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HOST-PARASITE RELATIONS OF CANVASBACK  
AND REDHEAD DUCKLINGS

by

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## ABSTRACT

Field observations of mixed broods and laboratory studies of visual imprinting and auditory discrimination learning were employed to compare behavior and to suggest possible mechanisms for species recognition in Redhead ducklings Aythya americana representing the parasitic segment of the Redhead population and non-parasitic Canvasback ducklings Aythya valisineria.

With increased age of broods, brood hens became increasingly absent, ducklings behaved more independently and there was a decline in aggression to non-brood members. Spacing between brood mates increased as a result of inter-specific aggression initiated by Redhead ducklings, but there were no observations of permanent species segregation, possibly due to the close confines of the brood habitat. Species differences in extent of aggression, neck-stretch and head-throw displays suggest possible area for species recognition by Redhead and Canvasback ducklings during the brood period.

The capacity to learn visual and auditory discriminations was compared between Redhead and Canvasback ducklings in the laboratory. The two species learned a visual discrimination equally well, but Canvasback ducklings performed significantly better in learning an auditory discrimination.

Visual imprinting by parasitic Redhead ducklings is well developed and could facilitate the formation of parent-young relationships. The reduced auditory learning in the young Redhead raises the possibility that auditory stimuli may be particularly important for subsequent species recognition in brood parasites.

GENERAL INTRODUCTION

Species recognition and the formation of attachments to the biologically correct species is generally acknowledged to be of fundamental importance to normal reproductive biology in the family Anatidae (see Sluckin 1965; Bateson 1966). It is especially important in the subfamily Anatinae, in which the temporary pair bond situation requires the female to select a new mate every year on the wintering ground or during migration. In those closely related species which are sympatric on the pairing grounds, pronounced sexual dimorphism and elaborate courtship displays facilitate the prevention of interspecific hybrids (Sibley 1957).

The Redhead, Aythya americana and the Canvasback, Aythya valisineria represent two such closely related species, both in their courtship displays and to a lesser extent, gross morphology (Weller 1967). Although some differences exist in their wintering grounds, migration routes and breeding range (Stewart, Geis and Evans 1958; Weller 1964), the two species exist sympatrically. Species recognition based on early learning is further complicated in the Redhead by its semiparasitic habit (Weller 1959), which results in a certain percentage of the population being raised by foster parents, of which the Canvasback is the principal species. Under these circumstances, if conventional imprinting of Redhead ducklings to their foster

parent occurred, the frequency of interspecific courtship and the possibility of hybrids between these two species would be expected to increase. Although reports of interspecific courtship have been advanced by several investigators (Hochbaum 1944; pers. obs.), no wild hybrids appear to have been reported between the Redhead and Canvasback (Gray 1958). This lack of wild hybrids suggests that the relationship between imprinting and subsequent mate selection is modified in the semi-parasitic Redhead. The present study was therefore initiated to investigate the early development of behavior in parasitic Redhead ducklings compared to non-parasitic Canvasback ducklings, and to assess the effects of imprinting and subsequent social interactions on mixed brood behavior and species recognition.

PART I. BEHAVIOR IN MIXED BROODS

## INTRODUCTION

Several investigators (Low 1945; Erickson 1948; Wingfield 1951; Spencer 1953; Weller 1959; Olson 1964; Lokemoen 1966; and others), have reported the occurrence of parasitic egg laying in the Redhead, Aythya americana. A search of the literature, conducted by Weller (1959), revealed parasitic intrusions on 11 species of the sub-family Anatinae. The Canvasback, Aythya valisineria however, was shown to be the principal host species, apparently because of similarities in habitat preference on the breeding range (Weller 1959).

Olson (1964) has demonstrated that the frequency of egg parasitism in a given habitat bears a direct relationship to the number of breeding Redheads. On small water areas, where Redheads are less numerous than on large marsh situations, the absolute frequency of egg parasitism is less. The success of egg parasitism on these small habitats however, may result in up to 50% of the Redheads produced in a given year being raised by Canvasback foster parents (Olson 1964). In spite of this apparent importance of mixed broods to total productivity of the species, little information exists concerning the behavior of the Redhead duckling as a brood parasite, or on the effects,



if any, of this parasitism on the host ducklings. Part I of this thesis was designed to investigate these aspects of behavior for mixed broods on small water habitats.

In view of the involvement of early learning in facilitating the integration of young waterfowl broods (Ramsay 1951), the apparent need for some form of subsequent segregation from the foster family seems crucial to the biologically correct development of the parasitic Redhead duckling. Some of the mechanisms which may function to integrate or segregate waterfowl broods have been discussed by Collias and Collias (1956). They were able to attract a mixed brood of Canvasback and Redhead ducklings by calling to them, for example, suggesting that mechanisms such as responsiveness to adult calls may operate to promote integration early in the brood period. Segregative effects were also reported. By measuring aggressive encounters, Collias and Collias (1956) demonstrated that Redhead ducklings were dominant over Canvasback ducklings and that this tended to segregate the species, but they did not obtain complete segregation between these two species under the conditions of their study. Weller (1959) however, has shown that approximately 4 weeks after hatching, aggression between Redhead and Canvasback ducklings in naturally occurring mixed broods may act to segregate the ducklings into species groups. This observed segregation suggests that species recognition processes may be active at this

time to prevent the brood parasite from becoming irreversibly attached to the foster parent species by means of conventional imprinting (Sluckin 1965; Bateson 1966) or by subsequent sexual imprinting (Schutz 1965). A major objective of the present study was to identify and examine those factors which operate to integrate or segregate mixed broods under conditions present on the "pothole" breeding grounds in southwestern Manitoba.

## STUDY AREA

Brood observations were conducted on a 60-square mile block of predominantly agricultural land located one mile south of the town of Minnedosa, Manitoba. The study area was located in aspen parkland (Bird 1961). The topography was gently rolling. The geological history of the area (Ellis 1938) has generally resulted in the formation of numerous potholes which in some areas commonly exceeded 100 per square mile (pers. obs.). Various factors, including the fertility of the upland areas and the density of potholes have combined to make the area around Minnedosa the most productive in southwestern Manitoba and one of the most important breeding areas in North America (Bartonek and Hickey 1969).

Canvasback and Redhead populations have been monitored in this area by Stoudt (1971). A detailed investigation of the population dynamics of these two species in the Minnedosa area has been investigated by Olson (1964), who suggested that the Redhead may be replacing Canvasback breeding populations in certain habitats and competition for breeding habitat may exist between the two species. Several other investigators (Evans 1951; Dzubin 1955; Kiel 1955; Stoudt 1963; Bartonek

and Hickey 1969) have given detailed descriptions of the area and have discussed its use by waterfowl. Table 1 and Table 2 summarize waterfowl breeding pair and brood production data collected by the U. S. Fish and Wildlife Service on a 4-square mile beat-out area established south of Minnedosa (see Stoudt 1963, 1971).

TABLE 1. Indicated breeding pairs per square mile.<sup>a</sup>

Species	1963-1970 (mean)	1970	1971
Blue-winged Teal, <u>Anas discors</u>	30	25	33
Mallard, <u>Anas platyrhynchos</u>	16	12	16
Ruddy duck, <u>Oxyura jamaicensis</u>	10	13	21
Canvasback, <u>Aythya valisineria</u>	9	6	8
Lesser Scaup, <u>Aythya affinis</u>	6	5	5
Redhead, <u>Aythya americana</u>	6	4	4
Others	23	17	15
Total	100	82	102
American Coot, <u>Fulica americana</u>	104	129	161

TABLE 2. Brood populations per square mile.<sup>a</sup>

Species	1963-1970 (mean)	1970	1971
Blue-winged Teal, <u>Anas discors</u>	7.3	6.5	7.2
Canvasback, <u>Aythya valisineria</u>	3.6	2.5	3.8
Mallard, <u>Anas platyrhynchos</u>	3.4	2.2	2.5
Ruddy duck, <u>Oxyura jamaicensis</u>	2.5	6.2	7.5
Redhead, <u>Aythya americana</u>	1.0	1.3	2.0
Lesser Scaup, <u>Aythya affinis</u>	0.3	0.5	1.0
Others	4.9	4.0	3.2
Total	23.0	23.2	27.2
American Coot, <u>Fulica americana</u>	--	58	57

<sup>a</sup>Data summarized from Stoudt (1971).

## METHODS AND MATERIALS

Canvasback, Redhead and mixed Canvasback-Redhead broods observed on the study area during the 1970 and 1971 field seasons were recorded by species, age, location, number of ducklings and presence or absence of the brood hen. The age of both Canvasback and Redhead ducklings was approximated by the plumage subclasses described by Gollop and Marshall (1954). The reliability of assessing age-dependent behavioral characteristics based on these subclasses was validated by comparison with two marked, mixed broods of known age established in 1970. In these two cases, the hens were trapped in the later stages of incubation (approx. 20 days), using a slight modification of the automatic nest trap described by Weller (1957), and marked with yellow plastic nasal saddles (Sugden and Poston 1968). For unmarked mixed broods, the onset of the brood period was calculated by back-dating broods aged in the field.

Observations on mixed Canvasback-Redhead broods comprised 10-min intervals of time during which complete records were made on the activity, spatial distribution and various behavioral patterns in the ducklings. For each 10-min interval, the value tabulated for spatial distribution

represented an estimate of the maximum distance, in feet, over which the brood was spaced. These distances were divided into four categories: 0-10, 11-20, 21-30 and > 30 feet. The number of individuals of other species in the vicinity of the brood was also recorded in a similar fashion. Practice with decoys prior to the brood season enhanced the reliability of the estimates. Errors in distance estimation that may have occurred, were hopefully minimized by relatively large samples. For the purposes of this study, an "observation" is defined as the recorded behavior of the brood during a 10-min interval. Except where otherwise stated, the data analysis was based on the presence or absence of a given behavior pattern within an observation. Observations were obtained from an automobile or a collapsible 3 ft x 3 ft x 4 ft high green, sailcloth blind. Ten-power binoculars and a 25-power spotting scope were used.

## RESULTS

### Occurrence of Mixed Broods at Minnedosa

The approximate dates that broods were present on the study area are given in Table 3. Canvasback, Redhead and mixed Canvasback-Redhead broods observed on the study area during the summers of 1970 and 1971 are presented in Table 4. As in Table 3, mixed broods are separated from those containing only Canvasback or Redhead ducklings. For 1970, 44% of the broods raised by Canvasback hens contained Redhead ducklings compared to 52% for 1971. Of the total Redhead ducklings observed for both years, 26% and 35% respectively, were reared by Canvasback foster parents. Redhead ducklings accounted for 36% and 41% of the ducklings in mixed broods in 1970 and 1971 (Table 5). Although these data do not arise from an established transect or beat-out area, the per cent of Canvasback broods which contained Redhead ducklings agrees with Olson (1964) who stated that 47% to 55% of Canvasback broods observed on pothole habitats were mixed.

The number of parasites per mixed brood varied from one to seven ducklings (Table 5), although broods with a single Redhead occurred most frequently. Broods containing additional Redhead ducklings decreased significantly in



TABLE 3. Approximate dates that broods were found on the study area.

Brood description	Brood period	Peak numbers of broods <sup>b</sup>
1970		
Canvasback	June 5 - October 12	July 25 - August 24
mixed <sup>a</sup>	June 15 - October 13	July 25 - August 14
Redhead	July 5 - October 23	August 24 - September 13
1971		
Canvasback	May 25 - October 2	July 15 - August 4
mixed <sup>a</sup>	June 5 - October 2	July 25 - August 14
Redhead	June 15 - October 23	August 4 - August 24

<sup>a</sup>Broods consisting of a Canvasback hen and Redhead ducklings are classed as mixed broods.

<sup>b</sup>Peak numbers refer to the maximum number of broods observed on this study area.

TABLE 4. Canvasback, mixed Canvasback-Redhead and Redhead broods located on the study area at Minnedosa in 1970 and 1971.

Plumage class <sup>a</sup>	Number of broods		Average brood size		Total ducklings				
	Canvasback	Mixed Redhead	Canvasback	Mixed Redhead	Canvasback	Mixed Redhead			
1970									
I	18	4	20	6.7	7.8	7.1	120	31	141
II	11	13	1	5.8	5.6	4.0	64	73	4
III	-	6	-	-	6.2	-	-	37	-
Total (1970)	29	23	21	6.3	6.1	6.5	184	141	145
1971									
I	6	12	15	3.3	6.1	6.5	20	73	97
II	15	12	4	5.1	5.0	4.3	77	60	17
III	4	3	-	5.5	4.7	-	22	14	-
Total (1971)	25	27	19	4.8	5.4	6.0	119	147	114

<sup>a</sup>Plumage Class I corresponds to an age of up to 3½ weeks posthatch; Class II from 3½ to 7½ weeks posthatch and Class III from 7½ to approximately 9 weeks posthatch.

TABLE 5. Frequency and per cent of parasitic Redhead ducklings in mixed broods found on the study area at Minnedosa in 1970-1971.<sup>a</sup>

Number of Redheads	Number of Mixed broods	Total ducklings	Average brood size	Per cent parasitic Redheads <sup>b</sup>
1970				
1	8	53	6.6	15
2	7	32	4.6	44
3	4	23	5.8	52
4	2	16	8.0	50
5	2	17	8.5	58
1971				
1	11(1)	61	5.5	18
2	6(3)	18	3.0	67
3	5(1)	28	5.6	54
4	4	30	7.5	53
7	1	10	10.0	70

<sup>a</sup>Number of Canvasback broods containing only Redhead ducklings are given in brackets. These broods were considered "mixed".

<sup>b</sup>Redhead ducklings comprised 36% of the ducklings in mixed broods for 1970 compared to 41% for 1971.

frequency in both 1970 ( $p < .05$ ) and 1971 ( $p < .01$ ) (Rank correlation, Ferguson 1959). For both years however, the average number of Redhead ducklings per mixed brood was 2.3. On five occasions, Redheads were the only ducklings in the brood of the Canvasback female.

#### General Brood Activity

During the 1970 and 1971 field seasons, 739 10-min observations (123.2 hrs) were completed on 22 mixed broods in which the parasitic Redheads ranged in number from 1-5 ducklings (Appendix A). The number of observations on individual broods varied from one to 103. An average of 33.6 observations were recorded per mixed brood.

Time spent in cover: The brood was recorded as being in cover for those observations in which all of the ducklings were in the cover of the emergent edge vegetation for the entire 10-min period. Although broods of all ages spent a certain percentage of their time in cover (Table 6), age-dependent effects were observed, older broods spending less time in cover. All Class I broods combined spent 28% of the total number of observations in cover, significantly greater (2x2 test,  $X^2 = 8.1$ ,  $p < .01$ ) than the 18% recorded for Class II broods. Class II and Class III broods, however, spent approximately the same amount of time in cover ( $X^2 = .41$ ,  $p > .10$ ).

Feeding, sleeping and loafing: In view of the difficulty in determining the activity of mixed broods

TABLE 6. Per cent of observations in which mixed broods of various plumage classes were found in the cover of emergent vegetation.

Plumage <sup>a</sup> subclass	Number of broods	Total number of observations	Observations spent in cover <sup>b</sup>	Per cent of total obser- vations in cover
Ia	2	54	21	39
Ib	2	97	33	34
Ic	4	82	11	13
Total (Class I)	5	233	65	28
IIa	6	74	18	24
IIb	7	110	32	29
IIc	8	256	31	12
Total (Class II)	14	440	81	18
IIIa	8	66	10	15

<sup>a</sup>Age of the broods are based on the plumage subclasses described by Gollop and Marshall (1954).

<sup>b</sup>The amount of time spent in the cover of emergent vegetation in relation to the dominant vegetation type is presented in Appendix B.

while they were in the cover of emergent vegetation (see Table 6), analysis of brood behavior was restricted to those observations when the broods were recorded out of cover (Table 7).

Canvasback hens, while accompanying mixed broods, spent little time feeding. Hens were observed feeding in 25% of the Class I observations (Table 7A), then feeding decreased significantly for Class II ( $p < .001$ ) and again for Class III broods ( $p < .05$ , Table 7B), when temporary absences and desertions by the brood hens became more common (see following sections). Similar observations have been reported for the Ring-necked Duck Aythya collaris brood hens (Mendall 1958; Beard 1964), which do not usually feed when they accompany broods. Canvasback hens typically remained close to the ducklings during bouts of feeding and followed, rather than directed, the ducklings' feeding activities.

Excluding those observations in which mixed broods were in the cover of emergent vegetation, feeding occurred in 74% of the observations for Class I broods (Table 7A). The duration of feeding bouts ranged up to 110 mins with an average of 36 mins for mixed broods of all ages. The per cent of observations in which feeding was observed, however, decreased in Class II to 53% ( $p < .001$ , Table 7B), after which they remained relatively stable at 45% through Class III. Because the times spent feeding and loafing,

TABLE 7. Activity of mixed broods in relation to the age of the broods.  
Table based on observations recorded when the broods were out  
of cover.

A. Plumage subclass	Number of observations out of cover	Per cent of observations		
		hen feeds	brood <sup>a</sup> feeds	brood loaf <sup>a</sup> , sleeps, moves <sup>b</sup> ducklings behave independently
Ia	33	39	79	21(1) 12
Ib	64	23	81	19(1) 9
Ic	71	25	66	34(1) 25
Total (Class I)	168	25	74	26 17
IIa	56	5	38	63(4) 20
IIb	78	21	42	58(2) 14
IIC	225	7	61	39(1) 32
Total (ClassII)	359	9	53	47 26
IIIa	56	2	45	55(2) 43

B. Statistical comparison <sup>c</sup>	hen feeds	brood feeds	brood loafs or sleeps	ducklings behave independently
I vs II	I>III, p<.001	I>II, p<.001	I<II, p<.001	I<II, p<.02
II vs III	II>III, p<.05	II>III, n.s.	II<III, n.s.	II<III, p<.01

<sup>a</sup>One or more members of brood seen feeding during observation.

<sup>b</sup>Number of observations in which broods were observed moving from place to place are given in brackets.

<sup>c</sup>Comparisons based on 2x2 test (Ferguson 1959).



sleeping or moving are inversely proportional, a corresponding increase in this latter behavior was observed as the broods became older. Significance levels, identical to those for feeding, are included in Table 7B. Those findings for Class II and III are contrary to Beard (1964), who demonstrated that in waterfowl broods of various species, excluding Canvasback and Redhead, feeding occupied approximately three fourths of their time. These differences may suggest effects due to habitat (large marsh vs small water area) and food availability.

Feeding observations in which the brood mates behaved "independently", i.e., one or more fed while others slept or remained in cover, were further separated and expressed as a per cent of the total observations recorded when the broods were out of cover (last column, Table 7A). During the latter part of the brood period, the independent behavior by brood mates was observed on several occasions (Table 7A). Compared to relatively few observations of independent behavior in Class I broods (17%, Table 7A), there was a significant increase for Class II ( $p < .02$ ) and Class III broods ( $p < .01$ , Table 7B). These results provide evidence that more of the older broods had ceased, at least temporarily, to function as closely integrated units.

Temporal differences: To determine if there was a daily schedule of brood activity, the per cent occurrence of a given behavior pattern (Table 8), was compared between

TABLE 8. Activity of Class I and Class II broods in relation to the time of day.

Time period <sup>a</sup>	Total number of observations	Number of broods	Per cent of observations in which activity occurred		
			in cover	feeding	sleeping & loafing
Class I					
0400-0900	87	4	37	48	15
1000-1500	97	4	26	55	20
1600-2100	49	2	16	62	22
Class II					
0400-0900	156	10	22	38	40
1000-1500	98	7	5	71	23
1600-2100	186	12	22	28	49

<sup>a</sup>Central standard time.

three observation periods; morning, 0400-0900 hrs, afternoon, 1000-1500 hrs, and evening, 1600-2100 hrs Central Standard Time. As shown in Table 8, no clear relationship was found between the time of day and the feeding activity or sleeping and loafing of Class I broods ( $p > .05$ ). The amount of time broods spent in cover during the morning, however, was significantly greater than during the evening observation periods (2x2 test,  $\chi^2 = 6.3$ ,  $p < .02$ ). For Class II broods, the afternoon observation period differed from both the morning and evening periods. Broods spent less time in cover during the afternoon than in the morning (2x2 test,  $\chi^2 = 13.6$ ,  $p < .001$ ) or evening ( $\chi^2 = 14.2$ ,  $p < .001$ ) observation periods. Also observed was an increase in feeding (decrease in loafing or sleeping) in the afternoon compared to the morning ( $\chi^2 = 27.2$ ,  $p < .001$ ) or evening periods ( $\chi^2 = 48.2$ ,  $p < .001$ ).

The absence of a daily schedule of brood activities has been observed for the Canvasback (Hochbaum 1944), Ring-necked Duck (Mendall 1958; Beard 1964) and for several other species of waterfowl of various ages (Beard 1964). Low (1945), however, observed that "broods were more easily seen early in the morning and late in the afternoon during the feeding periods." The data presented in Table 8, for at least Class II broods, are consistent with the observations of Low (1945) in that they indicate differences during the day, but differ in that the peak

of feeding in Class II broods was greatest during the mid-day. The increase in feeding observed during the evening for Class I broods may reflect an effect of the small sample of broods observed.

Spacing of mixed broods: As described above (Table 7A), when broods became older, ducklings were increasingly independent of their brood mates. This increased independence of the older ducklings was further evidenced by the distance over which the brood was spaced (Table 9). These estimates, particularly during bouts of feeding, varied proportionately with the age of the brood. The percentage of observations in which broods were spaced over a particular distance are given in Table 9A. During feeding, and to a lesser extent loafing or sleeping, there was a significant increase (Table 9B) in the time older broods were spaced greater than 30 ft. These observations are consistent with those described for the Blue-winged Teal, Anas discors (Bennet 1938), Ring-necked duck (Mendall 1958) and for several other waterfowl species, excluding the Canvasback and Redhead (Beard 1964).

Possible segregation between Canvasback and Redhead ducklings in mixed broods was assessed by determining the instances in which the species were either spatially separated (> 30 ft), or segregated by habitat such that one species was in the open or visible to the observer, while the other species remained in cover. With the exception of

TABLE 9. Spacing of the brood members in relation to age and activity.

A. Activity of the brood	Age class	Number of observations	Per cent of observations brood spaced <sup>a</sup>			
			0-10	11-20	21-30	>30
Feeding	I	125	44	36	14	7
	II	192	21	23	15	40
	III	25	0	0	4	96
Sleeping or loafing	I	43	88	9	0	2
	II	167	56	16	7	22
	III	31	19	6	0	77
B.		Statistical comparison <sup>b</sup>	Feeding	Loafing or sleeping		
		I vs II	I < II, p < .001	I < II, p < .05		
		II vs III	II < III, p < .001	II < III, p < .001		

<sup>a</sup>Distances estimated in feet.

<sup>b</sup>Comparisons, based on 2x2 tests, between proportions of observations greater than and less than or equal to 30 ft (Ferguson 1959).

three observations in Class III, segregation was recorded only during those observations in which the broods were feeding. The proportion of observations in which segregation occurred did not differ significantly between age classes, although there was a slight tendency for these to increase with the age of the broods. Expressed as a percent of the observations in which the broods were observed feeding, species segregation occurred in 5% of the Class I observations compared to 9% and 16% for Class II and Class III.

With increased spacing of broods and independence of the ducklings after approximately 5 wks (subclass IIb), Beard (1964) observed that brood mates "rarely assembled as a whole brood." Mixed broods of all ages observed in the present study were frequently seen together during observations in which sleeping or loafing occurred. In addition, with the exception of one marked mixed brood from which the two Redhead ducklings disappeared, no permanent segregation of Redhead and Canvasback ducklings was observed. For those observations in which the ducklings in individual broods became divided into groups, frequent interchange between groups resulted in Canvasback and Redhead ducklings remaining together for the majority of the time.

Attendance of brood hens: Canvasback hens usually tended their young in mixed broods in the Class I and subclass IIa stages of development although they temporarily

deserted them for short periods of time (Table 10). The extent and duration of these temporary absences varied, but were most common in the afternoon observation periods. Hens were absent from Class I and subclass IIa broods for 15% of the 132 observations between 0400 and 0900 hrs, for 20% of the 98 observations between 1000 and 1500 hrs, but were never absent in 77 observations from 1600 to 2100 hrs.

Permanent desertions were first observed during the IIb stage of development (Table 10). There was subsequently, a marked increase in the number of desertions as evidenced by the increase in the number of observations brood hens were absent from Class I to Class II ( $2 \times 2$  test,  $\chi^2 = 94.6$ ,  $p < .001$ ) and from Class II to Class III broods ( $2 \times 2$  test,  $\chi^2 = 48.0$ ,  $p < .001$ ). For both 1970 and 1971, the desertion rate of Canvasback hens attending broods containing only Canvasback ducklings, supports these results. All 9 broods observed in the IIa stage were accompanied by hens. Of the 21 broods observed at later stages of development, 7 broods were deserted.

The effects of temporary absences on the ducklings were difficult to assess for individual mixed broods. It can be noted, however, that when the brood hens were absent, the ducklings of both species typically remained together as a brood. For one instance, two Redhead ducklings from one marked, mixed brood in the Ib stage, became markedly segregated (approx. 60 yds) from the 5 Canvasback ducklings,

TABLE 10. Attendance of brood hens related to the age of the brood. Table based on those mixed broods on which observations were made.

Plumage subclass	Total number of observations	Number of broods observed <sup>a</sup>	Number of broods deserted	Per cent of observations hen absent
Ia	54	2	0	17
Ib	97	2	0	11
Ic	82	4	0	6
IIa	74	6	0	20
IIb	110	7	2	20
IIc	256	8	5	69
IIIa	66	8	6	94

<sup>a</sup>Represents a cumulative record of broods. A given brood may have been observed in one or more subclasses.



but were reunited with the brood after the hen returned.

Permanent desertions and the increasing absence of brood hens occurred in conjunction with several previously described behavior patterns. The spacing of the ducklings (Table 9) increased proportionately, in addition to increases in the per cent of observations in which independent behavior occurred (Table 7). The relationships between permanent desertions and aggression involving the brood hen and ducklings are presented in following sections.

Differences between Redhead and Canvasback ducklings during feeding, loafing and sleeping: Both Canvasback and Redhead ducklings feed by diving. As described by Dewar (1924), a bird's diving efficiency can be measured by comparing the time spent submerged to the total time spent diving. Dow (1964) suggested that this dive/pause ratio, because it is largely independent of water depth, should remain approximately constant for a given species. For the purpose of the present study, therefore, possible feeding differences between Canvasback and Redhead ducklings in mixed broods were assessed by comparing dive/pause ratios between the species in the mixed broods observed. The diving schedule for a given duckling was recorded on a tape cassette recorder. As the tape was played back, the time submerged and the time spent on the surface were determined using a stopwatch. It was not possible to obtain a complete record for ducklings of all ages. Subclasses Ic, I Ib, and

IIc, however, were represented.

The dive/pause ratios for both species increased from subclass Ic to class II (Table 11), indicating a greater increase in the time submerged relative to the time spent on the surface. Beard (1964) observed a similar trend for the Hooded Merganser Lophodytes cucullatus. Comparisons between dive/pause ratios for individual dives, however, revealed a significant difference ( $Z = -1.74$ ,  $p < .05$ , Mann Whitney U Test) between Redhead and Canvasback ducklings in subclass Ic. No differences were observed for subclass IIb ( $Z = 2.43$ ,  $p > .05$ ) and subclass IIc ( $Z = 4.15$ ,  $p > .05$ ) broods. The similarity of dive/pause ratios of older birds indicates that species differences in the dive/pause ratio cannot explain the increase in spacing and segregation of older broods.

The exact location of the ducklings during feeding was not recorded in detail, but it was evident that Redhead ducklings utilize the emergent edge vegetation during feeding more heavily than Canvasback ducklings. Other differences in feeding between Redhead and Canvasback ducklings have also been observed by Bartonek and Hickey (1969). These authors found that animal material comprised 96% of the food consumed by Canvasbacks compared to only 43% for Redhead ducklings.

Quantitative data indicating species differences during loafing or sleeping were not obtained. Observations

TABLE 11. Diving times of Canvasback and Redhead ducklings in mixed broods.

Plumage subclass	Species	Position of birds	Number of observations	Time in seconds		Dive/pause ratio
				Mean $\pm$ SE	Range	
Ic	Canvasback	submerged	23	5.0 $\pm$ 0.50	2.5-11	.8
		surfaced	23	5.9 $\pm$ 0.48	2.5-13.5	
	Redhead	submerged	30	3.5 $\pm$ 0.17	2.0-5.0	.4
		surfaced	30	9.2 $\pm$ 0.77	3.0-19.0	
IIb	Canvasback	submerged	26	13.3 $\pm$ 0.82	5.2-19.5	1.8
		surfaced	26	7.2 $\pm$ 0.54	1.0-11.8	
	Redhead	submerged	25	13.3 $\pm$ 0.52	9.0-20.0	1.3
		surfaced	25	9.9 $\pm$ 0.84	6.0-13.5	
IIc	Canvasback	submerged	66	17.3 $\pm$ 0.36	9.8-22.0	1.8
		surfaced	66	9.4 $\pm$ 0.50	5.0-24.0	
	Redhead	submerged	57	15.4 $\pm$ 0.50	6.0-20.5	1.5
		surfaced	57	10.6 $\pm$ 0.54	4.0-27.5	

of pseudo-sleeping (Cornwall and Bartonek 1963) and the results of Part II of this thesis however, suggest that Canvasback ducklings are more wary than Redheads. In addition, on at least one occasion Canvasback ducklings in an older mixed brood (IIc) were observed to assume the alert posture in response to a disturbance from agricultural activity. There was no comparable response from the Redhead ducklings.

### Aggression

For each aggressive encounter, the brood number, age of the brood, presence or absence of the brood hen and circumstance, including the birds in proximity to the brood, were recorded. Because the aggressor, in most cases, dominated a given aggressive encounter, analyses of aggression observed during the brood period was based on which individual initiated the interaction. To reduce interpretive errors, only those encounters involving an obvious (to the observer) chase or threat were classified as aggressive. Actual contact between participants was observed only rarely.

Aggression through the brood period: The per cent of the observations out of cover in which at least one aggressive encounter involving broods was initiated by either the brood hen, ducklings, or individuals outside the brood (attacks on brood), are given in Table 12 on an age dependent basis.

TABLE 12. Per cent of intervals in which aggression involving broods was initiated by the brood hen, ducklings, or individuals outside the brood, for observations out of cover. Total encounters are given in parenthesis.<sup>a</sup>

Age of brood	Brood hen	Ducklings		Individuals outside brood
		Redhead	Canvasback	
Ia	6 (2)	0	0	6 (2)
Ib	17 (11)	0	0	4 (3)
Ic	24 (21)	0	0	1 (2)
Total (Class I)	18 (34)	0	0	3 (7)
IIa	18 (15)	5 (3)	0	7 (5)
IIb	21 (28)	15 (14)	4 (3)	2 (4)
IIc	2 (5)	11 (30)	7 (16)	6 (21)
Total (Class II)	9 (48)	13 (47)	5 (19)	5 (30)
IIIa	0	4 (2)	0	5 (3)

<sup>a</sup>The per cent of individuals of various species present during those observation periods in which aggression was recorded are tabulated in Appendix C (columns 2, 4, 6), along with the per cent attacks by individuals of those species, or aggression directed at individuals of those species, by the brood hen and ducklings.

The number of attacks on broods (5th column, Table 12) remained relatively consistent throughout the brood period. There was no significant difference between Class I and Class II (2x2 test,  $\chi^2 = 1.1$ ,  $p > .05$ ) in which aggression was recorded in 3% and 5% of the observations respectively (Table 12). Similarly, attacks initiated on Class II and Class III broods did not differ significantly (2x2 test  $\chi^2 = .01$ ,  $p > .05$ ). With the exception of the attacks on Class I broods the aggressor was usually dominant, of 30 attacks on Class II ducklings, the brood hen was away for 20 and the aggressor won in 26. Of 7 attacks on Class I broods, the brood hen was never away and the aggressor won in only 3 instances. The greater dominance by aggressors in older broods presumably relates to the fact that brood hens had become increasingly absent by stage II (see Table 10) and increased spacing among brood mates (see Table 9) facilitated attacks on ducklings without retaliation by brood hens.

Attacks initiated by brood hens to individuals outside the brood (2nd column, Table 12) decreased significantly (2x2 test,  $\chi^2 = 8.8$ ,  $p < .01$ ) from 18% in Class I to 9% in Class II. Brood hens won all of the aggressive encounters they initiated to individuals outside the brood with the exception of one encounter in subclass Ic which was recorded as recorded as a draw.

Aggressive encounters initiated by ducklings were

first observed in subclass IIa, when Redheads were aggressive during 5% of the observations (Table 12). By the end of Class II, aggression initiated by Redhead ducklings was observed in 13% of the observations compared to 5% for Canvasback ducklings. The outcome of the aggression initiated by the ducklings appeared to be independent of the presence or absence of the brood hen. For the Class II subclasses, for example, ducklings won all but one encounter, even though the hen was present for all 3 attacks in stage IIa, and for 16 out of 17 attacks in IIb, but only 6 of 46 in IIc.

Differences between Redhead and Canvasback ducklings:

Differences in the frequency of aggression initiated by Redhead and Canvasback ducklings are shown in Table 12 in relation to the age of the brood. The relative number of Redhead and Canvasback ducklings, however, and hence the opportunity for aggression by Redhead and Canvasback ducklings, varied between the mixed broods observed. The number of aggressive encounters initiated by Redhead and Canvasback ducklings to individuals outside the brood or to brood mates of the opposite species are given in Table 13 in relation to the number of ducklings of both species in individual mixed broods.

A total of 49 attacks, or 1.7 attacks per duckling, by Redhead ducklings to non-brood members were observed compared to 19 attacks, or .7 per duckling by Canvasback ducklings. Relative to the opportunity for aggression by

TABLE 13. Number of aggressive encounters initiated by Redhead and Canvasback ducklings to individuals outside the brood and to brood mates.

Brood number	Number of Redhead ducklings	Number of Canvasback ducklings	Aggressive encounters initiated by		Aggression between brood mates	
			Redhead	Canvasbacks	Redhead	Canvasback
1	3	3	1	0	0	0
2	2	2	6	2	6 (1) <sup>a</sup>	0
3	2	4	5	2	2	0
4	4	3	2	0	0	0
5	4	5	1	0	1	0
6	2	3	1	0	0	0
7	5	3	20	12	6 (1)	0
8	3	1	7	2	3 (2)	0
9	4	3	6	1	0	0
Total	29	27	49	19	18 (4)	0

<sup>a</sup>Figures in parenthesis represent attacks initiated by Redhead ducklings to Redhead brood mates.



individuals of both species, Redhead ducklings were significantly ( $X^2 = 11.2$ ,  $p < .001$ ) more aggressive to outsiders than their Canvasback brood mates. Aggression between brood mates was observed in 5 mixed broods in which Redhead ducklings attacked and dominated Canvasbacks in 14 encounters. Although Redheads were more aggressive to Canvasback brood mates, the number of aggressive encounters initiated by Redheads to Canvasback or to Redhead brood mates did not differ significantly ( $X^2 = 3.0$ ,  $p > .05$ ), possibly due to the small sample of broods in which aggression was observed. There were no attacks initiated by Canvasback ducklings to Redhead brood mates.

Tolerance of brood hen and ducklings: To determine the tolerance of the brood hen and ducklings to non-brood members, a space around a given mixed brood was defined using three previously mentioned categories: 0-10, 11-20 and 21-30 feet. Because there was an age-dependent increase in the distance over which the brood mates were spaced (see Table 9) the distance of an intruding individual was estimated from the nearest brood member. The maximum penetration of this 0-30 foot space was determined for those observations in which non-brood members were observed in the vicinity of mixed broods. For example, if an intruder was recorded within 0-10 feet from at least one brood member for a given 10-min observation, it was credited with passing through the 11-20 and 21-30 foot intervals

unless it remained in the 0-10 ft interval for more than one observation period in which case it was recorded as passing through the other intervals only once. The number of observations in which intrusions were observed in the specified intervals therefore represents a cumulative record of violations of this "brood space". The per cent of these intrusions in which aggression was recorded for the brood hen or ducklings is presented in Table 14. To facilitate comparisons between hens and the brood to determine their relative effectiveness in maintaining a "brood space", ducklings in a given brood were considered as a "unit".

For hens attending broods in the Class I stage of development, aggression was observed for 67% of the intrusions in the 0-10 ft interval compared to 7% and 3% in the 11-20 and 21-30 ft intervals respectively (Table 14). In Class II, however, brood hens became more tolerant of intrusions (2x2 test,  $\chi^2 = 38.9$ ,  $p < .001$ ) responding to 19% of the intrusions in the 0-10 ft interval and to only 1% in the 11-20 ft interval. In conjunction with the observed decrease in aggression by hens there was a significant (2x2 test,  $\chi^2 = 35.5$ ,  $p < .001$ ) increase in the proportion of observations in which intrusions occurred in the 0-10 ft interval by non-brood members between Class I and Class II (Table 14), probably due, in part, to increased spacing of brood mates (see Table 9) and the resulting increase in the

TABLE 14. Aggression by brood hens and ducklings to individuals in proximity to the brood.

Age class	Distance <sup>a</sup>	Number of observations <sup>b</sup>	Per cent aggression per intrusion by	
			brood hen	ducklings
I	0-10	42	67	0
	11-20	58	7	0
	21-30	78	3	0
II	0-10	189	19	28
	11-20	189	1	0
	21-30	209	0	0
III	0-10	15	0	13
	11-20	19	0	0
	21-30	22	0	0

<sup>a</sup>Distance in feet from nearest brood member.

<sup>b</sup>Number of observations in which individuals were recorded in the specified intervals.

probability that other birds will be in their vicinity.

In Class I, broods were never aggressive. Aggression increased significantly in Class II broods (2x2 test,  $X^2 = 15.3$ ,  $p < .001$ ). Class II broods were significantly more aggressive than Class II hens (2x2 test,  $X^2 = 4.3$ ,  $p < .05$ ), due primarily to the absence of hens in 69% of the observations for subclass IIc (see Table 10). Brood aggression in Class II was, however, considerably less than for hens in Class I (2x2 test,  $X^2 = 38.9$ ,  $p < .001$ ), suggesting that ducklings may never be as aggressive as hens with Class I broods. Brood aggression remained consistent (2x2 test,  $X^2 = 1.4$ ,  $p > .05$ ) between Class II and Class III even though there was a significant decrease (2x2 test,  $X^2 = 13.0$ ,  $p < .001$ ) in the number of intrusions.

#### Agonistic Displays

Neck-stretch display: The function of the Neck-stretch display in courtship and pair maintenance has been described for both the Canvasback and Redhead by Hochbaum (1944) and Johnsgard (1965) and for the Redhead by Weller (1967). In giving the display, a male Canvasback "raises his head as high as the neck, held stiff and straight, will reach . . . sometimes turning his head stiffly from one side to the other, or bobbing his bill" (Hochbaum 1944: 23-24). Neck-stretching is an element of the inciting display of Canvasback females but may be given in response to a male's

display. In males it serves as both a hostile display and sexual display (Johnsgard 1965). The display also occurs in Redhead females but "lacks such extreme Neck-stretching as occurs in the Canvasback" (Johnsgard 1965: 232). The display is also given by males, but as in the female, is given less frequently and is not as conspicuous as the comparable display in Canvasbacks. Within broods, the display can be initiated by either the hen or one or more of the ducklings. Other members of the brood may respond by also giving the display.

Hochbaum (1944: 20) observed the display in downy (Class I) Canvasback and Redheads and suggested that it was a fear reaction in birds of this age. In mixed broods at Minnedosa, the Neck-stretch display was first observed in subclass Ic (Table 15), when all brood members, including brood hens, were observed to initiate the display. Although the frequency of the display was variable between subclasses, there was no significant change (Table 15B) in frequency from subclass Ic through to the end of subclass IIc, after which the display was not seen. Based on the number of Redhead and Canvasback ducklings (Table 16) there was no significant difference ( $\chi^2 = 1.6$ ,  $p > .05$ ) in the observed frequency of displays between species.

The context in which Neck-stretch displays were given was variable. In order of decreasing frequency, displays were observed when broods were moving from place

TABLE 15. Per cent of intervals in which the Neck-stretch display was initiated by the brood hen or ducklings for observations out of cover. Totals are given in parenthesis.

A. Age of brood	Brood hen	Ducklings	
		Redhead	Canvasback
Ic	7% (5)	6% (6)	21% (20)
IIa	4 (2)	5 (3)	11 (6)
IIb	3 (2)	12 (13)	6 (5)
IIc	0.9 (2)	6 (18)	8 (20)

B. Statistical comparison <sup>a</sup>	Brood hen	Redhead	Canvasback
Ic vs IIa	Ic > IIa, N.S.	Ic > IIa, N.S.	Ic > IIa, N.S.
IIa vs IIb	IIa > IIb, N.S.	IIa < IIb, N.S.	IIa > IIb, N.S.
IIb vs IIc	IIb > IIc, N.S.	IIb > IIc, N.S.	IIb < IIc, N.S.

<sup>a</sup>Comparisons based on 2x2 test (Ferguson 1959).

TABLE 16. Number of observations of the Neck-stretch display initiated by Redhead and Canvasback ducklings.

Brood number	Number of Redhead ducklings	Number of Canvasback ducklings	Observations of neck-stretch	
			Redhead	Canvasback
1	3	3	2	9
2	2	2		3
3	2	4	2	7
4	4	3	2	
5	4	5	4	1
7	5	3	7	10
8	3	1	8	
9	4	3	9	2
10	1	5	2	12
11	4	3	4	6
12	3	2		1
<hr/>				
Totals				
11	35	34	40	51

to place, during bouts of feeding, loafing, or after aggressive encounters. In many cases, the display did not appear to be directed to a specific individual, and there were several instances in which no obvious response was given by brood mates. In response to the Neck-stretch display, brood mates also displayed.

The frequency of response by brood mates to displays initiated by hens and Redhead or Canvasback ducklings is documented in Table 17. Both Canvasback and Redhead ducklings responded equally well (2x2 test,  $\chi^2 = .7$ ,  $p > .05$ ) to displays initiated by brood hens. Similarly, when the display was initiated by Redhead ducklings, the response by other Redhead and Canvasback brood mates did not differ. When displays were initiated by Canvasbacks, however, the Canvasback ducklings responded significantly (2x2 test,  $\chi^2 = 6.6$ ,  $p < .02$ ) more than Redheads. In addition, the response of Canvasbacks was greater ( $\chi^2 = 8.7$ ,  $p < .01$ ) when Canvasbacks initiated the display than when it was initiated by Redheads. Redheads, in contrast, responded equally (2x2 test,  $\chi^2 = .38$ ,  $p > .05$ ) to displays initiated by both species.

Head-throw: Johnsgard (1965) described the Head-throw display as a "toss of the head back 180 degrees to the base of the tail." Detailed descriptions of the Head-throw and its function in the courtship of male Canvasbacks and Redheads are given by Hochbaum (1944) and



TABLE 17. Response frequency by brood mates to Neck-stretch displays initiated by brood hens and Redhead and Canvasback ducklings.

Display initiated by	Number of obs. Neck-stretch	Response by <sup>a,b</sup>			No response
		Canvasback	Redhead	Hen	
Brood hen	11	7	4	-	2
Canvasback	51	22	10	5	19
Redhead	40	5	10	5	21

<sup>a</sup>Response by at least one individual.

<sup>b</sup>Responding individuals also gave the display.

Weller (1967). Weller (1967) summarized the differences in the display between the two species as "extreme and fast versus short and slow" for Redheads and Canvasbacks respectively. Both Hochbaum (1944: 21) and Weller (1967) have observed the display in young Redheads, 7½-12 weeks of age.

In the present study, indications of this display were first observed in subclass Ic, in which a Canvasback duckling gave a "partial" Head-throw. Other observations include 10 in subclass IIc and 2 in Class III, of which Redheads gave the display 8 times and one time respectively. In two separate 10-min observation periods, the display was given 3 times by two Redheads and two times by two Canvasback ducklings.

The context in which the displays were given was variable. In one observation the display preceded aggression initiated by the displaying duckling. The display was observed in lone individuals (> 10 ft from brood mates) and individuals in close association with brood mates. In two cases, the previously mentioned Neck-stretch display was given after the Head-throw by the displaying individual. The Kinked-neck call (Weller 1967) was associated with only one Head-throw display but was heard at least two other times in subclass IIc broods.

## DISCUSSION

### Brood Integration

Under natural conditions, normal brood integrity is determined by the age of the ducklings and the stage which the brood hen has reached in the annual reproductive cycle (Beard 1964). Early in the brood period, the presence of the hen promotes brood integration by providing for the developing ducklings a combination of visual and auditory stimuli upon which they can imprint. In addition, the parent also provides tactile and thermal stimulation (Gottlieb and Simmer 1969). The importance of the hen as an integrating factor has been described by Collias and Collias (1956). As a result of the normal establishment of parent-young relationships, the ducklings perform most of their activities within a certain distance of the hen (Bateson 1963) which gradually increases as the brood becomes older.

For mixed broods, the results of Part I of this study suggest, in accordance with the findings of Beard (1964), age-dependent factors effecting the integration of Redhead and Canvasback brood mates. In conjunction with, and partially as a result of the increased absence of brood hens and the occurrence of permanent desertions in subclass

IIc (see Table 10), several significant changes occurred in the behavior of the developing ducklings. Brood mates became increasingly independent (see Table 7) and as the age of the ducklings increased, comparable increases occurred in the spacing of mixed broods (see Table 9) particularly during bouts of feeding.

During this time, the aggressive behavior of the brood hen and ducklings, when directed to other hens and ducklings is thought to maintain brood spaces and reduce additions to the brood, thereby maintaining brood size within manageable limits (Collias and Collias 1956). In the present study, aggression directed at non-brood members also occurred, and hence may have acted as an integrating mechanism. Although ducklings were significantly more aggressive than hens attending Class II broods, it should be noted that their success in maintaining the "brood territory" was not as great as the brood hens' success in Class I. Hence, as aggression and active defense by the hen declined with the increasing absence of brood hens in Class II (see Table 14), there was a decrease in size of the actual area defended. Similarly, ducklings and hens attending Class II broods were more tolerant of intrusions in the 11-20 ft interval (see Table 14). The integrating effects of aggression, therefore, appear to decline as broods become older. Despite these changes over the brood period, however, relatively few observations occurred in

which there was actual segregation between Redhead and Canvasback ducklings. Although daily activities were conducted over increasingly greater distances, brood mates remained responsive to each other, and where groups of ducklings occurred, there was frequent interchange. This result suggests that other integrating mechanisms were present.

Several investigators have recorded the use of calling by hens to direct broods (Bennet 1938; Hochbaum 1944; Sowls 1955; Mendell 1958; Beard 1964). Importance has also been ascribed to duckling contentment twitters (Collias and Collias 1956). Visual stimuli are also known to attract ducklings (see Sluckin 1965; Bateson 1966). Similarly, the ability of both parasitic Redhead and Canvasback ducklings to respond to both visual and auditory stimuli (Part II, this thesis) presumably facilitates early parent-young relationships and brood integration.

#### Brood Segregation

In typical, non-parasitic Anatinae, parent-young relationships and bonds between brood mates begin to deteriorate as the brood becomes older (Beard 1964). Parental vocalizations typically decrease and the hen leaves the brood more frequently and no longer attempts to maintain a tight brood formation. The ducklings feed over greater distances and at approx. 5 wks become increasingly

independent (Bennet 1938; Mendall 1958; Beard 1964). Comparable results were obtained in the present study for mixed broods of Canvasback and Redhead ducklings.

For single species families, Beard (1964) documented final and complete break-up to occur where young were 7-8 wks old but both Munro (1949) and Beard (1964) state that it was common to see ducklings at this age accompanied by hens. Observations on Canvasbacks and Redheads in mixed broods by Weller (1959) indicate that when ducklings were approximately 4 wks old, they segregated into species groups in the course of their daily activities. Collias and Collias (1956), however, never achieved complete segregation between Redhead and Canvasback ducklings under the conditions of their study. Similarly, for the mixed broods observed on small water habitats in the present study, segregation of the brood mates into species groups was never complete. Even during the last week of the flightless period, when broods were 8-9 wks old, species segregation was observed in only 16% of the observations.

Weller (1959), in agreement with the findings of Collias and Collias (1956) that Redhead ducklings were dominant over Canvasbacks (as evidenced by aggressive encounters) suggested that interspecific aggression within the brood was one possible reason for the segregation he observed between species in mixed broods. In addition, he suggests that the reported tendency for the Redhead

ducklings to be lost from mixed families (Erickson 1948) may be a result of increased interspecific aggression between the brood mates. For the mixed broods observed during the present study, Redheads were significantly more aggressive to non-brood members than were Canvasbacks but were not significantly more aggressive to Canvasback than to Redhead brood mates (see Table 13). Although the sample size indicated in Table 13 is not large, these results raise some question as to the extent to which interspecific aggression would be expected to segregate Redhead and Canvasback ducklings into species groups. In agreement with this interpretation, it can be noted that although there were increases in brood spacing coincident with interspecific aggression in Class II (see Table 9), there were no instances of permanent segregation in any of the broods observed at that time. Although experimental proof is lacking, it remains possible that observed intra-brood aggression might tend to produce segregation, but this tendency was counteracted, at Minnedosa by the close confines of the small pothole habitat in which these broods were reared.

#### Species Recognition

The differences in frequency of aggression initiated by Redhead and Canvasback ducklings provide one possible stimulus basis for the development of recognition of species

by ducklings in mixed broods. Evidence obtained in this study (above, and Part II) suggests that species differences in response to displays may also be relevant.

The Neck-stretch display was observed in brood hens as well as Redhead and Canvasback ducklings. Although the context in which the displays were given was variable, the fact that the Neck-stretch display was observed in conjunction with disturbances involving the brood (Hochbaum 1944; this study) suggests that the display has a possible integrating function, particularly when brood hens were present. Differences in the form which the display takes between Canvasback and Redhead ducklings have been recorded, however, and analysis of my data (Table 17) revealed differences in the response of Redhead and Canvasback ducklings. In particular, Canvasback ducklings responded significantly more to displays given by Canvasbacks than by Redheads. It is possible, therefore, that the Neck-stretch may serve as a cue for subsequent species recognition, at least in the Canvasback. Species differences in other visual displays such as the Head-throw, and differences in voice, provide additional possibilities for species recognition. The reduced auditory discrimination learning, found in the Redhead (Part II, this thesis) raises the interesting possibility that innate responses to auditory stimuli (cf Gottlieb 1971) may be particularly important for species recognition in parasitic Redhead ducklings.



PART II. IMPRINTING OF THE YOUNG

## INTRODUCTION

The occurrence of egg parasitism has been well documented for the Redhead Aythya americana, a semiparasitic species of waterfowl (Weller 1959). Three distinct types of nest behavior are found in different individual females: normal nesting, semiparasitism and obligate parasitism. Because of the similarities in breeding range and habitat preference, the Canvasback Aythya valisineria is the principal host species. This condition commonly results in the formation of mixed broods of Redhead and Canvasback ducklings (Weller 1959; Part I, this thesis).

As a brood parasite, an individual Redhead duckling appears to be faced with two special problems: it must recognize the foster parent to maintain continuity of parental care, and it must be able to recognize its own species for biologically correct mate selection. Because a foster parent will brood a Redhead duckling much as she would her own young (Weller 1959), the solutions to the above problems must rest with the early development and behavior of the parasitic duckling. Investigation of this development constitutes the primary objective of Part II of this thesis.

### Species Recognition

Sluckin (1965) states that sexual responses may be directed to objects which resemble those to which filial responses were directed, including foster parent species (see also Craig 1908, 1914; Goodwin 1948; Lorenz 1955; Steven 1955; Heinroth and Heinroth 1959; Hess 1959; Kear 1960). Courtship fixations to foster species are not necessarily irreversible, in that the fixated individual may still mate successfully with its own species. Reports of such reversals have been advanced for pigeons Columba livia (Goodwin 1948), a female Hawfinch Coccothraustes coccothraustes (Kear 1960), the Mallard Anas platyrhynchos (Shutz 1965) and for several species of waterfowl at the Wildfowl Trust in Slimbridge, England where domestic hens are commonly used as foster parents (Fabricius 1962). Bateson (1966) states that in some cases, mate selection is determined by the early filial preference. He cites the parasitic species however, as evidence that correct mate selection does not always depend on visual imprinting early in the life of the individual.

Early workers (Ramsay and Hess 1954) have demonstrated that naive young chicks Gallus gallus can exhibit a preference for the parental calls of their own species without prior experience with them. More recently, such species recognition of vocalizations has been demonstrated even before visual imprinting has occurred (Gottlieb 1965,

1966, 1971). The strength and early occurrence of this recognition prompted Gottlieb (1965) to state that visual imprinting, although important, plays only a "supporting role" in species recognition. Ducklings apparently exhibit no species specific visual preference when auditory stimulation is withheld (Gottlieb 1971). Published accounts thus provide evidence that species recognition by voice may occur in the absence of prior experience with species typical vocalizations. They also suggest that visual imprinting, although relevant, may be of secondary importance, thus permitting correct mate selection even when young are reared by foster parents.

#### Individual Recognition

The mechanisms responsible for an early development of recognition and attachment to individual parents have been less thoroughly studied (Beer 1970b). Observations of artificially created mixed families have been employed by several workers to investigate some aspects of the formation of family bonds and parent-young relationships (Schooland 1942; Cushing and Ramsay 1949; Collias and Collias 1956). Cushing and Ramsay (1949) and Ramsay (1951) suggested that filial attachments may be established by an imprinting process which acts at the time of hatching. Collias and Collias (1956) have advanced a somewhat contrasting view. Their observation of a poor following response in Mallard

ducklings raised with a Ring-necked Duck foster parent suggests that other mechanisms may operate to facilitate normal family intergration and segregation. Alley and Boyd (1950) considered parent-young relationships only as part of the larger problem of species recognition.

Bateson (1966) has suggested that individual recognition may constitute a result of visual imprinting. Other evidence however, indicates the importance of the auditory modality for an early development of individual recognition (Ramsay 1951; Tschanz 1965, 1968; McBride et al 1969; Beer 1969, 1970a; Evans 1970a, 1970b; Stevenson et al 1970; White 1971). Although the mechanisms for early auditory learning remain doubtful (Beer 1970b), a recent study (Evans and Mattson 1972) provides evidence that in domestic chicks, early learning of individual parental vocalizations may be mediated by association with a familiar visual stimulus (see also Evans 1972).

#### Semiparasitic Species

Although there are numerous publications devoted to early learning and imprinting in young birds (Sluckin 1965; Bateson 1966), there is a paucity of information on imprinting in semiparasitic and parasitic species of waterfowl. Because of the parasitic nature of the Redhead, Collias and Collias (1956) suggested that a Redhead duckling might have a strong tendency to follow a foster parent. Weller (1968) however, questions the occurrence of imprinting

in parasitic species. He states, as evidence, the reported tendency of Redhead ducklings to leave rather than remain with the foster parent (Weller 1959). This same tendency has been reported for the completely parasitic Black-headed Duck Heteronetta atricapilla (Weller 1968). In at least some habitats however, it has been found (Part I, this thesis) that many mixed broods of Redhead and Canvasback ducklings remain intact at least until the end of the flightless period, thus casting doubt on the generality of the earlier findings.

Evidence described above indicates that in non-parasitic species, auditory discriminations and to a lesser extent, visual imprinting, are both involved in the normal establishment of parent-young relationships and species recognition. The situation in semiparasitic species however, remains obscure. The present study was designed to examine the possibility that the capacity to learn discriminations in the auditory and visual modalities may differ between a parasitic species, the Redhead, and a closely related non-parasitic species, the Canvasback.

## MATERIALS AND METHODS

### Subjects

Canvasback and parasitically laid Redhead eggs were collected at Delta, Manitoba from wild nests, the Redhead eggs from either Canvasback nests or Redhead "dump nests" (Weller 1959). Eggs were placed in a forced-draft humid-air incubator until the pipping stage at which time they were transferred to individual compartments in an electrically operated, still-air hatching tray where they were allowed to hatch. After drying, each duckling was individually marked with a felt marking pen and placed in the rearing facilities. A total of 16 Redhead and 16 Canvasback ducklings was used.

### Rearing Conditions

Ducklings were reared in a sound-attenuated cupboard provided with a continuous background of white noise produced by a Grason-Stadler Model 901B generator. Within the cupboard, species groups of 4-6 individuals were placed in separate rearing cages constructed of plywood and finished with low gloss grey paint. Each cage measured 50 cm x 35 cm x 25 cm high. A wire-mesh floor ensured traction for the developing ducklings. Continuous light and heat were supplied by a 25 watt incandescent bulb placed

near the top of each cage. Room temperature was held at approximately 30 C. Food was withheld for the duration of the experiment. Water was provided ad lib.

### Apparatus

A separate sound-attenuated room housed both the training and test pens. As for rearing, a continuous background of white noise was provided.

Visual training: Three identical, grey plywood pens were used for visual training. Individual pens measured 80 cm x 50 cm x 25 cm high. A plywood partition divided each pen into two 40 cm x 50 cm x 25 cm high training compartments, an arrangement which allowed six ducklings to be trained simultaneously. Traction was provided by mixing fine sand into the floor paint. The end of each training compartment was partitioned into a 10 cm section by a 1.26 cm wire screen. These end sections contained a conspicuous visual stimulus attached to the lower end of a moveable pendulum which was driven through an arc of approximately 10 cm at a rate of 35 cycles per min. By arranging the training pens in parallel, it was possible to drive all six pendulums by a single electric motor.

Auditory discrimination training: This was conducted in two identical grey, plywood "tip-floor" pens of the type previously used to train domestic chicks (Evans 1972). Pens measured 117 cm x 40 cm x 30 cm high above the level of the tip floor. A section 30 cm in length was partitioned off at



each end of the pen by a 1.26 cm wire screen. The center compartment consisted of a 57 cm tip floor, constructed in such a way that either end could be depressed by the weight of a duckling.

In each end compartment was placed a conspicuous visual stimulus on the lower end of a pendulum, as previously described, and a loud speaker fixed to the floor behind the visual stimulus. Each loud speaker was wired to two Sony Model TC 800 tape recorders, modified for an increase in amplification. Synchronization between the output from each tape recorder and the onset and duration of the visual stimuli was accomplished by the use of a time interval generator. The auditory and visual stimuli were also controlled by separate microswitches located under the tip floor in such a way that when a duckling approached the stimuli active at one end of the pen, these would be deactivated and the stimuli at the other end of the pen would be activated. This arrangement created a continuous "approach" schedule: regardless of the stimulus or combination of stimuli used, the duckling was always in a position where it could approach the stimuli which were active at the opposite end of the pen.

A continuous record of a duckling's approach responses and "jumps" when at either end of the pen, was obtained from an Esterline Angus event recorder connected to a third microswitch located under the tip floor. The

schedule of auditory and visual stimulus presentation was automatically controlled by a time interval generator. A record of stimulus presentation during the training procedure was also obtained by connecting the time interval generator to the event recorder.

Testing: By appropriately altering the combination of stimuli used and the schedule of stimulus presentation, the above described tip-floor pens were also used for testing auditory and visual discriminations.

### Stimuli

Sluckin (1965) and Bateson (1966) reviewed the findings of several investigators that a variety of visual stimuli elicit approach responses in ducklings and chicks. The present experiment employed stimulus patterns similar to those successfully used by Smith and Hoyes (1961), Evans (1972) and Evans and Mattson (1972). Two visual stimuli were used: a 12.5 cm white cardboard disc and a 12.5 cm white, two-dimensional, cardboard square. To make these stimuli more conspicuous (see Bateson 1964a), 1.9 cm vertical green stripes were affixed to the circle, 1.9 cm horizontal brown stripes to the square. Movement of the pendulums to which these patterns were attached further enhanced the attractiveness of the visual stimuli by producing the "visual flicker" effect described by James (1959). In a preliminary simultaneous choice test conducted with 12 naive Mallard ducklings, the two visual stimuli were

found to be equally attractive ( $T = 30$ ,  $p > .10$ , Wilcoxon matched-pairs signed-ranks test).

Previous workers have found that a sporadic oscillating movement (Salzen and Sluckin 1959a; 1959b) and movement at right angles to the subject's line of vision (Smith 1960; Smith and Hoyes 1961), enhance the attracting power of a visual model. In this study therefore, as in Evans (1972), the definition of a "visual stimulus" in subsequent text will apply only when the pendulum to which it is attached is activated. A motionless model, although it remains in full view of the subject, will not constitute a visual stimulus (see also Hoffman et al 1970).

The characteristics of the two auditory stimuli employed in the experiment were similar to those that have been previously found to attract chicks (Collias 1952; Collias and Joos 1953) and wild ducklings (Collias and Collias 1956). Each of the calls consisted of five repetitions of a low pitched, voice-produced component note (Fig. 1). The component note in one call was the word "plop"; in the other call the word "brupp", a note which has been found to attract domestic chicks (Evans 1972). Both calls were produced as variations of the word "kuk", described by Collias and Collias (1956) as the component note of the Canvasback broody call and by Weller (in Collias and Collias 1956) as a note similar to that in the Redhead broody call.

FIGURE 1. Sonograms of the auditory stimuli employed in auditory discrimination training; top "Plop" call, bottom "Brupp" call. K-missilizer setting: 50-5000 cps, wide band.

KC PER SEC

0 1 2 3

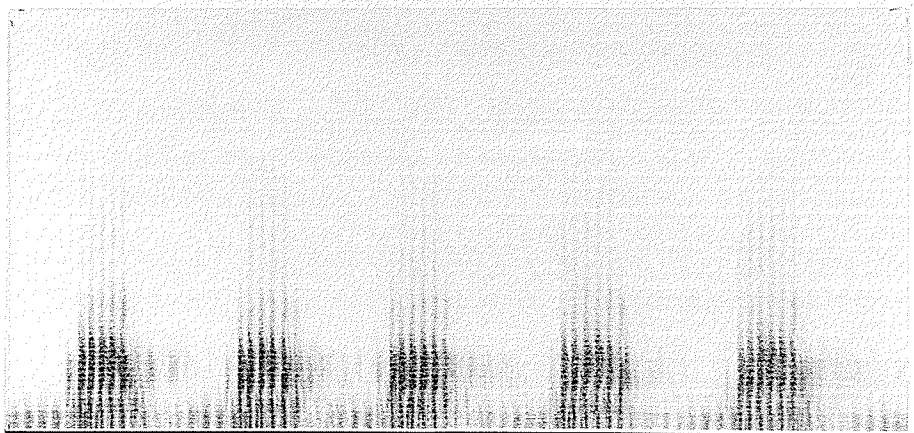
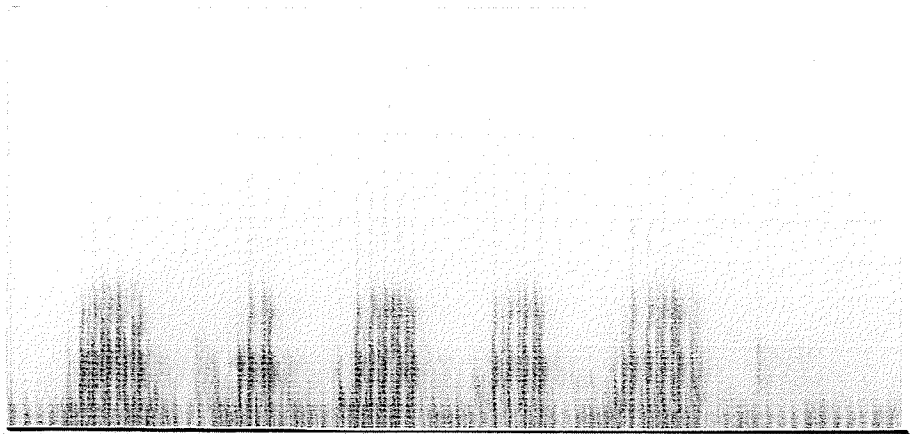
KC PER SEC

0 1 2 3

0

.5  
SEC

1.0



Sonogram analysis revealed that the calls also differed in frequency and to a lesser extent, duration. The "plop" call contained sound up to approximately 2500 c.p.s. with the maximum sound pressure occurring from 50-1065 c.p.s. compared to sound up to 2685 c.p.s. for the "brupp" call with a maximum sound pressure range of 50-695 c.p.s. Duration of the "plop" call was .98 secs compared to 1.05 secs for the "brupp" call. A continuous tape loop was made for each call and the call rate was equated between the loops at approximately 25 per minute.

#### Training Procedure

Initial visual training was conducted when the post-hatch age was from 12-20 hrs. Ducklings of known age ( $\pm 1$  hr) were placed individually in the visual training pens where they received 6 hr massed exposure to one of the moving models. Stimulus presentation was balanced so that one-half of the ducklings of each species was trained with each visual stimulus. The model to which a given duckling was trained will hereafter be referred to as the "visual imprinting stimulus".

Auditory discrimination training commenced from 24-30 hr post hatch. The ducklings were placed singly in the tip-floor pens which contained their visual imprinting stimulus affixed to each pendulum. Each duckling was trained for 8 successive 10-min periods; each period consisted of a 5-min interval with one of the calls presented

in association with the visual imprinting stimulus activated and the other 5-min interval with the other call presented with the pendulums deactivated. The visually associated auditory stimulus will be referred to as  $S^+$  in the following text, the other auditory stimulus as  $S^-$ . Stimulus presentation was scheduled independently for each of the two tip-floor pens. This arrangement allowed one duckling to receive a given auditory stimulus as  $S^+$  while the same auditory stimulus constituted  $S^-$  for the duckling in the other pen. One-half of the ducklings of each species received the "plop" call as  $S^+$ ; the other half the "brupp" call as  $S^-$ .

#### Testing Procedure

The auditory discrimination test commenced 5 min after the completion of training. The test procedure lasted for 3 successive 10-min periods. As in training each 10-min period was divided into two 5-min intervals, one for presentation of  $S^+$ , the other for  $S^-$ . For the test procedure, however, the visual stimuli were never activated although they remained attached at all times to the motionless pendulums at either end of the apparatus. The number of times each duckling crossed the tip-floor and the number of "jumps" while at either end were recorded.

During the test procedure, any consistent, differential response rate to  $S^+$  and  $S^-$  constituted evidence that

the ducklings could discriminate between them and, further, that learning had occurred as a result of the training procedure.

To determine if the ducklings had acquired a preference for, or imprinted to the visual imprinting stimulus, a simultaneous choice test was conducted at approximately 36 hr post hatch, at least 5 hr after the termination of the preceding auditory tests. Ducklings were placed singly in the tip-floor pens. The visual imprinting stimulus was placed on the pendulum in one end compartment; the second unfamiliar visual stimulus at the other end. Both pendulums were activated and remained so for the duration of the test. Auditory stimulation was withheld. Each duckling was released on the tip-floor on the side opposite the visual imprinting stimulus. For each duckling, the number of jumps in the apparatus and the time spent in the side of the pen nearest the visual imprinting stimulus were recorded for 3 successive 10-min intervals.

#### Treatment of Data

Unless otherwise stated, significance levels are based on Wilcoxon matched-pairs signed-ranks tests for correlated samples and Mann-Whitney U tests for independent samples (Ferguson 1959).

To facilitate interpretation of the results, a test score (see Evans 1972) was calculated for data from each



individual, based on the number of responses to  $S^+$  and  $S^-$  during the training or testing periods:

$$\text{Test score (\%)} = \frac{S^+ - S^-}{S^+ + S^-} \times 100$$

Test scores so calculated are independent of absolute response rates, but can range from minus 100% to plus 100% depending on the relative number of responses to  $S^+$  or  $S^-$ . The presence of zero scores would indicate no preferential response to either stimulus.

## RESULTS

### Learned Discriminations

Visual: The establishment of a marked preference for the visual imprinting stimulus was evident for both species. Of the 16 Redhead ducklings tested, 15 spent most of the test period nearest the familiar stimulus ( $\chi^2 = 12.25$ ,  $p < .001$ ). Similarly, 15 Canvasback ducklings registered a positive response in the test situation ( $\chi^2 = 12.25$ ,  $p < .001$ ). Redheads spent 81% of the total time in the test apparatus with their visual imprinting stimulus compared to 83% for Canvasback ducklings.

The average time positive, standard deviation and the observed range of responses for each of the 3 successive 10-min test periods are given in Table 18. Although the range of responses for Redhead ducklings was greater, there was no significant difference ( $U = 120.5$ ,  $p > .10$ ) between the individual response times of the two species. The median time positive was 1573 secs for Redhead ducklings compared to 1671 secs for Canvasback ducklings.

Auditory: Only Canvasback ducklings were able to effectively discriminate between the  $S^+$  and  $S^-$  stimulus conditions (Tables 19 and 20). For the training session, all 16 Canvasback ducklings exhibited a greater number of

TABLE 18. Average time positive, standard deviation and the observed range of responses for Canvasback and Redhead ducklings during the 10-min visual test periods.<sup>a</sup>

Test period	Canvasback			Redhead		
	Mean	S.D.	Range	Mean	S.D.	Range
1	534.3	95.8	326-600	504.6	123.4	270-600
2	500.1	139.5	210-600	499.7	142.7	195-600
3	464.3	140.1	259-600	475.7	148.0	0-600

<sup>a</sup>Time in seconds.

approaches to  $S^-$  ( $T = 0$ ,  $p < .01$ , two-tailed test). For the test session, a similar response was observed for 14 of the Canvasback ducklings ( $T = 12$ ,  $p < .01$ ). In contrast, only nine Redhead ducklings registered a greater number of approaches to  $S^-$  during both the training ( $T = 62$ ,  $p > .05$ ) and test sessions ( $T = 67$ ,  $p > .05$ ). Canvasbacks exhibited a significant preference for the "plop" call ( $U = 9.0$ ,  $p < .05$ ). Redhead ducklings however, showed no preference for either call ( $U = 24.5$ ,  $p > .05$ ).

For the Canvasback ducklings, the average number of approaches to  $S^-$  remained relatively uniform from the first training period to the completion of the test session (Table 19). The proportion of responses given during the  $S^-$  stimulus condition increased however, due to a decrease in the number of approaches to  $S^+$  as training progressed. Redhead ducklings exhibited a comparable response pattern, in that a minor decrease is evident in the average number of approaches during the presentation of  $S^+$  and the approaches to  $S^-$  are relatively constant (Table 20). In both species, responses to  $S^+$  during testing showed an initial increase followed by an apparent decline. Differences between  $S^+$  and  $S^-$  decreased significantly with successive testing for Redheads ( $p < .05$ , Friedman two-way analysis of variance by ranks). The response selectivity of the Canvasback ducklings however, remained stable during the test periods ( $p > .05$ ).

TABLE 19. Average number of approach responses given by Canvasback ducklings to auditory stimuli either paired with a visual stimulus ( $S^+$ ) or presented alone ( $S^-$ ) during training.

Successive 10-min periods	Responses to $S^+$		Responses to $S^-$		Sig. level <sup>a</sup>
	mean	S.D.	mean	S.D.	
Training					
1	20.0	17.1	30.4	18.0	.01
2	19.3	13.1	36.3	16.9	.01
3	14.6	8.6	37.9	17.2	.01
4	11.2	6.6	33.7	14.2	.01
5	11.1	6.4	36.3	15.7	.01
6	9.9	5.0	34.6	16.0	.01
7	9.1	4.2	34.9	14.4	.01
8	9.3	4.5	33.4	14.8	.01
Testing					
1	26.2	15.2	38.9	14.8	.01
2	19.6	14.4	30.0	12.3	.05
3	15.6	13.9	30.3	13.3	.01

<sup>a</sup>Significance levels are based on Wilcoxon matched-pairs signed-ranks tests.

TABLE 20. Average number of approach responses given by Redhead ducklings to auditory stimuli either paired with a visual stimulus ( $S^+$ ) or presented alone ( $S^-$ ) during training.

Successive 10-min periods	Responses to $S^+$		Responses to $S^-$		Sig. level <sup>a</sup>
	mean	S.D.	mean	S. D.	
Training					
1	19.7	12.9	16.6	7.1	n.s.
2	23.6	10.3	19.1	10.4	n.s.
3	19.6	11.7	19.7	9.4	n.s.
4	21.1	13.5	19.9	9.0	n.s.
5	17.0	12.5	18.8	9.7	n.s.
6	17.9	12.6	22.2	8.6	n.s.
7	17.5	14.3	21.3	11.1	n.s.
8	17.8	12.3	21.1	9.3	n.s.
Testing					
1	21.6	15.6	18.6	8.1	n.s.
2	17.4	11.8	19.0	9.1	n.s.
3	18.0	8.9	19.1	5.7	n.s.

<sup>a</sup>Significance levels are based on Wilcoxon matched-pairs signed-ranks tests.

To further compare the number of approaches of Redhead and Canvasback ducklings to both auditory stimulus conditions, statistical tests were conducted between the response totals of individual birds for each species during the training and test sessions (Table 21). There was no significant difference between species in the number of approaches to  $S^+$ . The primary difference between the species appeared to be in the number of approaches during the presentation of  $S^-$ , which were significantly greater ( $p < .01$ ) for Canvasback ducklings for both the training and test periods.

Test Scores: Rank correlation coefficients were calculated using the test scores of individual birds for both species to determine if a relationship existed between the relative number of approaches given to  $S^+$  and  $S^-$  during training and the subsequent test session. A significant relationship was found for Redhead ( $r = .594$ ,  $p < .05$ ) but not for Canvasback ducklings ( $r = .262$ ,  $p > .05$ ). This difference was possibly due to a marked increase in the number of approaches and jumps to  $S^+$  by Canvasback ducklings during the test session.

### Jumps

Additional evidence concerning the acquisition of the capacity to discriminate between the  $S^+$  and  $S^-$  stimulus conditions was obtained through the analysis of the number

TABLE 21. Significance levels for tests conducted between the individual response totals for each species during the training and test periods. Comparisons are based on the number of approaches.

Comparison made	Value of U <sup>a</sup>	Sig. level
Training		
Canvasback vs Redhead		
s <sup>+</sup>	U = 77.5	p > .05
s <sup>-</sup>	U = 42	p < .002
Testing		
Canvasback vs Redhead		
s <sup>+</sup>	U = 120	p > .10
s <sup>-</sup>	U = 35	p < .002

<sup>a</sup>Significance levels are based on the Mann-Whitney U test for independent samples.



of jumps by Redhead and Canvasback ducklings during the training and test sessions. Because of the small number of jumps to  $S^+$  during training, values for each bird were obtained by dividing the total number of times it jumped to  $S^+$  or  $S^-$  during training or testing by the number of 10-min periods in that particular stimulus condition, to give the average number of jumps per training or test period (Table 22). Jumps during visual testing were also included for comparison. To facilitate comparisons between the jumps and approach responses, the average number of crosses per 10-min period were also calculated and included in Table 22.

The greatest number of jumps occurred in those periods in which the visual imprinting stimulus was either deactivated or else presented in association with a strange visual stimulus as it was in the visual discrimination test. Both jumps and approaches were prominent responses of Canvasback ducklings to the  $S^-$  and, to a lesser extent, the  $S^+$  test condition. The average number of jumps performed by Redhead ducklings reveal a similar trend but the differences are less great (Table 22).

Significance levels given in Table 23, based on response totals of individual birds, demonstrate that both Redhead and Canvasback ducklings registered a significantly greater number of jumps to  $S^-$  than to  $S^+$  during the training session. Only the Canvasback ducklings however showed a

TABLE 22. Average number of approach responses and jumps per 10-min of training and testing for Canvasback and Redhead ducklings. Jumps given during the visual test session are included for comparison.

Stimulus condition	Canvasback (n = 16)			Redhead (n = 16)		
	Approaches mean	Approaches range	Jumps mean range	Approaches mean	Approaches range	Jumps mean range
Training						
S <sup>+</sup>	208.6	148-320	1.1 0-5	317.1	272-378	2.8 0-10
S <sup>-</sup>	554.5	487-605	60.6 7-90	317.1	266-355	38.3 15-70
Testing						
S <sup>+</sup>	327.7	250-419	31.7 22-40	303.7	278-345	21.7 19-25
S <sup>-</sup>	528.7	480-622	119.0 97-149	302.3	298-305	51.0 25-71
Visual	-	-	92.0 70-127	-	-	44.3 30-68

significant difference during the test session when visual stimuli were inactivated. A further comparison was conducted between the species in order to determine if a comparable number of jumps were given during the  $S^+$  and  $S^-$  test periods. This proved to be the case, neither Redhead nor Canvasback ducklings giving a significantly greater response rate (Table 23).

TABLE 23. Significance levels for tests comparing the number of jumps between different stimulus conditions and between Canvasback and Redhead ducklings.

Comparison made	Test	Sig. level
Training: $S^+$ vs $S^-$		
Canvasback	Wilcoxon	$T=0, p<.01$
Redhead	Wilcoxon	$T=3, p<.01$
Testing: $S^+$ vs $S^-$		
Canvasback	Wilcoxon	$T=8.5, p<.01$
Redhead	Wilcoxon	$T=30.5, p>.05$
Testing: Canvasback vs Redhead		
$S^+$	Mann-Whitney	$U=117.5, p>.10$
$S^-$	Mann-Whitney	$U=111, p>.10$

## DISCUSSION

The finding that a significant proportion of Redhead and Canvasback ducklings spent the majority of time in the visual test apparatus adjacent to the visual imprinting stimulus shows that both species were able to learn a visual discrimination of the type commonly considered to be manifestations of early imprinting (Sluckin 1965; Bateson 1966). The auditory data, however, lead to the somewhat different conclusion, that only Canvasback ducklings were able to learn the auditory discrimination. Redhead ducklings, in contrast, proved to be resistant to learning in the auditory modality, at least under the experimental conditions employed in this study. It is not certain from the present results whether the differences in auditory discrimination learning between Canvasback and the parasitic Redhead duckling reflects an inability of the latter to discriminate between the stimuli used, or to a failure of the visual imprinting stimulus to selectively alter responses to the two stimuli in the latter species.

Reinforcing properties associated with visual imprinting stimuli have been demonstrated by several investigators for non-parasitic ducklings, Black Duck Anas rubripes, Mallard Anas platyrhynchos (Peterson 1960; Hoffman et al

1966) and domestic chicks, Gallus gallus (Campbell and Pickleman 1961). More recently, it has been demonstrated in domestic chicks that the visual imprinting stimulus may mediate the acquisition of an auditory discrimination using either artificial (Evans 1972) or biologically relevant vocalizations (Evans and Mattson 1972).

Differences are present, however, between the results of the present study and the comparable studies conducted with domestic chicks. For chicks, auditory discrimination was shown by a preponderance of approaches given during the presentation of the auditory stimulus ( $S^+$ ) that was paired with a visual stimulus during training, due apparently to habituation of approach responses to the  $S^-$  stimulus condition (Evans 1972; Evans and Mattson 1972). This habituation (Thorpe 1963) was lacking, in the present study, for either species of duckling. In chicks, a virtual absence of jumps during the training and test periods (Evans pers. comm. and pers. obs.) suggests a further difference between the two groups. The fewer jumps and fewer responses to  $S^-$  relative to  $S^+$  in chicks suggests that they were generally less fearful (cf Salzen 1962) than Canvasback or Redhead ducklings.

Although the present study provides further evidence that visual imprinting stimuli may mediate the development of auditory discriminations in at least one species of duckling, the results for the Redhead ducklings also suggest

that semiparasitic species may exhibit a reduced capacity to learn an identical auditory discrimination. Resistance to learning in a semiparasitic species may be particularly significant in view of the natural situation. A Canvasback foster family may spend considerable time on the nest before departure (Collias and Collias 1956) and then remains together for at least 15 days and generally much longer (Part I, this thesis). During this period a parasitic Redhead duckling receives a combination of auditory and visual stimuli at a time when young ducklings of non-parasitic species are susceptible to learning in these modalities. Resistance to learning in the auditory modality may therefore function at this time to prevent the brood parasite from becoming irreversibly attached to vocalizations of the foster species.

Gottlieb (1970) has demonstrated that in several species, including wild Mallard ducklings, recognition of species specific maternal vocalizations can occur in the absence of prior experience with them. If this result applies to the Redhead, then such recognition, coupled with the above demonstrated resistance to modification by early learning, would appear to constitute a highly adaptive mechanism favoring ultimate selection of a mate of the proper species.

## SUMMARY

Field observations on mixed broods of Canvasback and Redhead ducklings were conducted on pothole habitat in Minnedosa. Both field observations and additional laboratory studies to determine the capacity to learn visual and auditory discriminations, were designed to compare the behavior of the two species and to suggest a possible mechanism for species recognition.

1. The time mixed broods spent in the cover of emergent vegetation decreased significantly from Class I (age: to  $3\frac{1}{2}$  weeks) to Class II (age:  $3\frac{1}{2}$  to  $7\frac{1}{2}$  weeks) but, remained relatively constant to the end of Class III (age:  $7\frac{1}{2}$  to  $\approx 9$  weeks).

2. For those observations recorded while mixed broods were out of cover, Class II broods spent significantly less time feeding than Class I broods. There was a corresponding increase in the time spent sleeping and loafing. In conjunction with these changes over the brood period, ducklings became significantly more independent and ceased to conduct their daily activities as a "unit". Significant increases in the spacing of brood mates and the number of observations of independent behavior increased in proportion with the absence of brood hens. Permanent desertions



were first observed in subclass IIb and increased to 75% of broods by Class III.

3. Increased absence of brood hens was paralleled by a comparable decrease in aggression initiated to individuals outside the brood. Although Redhead and Canvasback ducklings were aggressive by subclasses IIa and IIb respectively, they were less aggressive than brood hens and consequently were less active in the defense of the brood territory.

4. Redhead ducklings were significantly more aggressive than Canvasback ducklings. There were no instances where Canvasback ducklings were aggressive toward Redhead brood mates. Although spacing increased in conjunction with aggression, there were no observations of permanent segregation between Redheads and Canvasbacks, possibly due to the close confines of the brood habitat.

5. Observations of Neck-stretch were first observed in subclass Ic and remained relatively constant to the end of the brood period. Canvasback ducklings responded significantly more to display initiated by other Canvasback ducklings than to those initiated by Redheads. This difference, in conjunction with species differences in the form of the Head-throw display and frequency of aggression, suggests that those behavior patterns could serve as possible cues for species recognition which could promote the ultimate segregation of Redhead and Canvasback

ducklings in mixed broods.

6. Laboratory studies were conducted on 16 Redhead and 16 Canvasback ducklings to test their ability to learn visual and auditory discriminations. Both Redhead and Canvasback ducklings learned a visual discrimination equally well but Redheads were significantly less proficient in learning an auditory discrimination. Additional evidence obtained from the number of "jumps" by ducklings in the test apparatus indicated that Canvasback ducklings are more wary than Redheads. These results suggest that visual imprinting may serve to promote brood integration and the formation of parent-young relationships early in the brood period. The reduced auditory learning in the Redhead, however, suggests that auditory stimuli may serve a more important role in subsequent species recognition.

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APPENDICES

APPENDIX A. Observations on mixed broods at Minnedosa.

Brood number	Number of Redheads	Number of Canvasbacks	Number of 10-min observations	Age(s) at which brood was observed
*1	3	3	103	Ia-IIIa
2	2	2	78	IIb-IIIa
3	2	4	38	IIa-IIb
4	4	3	36	IIa-IIb
5	4	5	37	IIa-IIb
6	2	3	7	IIc
7	5	3	98	IIc-IIIa
8	3	1	45	IIb-IIc
9	4	3	49	IIc
10	1	5	34	Ic
11	4	3	28	Ic
12	3	2	36	IIc-IIIa
*13	2	5	100	Ia-Ib
14	3	3	5	Ic
15	2	2	6	IIa
16	2	3	1	IIa
17	1	3	3	IIb
18	3	3	2	IIIa
19	1	5	2	IIIa
20	5	3	3	IIIa
21	2	2	14	IIc
22	3	3	14	IIIa

\* Marked broods.

APPENDIX B. Per cent of observations mixed broods spent in cover in relation to the dominant vegetation type.

Pothole type <sup>a,b</sup>	Number of potholes	Number of broods	Total observations	Per cent of observations in cover
Class I				
Whitetop, <u>Scolockloa festuacea</u>	2	2	111	26
Bulrush, <u>Scirpus acutus</u>	2	3	94	36
Cattail, <u>Typha latifolia</u>	0	0	0	0
Mixed and denuded	1	1	28	7
Class II				
Whitetop	4	4	30	27
Bulrush	6	10	376	18
Cattail	1	1	34	15
Mixed and denuded	0	0	0	0

<sup>a</sup>Classification of pothole types was based on the system described by Evans (1951) using the dominant vegetation type.

<sup>b</sup>Potholes were subjectively classified.

APPENDIX C. Aggressive encounters initiated by individuals outside the brood, by the brood hen, and by the ducklings in relation to the proportion of individuals of various species present.

Species	Per cent individuals present	Per cent attacks to brood	Per cent individuals present	Per cent attacks by brood hen	Per cent individuals present	Per cent attacks by ducklings
Coot	67.0	50.0	69.5	29.3	67.2	49.3
Grebe	9.6	17.5	8.2	30.5	5.7	6.0
Dabbling	8.2	0.0	7.3	7.3	16.7	14.9
Diver	10.4	2.5	8.0	6.1	1.8	1.5
Redhead	1.1	7.5	0.5	4.9	1.2	6.0
Canvasback	0.9	0.0	2.5	9.8	2.9	9.0
Other duck broods	2.7	22.5	4.1	12.2	3.5	14.0