

is no obvious leader. Any intermediate echelon will suffice for purposes of visual communication, as long as its angle is not so acute as to put following birds in the blind area. A V is two echelons joined at the apex, and it is perhaps not surprising that echelon flight is common, while V-formation flight is not. If there is functional advantage to the V, it is evidently not of great significance.

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Differential Contribution of the Sexes to Prefledged Young in Red-throated Loons

T. E. REIMCHEN AND SHEILA DOUGLAS

Department of Zoology, University of Alberta, Edmonton, Alberta T6G 2E9, Canada

The extent of parental investment by each sex is relevant to analyses of mating systems (Kleiman 1977; Ralls 1977; Searcy 1979; Yasukawa 1979, 1981), yet empirical data on time budgets and resource acquisition by each sex are still limited for many taxa. Loons (Gaviidae) are monogamous (Cramp and Simmons 1977) and monomorphic in plumage patterns, and from general theory (Ralls 1977) the sexes could be expected to have roughly equal investment in raising the young. Yet in the 4 loon species, there is moderate size dimorphism, males being 10-15% larger. Greater size may be advantageous for territorial defense or may allow niche partitioning with the female (Selander 1966, Reynolds 1972). However, size dimorphism resulting from sexual selection (Trivers 1972) could indicate reduced male investment. Field studies of loons (Olson and Marshall 1952; Hall and Arnold 1966; Braun et al. 1968; Sjölander and Agren 1972, 1976; Furness 1983; Reimchen and Douglas 1984) indicate that both sexes contribute to raising the young, but the relative investment has not been determined for any of the species.

Red-throated Loons (*Gavia stellata*) on the Queen Charlotte Islands, British Columbia, feed their young marine fish, flying from the lake nesting territory to the ocean for prey throughout the 50-day prefledging period (Reimchen and Douglas 1980, 1984). For

each sex we documented the number and taxa of fish brought to the young and the time budget for foraging flights, brooding, attending, and territorial defense for a nesting pair in 1982 and 1983. Observations were made continuously from predawn to dusk (21 days in 1982, 19 days in 1983), including the first 6 days following hatching and thereafter at intervals over the prefledging period. For the 1982 data, weights of fish were calculated from video tape recordings of feedings (details in Reimchen and Douglas 1984); mean weights for each taxa were determined and used for estimating fish weights for the 1983 data. The pair also nested during 1984, and we supplemented the previous data with records of the proportion of foraging flights made by each sex.

Differentiation of the sexes was made during observations of copulation, which confirmed a marginal size dimorphism, and by a difference in the number and spacing of vertical white lines on the back of the neck, the female having 6-7 lines and the male 10 lines. For each sex, the neck patterns on the breeding plumage were similar over the 3 yr.

Summarized data for 1982 and 1983 are shown in Table 1. Duration of each flight to the ocean to obtain food for the young was significantly shorter for the male than for the female during the first 6 days after hatching; by the third time block (days 27-48) male

flight durations had increased by approximately 200%, while female durations showed a 50% increase. In 5 of the 6 paired comparisons, variance of flight durations was significantly higher for the male (range 11-562 min) than for the female (15-227 min). In 1982, the male made more flights in the morning than later in the day ($\chi^2_3 = 8.76, P < 0.05$), while the female's flights were distributed evenly throughout the day. This trend was not evident in 1983 ($\chi^2_3 = 0.78, P > 0.5$).

The female made significantly more foraging flights and brought more fish to the young than did the male (paired *t*-test; 1982: female, *n* = 140 fish, male, *n* = 88, *t* = 4.31, *P* < 0.001; 1983: female, *n* = 105 fish, male, *n* = 88, *t* = 2.69, *P* < 0.02; 1984: female, *n* = 148, male, *n* = 114, *t* = 2.86, *P* < 0.01). Numbers were similar for the 2 sexes during days 1-6, but thereafter the contribution of the male progressively decreased (Table 1). This trend also was present at the 1984 nest, where male flights decreased from 52.5% of the total (*n* = 59) near hatching to 39.0% (*n* = 100) prior to fledge. The similar investment near hatching coincides with a period when the greatest numbers of fish are required daily. At this time, the young are incapable of swallowing large fish, and the diet is made up of numerous small fish (Reimchen and Douglas 1984).

The fish brought to the young belonged to 6 taxa: Ammodytidae (mean wt 1.5 g), Pholidae (4.1 g), Stichaeidae (7.0 g), Clupeidae (10.5 g), Gadidae (8.0 g), and Embiotocidae (22.5 g). In 1982 and 1984, the male brought proportionally more of the larger fish taxa (Gadidae, Stichaeidae, and Embiotocidae) and the female more of the smaller taxa (Ammodytidae and Clupeidae; 1982: $\chi^2 = 23.4, P < 0.01$; 1984: $\chi^2 = 8.0, P < 0.05$). In 1983, the proportions of Clupeidae and Embiotocidae were similar for the 2 sexes, although the female returned more Pholidae and the male more Ammodytidae ($\chi^2 = 19.0, df = 3, P < 0.01$). Differences between the sexes in mean weight of fish brought (Table 1) are largely a reflection of differences in the proportions of each of these taxa of prey. In 1983, we classified Clupeidae and Embiotocidae into 3 relative size classes. In both taxa, the male brought relatively more of the larger size classes than did the female (Fisher's Exact test: Clupeidae, *P* = 0.05; Embiotocidae, *P* = 0.03). These differences suggest a niche separation in marine foraging by the two sexes; alternatively, the larger male may be capable of carrying heavier fish in flight and accordingly selects larger prey than the female.

There were no differences between the sexes in the number and taxa of fish brought to 4-6-week-old chicks on the Shetland Islands (Furness 1983). Because the major prey offered were small-bodied fish (Ammodytidae, Pholidae), large numbers were provided daily; under these conditions similar numbers of flights by the male and female may be necessary, as was observed during the 6 days following hatch.

TABLE 1. Summarized data on parental activities at 2 nests of the Red-throated Loon. Numbers of observation days for each time block are shown in parentheses and represent continuous observations from dawn to dusk. Comparison of means (*t*-test with unequal variance) and variance (*F* test) shows levels of significance.^a SE = one standard error.

	1983											
	Days 1-6 (6)		Days 7-26 (7)		Days 27-43 (6)		Days 1-6 (6)		Days 7-26 (5)		Days 27-48 (7)	
	Female	Male	Female	Male	Female	Male	Female	Male	Female	Male	Female	Male
Duration of foraging flights (min)	\bar{x} 45.4	37.6	47.9	54.3	61.8	171.4***	44.6	28.8***	68.1	87.1	66.2	107.5*
	SE 3.6	4.1*	4.2	7.2*	7.1	50.2***	3.5	2.7	10.0	19.4*	6.2	16.4***
	<i>n</i> 45	39	51	34	45	14	33	35	27	20	41	25
Number of fish/day	\bar{x} 7.3	6.8	7.3	4.7*	7.5	2.3*	5.5	5.8	5.4	4.0	5.9	3.3*
	SE 0.9	0.4	1.1	0.4	0.7	0.3	0.4	0.7	0.7	0.6	0.7	0.4
Weight of each fish (g)	\bar{x} 5.3	7.9*	11.7	15.7*	15.6	15.4	12.0	5.9**	14.9	21.7***	16.0	16.5
	SE 0.5	0.9***	0.6	1.8***	0.9	1.7	1.6	1.1	1.1	1.6	1.0	1.6
	<i>n</i> 44	41	51	33	45	15	32	37	27	21	39	24
Contribution by weight to diet of young (%)	\bar{x} 64.1	35.9	65.2	34.8	78.9	21.1	63.3	36.7	51.9	48.1	60.8	39.2
	SE 8.3	8.9	5.8	6.3	4.7	4.0	8.3	8.7	6.0	6.0	5.7	5.2
Brooding and attending (h/day)	\bar{x} 0.4	0.4	0.6	0.9	0.7	0.9	0.6	0.6	0.5	0.9	0.4	0.7
	SE 0.4	0.4	0.6	0.9	0.7	0.9	0.6	0.6	0.5	0.9	0.4	0.7

^a * *P* < 0.05; ** *P* < 0.025; *** *P* < 0.001.

TABLE 2. Number of territorial events and parental response to incursions by conspecifics (RTLO) and Common Loons (COLO) during pre fledging period. See text for description of behavioral responses.

	1982				1983			
	RTLO		COLO		RTLO		COLO	
	Female	Male	Female	Male	Female	Male	Female	Male
Low intensity	14	17	3	5	4	5	13	9
Moderate intensity	40	37	7	14	6	6	3	19
High intensity	7	14	3	14	2	2	4	77
Chi-square	0.51		0.60		0.21		33.84 ^a	

^a $P < 0.001$.

Approximately 15% of the fish were not eaten by the young. The three principal reasons for feeding failure were 1) chick satiated, 2) fish too large for swallowing, and 3) territorial disturbance immediately prior to the feeding that caused the adult to swallow the fish before offering it to the young. There was a significant trend ($\chi^2_4 = 29.4$, $P < 0.001$) for the male to bring fish that were too large (male = 11.4% of fish, female = 1.8%) and to be more likely to swallow the fish during territorial intrusions (male = 6.2%, female = 1.0%). Failures for the female occurred primarily when the young were satiated. Frequency of all failures was generally greater for the male than for the female (1982: male = 39.8%, female = 6.4%, $\chi^2 = 4.33$, $P < 0.05$; 1983: male = 22.5%, female = 15.7%, $\chi^2 = 1.0$, $P > 0.5$; 1984: male = 12.3%, female = 1.4%, Fisher's Exact test, $P = 0.002$).

Tabulating differences between the sexes in numbers of foraging flights, average weight of fish, and feeding success rate showed that total contribution to grams of food consumed by the young was considerably greater for the female (70.9% in 1982, 58% in 1983) than for the male. Differential contribution was evident in each time block during both years (Table 1).

Time spent brooding (on nest) and attending during daylight was similar for the sexes throughout the pre fledging period (Table 1). We could not determine the contribution of each parent during darkness, although the female generally brooded on the nest at dusk.

Territorial defense against intrusions by nonbreeding Common Loons (*Gavia immer*) and Red-throated Loons represented a small proportion of the total time budget (3.9% in 1982, 1.6% in 1983). The male spent relatively more time in defense (1982: male, 15.3 h; female, 10.6 h; paired t -test₁₈ = 2.06, $0.05 < P < 0.10$; 1983: male, 6.6 h; female, 0.6 h; $t_{17} = 4.08$, $P < 0.001$) and defended a much larger area (up to 400 m from the nest) than did the female (up to 50 m). When the female attended alone, she responded to conspecifics but rarely defended against Common Loons. In contrast, the male, when sole attendant, defended against all intruding conspecifics and Common Loons. When both adults were attending, the male maintained the

principal defense: of 69 encounters, the pair defended jointly in 20 cases, the male defended alone in 47, and the female alone in 2 cases.

The sexes also differed in intensity of response to territorial intruders (terminology follows Huxley 1923). We categorized territorial response as (1) low intensity (no vocalizations, noncontact): alert, stretched neck, flattening, bill-dipping, retreat; (2) moderate intensity (displays and vocalizations): wail, slow quack, penguin, splash-dive, plesiosaur; and (3) high intensity (direct attack): swim-fly, surf and fly at intruder, underwater attack, surface lunge. The female responded to Common Loons with low and moderate intensity, generally retreating closer to the nest or shore with the young, while the male responded predominantly with direct attack (Table 2). The primary responses of both sexes to conspecifics were of moderate intensity. Attack was rare and occurred only when the intruding Red-throated Loon approached the young. Territorial defense may be of immediate value, as we observed 3 instances of attack on the young by adult conspecifics when the parents were on simultaneous foraging flights.

A time budget for each sex was constructed and energy requirements/h were calculated for body weights of 1,600 g (female) and 1,800 g (male; Cramp and Simmons 1977 for mean wt) at 15°C using equations for existence energy (EE) from Kendeigh (1970). We assumed no additional demands above EE for brooding, attending, and low-intensity territorial defense but a 20% increase for moderate-intensity and a 40% increase for high-intensity defense, foraging, and flight (e.g. Wiens and Scott 1975). Daily energy expenditure was 239.4 kcal for the female and 243.4 kcal for the male, representing an estimated increase of 35.4% and 27.4% above EE for female and male.

In summary, the female contributed considerably more to the diet of the young and the male more to territorial defense, resulting in a similar energetic investment by the 2 sexes during the pre fledging period. While data on a single pair provides only limited insight into the evolution of size dimorphism in this species, these observations are consistent with elements of both role partitioning (Andersson and Norberg 1981) and niche separation (Selander 1966).

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A New Species of Teal from the Pleistocene (Rancholabrean) of Wyoming

STEVEN D. EMSLIE

Department of Zoology, University of Florida, Gainesville, Florida 32611 USA

The late Pleistocene fossil avifauna from Little Box Elder Cave, Converse County, Wyoming consists of 1,051 identifiable bones representing 84 taxa and 71 species (Emslie in press). These remains include 65 Anatidae bones identified as *Branta canadensis*, *Anas crecca*, *A. platyrhynchos*, *A. acuta*, *A. discors* or *A. cyanoptera*, *A. clypeata*, *Anas* spp., *Aythya collaris*, and *Mergus merganser*. In addition to these 65 bones is one Anatini carpometacarpus that differs in morphology and is considerably smaller than any other Recent or fossil teal from North America. This bone is described here as a new species.

Skeletal specimens of Recent species used for comparison include *Nettapus auritus* (1♂), *N. coromandelianus* (1♀), *Anas crecca* (24♂, 10♀, 13?), *A. querquedula* (2♂, 1♀), *A. discors* (14♂, 17♀, 1?), *A. cyanoptera* (5♂, 5♀), *A. hottentota* (3♂), *Aythya affinis* (1♂, 1♀), *Histrionicus histrionicus* (1♀), *Bucephala albeola* (1♂, 3♀), *Amazonetta brasiliensis* (1♂, 1♀), and *Oxyura jamaicensis* (2♂, 1♀). Specimens of North American teals examined are from a variety of geographic locations including Alaska, Montana, Utah, California, Arizona, Minnesota, and Florida to ensure that extremes in size and osteological characters were encountered. Fifteen