Sizes (total length) of yellow perch fed to back-brooded (BB) and free-swimming (FS) young by male and female Western Grebes at Duck Lake in 1982 and 1983. *G*-tests used for all comparisons.

Size class (cm)	Male		Female	
	BB	FS	BB	FS
1982				
0–4.9	17	42	27	48
5–9.9	3	14	0	5
10+	0	3	0	0
1983				
0–4.9	126	0	263	3
5–9.9	55	28	35	31
10+	1	3	0	0

BB vs. FS, 1982—Male: $G = 1.6$, $P > 0.05$; —Female: insufficient data.
BB vs. FS, 1983—Male: $G = 63.4$, $P < 0.01$; —Female: $G = 95.4$, $P < 0.01$.
Male vs. Female—1982: $G = 14.3$, $P < 0.01$; —1983: $G = 27.8$, $P < 0.01$.
1982 vs. 1983—Male: $G = 6.2$, $P < 0.05$; —Female: $G = 10.1$, $P < 0.01$.

ing to swallow them), and since the size of fish that young can swallow is smaller, depending upon the size of the chick, fewer pumpkinseed were available for parents to feed to chicks in 1982. Similarly, intermediate-sized perch are more important for chicks than large perch since they can be eaten when the chicks are smaller.

Thus the overall biomass of perch and pumpkinseed was not significantly different between years, but the sizes were. Since fewer intermediate-sized perch and pumpkinseed were present in 1982 than in 1983, 1982 was a year of relative food scarcity for parents feeding offspring.

BEHAVIOR OF ADULTS

Parents performed two distinct roles during brood rearing: foraging and brooding. Diving and swimming were the primary activities of a foraging parent, whereas brooding parents sat, slept, or preened while tending young. Early in brood rearing, one parent had to brood offspring on its back, leaving only one parent to forage. Later when the chicks could thermoregulate and swim on their own (i.e., were no longer back-brooded by parents), both parents were able to forage simultaneously. The transition between the back-brooding and free-swimming stages was gradual. Chicks were back-brooded more or less continualiy for the first 2 weeks but with decreasing frequency thereafter. Here we arbitrarily defined two phases of the brood rearing: we referred to weeks 1–3 of brood rearing as back-brooding, and weeks 4–10 as free-swimming.

Females foraged more than males during back-brooding when prey were abundant (1983) but not when prey were scarce (1982; Tables 1, 2). Both males and females foraged more in 1982 than in 1983 (primarily an increase in time spent swimming), but males increased their foraging effort more than females in 1982, and the amount of time males and females spent foraging was roughly equivalent (Tables 1, 2).

The roles of males and females reversed during free-swimming. Males foraged more than females in both years. However, both males and females foraged longer in 1982 when year-class-one perch were relatively scarce (Tables 1, 2).

SIZE AND SPECIES OF FISH FED TO BROOD

Yellow perch and pumpkinseed were the only fish fed to Western Grebe broods (Table 3). There was no significant difference in the proportion of all fish brought to the surface by parents that were fed to the young between 1982 (87.1%) and 1983 (84.6%) (Table 3). However, males ate a greater proportion, and females ate a smaller proportion of fish brought to the surface by parents in 1983 (12.6%) than in 1982 (6.7%) (Table 3).

Both males and females fed smaller fish to the brood during back-brooding than during free-swimming (Table 4) reflecting the larger size of fish that older young can eat. Some of the difference in the size of fish fed to back-brooded and free-swimming young may have been attributable to the growth of young-of-the-year (YOY) yellow perch. For example, the mean total

TABLE 5. Number of 20-min periods with and without fish delivered to the brood by male and female Western Grebes at Duck Lake during back-brooding (BB) and free-swimming (FS) periods in 1982 and 1983. *G*-tests used for all comparisons.

Period	Sex	Number of 20-min periods	
		With	Without
1982 BB	male	22	10
	female	25	13
FS	male	36	10
	female	26	15
1983 BB	male	102	60
	female	77	85
FS	male	25	20
	female	24	17

BB 1982 vs. 1983—Male: $G = 0.4$, $P > 0.1$; —Female: $G = 4.2$, $P < 0.05$.
FS 1982 vs. 1983—Male: $G = 5.4$, $P < 0.05$; —Female: $G = 0.2$, $P > 0.05$.
Male vs. Female, BB—1982: $G = 0.1$, $P > 0.5$; —1983: $G = 7.8$, $P < 0.01$.
Male vs. Female, FS—1982: $G = 2.3$, $P > 0.05$; —1983: $G = 0.1$, $P > 0.5$.

TABLE 6. Number of fish fed to brood by male and female Western Grebes at Duck Lake in 20-min periods with prey deliveries during back-brooding (BB) and free-swimming (FS) periods in 1982 and 1983.

Period	Sex	Fish/20 min			
		1	2	3	>3
1982 BB	male	7	0	0	3
	female	6	2	0	5
FS	male	3	1	1	5
	female	4	3	1	7
1983 BB	male	20	18	7	15
	female	22	19	11	33
FS	male	14	3	2	1
	female	7	9	1	0

Male, BB 1982 vs. 1983: $G = 0.1$, $P > 0.5$.
Female, BB 1982 vs. 1983: $G = 0.0$, $P > 0.5$.
Male, FS 1982 vs. 1983: Fisher exact test, $P = 0.009$.
Female, FS 1982 vs. 1983: Fisher exact test, $P = 0.002$.

length of YOY perch increased from 36.8 mm (*SD* = 6.5 mm, $n = 83$) on 20 July 1982 to 48.1 mm (SD = 6.7 mm, $n = 55$) on 24 August. However, we consider this to be of only minor importance since on the latter date (which was also the last day on which grebes were observed that year) most YOY perch were still less than 5 cm (38 of 55, 69%), and at earlier dates, when most observations of free-swimming young were made, an even greater proportion of YOY perch would have been less than 5 cm in length.

Males fed larger fish to the brood than females (Table 4). The failure of year-class-one yellow perch in 1982 affected the size of fish fed to the brood; both males and females took more 5–9.9 cm perch in 1983 than in 1982. In 1982, males and females fed a greater proportion of YOY perch to the brood than in 1983 (Table 4); also, parents fed pumpkinseed to the brood in 1982 but not in 1983.

FREQUENCY OF PREY CAPTURES

Even though males and females foraged more, females (but not males) delivered fish to the brood less frequently during back-brooding in 1982 than in 1983 (Table 5). However, males (but not females) delivered fish to the brood less frequently during free-swimming in 1982 than in 1983 (Table 5).

Males and females delivered fish with similar frequency during back-brooding in 1982 (Table 5). However, females delivered prey to the brood more frequently than males during back-brooding in 1983 (Table 5). Males and females delivered fish to the brood with similar frequency during free-swimming in 1982 or 1983 (Table 5). Parents brought more fish to the brood during free-swimming (but not back-brooding) in 1982 than in 1983 (Table 6).

DISCUSSION

Differences in predator size usually correspond to differences in prey-size optima (Wilson 1975), and Fjeldså (1981) suggested that in grebes, dimorphic parents may be able to collect a broader range of prey for the young more efficiently than monomorphic parents. Our data support Fjeldså's thesis. In both years, males fed larger fish to the young than females and this difference was exaggerated in 1982 when year-class-one yellow perch were scarce. In 1982, both males and females fed predominantly YOY yellow perch to young. Also, parents fed pumpkinseed to the brood in 1982 but not in 1983. Thus when year-class-one perch were scarce, parents exploited a broader range of prey. An expansion of diet breadth when the abundance of the highest ranked prey declines is a standard prediction of foraging theory (the prey model; Stephens and Krebs 1986).

In monogamous species, size dimorphism may be used to advantage when performing various tasks simultaneously if members of the pair coordinate their activities so that each individual specializes in behaviors for which its size makes

it better suited (Martindale and Lamm 1984). Differences in the foraging roles of male and female Western Grebes during brood rearing are consistent with differences in body size. Females foraged more when young were small and could eat only small fish, and males increased their effort when the young were larger. As a function of their smaller body size, females probably harvest smaller, more numerous fish, more cheaply than males, predisposing them for feeding small young. Conversely, males may better expend their foraging effort harvesting larger fish. Reynolds (1972) and Mosher and Matray (1974) similarly suggested that smaller body size in male raptors may be a result of selection for greater foraging efficiency.

Alternatively, larger body size may better suit male grebes for back-brooding young, perhaps by being able to brood more young, or fend off predators, or both. The latter has been suggested as an explanation for reversed sexual dimorphism in raptors (Storer 1966, Snyder and Wiley 1976). As a consequence of spending more time brooding young, males may forage less.

Parents compensated for the failure of year-class-one yellow perch by working harder, and by capturing more (but smaller) fish. Both males and females exhibited behavioral flexibility in the face of variable food supplies. In doing so, parents may buffer offspring from the effects of resource variability.

That males increased their foraging effort and ate a smaller proportion of fish that the parents brought to the surface in 1982, whereas females did not, suggests that females normally work harder than males during brood rearing (i.e., would pay higher marginal costs for additional work).

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LITERATURE CITED

BUTLER, R. W., B. G. STUSHNOFF, AND E. MCMACKIN. 1986. The birds of the Creston Valley and southeastern British Columbia. Can. Wildl. Serv. Occas. Pap. No. 58.

CLADY, M. D. 1976. Influence of temperature and wind on the survival of early stages of yellow perch, *Perca flavescens*. J. Fish. Res. Board Can. 33:1887–1893.

CRAIG, J. F., AND C. KIPLING. 1983. Reproduction effort versus the environment; case histories of Windermere perch, *Perca fluviatilis* L., and pike, *Esox lucius* L. J. Fish. Biol. 22:713–727.

FJELDSÅ, J. 1981. Comparative ecology of Peruvian grebes—a study of the mechanisms of evolution of ecological isolation. Vidensk. Medd. Dan. Naturhist. Foren. 136:57–95.

FORBES, L. S. 1988. Feeding behaviour of Great Blue Herons at Creston, British Columbia. Can. J. Zool. 65:3062–3067.

GODFREY, W. E. 1986. The birds of Canada. Revised edition. National Museum of Natural Sciences, Ottawa.

HERMAN, S. G. 1973. Cyclic fluctuations in feeding rates and body weight in captive Western Grebes, *Aechmophorus occidentalis*. Ph.D.diss., Univ. of California, Davis.

HOKANSEN, K.E.F., AND C. F. KLEINER. 1974. Effects of constant and rising temperatures on survival and developmental rates of embryonic and larval yellow perch *Perca flavescens* (Mitchill), p. 437–448. *In* J.H.S. Blaxter [ed.], The early life history of fish. Springer-Verlag, New York.

JOBES, F. W. 1952. Age, growth and production of yellow perch in Lake Erie. U.S. Fish Wildl. Serv. Fish. Bull. 70. 52:205–266.

JOERIS, L. S. 1956. Structure and growth of scales of yellow perch of Green Bay. Trans. Am. Fish. Soc. 86:169–194.

MARTINDALE, S., AND D. LAMM. 1984. Sexual dimorphism and parental role switching in Gila Woodpeckers. Wilson Bull. 96:116–121.

MOSHER, J. A., AND P. F. MATRAY. 1974. Size dimorphism: a factor in energy savings for broad-winged hawks. Auk 91:325–341.

PALMER, R. S. 1962. Handbook of North American birds. Vol. 1. Yale Univ. Press, New Haven, CT.

REYNOLDS, R. T. 1972. Sexual dimorphism in accipiter hawks: a new hypothesis. Condor 74:191–197.

SNYDER, N.F.R., AND J. R. WILEY. 1976. Sexual size dimorphism in hawks and owls of North America. Ornithol. Monogr. No. 20. American Ornithologists' Union, Washington, DC.

STEPHENS, D. W., AND J. R. KREBS. 1986. Foraging theory. Princeton Univ. Press, Princeton, NJ.

STORER, R. W. 1966. Sexual dimorphism and food habits in three North American accipiters. Auk 83:423–436.

WILSON, D. S. 1975. The adequacy of body size as a niche difference. Am. Nat. 109:769–784.