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FOOD FLIGHTS OF RED-NECKED GREBES DURING THE BREEDING SEASON

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Abstract.—Red-necked Grebes (*Podiceps grisegena*) nested behind a dyke at Creston, British Columbia, and flew up to 2.5 km to an adjacent lake to forage for their young. Other Red-necked Grebes nested on the same lake and swam to foraging areas accompanied by their young. There were significant differences in size of prey chosen for chicks by "fliers" and "swimmers." As predicted by central place foraging theory, birds that flew to and from foraging areas, at a higher energetic cost, chose larger prey than those that foraged with their chicks. Small fish (<50 mm in length) were avoided by "fliers," although "swimmers" fed such fish to their young. "Fliers" also took a greater proportion of large fish (>75 mm in length) from the lake than did the "swimmers." Yellow perch was the preferred prey species; however, grebes broadened their diet to include more pumpkinseed and bass following a year-class failure of perch. The effect of flying to forage on an individual's lifetime reproductive output is unknown.

VUELOS DE ALIMENTACIÓN DE *PODICEPS ARISEGNA* DURANTE LA ÉPOCA DE REPRODUCCIÓN

Resumen.—Individuos de zaramago (*Podiceps arisegna*) anidaron detras de un dique en Creston, Columbia Británica, y volaron hasta 2.5 km a un lago aledaño para alimentarse y luego poder alimentar a sus crias. Otros zaramagos anidaron en el mismo lago y nadaron a áreas de alimentación acompañados de sus crias. Hubo diferencias significativas en el tamaño de presa escogidas para los juveniles por parte de los "voladores" y "nadadores." Según lo predicho por la "teoría central del lugar de forrajeo" las aves que vuelan a y desde áreas de forrajeo, a un costo energético mayor, escogieron presas más grandes que aquellos que nadaron para alimentarse con sus crias. Peces pequeños (<50 mm de largo) fueron evitados por los "voladores" a pesar de que los "nadadores" alimentaron a sus crias con dichos peces. Los "voladores" también tomaron una mayor proporción de peces grandes (>75 mm de largo) del lago que los "nadadores." La perca (*Perca flavescens*) fue la presa preferida. Sin embargo, los zaramagos ampliaron su dieta para incluir otras especies siguiendo un año malo reproductivo para la perca. Se desconoce el efecto que pueda tener en la productividad reproductiva de por vida de los zaramagos el volar a otras áreas para alimentarse.

In the spring and summer of 1982, 1983, and 1984, I observed Red-necked Grebes (*Podiceps grisegena*) flying with fish in their bills. The grebes caught the fish in Duck Lake, a shallow, eutrophic lake in southeastern British Columbia, and carried them over a dyke to an adjacent marsh. Upon landing, the grebes presented the prey to their young, who remained behind the dyke until they were capable of flight. Typically, Red-necked Grebes do not fly to foraging areas. Usually, they swim, with young accompanying the foraging adult, either brooded on the back of the other parent, or, when 2–3 wk of age, swimming alongside. This more typical behavior was exhibited by another group of Red-necked Grebes that both nested and foraged on Duck Lake. Their presence allowed me to compare the two foraging methods and test predictions based on central place foraging theory.

According to central place foraging theory, prey selection changes as a function of distance from a central place. The theory assumes that individual fitness increases if an animal maximizes its net rate of energy return (Orians and Pearson 1979). I expected, therefore, to see differences in prey choice between the two groups of Red-necked Grebes feeding in Duck Lake. Lake-nesting grebes rarely foraged more than 100 m away from their chicks. Grebes that nested behind the dyke, however, flew up to 2.5 km from their chicks to forage in the lake. In addition, I assumed that the energetic cost of flight is great for grebes, as their wing-loading is high (Storer 1958), and they must run along the water to become airborne. Red-necked Grebes can carry a single food item per trip in their bills, regardless of the size of that item. Therefore, birds that flew to Duck Lake foraging areas should choose larger, more profitable prey than those which did not fly.

STUDY AREA

This study was conducted at the Creston Valley Wildlife Management Area (49°14'N, 116°38'W), near the town of Creston, in southeastern British Columbia (Fig. 1). The study site was Duck Lake (1300 ha in size) and an adjacent marsh, separated from the lake by a dyke. Red-necked Grebes nested in both the lake and the marsh, in two distinct habitat types. Duck Lake has no emergent vegetation except for bands of very dense cattail (*Typha latifolia*) and sedges (*Carex* spp.) scattered along the shoreline. The dominant submergent in Duck Lake is water milfoil (*Myriophyllum spicatum*) with white water crowfoot (*Ranunculus aquatilis*), common bladderwort (*Utricularia vulgaris*), and sago pondweed (*Potamogeton pectinatus*) occurring as well. Nests on Duck Lake were built on the open water on mats of water milfoil which accumulated through the spring and summer.

The marsh, located behind the dyke, has loose stands of cattail, bulrush (*Scirpus acutus*) and grasses. Submergent vegetation includes sago pondweed, common bladderwort, Rocky Mountain elodea (*Elodea canadensis*) and white water crowfoot. Red-necked Grebes nested here in the loose stands of cattail. There is an area of open water, approximately 100 m by 600 m in size, between the cattails and the dyke. This open water is critical for grebes nesting in the marsh, for they must run along it in order to take off to fly to their foraging areas in Duck Lake.

METHODS

I observed Red-necked Grebe broods with a spotting scope from late May through August in 1982, 1983, and 1984. When birds were within 100 m, it was possible to identify individual adults by differences in the grey and white patterns on their cheeks. I identified chicks by the pattern of striping on their heads. This, plus fidelity to their territories (maintained throughout the pre-fledging period behind the dyke) allowed me to follow individual broods from one observation period to the next.

Observation periods were 3 h long and I collected 384 h of data on

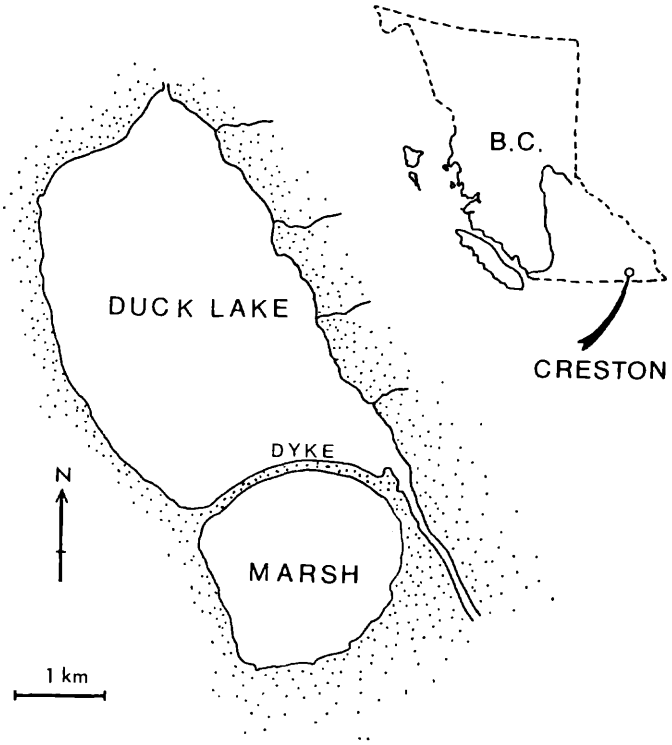

FIGURE 1. The study area.

broods behind the dyke in 1983 (24 broods), and 348 h in 1984 (27 broods). Some preliminary data were also collected in June of 1982 behind the dyke (5 broods). Feeding data from outside the dyke are limited to those collected from five broods (69 h) in 1983. I classified broods behind the dyke as 'early,' if the first egg hatched prior to 20 Jun., and 'late,' if it hatched on or after this date. This was the approximate mid-point of the hatching period in this area. No broods on the lake hatched prior to this date, so all were considered 'late.'

Red-necked Grebes present prey whole, bill-to-bill to the young. I recorded prey items fed to the young behind the dyke from the time the chicks hatched until they were 49 d old (wk 7), and in the lake, until chicks were 28 d old. It was possible to make direct comparisons of prey choice between marsh- and lake-nesting birds only in 1983, as no young hatched on the lake in 1984. When I did compare them, I included only those whose chicks were the same age at the same time of year to avoid the confounding effects of chick age and fish growth through the summer season.

I identified prey items as invertebrate (principally Odonate larvae) or

fish, and recorded where they were caught. To obtain a measure of size of prey taken, I compared them to the length of the adult's culmen. A value of 50 mm was used to represent 1 culmen length and was derived from the range given for males and females in Palmer (1962), which is 48.5–56.0 mm for males and 45–50 mm for females. Fish were placed into 4 size classes: Small: 1 culmen or less (≤50 mm), Medium: 1.1–1.5 culmens (51–75 mm), Large: 1.6–2 culmens (76–100 mm), and Very Large: greater than 2 culmens (>100 mm). As no attempt was made to determine total caloric intake of the young, this classification was considered adequate. When fish were flown in to young, I did not estimate their size until the adult had landed and was swimming to the young with the prey.

It was possible to identify by species only those fish that were >50 mm in length. I therefore calculated the relative abundance of each species in the diet based only on fish >50 mm. All data presented are based on the numbers of prey of each type given, not on their weights. Chi-squared analyses were used to test for differences in prey choice between 'early' and 'late' broods in the marsh, as well as differences between birds which flew and swam to foraging areas in Duck Lake. I refer to the marsh-nesting grebes as "fliers" throughout, as all birds nesting in this area did fly to the lake. I have called the lake-nesting grebes "swimmers."

RESULTS

Red-necked Grebes that nested in the marsh ("fliers") obtained part of their chicks' diet locally, and part from Duck Lake. Grebes that nested on the lake ("swimmers") obtained all their chicks' prey from the lake. The "fliers" foraged in the same areas of the lake as did the "swimmers"; however, there were significant differences between them in the size of prey they selected for similarly-aged young. The "fliers" took no small fish (≤50 mm) from the lake, whereas the "swimmers" did (Fig. 2). "Fliers" fed small fish to their young, but these were obtained locally, behind the dyke, not flown in. In addition, whereas both groups took more medium than large fish from Duck Lake, the "fliers" took many more large fish than did the "swimmers" (40.5% versus 17.9%) (Table 1). This difference in prey choice between medium and large fish is significant ($\chi^2 = 9.28$, df = 1, $P < 0.005$), and was consistent for chicks in all age categories sampled (Fig. 2). Both groups took a similar proportion of very large fish; however, the sample sizes for this category are too small for this to be meaningful.

Parents of both 'early' and 'late' broods behind the dyke began to fly fish back from Duck Lake when young were in their second week. The proportion of the diet that was flown in increased as the chicks grew (Fig. 3). In 1983 and 1984, 630 items were flown in to chicks of all ages, and 99.7% of these were fish in the medium to very large size categories; only two fish were less than 50 mm in length. In 1982, 100% of the fish flown back were over 50 mm in length ($n = 45$). Sampling of the fish population in the lake was carried out in 1982 and 1983, and revealed

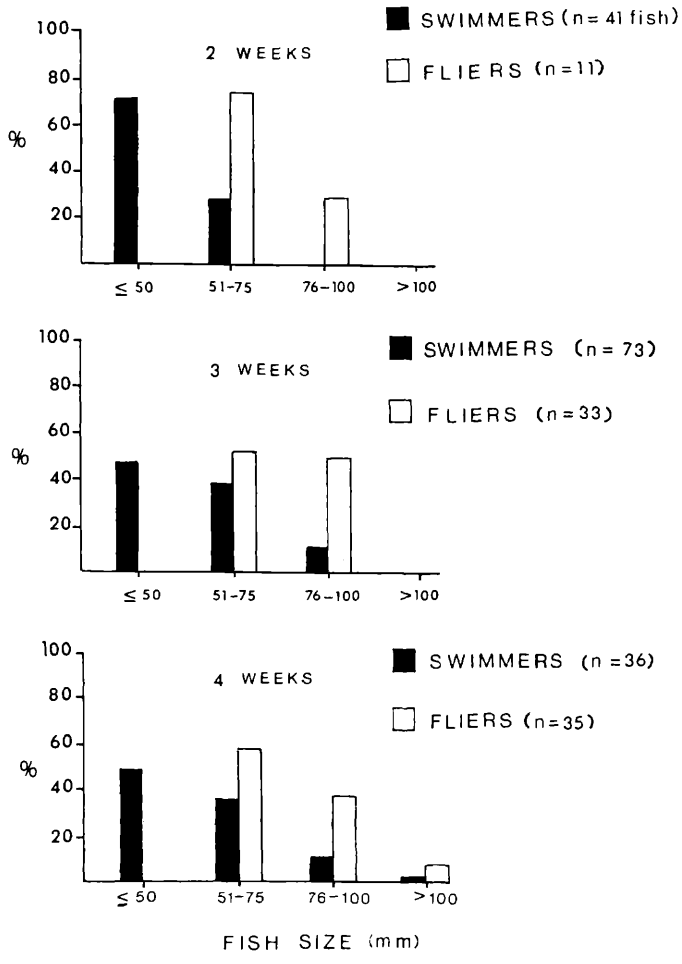

FIGURE 2. Size distribution of fish taken from Duck Lake (%) by "swimmers" versus "fliers" for broods aged 2–4 wk. Data were collected 3 Jul.–18 Aug. 1983.

that fish less than 50 mm in length were available during the brood-rearing periods of both these years (Forbes 1985). No fish sampling was carried out in 1984.

In contrast to this, only 3.6% of the 1540 fish caught locally behind the dyke were medium to very large; 96.4% were small. These small, locally caught fish were maintained in the diet of chicks of all ages, in both 'early' and 'late' broods (Figs. 4 and 5); adults responded to increasing food demands of growing chicks by increasing the proportion of the diet that was composed of fish in the medium to very large size categories, flown in from Duck Lake.

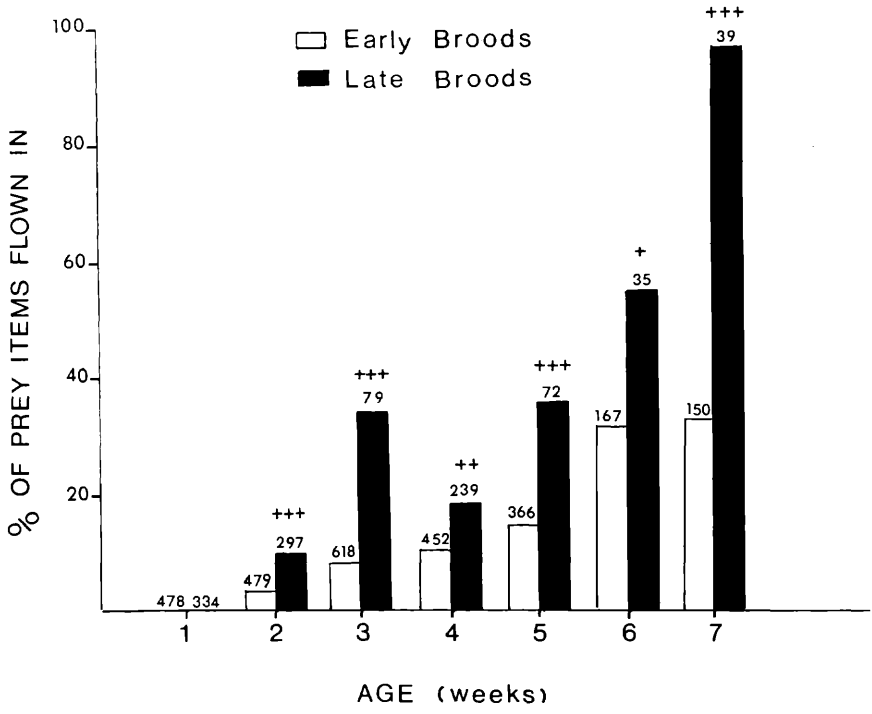

FIGURE 3. The proportion of the chicks' diet that was flown back from Duck Lake. This calculation is based on the number of prey items in the diet, not their weight. Significance levels from χ^2 tests between 'early' and 'late' broods: + $P < 0.05$, ++ $P < 0.005$, +++ $P < 0.001$.

Grebes also fed invertebrates, primarily dragonfly (Anisoptera) and damselfly (Zygoptera) larvae, to their young (Figs. 4 and 5). Their contribution to the diet decreased as chicks grew, and fewer invertebrates were fed to chicks in 'late' broods than in 'early' broods. They were totally eliminated from the diet of 'late' broods when chicks reached 6 wk of age (Fig. 5).

During 1983 and 1984, yellow perch (*Perca flavescens*) was the species

TABLE 1. Relative amounts of medium (51–75 mm), large (76–100 mm) and very large (>100 mm) fish taken by "fliers" versus "swimmers" in Duck Lake. The data were collected from 3 Jul.–18 Aug. 1983.

	51–75 mm		76–100 mm		>100 mm		Hours observed
	n	%	*n*	%	*n*	%	
Fliers (n = 79)	45	57.0	32	40.5	2	2.5	57
Swimmers	54	80.6	12	17.9	1	1.5	42

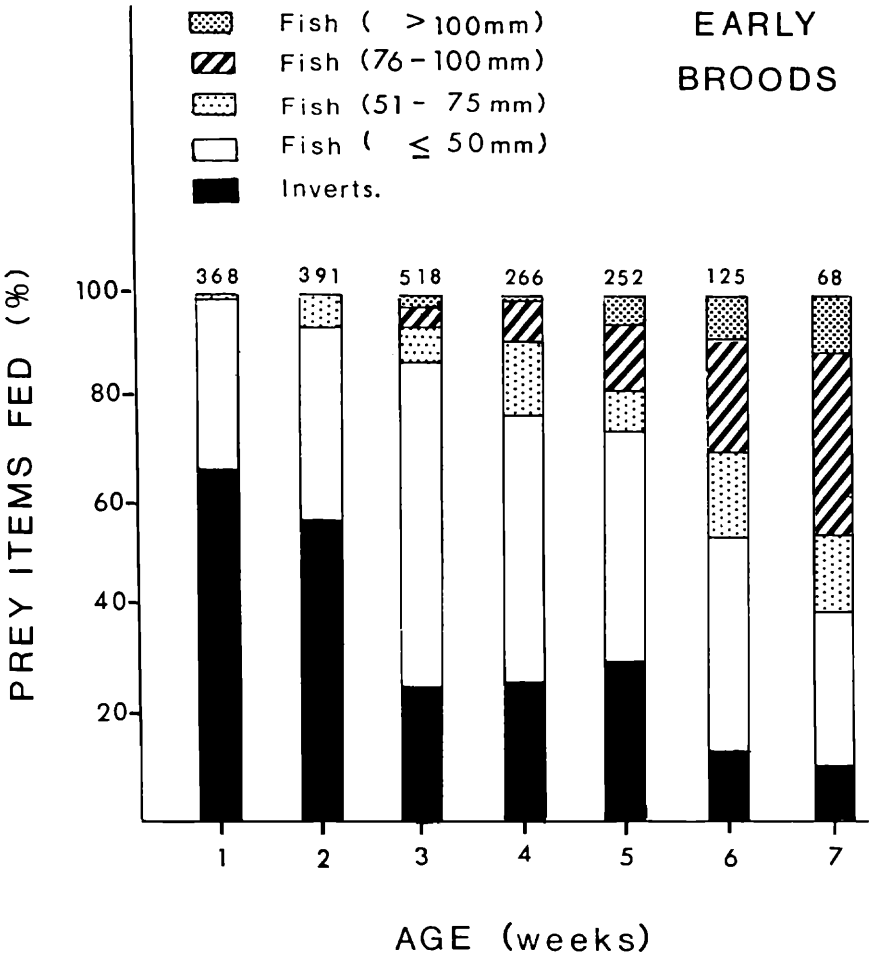

FIGURE 4. The relative contribution of different prey items to the diet of chicks in 'early' broods behind the dyke. Data from 1983 and 1984 are combined as there was no significant difference between years.

flown in most frequently and made up 96.0% and 97.3% of the total fish flown back to the marsh (Table 2). Pumpkinseed sunfish (*Lepomis gibbosus*) made up only 2.7% of the fish in both years and largemouth bass (*Micropterus salmoides*) only 1.4% in 1983. In 1982, perch was the dominant choice as well, but they made up only 64.4% of the fish flown in, whereas pumpkinseed and bass increased to 26.7% and 8.9%, respectively. This difference in prey choice between 1982 and 1983 is significant ($\chi^2 = 62.98$, df = 1, $P < 0.001$). Preliminary data obtained from broods in the lake in 1982 indicate that these birds also broadened their diet in that

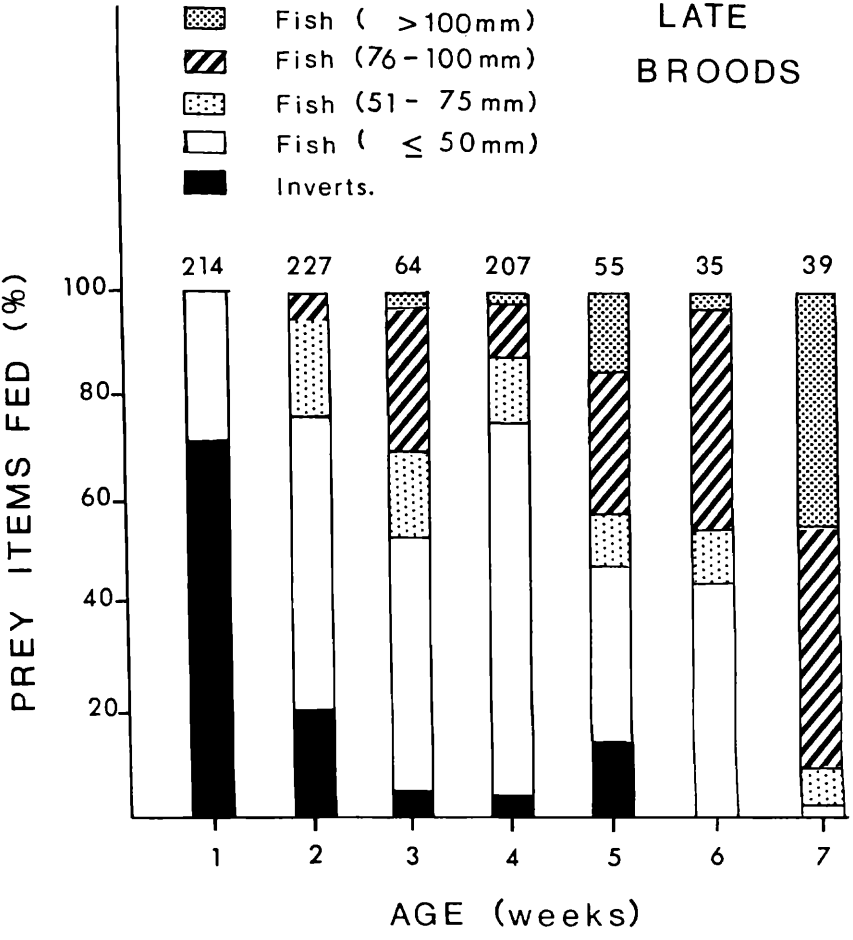

FIGURE 5. The relative contribution of different prey items to the diet of chicks in 'late' broods behind the dyke. Data from 1983 and 1984 are combined as there was no significant difference between years.

year to include more pumpkinseed; 4 out of 53 fish in the medium, large, and very large size categories were pumpkinseed. In 1983, however, all fish in these size categories were perch.

DISCUSSION

Following the construction of the dyke in 1970, water levels stabilized and the resultant growth of emergent vegetation behind it created good quality nesting habitat for Red-necked Grebes. It also made it necessary for those birds nesting behind it to fly to their foraging areas in the lake. The extra distance between adults and their chicks represents an addi-

TABLE 2. Fish species flown into the marsh from Duck Lake.

Year	*n*	Yellow Perch	Pumpkinseed	Largemouth Bass
1982	45	64.4%	26.7%	8.9%
1983	296[a]	96.0%	2.7%	1.4%
1984	328	97.3%	2.7%	0.0%

[a] 302 fish were flown in this year; however, six were not identified.

tional energetic cost borne by the marsh-nesters, over and above the cost of flight, which is probably high because of the grebes' high wing-loading. The prediction, based on central place foraging theory, that the "fliers" would take larger, more profitable prey than the "swimmers" was borne out in this study.

In addition to the costs of flight itself, carrying fish in their bills may also be an extra burden for Red-necked Grebes when they fly. It has been demonstrated in the morphologically similar Red-throated Loon (*Gavia stellata*) that the energetic cost of flying fish back to young has an effect on reproductive success, and fish carried in the bill impose difficulties during take-off and climbing (Norberg and Norberg 1971). Red-throated Loons exhibit foraging adaptations to minimize the cost of these flights—the items they bring back for young are close to optimal size (Reimchen and Douglas 1984).

I assume that, if larger fish were available behind the dyke in sufficient quantities, adults would not fly to the lake to forage. The small, locally caught fish were maintained in the diet of chicks of all ages; however, 'late' broods behind the dyke depended more heavily on fish flown in than did 'early' broods. The reason for this was not discovered; however, a possible explanation may be the fact that brood densities were extremely high (0.4 ha per pair), causing depletion of the local fish population. This may also explain, in part, the 'early' broods' greater dependence on invertebrates, the availability of which would be influenced not only by predation, but also by their emergence throughout the summer as adult dragonflies and damselflies.

A prediction of optimal foraging theory is that the degree of use of a prey species of lower rank is not related to the abundance of that species but to the abundance of prey of higher rank (Pyke et al. 1977). Sampling of Duck Lake fish populations (Forbes 1985) revealed that in 1981 there was a year-class failure of yellow perch. Perch in the medium to very large size categories were therefore not as available in 1982 as they were in 1983 and 1984. This may explain why the grebes' diet broadened in 1982 to include a greater proportion of pumpkinseed and bass. The sampling also revealed that there were proportionately more pumpkinseed in the 80–120 mm size range available in 1983 than in 1982 (Forbes 1985). These were not selected by the grebes, which strongly suggests that yellow perch are the preferred prey species for Red-necked Grebes

at Duck Lake. Yellow perch were also commonly eaten by Red-necked Grebes at Pine Lake, Alberta (Riske 1976).

I know of no other references in the literature to Red-necked Grebes flying to forage for their young, and references to other grebe species doing so are limited. Great Crested Grebes (*Podiceps cristatus*) flew 2–3 km from salt water areas of the Limfjord to their breeding grounds in the marshlands of northwestern Jutland with fish in their bills (Kortegaard 1973). Similarly, a population nesting behind a dyke in east-Flevoland, the Netherlands, flew over the dyke to a lake to forage for their young (Leys et al. 1969). On the other hand, studies on Western Grebes (*Aechmophorus occidentalis*) in Manitoba revealed that their pectoral muscles atrophied to 40–60% of their migratory flight mass (G. Nuechterlein, pers. comm.), and there are no reports of parents of this species flying in the breeding season. A colony of Western Grebes nested on Duck Lake while the present study was carried out, and they were never seen behind the dyke.

The long-term productivity of the Red-necked Grebes that nest behind the dyke is unknown; the effect of flying to foraging areas, rather than swimming, on an individual's lifetime reproductive output may be a negative one because of higher energetic demands. On the other hand, flying to foraging areas may allow the birds to gather information on different areas of the lake more efficiently than they could if they were restricted to swimming. It is also unknown whether it is characteristic of older, more experienced birds to nest in the more protected habitat behind the dyke. Long-term studies are needed to answer these questions.

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