DOCTORAL DISSERTATION SERIES
Publication No.: 18,597

AUTHOR: Milton Webster Weller, Ph. D., 1956
University of Missouri

TITLE: PARASITIC EGG LAYING IN THE REDHEAD (AYTHYA AMERICANA) AND OTHER NORTH AMERICAN ANATIDAE

University Microfilms, Ann Arbor, Michigan

The undersigned, appointed by the Dean of the Graduate Faculty, have examined a thesis entitled PARASITIC EGG LAYING IN THE REDHEAD (AYTHYA AMERICANA) AND OTHER NORTH AMERICAN ANATIDAE

presented by Wilton Webster Weller

a candidate for the degree of Doctor of Philosophy

and hereby certify that in their opinion it is worthy of acceptance.

Wm. H. Elder

Thomas S. Baskett

E. M. Fisher

Dr. Milton Webster Weller
Doctor of Philosophy
University of Missouri
August 1956

PARASITIC EGG LAYING IN THE REDHEAD (AYTHYA AMERICANA) AND OTHER NORTH AMERICAN ANATIDAE

by Milton Webster Weller

William H. Elder — Dissertation Superviser

ABSTRACT

It is well known that the redhead duck lays eggs in the nests of other birds as does the European cuckoo. The purpose of this study was to determine the origin and degree of development of this behavior in the redhead, appraise the effect of this parasitism on the productivity of the host and parasite, and evaluate management procedures designed to reduce the degree of parasitism.

The study was conducted in the Delta Marsh in Southern Manitoba and the Knudson Marsh in Utah. Nests were visited weekly and each egg was examined with a field candler to determine when each was layed; thus the relation of parasitic laying to normal nesting was established. Parasitizing and incubating hens were studied by watching from blinds placed at nests and by trapping females and marking them with plastic head tags.

Parasitic females searched marsh vegetation for nests in which to lay. Usually four minutes were required for the hen to lay. The male waited nearby. Laying occurred at all hours of the day but was most frequent in the morning. Both yearling and adult females layed parasitically. The average number of parasitic eggs layed by each female was eleven. As many as thirteen females were trapped on one nest. More than one half of the parasitic eggs were deposited after the host started incubation and thus were destined not to hatch.

If the host was on the nest, she threatened and pecked the intruding parasitic hen but could not always deter her. Occasionally the host ejected or buried the parasitic egg but usually accepted it. Continued parasitic intrusion seldom caused nest desertion in canvasbacks or mallards but redhead females commonly abandoned their nests because they were much less broody.

Parasitism reduced clutch size of the host by twenty percent and reduced both egg and nest success when it was severe. Of all hosts, the canvasback suffers most severely from redhead parasitism because the breeding range and nesting habitat of the two species are identical.

No relationship was found between degree of parasitism and cover quality, water fluctuations, or disturbance by the investigator; but it was influenced by nesting chronology of the host, location of the host's nest, and the abundance of hosts and parasites.

Approximately ten percent of redhead females nested normally and did not lay parasitically, fifty to sixty percent layed parasitically and later constructed nests of their own, while the remaining one third were completely parasitic.

Parasitic laying in the redhead is in the developmental stage and is occurring as a natural consequence of the deterioration of normal maternal instinct. The cause of this may never be known but probably resulted from variation in the synchronization of nest building and laying and the normal broodiness that follows. Three stages follow this: laying in other birds' nests and later constructing a nest, laying in other birds' nests followed by the use of an old nest for laying and incubating, and finally parasitic laying

alone with no attempt at nesting.

As a result of the redhead's parasitic habits and weakened maternal instincts, the balance between natality and mortality are so close that the size of the redhead population must be closely watched. Where possible, its nesting habitat should be managed to prevent nest losses from flooding.

TABLE OF CONTENTS

CHAPTER PAGE

LIST OF TABLES

LIST OF FIGURES

FIGURE PAGE

CHAPTER I

INTRODUCTION

Few birds have attracted more attention than those which have deviated from the usual pattern of nesting and rearing and have come to lay their eggs in the nests of other birds. Both laymen and scientists have devoted their lives to studying these birds, e.g. Stuart Baker, Edgar Chance, and Herbert Friedmann. Yet many problems remain unsolved. This mode of reproduction has been reported in five of 170 known families of birds. Of these, the ducks have received little attention, the weaver birds still present many problems, and so do the well-studied cuckoos, cowbirds, and honey-guides. Many simple details of behavior as well as basic biological facts necessary to understand the origin of parasitism remain unknown.

Investigators who have written on this breeding parasitism have suggested possible pathways by which the behavior may have evolved. They frequently cite the promiscuous egg laying of waterfowl as an example of an early stage of parasitism, for these species construct nests of their own in addition to laying in other birds' nests. But details of behavior and its biological implications have been considered but little.

Parasitism was frequently observed while the writer

studied plumages of the redhead at the Delta Marsh in southern Manitoba. The great abundance of redhead and ruddy duck eggs found in nearly every duck nest appeared of great importance to the reproductive success of both the parasitic and the parasitized species. Because of the apparent importance of this subject, parasitism became the foremost problem for investigation.

Answers to the following major questions were sought: What is the behavior of the parasitizing female? What effect does parasitism and its associated behavior have on the productivity and welfare of the host and parasite? Are there any basic differences in the breeding biology of the redhead and a more normal species, such as the mallard or canvasback, which might suggest the cause and pattern of evolution of the parasitic habit? And finally, is parasitism influenced by any environmental conditions which might be controlled or managed to reduce its frequency?

During 1952 and 1953, some data on parasitism were gathered, and the field seasons of 1954 and 1955 were devoted to full time research on this subject.

The study could not have been undertaken without financial aid from the E. Sydney Stephens Fellowship fund of the University of Missouri and research grants from the Delta Waterfowl Research Station.

Professor William H. Elder, University of Missouri, and H. Albert Hochbaum, Director, Delta Waterfowl Research Station,

deserve special thanks for their advice, constructive criticism, and encouragement throughout the study. Peter Ward and Dr. Frank McKinney of the Delta Station and Arthur S. Hawkins, Merrill Hammond, and Dr. Thomas S. Baskett of the U. S. Fish and Wildlife Service, offered many valuable suggestions during the investigation.

George P. Dellinger and Michael C. Milonski assisted in the field work during the summers of 1952 and 1954, respectively. Harold F. Duebbert helped in the 1955 egg-marking experiments.

Advice on certain phases of the study were given by: Dr. Herbert Friedmann, U. S. National Museum, Dr. Nicolas Collias, Illinois State College, Dr. Martin Moynihan, Harvard University, Dr. Clinton Conaway, University of Missouri, and Cecil S. Williams, U. S. Fish and Wildlife Service. Cecil Williams and Dr. William H. Marshall, University of Minnesota, allowed the examination of unpublished data.

During the field season in Utah, the writer received utmost cooperation from Dr. Jessop B. Low, Dr. Allen W. Stokes, and Robert I. Smith of the Utah Wildlife Research Unit. Noland Nelson, Utah State Department of Fish and Game, offered suggestions and provided unpublished data for use.

Mr. James F. Bell, Minneapolis, Minnesota, and Mr. Earl J. Knudson, Salt Lake City, Utah, kindly granted permission to conduct investigations on their property.

Much credit is due my wife for her continued encouragement and help.

CHAPTER II

REVIEW OF THE LITERATURE

A vast literature is available on parasitism in such groups as cuckoos and cowbirds and provides a good background for research on other parasitic species. Few comprehensive investigations of parasitism in waterfowl have been made and none has been published; however, many valuable contributions have come from these endeavors. It is essential that they be compiled for comparison with similar studies in other groups so the gaps in the knowledge of parasitism in waterfowl can be seen.

TERMINOLOGY

It may be argued that the term parasitism should not be applied to birds because it commonly connotes a method of obtaining food, rather than a means of reproduction. The word actually means "one which eats beside another" (Rothchild and Clay 1952:3) but it is never used in that way. Most definitions denote the feeding process of a small organism that lives in or on a larger one at the latter's expense. Similar behavior in animals like vampire bats, lampreys, and birds, cannot be classified so simply and it is necessary to refer to broader definitions which consider the population aspects. Thus Elton (1927:72) and Odum (1953:166) consider predators and parasites alike in that they both benefit through their

detrimental effect on other organisms. Because the aberrant laying habits of some birds are detrimental to the host at the family or population level, but are clearly not predation, the term parasitism seems justifiable.

Friedmann (1929b) did not consider parasitism in birds as "true parasitism in the real biological sense" but suggested that it might be called "social or breeding parasitism for want of a better term." The former term has come into more common usage although the latter is more correct. Recently, the term "brood parasitism" (Brutparasitismus of Makatch 1927), has been used, and seems to be the presently accepted term (Miller 1946, Friedmann 1949, 1955, Rothchild and Clay, op. cit.). It is, without doubt, superior to "social parasitism" for waterfowl, but allows some confusion with the "stealing" of broods which may occur.

Allen (1925:212-215), Davis (1940a), suggested that parasitism developed along two distinct lines: nest parasitism, in which the bird used old nests of other birds but incubated and reared its own young in normal manner, and egg parasitism, in which a species dropped eggs in the nests of other birds and later constructed and maintained a nest. Complete parasitism could have arisen, according to Davis, through either of these deviations from the normal. However, these terms have not been widely used; perhaps their meanings are not self-evident and perhaps because parasitism is not clearly divisible in this manner.

Numerous other terms have been used for parasitism in

species which lay eggs in the nests of other birds but also build nests of their own. Job (1902:201) called the ruddy duck "semi-parasitic," a term also used by Hudson (1920,1:91) to describe the activities of certain South American birds. Bent (1907), impressed by nests containing both redhead and canvasback eggs, assumed that both species participated in the careless laying of eggs and called them "dumping" nests. Williams and Marshall (1938) recognized large clutches of redhead eggs as the product of more than one female and called them "community" nests. Davis (1940a, 1940b) referred to the nests of the ani and the guira cuckoo as "communal." Stoddard (1931:38) and Low (1945) spoke of large quail and redhead clutches, respectively, as "compound" and Low referred to the laying process as "promiscuous egg laying": Allen (1925:213) and Davis (1942) also used this term.

Birds are not unique in the development of parasitic reproduction; it is common among ichneumon wasps. Entomologists have applied the adjective "parasitoid" to this group because they lay their eggs among another insect's eggs or larvae and the developing ichneumon slowly devours them as its sole food supply (Elton, op. cit.:78-79).

Both wasps and birds may be classified as "temporary" rather than "permanent" parasites, because they are free living during a major part of their life cycle. Some birds are "obligate" parasites--like the cowbird and cuckoo--because they are restricted to the parasitic mode of reproduction (Rothchild and Clay, op. cit.:7). Others, like the redhead,

may be termed "non-obligate" for they are thought to nest as well as parasitize.

PARASITIC EGG LAYING AMONG BIRDS

Honey-guides (Indicatoridae)

An excellent summary and evaluation of the literature on honey-guides, plus a wealth of new field data, were recently presented by Friedmann (1955:14-20). He believes that the parasitic mode of reproduction is more ancient in this group of birds than in any other. Several characteristics of the group give evidence of this. Firstly, most courtship and all nesting behavior has been lost. Secondly, all of the nine African and the two Asiatic species are thought to be parasitic, although details are known for only four of the African species. And, lastly, a structural modification in the beak of the young parasite has evolved which is used to eject nest mates. This is a very sharp hook present only during the early days of life when the nestling uses it to seize its nest mates and toss them from the nest. In this way, competition for food is avoided. It is apparent that such an adaptation must have required a long time to develop; thus any clues to the origin of the habit are lost in the past (ibid.:17).

Little is known of the behavior of the parasitizing female except that she is very aggressive, often opposing the defensive actions of both members of the nesting pair. The

eggs are plain white, often smaller than those of the host, and usually are laid in the nests of closely related, hole-nesting species (woodpeckers and barbets). One egg is laid in each nest before incubation starts.

Cuckoos (Cuculidae)

Most famous of avian parasites are the cuckoos. Approximately 80 of the 200 species of this family are parasitic (Makatch, 1937), and they are found on all major continents. The host-parasite relationships of African cuckoos have been studied by Friedmann (1948), those of India and Malaya by Baker (1942), and those of Australia by Serventy and Whittel (1951). The most extensive studies have been done on the European cuckoo (Chance, 1922, 1940; Makatch, op. cit.) but some aspects of the behavior of this bird are still little known.

Courtship and pairing in the cuckoo have not been well described. The role of the male in defence of territory is not clear-cut although the female is known to defend a territory to which she returns yearly (Chance, 1940:170, Chance and Hahn, 1942). Within this territory, the female watches the nesting activity of other birds and deposits all her eggs. The sight of the host's nest building activities are apparently sufficient to stimulate ovulation in the cuckoo (Baker, 1922, 1942; Chance, 1922). It is probable that the number of eggs laid is determined by the number of nests available (Chance, 1940:3-4), for artificial nests were always utilized.

The presence of several fascinating adaptations indicates that in cuckoos this behavior is very old, as in honey-guides. The most amazing adaptation is the evolution of egg mimicry; the eggs of a particular female greatly resemble those of her host. Comparisons of eggs of cuckoos and their hosts show almost unbelievable similarity (Chance, 1940, Baker, 1942). The Indian koel cuckoo has evolved such a degree of perfection that its eggs not only match those of the crow which it commonly parasitizes, but parallel the geographic variation of egg color in the crow (Baker, 1923). Egg mimicry apparently developed by the host's ejection of eggs unlike her own. This resulted in the survival of the fittest; only those parasitic eggs similar in color were hatched and resulted in strains of cuckoos laying one type of egg adapted to certain fosterers (Darwin, 1889-I: 330-336, Baker, 1923, Jourdain, 1925). Such host specificity developed for species with which the cuckoo was ecologically associated (Friedmann, 1928).

A second adaptation of the cuckoo is the speed with which the female lays her egg--a matter of seconds. The method of deposition, however, has been very controversial. Some investigators believed that the egg was laid on the ground and was carried with the bill to the nest, probably because they had seen cuckoos carrying eggs away from nests. Others believed the feet were used. Most workers now agree (Chance, 1940:144-145) that the egg is expelled directly from the oviduct into the nest--even in nests with a small opening

where the cuckoo cannot sit!

A third specialization is found in the young cuckoo. Its back is concave and during the first four days of life it instinctively pushes backwards when an object rests against this area. The result is the ejection of the nest mate or egg and, as in the honey-guides, reduced competition for parental care.

Many other members of the cuckoo family are aberrant in their breeding habits. The North American black- and yellow-billed cuckoos construct very poor nests and commonly lay eggs in the nests of other birds (Davidson, 1887, Herrick, 1910, Barrows, 1912:95, Bent, 1940:56-57, Spencer, 1943). Another North American member of the family, the roadrunner, is irregular in its laying habits. Miller (1946) states that eggs may be laid in a nest as late as the hatching period of the first laid egg; he assumes that this is done by the nesting female. It appears more likely to be a case of parasitism by another female; intraspecific parasitism was also reported in a raven nest by Pemberton (1925).

Among the cuckoos of South and Central America, the smooth-billed ani (Davis, 1940a) and the guira cuckoo (Davis, 1940b) are both reported to be communal in nesting habits. All construct nests, however; the guiras build nests in close association and several females lay eggs in one nest. The anis are even more sociable, many pairs constructing a single nest in which most females lay. Territorial defence by the

pair is weak but defence by the flock is strong. Davis (1942) suggested that these nesting habits represent a modification of egg parasitism and the development of social and nesting behavior. Makatch (1934) thought that this type of nesting was a stage in the development of complete parasitism while Daguerre (1924) considered this a secondary modification of parasitism which arose by one pair parasitizing another. Davis considered the latter improbable because it presupposed the existence of a parasitic and a non-parasitic phase within the species, a theory which Davis could not substantiate.

Weaver finches (Ploceidae)

The weaver finches are a large family with a variety of nesting habits ranging from colonial nesting to complete parasitism (Friedmann, 1949). Habits vary within sub-families and species; unfortunately, less is known of the parasitic species than of the colonial nesters.

In the typical weavers (apparently polygamous), the males build colonial nests and the number of a male's females is determined by the number of nests he can construct. The cuckoo finch is completely parasitic and builds no nest.

The buffalo weavers build less elaborate (even crude) nests but are also colonial in their habits. The most elaborate nests are made by the social weavers; these are colonial and may be 15 by 25 feet.

The common English sparrow, a member of the true weaver finch group, constructs a simple nest but is comparatively

normal in its nesting habits (i.e., it rears a brood).

Another sub-family (the indigo and widow birds), are all thought to be parasitic or else they use old nests for egg laying. Thus within this one large family of nest specialists, parasitism has developed in two widely separated subfamilies, i.e. the typical weavers and the indigo birds.

Cowbirds (Icteridae)

The cowbirds are a small group of the New World Icteridae in which parasitism has developed more recently and in which various stages of development are found. For this reason, and because of the intensive research on these birds, this group has revealed more of the origin of parasitic reproduction than has any other group. These various stages of parasitism were studied by Hudson (1920, I:69-114) and considered by Allen (op. cit.), Jourdain (op. cit.), and others. The most comprehensive study was by Friedmann in his classical work, "The Cowbirds" in 1929. Parasitism in cowbirds may be summarized as follows:

The bay-winged cowbird is the most normal in its nesting habits. It lays its eggs in other birds' nests which it sometimes acquires forcibly. It may then do some nest repairing. The screaming cowbird, like the bay-wing, lacks elaborate courtship behavior and is monogamous. It is completely parasitic, however. It is of interest that the bay-wing breeds late in the summer when there is an abundance of old nests; the screaming cowbird also lays late and as a result,

parasitizes mainly the bay-winged cowbird.

The Argentine or shiny cowbird is also parasitic although the behavior is hardly developed to perfection. It often lays more than one egg in a nest and drops eggs on the ground. By placing old nests in conspicuous places, Hudson (op. cit.:74) found that the Argentine cowbird would even lay in unattended nests. It is, nevertheless, very successful in maintaining a high population density, possibly because it is an early breeder and its habitat preferences result in an abundance of hosts (Friedmann, 1928).

The North American cowbird is also very abundant. It parasitizes several hundred species of small songbirds (Friedmann, 1929a, 1931, 1934). Much material on the behavior of the female of this species has been contributed by Hahn (1937, 1941) in his work on the ovenbird. By careful nest observation, Hahn found that the cowbird watches nest construction in its home area and, as in cuckoos, is probably stimulated to ovulate in this way. He found that the cowbird took an egg from the nest prior to or following the deposition of its own egg. The host's egg is usually eaten. The cowbird, like the cuckoo, can deposit its egg in a few seconds.

Nice (1937:163-164) considered the parasitic habit in cowbirds imperfectly developed because it often deposits more than one egg in a nest. In her well-known work on the song sparrow, she found that cowbirds laid more than one egg in 30 percent of the parasitized nests and often laid as many as three. Eggs were also laid in nests in which incubation had

started and in unattended nests. Berger (1951) reported similar behavior suggesting the cowbird was not as highly specialized as the cuckoo.

Quails and pheasants (Phasianidae)

Although no obligate parasites are known from this group, they are of interest because they commonly drop eggs in the nests of other birds. They apparently later nest.

Of the bob-white quail, Stoddard (1931:27) states: "When quail are abundant and nesting cover is scarce and short . . . two or even three quail hens occasionally deposit eggs in the same nests." He was able to observe this from a blind but gave no details of the procedure. He found that early clutches averaged slightly larger because of the prevalence of early compound clutches which were found mainly before nesting cover became dense. Of 394 complete clutches, 32 were of 20 or more eggs, and one contained 28 eggs. Single eggs were often found scattered on the ground; Stoddard attributed these to hens with destroyed nests or to those that could not reach their nests before the egg had to be laid. In captivity, he was able to verify that hens with nests destroyed either dropped a few eggs on the ground or stopped laying.

An interesting case of interspecific parasitism involving bob-whites and chickens was found by Stoddard in a farmyard. Bob-whites parasitized the chicken nests and the bantams parasitized nests of the bob-white. Interspecific parasitism by bob-whites was also reported by Blain (1954) who found their

eggs in a pheasant nest. Baskett (1947) noted laying by domestic chickens in pheasant nests. Bleitz (1956) reported an egg of the California quail in a bob-white's nest.

The exotic ring-necked pheasant commonly deposits its eggs in the nests of other species of birds as well as in those of other pheasants. In Iowa, where pheasants nest close to water areas used by ducks, Bennett (1936, 1938a: 47-67) found that nearly five percent of blue-winged teal nests, and a few mallard and shoveller nests were parasitized. He suggested that variations in the degree of parasitism reflected differences in the pheasant density, a view supported by Glover (1956) in later work on the blue-winged teal. Girard (1939), Williams and Nelson (1943), Wingfield (1951), Fuller (1953) and Miller and Collins (1954) also reported pheasant eggs in duck nests.

Baskett (op. cit.) found intraspecific parasitism indicated by dump nests common in pheasants in Iowa. Nests were classified as dump nests only when the rate of egg laying exceeded one per day or when clutches were large and the eggs scattered. Dump nests made up only two percent of the unsuccessful nests while losses due to unknown causes were 12 percent. It is possible that some of the latter losses were also caused by undetected pheasant parasitism.

When Meyer, Kabat, and Buss (1947) developed the technique for counting ovulated follicles they were able to determine the number of eggs laid by hen pheasants. They found (Buss, Meyer, and Kabat, 1951) that wild hens laid as many as

50 eggs per season; those hens collected latest in the season had laid the most eggs. Twelve hens collected in one year averaged 16 eggs while those collected in another area another year averaged 31 eggs. There was no knowledge of re-nesting, population density, etc., but it was apparent that hens commonly laid far more than twice the normal clutch of eggs. They concluded that the egg laying behavior of wild hens was similar to that observed in captive hens; penned birds laid four to 27 eggs on the ground, up to 24 eggs in nests which were not incubated, and finally six to 13 eggs in nests which they then incubated.

Stokes (1954) observed much parasitism or dump nesting on Peelee Island, Ontario. Pheasant populations were very high and he noted that the amount of parasitism and the density of the nesting population correlated highly. Stokes concluded that laying behavior was similar to that observed in captivity by Buss, Meyer, and Kabat (op. cit.). From 35 to 39 percent of nests observed were deserted; many of these were large clutches. Stokes considered nest abandonment inherent in the pheasant, and suggested that eventual control of the very high Peelee Island pheasant population "may be a rate of nest abandonment so high that nesting success barely compensates for annual mortality."

Other families

It is obvious from the literature that most species will on occasion lay their eggs in the nests of other birds;

many seem to do so commonly but too little is known to determine its frequency of occurrence. Abbott (1902) reported the eggs of the eared grebe in western grebe's nests and Wolf (1953) found two pied-billed grebe eggs in the nest of a western grebe. Bernard Gallóp (in litt.) observed an egg of the black tern in a redhead "dump" nest. Allen (1932) reported the egg of the royal tern in the nest of a laughing gull, while Beresford (1922) noted a curlew's egg in the nest of a wild duck.

Adam (1908) found that the common rhea of Argentina frequently laid eggs in other rheas' nests. Of this bird Hudson (op. cit.:235) wrote:

> Several females lay in one nest, which is merely a slight depression lined with a little dry rubbish; as many as fifty eggs are sometimes found in one nest. A great many wasted or huacho eggs, as they are called, are found at a distance from the nest.

Darwin (op. cit.:330-336) reported picking up 20 "lost and wasted" eggs of the rhea and cited this as an example of imperfection of a habit better developed in the ostrich, wherein "several hen-birds unite and lay first a few eggs in one nest and then in another; and these are hatched by the males." He attributed this behavior, as he did the development of parasitism in the cuckoo, to the fact that the birds lay a large number of eggs but at intervals of two or three days; thus the eggs would otherwise have to lie unincubated for a long period of time or eggs would hatch at considerable intervals if incubation were started with the first egg.

Ritter (1938:66) reported the California woodpecker to be a highly social bird and probably communal in nesting habits. Records of nests containing as many as 12 to 17 eggs were cited, while the average clutch was only four or five.

Among the passerines, the eggs of the house finch (Shepardson, 1915) and the brown thrasher (Bailey, 1887) have been reported in the nests of other birds. Joint nestings involving the laying of eggs by two species in one nest with the result that both incubate side by side are not uncommon. This has been reported for the cardinal and song sparrow (Brackbill, 1952), the mourning dove and the cuckoo (Davidson, op. cit.), and the mourning dove and the American robin (Raney, 1939). Similar nestings have been reported for the European robin and the redstart (Balsac, 1926). Lack (1946: 71), in his "The Life of the Robin," reported this occurrence as fairly common. Undoubtedly numerous other cases are known and have been reported but since they more clearly represent conflicts in nest site selection than parasitism, the above are sufficient to indicate its occurrence.

Waterfowl (Anatidae)

North American species. Of all the non-obligate parasites, the North American waterfowl are most noted for the laying of eggs in the nests of other birds. Since the late 1800's, when ornithologists first studied the waterfowl nesting areas of the American prairies, numerous records of nests containing the eggs of more than one female or one species

have been reported. These records, with the exception of those which were not clearly stated, are tabulated in Table I. This not only gives some idea of the widespread occurrence of parasitism or dump nesting among North American waterfowl, but is also a crude index to the species most given to this behavior.

Job (1898, 1902:205), one of the earliest workers to report this behavior, was impressed by the commonness with which the ruddy duck laid its eggs in other nests and termed it "semiparasitic." Bent (1902) also noted this habit but found more parasitism by redheads than by ruddy ducks. Of the redhead he stated (1907):

> A few eggs of this species were generally to be found in all the canvasback's nests. These two species have a peculiar habit of building what we called dumping nests in which large numbers of eggs are deposited but apparently not incubated; we found two such nests, one of which contained 19 eggs, 9 of the redhead and 10 of the canvasback, piled up indiscriminantly and some of which had rolled out of the nest which was partially broken down and evidently deserted.

Willet (1906) found mixed clutches of blue-winged, green-winged teal, mallards, canvasbacks and shovellers. He found parasitism by the larger species on the teal most common but gave no accurate details of individual nest records.

The most extensive data on parasitism among waterfowl have been obtained during productivity and life history studies designed to find facts useful to management and conservation of waterfowl. Williams and Nelson (1943), in their comprehensive investigation of the redhead in Utah, found large

TABLE I. Reports of parasitic egg laying among North American waterfowl. The area of observation and the authority follow each host.

Species parasitized by the redhead:		
Coot	California	Bryant, 1914
American bittern	Iowa	Low, 1945
Pintail	Utah	Williams and Nelson, 1943
"	Idaho	Bizeau, 1951, Steel, 1952
"	Utah	Fuller, 1953
Mallard	Utah	Williams and Nelson, 1943
"	Iowa	Low, 1945
"	Idaho	Bizeau, 1951, Steel, 1952
"	Utah	Wingfield, 1951
"	Utah	Wolf, 1952
Gadwall	Utah	Nelson, 194
Cinnamon teal	Utah	Williams and Nelson, 1943
" "	Utah	Wingfield, 1951
" "	Utah	Spencer, 1953
Canvasback	North Dakota	Job, 1898, 1899, 1902:187
"	North Dakota	Bent, 1902
"	Manitoba	Macoun and Macoun, 1909
"	Iowa	Bennett, 1937
"	Manitoba	Hochbaum, 1944:91
"	Idaho	Low and Nelson, 1945
"	Oregon	Erickson, 1948a, 1948b
"	Idaho	Bizeau, 1951, Steel, 1952
Redhead	North Dakota	Bent, 1902
"	Colorado	Rockwell, 1911
"	California	Willet and Jay, 1911
"	Saskatchewan	Bent, 1923:178
"	Iowa	Bennett, 1938b
"	Saskatchewan	Furniss, 1938
"	Utah	Williams and Nelson, 1943
"	Iowa	Low, 1945
"	Oregon	Erickson, 1948a
"	Idaho	Bizeau, 1951, Steel, 1952
"	Utah	Wingfield, 1951
"	Utah	Wolf, 1952
"	California	Miller and Collins, 1954
Lesser Scaup	?	Macoun and Macoun, 1909
" "	Idaho	Bizeau, 1951, Steel, 1952
Ruddy duck	North Dakota	Bent, 1902
" "	Iowa	Low, 1945
" "	Utah	Wingfield, 1951
" "	Utah	Wolf, 1952

TABLE I. (cont'd) Reports of parasitic egg laying among North American waterfowl. The area of observation and the authority follow each host.

Species parasitized by the ruddy duck:		
Western grebe	North Dakota	Bent, 1902
" "	Utah	Wolf, 1953
Coot	Iowa	Low, 1941
"	Manitoba	Weller, 1955
Mallard	Idaho	Bizeau, 1951, Steel, 1952
"	Utah	Wingfield, 1951
Canvasback	North Dakota	Bent, 1902
"	?	Macoun and Macoun, 1909
"	Manitoba	Hochbaum, 1944
"	Oregon	Erickson, 1948a
Redhead	North Dakota	Job, 1898, 1899, 1[illegible]97
"	California	Bryant, 1914
"	Montana	Weydermeyer, 1933
"	Iowa	Bennett, 1938b
"	Utah	Williams and Nelson, 1943
"	Iowa	Low, 1941, 1945
"	Oregon	Erickson, 1948a
Ruddy duck	?	Bent, 1925:155
" "	Montana	Weydermeyer, 1931
" "	Iowa	Low, 1941
" "	California	Miller and Collins, 1954
Species parasitized by the mallard:		
Pintail	Utah	Fuller, 1953
Mallard	?	Phillips, 1923
Cinnamon teal	Utah	Wingfield, 1951
" "	Idaho	Bizeau, 1951, Steel, 1952
Canvasback	?	Bent, 1923:193
Redhead	Utah	Williams and Nelson, 1943
"	Oregon	Erickson, 1948a
"	Utah	Wingfield, 1951
Ruddy duck	Utah	Wingfield, 1951
Species parasitized by the lesser scaup:		
Gadwall	North Dakota	Bent, 1902
"	Saskatchewan	Macoun and Macoun, 1909
"	Saskatchewan	Ferry, 1910
Shoveller	North Dakota	Job, 1898, 1899, 1902:192
Greater scaup	Saskatchewan	Macoun and Macoun, 1909
Redhead	?	Phillips, 1925
White-winged scoter	North Dakota	Bent, 1902

TABLE I. (cont'd) Reports of parasitic egg laying among North American waterfowl. The area of observation and the authority follow each host.

Species parasitized by the Fulvous tree duck:		
Redhead	California	Shields, 1899
Fulvous tree duck	California	Barnhart, 1901
" " "	Argentina	Hudson, 1920
" " "	California	Dickey and Van Rossem, 1923
Species parasitized by the pintail:		
Canada goose	Idaho	Bizeau, 1951
Mallard	Utah	Wingfield, 1951
Redhead	Utah	Williams and Nelson, 1943
"	Iowa	Low, 1945
Species parasitized by the cinnamon teal:		
Mallard	Utah	Wingfield, 1951
Redhead	Utah	Williams and Nelson, 1943
"	Utah	Wingfield, 1951
Ruddy duck	Utah	Wingfield, 1951
Species parasitized by the shoveler:		
Mallard	?	Phillips, 1923
American widgeon	North Dakota	Job, 1898, 1899, 1902:192
Cinnamon teal	Utah	Spencer, 1953
Redhead	Utah	Williams and Nelson, 1943
Species parasitized by canvasback:		
Redhead	Manitoba	Hochbaum, 1944:49
"	Oregon	Erickson, 1948a
Canvasback	Saskatchewan	Furniss, 1938
"	Oregon	Erickson, 1948a
Species parasitized by the wood duck:		
Wood duck	?	Sampson, 1901
" "	?	Barrow, 1912:89
" "	Iowa	Leopold, 1951
" "	Massachusetts	McLaughlin and Grice, 1952
Species parasitized by the gadwall:		
Gadwall	North Dakota	Hammond, 1941
Redhead	Utah	Williams and Nelson, 1943
?	Utah	Wingfield, 1951

TABLE I. (cont'd) Reports of parasitic egg laying among North American waterfowl. The area of observation and the authority follow each host.

Species parasitized by the American eider:		
Herring gull	Maine	Gross, 1938
" "	?	Barker, 1938
American eider	Maine	Gross, 1938
Species parasitized by the Canada goose:		
Osprey	Alberta	Fannin, 1894
Canada goose	Idaho	G. H. Jensen, *in litt.*
Species parasitized by the greater scaup:		
Greater scaup	?	Bent, 1923
Greater scaup and Old Squaw (joint nesting)	?	Phillips, 1925
Species parasitized by the white-winged scoter:		
Widgeon	North Dakota	Job, 1898, 1899, 1902:201
Gadwall	North Dakota	Job, 1898, 1899, 1902:201
Lesser scaup	North Dakota	Job, 1898, 1899, 1902:201
Species parasitized by the American goldeneye:		
Pintail	Manitoba	Arnold, 1894
Goldeneye	Maine	Brewster, 1900
Species parasitized by the hooded merganser:		
Goldeneye	Maine	Brewster, 1900
Wood duck	?	Peck, 1917
Species parasitized by the blue-winged teal:		
Pintail	North Dakota	Henry, 1940
Species parasitized by the Barrows goldeneye:		
Barrows goldeneye	?	Phillips, 1923
Species parasitized by the bufflehead:		
Bufflehead	?	Phillips, 1923
Species parasitized by the red-breasted merganser:		
Domestic fowl	Wisconsin	Strong, 1912

clutches, which they called "community nests" (intraspecific laying) and "parasitism" (interspecific laying) common. They state:

> Community nesting is regarded as the most important single cause limiting the production of redhead ducks in Utah. Should comparable circumstances be found on other major breeding grounds, the riddle to the redhead duck depletion would likely be answered. Community nesting is not only responsible for much of the desertion losses and losses of eggs pushed out of nests . . . but also for the majority of unhatched eggs to be found in large sized clutches (compound nests) and in parasitized nests including both those of redheads containing eggs of other ducks and of mallards, cinnamon teal, etc., containing redhead eggs. In both instances, the parasitism very likely originated with the redhead rather than the other species, the latter retaining incubation of the nest in most instances.

In some areas of Utah, these workers found that 30 percent of the nests of other species of ducks were parasitized by redheads, while the average figure was six percent for over 5,000 nests observed. This is the rate of interspecific parasitism and does not include intraspecific parasitism.

Hochbaum (1944:49) found that redheads, ruddy ducks, and occasionally lesser scaups, dropped eggs in the nest of canvasbacks but redheads did so commonly. Thus 22 of 38 canvasback nests contained an average of six redhead eggs. Hochbaum (op. cit.:91) noted that parasitically dropped eggs were fertile. In regard to the hatching success of these eggs he stated that "the number of redhead hatching from mixed clutches depends on the number intruded before incubation begins. Eggs laid after the clutch of the owner has been completed remain, in various stages of incubation, when the brood leaves."

Hochbaum (op. cit.:91) was able to observe female red-

heads resting near a canvasback's nest ". . . until the owner departed" and once saw a battle between a redhead and canvasback when the host returned unexpectedly. McKinney (1954), while observing the behavior of a female canvasback, saw and photographed an intruding redhead female laying an egg in the canvasback's nest while the latter was incubating. Although the canvasback pecked the redhead, the redhead remained about four minutes until she had laid her egg.

Low (1945) in his study of the redhead in Iowa found parasitism very common and an important cause of nest failure. Most nest desertions were caused by fluctuating water levels but he stated:

> Another factor responsible for unsuccessful nests was the intolerance of the nesting female toward other females or disturbance from ducks other than the rightful owners laying in the nests. The compound clutches, which usually occur early in the season, represented the laying, in addition to the rightful owner, of one or more females, probably before their nests were constructed or following an earlier nest failure.

The most thorough study of parasitism by the redhead was made by Erickson (1948a, 1948b) during his study of the canvasback in the Malheur Refuge in Oregon. Of 74 canvasback nests observed, 59 (80 percent) contained redhead eggs and these made up more than half of all eggs found in the nests. One canvasback nest contained, in addition to ten canvasback eggs, 48 redhead eggs! He found that many of these redhead eggs hatched and the young were commonly reared in canvasback broods.

Erickson observed that parasitizing female redheads

were usually accompanied by a mate which remained at some distance from the nest. Because the female had no nest duties, the male remained with her for several months.

In regard to the chronology of parasitism, Erickson found that, while the very earliest nests avoided extreme parasitism, early nests in general were more susceptible to parasitism than later ones. During three different years he found that the number of canvasback nests parasitized remained the same but that the number of eggs per nest varied.

Further valuable contributions to the knowledge of parasitism were made through the efforts of Wingfield (1951) in the Knudson Marsh in Utah. In this small area of high nesting populations, he found much inter- and intraspecific parasitism --especially by the redhead. Parasitism occurred in 69 percent of the nests of all species observed and was responsible for the majority of nest and egg losses. Because of the nature of Knudson Marsh (see "Methods and Study Areas" below), redheads nested close to mallards and cinnamon teal. Wingfield found that they parasitized 71 percent of the mallard nests and 79 percent of the cinnamon teal. The degree of intraspecific parasitism could not be determined but 26 of 151 redhead nests contained more than 18 eggs. The maximum was 50. A few records of parasitism by mallards, cinnamon teal, and ruddy ducks were also noted. Perhaps his most important contribution was data showing that the peak in the number of nests deserted because of parasitism by redheads preceded the peak of redhead nest initiation.

Spencer (1953) in a study of the cinnamon teal in Utah reported a high degree of parasitism of teal nests by the redhead, averaging 25 percent of the nests during the two years of study. He reported that teal often attempt to bury redhead eggs as songbirds do cowbird eggs (Arnott, 1890, Allen, 1925:206).

Foreign species. It is important to note that observations of waterfowl nesting behavior on all major continents indicate that most waterfowl tend to be "careless" with their eggs. Leverkuhn (1891), in his compilation of European records of nests containing the eggs of more than one species, reported eggs of the shelduck, shoveller, mallard, gadwall, white-eyed pochard, and common scaup, in the nests of other water birds. Bent (1923-25) reported large clutches of shelduck, tufted duck, and common pochard eggs which were probably the result of the laying of several hens. Durango (1940) and Koskimies and Routamo (1953) reported parasitism by the red-breasted merganser on the velvet scoter. Voohus (1947) noted parasitism of mallard and scaup nests by the red-crested pochard; these eggs usually failed to hatch because they were laid after incubation had started. Phillips (1926:109-110) also reported large clutches of this species which probably represented intraspecific parasitism. Jourdain (op. cit.) noted the commonness of this behavior among European ducks.

Gudmundsson (1932) reported compound nests common in European eiders. He suggested that such nests occurred when

an old female discovered that a young female had taken the adult's nest site of the previous year. The old bird laid anyway; both hens incubating the nest, alternately or simultaneously.

Serventy and Whittel (1951) reported that large clutches of duck eggs were often found in Australia and it is suggested that they were the product of more than one female. This is true of the blue-billed or Australian ruddy duck, a species which uses old nests in which to lay its eggs rather than constructing its own. This habit has also been reported for the Mediterranean white-headed ruddy duck (Phillips, 1926: 156) and the North American ruddy duck (Bent, 1925:154, Weydermeyer, 1931).

Another member of the sub-family of ruddy ducks, the black-headed duck, appears to be the only known obligatory parasite among the waterfowl. It inhabits deep lagoons of southern Paraguay and Uruguay, southeastern Brazil, and central Chile and Argentina (Wilson, 1920, Phillips, 1925:95). Typical of the group, it is a shy and retiring species (Wetmore, 1926). Its parasitic nature was first discovered in 1918 when duck eggs found in waterbirds' nests were attributed to the rosy-billed duck (Rodriguez, 1918). Daguerre (1920) proved these to be eggs of the black-headed duck by comparing them with an egg removed from the oviduct of a collected hen. Dabbene (1921) reported eggs of the black-head in the nest of a limpkin. Wilson (1923a) published a photograph of an uniden-

tified egg in the nest of a gull which Daguerre (1923) identified as an egg of the black-headed duck. Wilson (1923b) reported an egg of this species in the nest of the chimango or caracara. Daguerre (1922, 1924) wrote philosophically of the black-head and other parasites, as did Wilson (1926). Delacour and Mayr (1946) reported the egg of a black-headed duck in the nest of a coot. An interesting story cited by Phillips (1925:96) was a tale of a monk who was in charge of a museum in Santiago, Chile. He reported seeing a duck which he believed to be a black-headed duck, leave a hole in a tree followed by some young ducklings. No evaluation of this story was possible. While adding some intrigue to the mystery of the black-headed duck, Goodall, Johnson, and Phillippi (1951) concluded that there was little question as to the parasitic nature of the species. They found its eggs in coot nests commonly during the 1930's but reported the species decreasing in abundance in Chile because of marsh drainage and droughts. Emilie Zuberbuhler, an ornithologist in Buenos Aires, reports (in litt.) its status in Argentina to be somewhat better than that noted in Chile. He also reported finding its eggs in the nests of coots, caracara, herons and the crested screamer.

Nothing is known of the behavior of the female or the pair, the success of the eggs, or the general biology of the species.

Resume. Most species of waterfowl have been known to deposit their eggs in the nests of other associated birds.

Ducks apparently are easily stimulated to lay by the presence of a nest containing eggs. Two species, the redhead and the ruddy duck, are best known for this behavior. Reports indicate that redhead parasitism occurs throughout the breeding ground of the species and may be so frequent as to reduce production of other species greatly. Redheads nesting in a normal manner also may be affected by the intrusions of parasitic redheads. Some gain to the parasite is made by the young redheads reared in broods of other ducks but little is known of the effect of the habit at the population level.

It has been suggested that parasitism occurs either before nesting or following nest failure. Thus the amount of parasitism may be proportional to the amount of nest failure, as seen in areas with great water fluctuations. However, parasitism does occur in areas where there is no water fluctuation and most parasitism occurs prior to the period when most redhead nests are initiated.

Relatively little is known of the behavior of the parasitizing female but she will lay eggs in a nest while the owner is present. The laying requires approximately four minutes. The female may be accompanied by the male but he remains at some distance while she is parasitizing a nest.

Many questions remain: Are all redheads parasitic? Do they parasitize before nesting or is the behavior related to nest failure? Do parasitic females later construct and maintain a nest of their own? If so, how does the nesting behavior of the redhead differ from more normal species? What

factors influence parasitism and is it subject to management? What effect does this behavior have on the parasite and the host? Is the redhead truly in a developmental stage of parasitism or is it merely an example of unnecessary production spent in a conspicuous manner? Many more minor questions also remain.

CHAPTER III

STUDY AREAS AND METHODS

STUDY AREAS

Delta Marsh

Delta Marsh, at the south end of Lake Manitoba in south-central Manitoba, has been thoroughly described in the writings of Hochbaum (1944:3-12), Love and Love (1954) and Sowls (1955:2-3). Ecological features of the marsh pertinent to this investigation are summarized below.

The Delta Marsh lies between the beach ridge of Lake Manitoba and the higher prairie farmland to the south; it lies in a crescent 15 miles long around the southern end of the lake. The dominant vegetation is cane (Phragmites), but hardstem bulrush, cattail, and whitetop grass also grow in abundance. Water depth determines the species and abundance of plant growth; hardstem bulrush grows in water two to four feet deep, while cattail, Phragmites, and whitetop, in that sequence, require less water, the latter growing well if only temporarily inundated.

Whitetop and similar aquatic grasses form the wet meadows in which nest dabbling ducks like the mallard, pintail, shoveller, and blue-winged teal. The diving ducks, the redhead, canvasback, and ruddy, nest in bulrush, cattail and Phragmites of deeper marsh areas (Figure 1). The dense growth

Figure 1. Part of the Delta Marsh, beach ridge, and Lake Manitoba. The light colored vegetation is Phragmites, the dark is bulrush and cattail.

habits of Phragmites limit nesting to the edge of the stands (Ward, 1942) and prevent movements of divers to shallow meadows. In other marshes where Phragmites is less abundant, diving ducks are free to move from deep-water feeding areas to shallow water areas where they may nest. Thus in the Delta Marsh redheads are ecologically separated from the dabbling ducks, whereas they may nest side by side in other areas where deep marsh and meadow are less clearly divided.

At times of high water levels, when meadows are sufficiently deep to allow the feeding and courtship of divers, diving ducks may nest there, and at such times the marsh proper may have fewer nesting ducks than in drier years; the nesting of all species occurs nearer the marsh edge.

Whitewater Lake

Whitewater Lake is near the Turtle mountains near Boisevain in southwestern Manitoba. It is approximately three miles wide and five miles long but fluctuates greatly in size with changes in water levels because of its shallow basin. Maximum water depth is five feet and during periods of severe drought, the lake may dry completely. The dominant emergent vegetation is whitetop grass, hardstem bulrush, cattail and Phragmites. The latter is not abundant and thus the ducks can move from deep to shallow water areas. The species nesting there are the same as at the Delta Marsh.

Knudson Marsh

The Knudson Marsh is four miles west of Brigham, Utah, in the valley of the Bear River Bay of Great Salt Lake. It is an isolated, fresh water marsh, one and one-half miles north of the huge Bear River Migratory Bird Refuge. With the exception of a small ox-bow marsh one mile from the Knudson area, the nearest good nesting cover for diving ducks is about four miles.

The marsh is surrounded and dissected by flowing water in channels two to four feet deep. This water is a barrier to skunks and other land predators. These small streams meander, cutting new channels and silting in old ones which then serve as sites for the spread of vegetation. The channels allow the birds access to the nesting vegetation.

Heavily grazed saltgrass surrounds the marsh, beyond which are salt flats with the only vegetation being glasswort and greasewood.

The marsh is approximately 400 acres in size and is divided into two sections connected by a channel. The lower section is predominantly open water with an island of about 20 acres of vegetation. The area of the upper marsh is about 120 acres of vegetation and 55 acres of water. The vegetation of the upper marsh was mapped by Wingfield (1951) in 1950 and consisted of 56 percent hardstem bulrush, 24 percent Olney's three-square, 27 percent cattail, 6.5 percent saltgrass, and minor percentages of alkali bulrush and cane. Although the

water level was lower in 1955 than in 1950 and the vegetation was reduced in height, the percentage of each plant species was about the same.

Waterfowl used the old vegetation for nest material and concealment. This had been flattened by wind and snow and trampling by cattle during the previous fall. The resulting clumps of vegetation (Figure 2) offered excellent nest sites and the cattle trails were used by hens as pathways to their nests. Cattle on the range surrounding the marsh entered to feed on the green shoots of aquatic plants and thus kept old trails open and destroyed both old and new vegetation.

The marsh was used for nesting by redheads, mallards, cinnamon teal, gadwalls, pintails, ruddy ducks, and the Canada goose.

Ogden Bay Refuge

The Ogden Bay Refuge, near Ogden, Utah, is about 20 miles south of the Knudson Marsh. It is a man-made marsh of 14,000 acres of excellent waterfowl nesting and brood-rearing cover (Nelson, 1955:11). The dominant emergent plants are three-square and cattail with lesser amounts of hardstem bulrush. Water levels are controlled by gates and kept constant whenever the supply is sufficient. Species of nesting ducks are the same as those of Knudson Marsh.

Figure 2. Hardstem bulrush in the Knudson Marsh, Utah.

METHODS

Obtaining nest data

Nests were found by canoeing, walking, or wading. The distance of the observer from the female when she flushed from her nest was recorded on each visit as a measure of her broodiness or attachment to the nest. The presence of the drake was also recorded. The following information was recorded at each redhead and canvasback nest: location, composition and density of the cover, size of nest, water dept. amount c down (arbitrarily classified on a scale of one to five), and the number of eggs in the nest and outside on the ground or under the surrounding water. Only location, number of eggs, amount of down, and flushing distance were recorded for nests of species other than redhead or canvasback.

To determine the chronology of parasitism, all dates when parasitic eggs were laid were recorded. Dates were calculated for parasitic eggs laid prior to the observer's recording of the nest by determining the age of the embryos with a mailing tube field candler (Weller, 1956) and backdating to the approximate day of laying.

Disturbance at the nest was kept at a minimum. Nests were seldom conspicuously marked except in the Knudson Marsh where nest densities were extremely high. Here, willow poles bearing numbered tags were placed 15 feet from nests. Eggs were covered with down or other nest material after examination.

Observations of pairs, females, and broods

The female's manner of finding nests, the response of the host female, the actions of the parasite's mate, and similar details associated with this behavior were investigated by observations in the field. These observations were facilitated by use of blinds.

Observations of duck broods were made to determine how often redheads were reared in broods of other species and the effect of their presence on the behavior of the hen and her ducklings.

Nest trapping and marking of hens

Some interesting observations were made of unmarked female redheads but marked hens were necessary so that the investigator could know the breeding status of individual birds and determine whether parasitizing hens later nested.

One method of capturing hens was a drop trap tripped manually from a blind. The distance of the blind from the nest was determined by the height and density of the vegetation. The trap used by Sowls (1949) in the Delta Marsh for dabblers was modified for work with diving ducks. The size was reduced from a two-foot square to a 12-14" diameter round aluminum frame which was placed on the rim of the nest bowl and held the hen securely (Figure 3a). One inch mesh string netting was used to entangle the bird and partly compensate for the reduced size of the trap. Only incubating hens were captured successfully with this trap because parasitizing hens

Figure 3a. Drop-trap for capturing female diving ducks on a canvasback nest. Note plastic neck marker.

Figure 3b. Nest-basket with drop-door tripped by bird moving wire ring inside the nest.

were more wary and were frightened away by the presence of the blind and the trap.

Nest basket traps, as shown in Figure 3b, were tried in the hope that parasitizing hens would enter them. However, only one ruddy duck female was captured.

The equipment which finally proved successful for capturing both parasitizing and nesting females was a trap with the door released by a treadle well inside the trap (Figure 4). Use of this trap was possible only in Utah where duck nests were constructed on land rather than over water as in the Delta Marshes. The trap was made of 14 gauge welded wire fencing which enabled the trap to stand upright without other support. A single piece of this fencing was formed into a semi-circle, leaving an opening for the door. A roof, necessary even for diving ducks, and drop door were made of the same material. No lock was found necessary, for the bird pushed against the door rather than lifting it. Traps were examined one to three times daily.

Females were marked either with airplane dope (Sowls, 1949) or with a plastic neck tag (Figure 3a) similar to that used by Taber (1949) on pheasants, then weighed and released.

Inducing the laying of marked eggs

An attempt was made to make females lay distinctively marked eggs in order to determine how many were laid by a single parasitizing female, how many nests one female laid in, and how many hens laid in one nest.

Figure 4. Automatic nest trap containing a redhead female captured while parasitizing a mallard nest.

Because insertion of skin clips in the oviduct failed to produce marked eggs, the following dyes were tried: alizarin blue, alizarin red, brilliant green, eosin blue, gentian violet, methyl red, methylene blue, rhodamine, and safranin. Each of these substances was mixed with the minimum amount of beeswax necessary to form a pellet. The pellets were then implanted intraperitoneally or subcutaneously in domestic chickens. Only intraperitoneal methylene blue showed any influence on egg color; one gram of this dye per bird changed yolk color from yellow to lime green but did not affect the egg shell. However, this color was distinguishable through the field candler and thus seemed a practical field technique. Its major disadvantage was that only one female could be so marked in a study area.

Egg acceptance tests

Eggs are often found outside of parasitized duck nests on the ground or in the water and it is not known whether these are deliberately rolled from the nest. Because chances of observing how such eggs were lost from the nest were small, chicken eggs were marked conspicuously with India ink and placed in nests (Figure 5) when the female was laying or incubating, to determine her response.

Artificial nests

To test the presence of the nest with and without eggs as a factor possibly stimulating the deposition of parasitic

Figure 5. Conspicuously marked chicken egg in a redhead nest.

eggs, artificial nests of Phragmites or other vegetation were placed in habitat frequented by female redheads and ruddy ducks. In 1953, six artificial nests were modified as traps (Figure 3b) and placed in the Delta Marsh. In addition, four whitetop nests were made in a pen containing captive redheads. In 1954, twelve artificial nests of Phragmites were mounted on wooden platforms and placed in the Delta Marsh, and in 1955 the same number of nests were constructed of natural vegetation in the Knudson Marsh (Figure 6). In each test, half of the nests contained three to six fresh chicken eggs and half were left empty.

The Knudson Marsh tests were invalidated by the predation of the California gull. Even when molded plaster eggs were used in place of real eggs, the gulls carried them away.

Figure 6. Artificial nest constructed of three-square bulrush in the Knudson Marsh.

CHAPTER IV

RESULTS

BEHAVIOR OF THE PARASITIZING FEMALE

Locating the host's nest and laying

The redhead apparently discovers the nests it parasitizes by searching in nesting cover and, like the European cuckoo (Chance, 1921) and the North American cowbird, by observing the nest building and egg laying activities of the host (Friedmann, 1929a:187, Hahn, 1941). On numerous occasions at Delta, redhead pairs were observed swimming along the edge of nesting cover; the female entered the vegetation and remained out of sight for a minute or two while the drake remained at, or just inside, the edge of the nesting cover. On other occasions, redhead pairs were observed swimming in openings in dense vegetation used only for nesting. Little feeding was seen--preferred foods were in larger water areas. They seemed to be searching. It could not be determined whether these birds later nested in the same area and were thus searching for their own nest sites. If so, such searching preceded nest initiation by a month or more and the hens must have discovered other nests in the process.

In the Knudson Marsh, lone females were observed walking about on land--apparently searching for nests. One was seen to climb over the nest of a Canada goose which contained pipping eggs and was later observed climbing over vegetation several

feet high. She seemed to have no knowledge of a nearby redhead nest.

That females watch the activities of other females was noted in the Knudson Marsh. While the investigator was watching a redhead nest, a lone female redhead climbed over vegetation several feet in height and then disappeared. Another female then entered the nest and departed immediately. The first female met her mate and both observed intently the activities of the second female for a few moments, then all left the area. It was not known whether these females had parasitized the nest earlier, or even if one of them was the host, but their extensive searching of the area indicated no previous knowledge of the nest. The interest of the pair in another female suggests that parasitic hens may find nests by watching other parasitizing hens.

Another observation made in the Delta Marsh indicated that the parasite either knew the site of a canvasback nest containing redhead eggs or that she saw the hen near the nest as she flew over. While the investigator was in a blind near this nest, a pair of redheads flew by and landed, without hesitation, in a small water opening 50 feet away. After preening and loafing there for 50 minutes, the female left the male in the pool and swam directly to the canvasback nest.

A preliminary examination of the nest prior to laying is probably customary, and may stimulate ovulation as in cuckoos and cowbirds. This was apparent in nest-trapping parasitizing

females; in all which had not yet laid, the egg could be felt in the oviduct. Nor were these retained because of physiological stress of the capture. One collected from such a nest trap had an egg in the oviduct which still lacked the final shell coating. It is assumed that this female was trapped while examining the nest prior to laying. Moreover, because several other hens had been captured in this trap on preceding days, the female either had been unable to enter the trap on previous days or first discovered the nest when captured. In either case, a preliminary investigation of the nest preceded the final laying. Once, while the writer was observing a mallard nest, a redhead hen visited for a few seconds. About 45 minutes later a hen returned to the nest and remained four minutes (until disturbed). She did not lay an egg. That this was the same hen was indicated by the similarity of plumage and behavior in approaching the nest.

To test the influence of empty nests and unattended nests with eggs in inducing ovulation by redheads, 30 artificial nests were placed in natural vegetation in both the Delta and Knudson Marshes. No eggs were laid in any of these. One ruddy duck was captured in a basket-trap and palpation of the lower abdomen indicated that she held an egg in her oviduct. The slight use of these nests indicates that the activity of the host female is important in increasing the parasite's chances of finding the nest.

Although Hudson (1920, I:74-75), Nice (1937), and Berger

(1951) found that cowbirds laid in nests which did not contain eggs, this has not been reported for waterfowl. Only one uncertain case was found among ducks. A mallard was flushed from a scrape containing a few of her feathers and three unincubated eggs, two of the redhead and one of the ruddy. The nest was deserted and no other eggs were added. It appeared that both parasites had discovered the hen while she was making the scrape and deposited their eggs before the host laid. The sight of the host or the scrape may have stimulated laying by the parasites.

That the host is not the only stimulus to laying is shown by the fact that eggs, regardless of color, size, or shape, are also important, for ducks will lay in the nests of bitterns and rails (Figures 7a, b, c).

The redhead is very bold at the time of laying and may deposit her egg in spite of the presence of the host female. McKinney (1954) witnessed and photographed a redhead laying in a canvasback nest (Figure 8); despite much pecking by the host, she remained four minutes and laid her egg.

Parasitic laying was observed on three occasions during the present study. The first was a successful hen which took four minutes to lay in an unattended canvasback nest. The second case was that of a hen frightened by the camera shutter and the third was that of a hen frightened by the presence of a blind and nest trap.

Observations at the nest indicate that the redhead is

a. Ruddy duck egg in coot nest. Delta Marsh, Man.

b. Redhead egg in nest of sora rail. Photo by Lloyd Keith, Brooks, Alta.

c. Redhead egg in nest of American bittern. Whitewater Lake, Manitoba.

Figure 7. Duck parasitism on other marsh birds.

Figure 8. Redhead hen parasitizing a canvasback nest with the host present. Photo taken by Frank McKinney in the Delta Marsh, Manitoba.

not as highly adapted as the cuckoo or cowbird. Whereas the females of those species require only a few seconds to deposit their egg, the redhead remains on the nest about four minutes. During this period, movements which occur in normal nesting were observed. Two females which laid in unattended nests poked the eggs vigorously with their bills and changed their position on the nest--all in a hurried fashion. Even with the host present, McKinney (in litt.) photographed this poking by the parasitic hen. Females were never observed to add nest material and no down of the redhead was ever found in a parasitized nest.

During laying, the male usually accompanied the female. In two of three cases observed, the male awaited the female within 50 yards of the nest. Another male waited for a hen ten minutes after she had gone into nesting vegetation, presumably to parasitize a nest. Of 42 females trapped parasitizing nests, lone males were observed nearby on five occasions. While waiting, the male periodically called "meow" or "mer-ow" (whee-ough of Wetmore, 1920). A female occasionally was heard to utter a low "kuk-kuk-kuk" when at a nest but none of the parasitic hens observed was heard to call after leaving the nest. Other females, suspected of laying, were heard to call loudly "kurr-r-r-r" or "kurr-r-k" as they flew from nesting cover. This call attracted any lone males in the area and, presumably, her mate. After laying, the hen bathed and preened. Because the female has no nest duties and is undoubtedly sex-

ually receptive, the male remains with her throughout the parasitizing period and until the last days of egg laying or when she begins to incubate. Erickson (1948a) believed that males remained with parasitizing females as long as two months. Assuming a monogamous relationship, it appears that some males may remain with their females as long as three months because pairing occurs as early as March and nesting may not occur until June.

In more highly specialized parasites like the cuckoo and the cowbird, the time of egg laying has apparently been adapte to avoid the host's laying time. Thus cowbirds lay in the morning, preceding the laying period of the host (Hahn, 1941), while the European cuckoo lays in the afternoon, following the host's laying. In the redhead, parasitism was attempted at 8:55 A.M., 9:25 A.M., and 10:00 A.M. In the latter case, the hen laid sometime after 11:00 A.M. the next day--an interval of slightly more than 24 hours between eggs. For trapped hens, the following specific time periods could be assigned:

Between	3:30	P.M.	and	6:00	P.M.
	12:45	"	"	6:00	"
	12:45	"	"	7:25	"
	3:30	"	"	6:00	"
	1:30	"	"	7:30	"
	7:30	A.M.	"	11:30	A.M.
	11:30	"	"	7:30	P.M.

The other 35 females were trapped sometime between daylight and noon. Thus redheads seem to lay at all hours of the day although most authors agree that laying in other species occurs during the morning (Bennett, 1938a:47, Hochbaum, 1944:49,

sowls, 1955:95). However, Erickson (1948a) reported that canvasbacks laid at all hours of the day. Too little is known of laying periods in ducks to determine whether the pattern in redheads is significantly different from other species.

Data from trapped parasitizing females indicate that when the egg is fully formed there is little control over the time of laying. Trapped females had either already laid, or still held an egg in the oviduct. One female kept in a trap two hours did not lay. Another laid between 40 and 60 minut after capture, while a third laid in the investigator's lap five minutes after capture. In the latter case the egg was extruded in about one minute with six or seven pulsations of the oviduct. Thus it appeared that trapped females were on a preliminary visit, and would have returned to lay later, or that the bird was ready to lay when entering the trap and did so immediately.

On three occasions, when birds were in nest traps, single eggs were found outside, indicating that the second hen could not wait to lay. This also suggests that the hen lacked a knowledge of nearby nests or that she could not alter her laying pattern in the artificial situation.

Number of eggs laid per female

In an attempt to determine the number of eggs which a redhead female deposits parasitically, pellets of methylene blue dye were implanted intraperitoneally in a hen captured in the act of parasitizing a nest. Tests in captive birds showed

that this dye would change the color of the egg yolk from yellow-orange to lime green and that this could be recognized when the egg was examined with the field candler. Unfortunately, only one female could be so marked in a given area at one time. The first bird captured in the Knudson Marsh in 1955 was marked in this way but none of her eggs was found during the nesting period.

Because no measure of the number of eggs laid by individual females was obtained through the use of the dyeing technique, another approach was necessary: an average figure was calculated for all the females using the Knudson Marsh. The marsh was small and isolated and the vegetation sparse so that a high percentage of nests was found. A count of 936 parasitically-laid redhead eggs was made in all nests in the marsh. By ground and aerial counts, 90 to 95 females were estimated to be frequenting the marsh. If it is assumed that about five of these females did not lay parasitically (as explained below), about 87 females laid a minimum of 936 eggs for an average of 10.8 eggs per hen. This figure approximates that which might be expected of the first clutch of a redhead.

A second line of evidence as to the number of eggs laid per female was obtained in the Knudson Marsh by the discovery of eggs with an unusual shell structure and mottled appearance (Figure 9). No egg of this type had been observed in the Delta Marsh by the investigator, nor had Peter Ward,

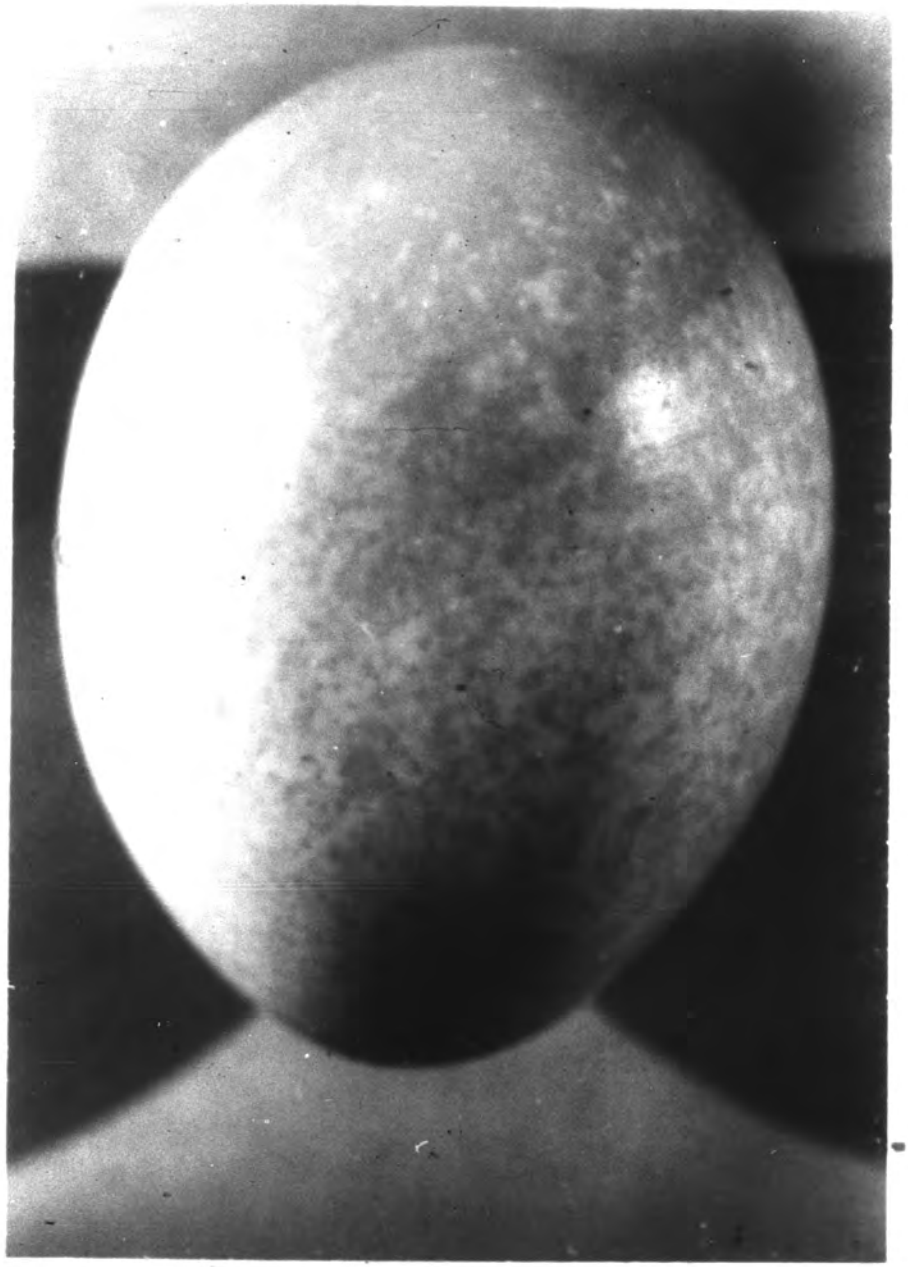


Figure 9. Redhead egg with mottled shell pattern found in Knudson Marsh, Utah.

Hatchery Superintendent of the Delta Waterfowl Research Station, ever seen one like it. These eggs were found in 15 nests of the redhead, mallard, and cinnamon teal in various parts of the Knudson Marsh. In all, 20 were found--seemingly a large number for one female to lay. On June 10, a female died in one of the traps; the freshly laid egg in the nest was of the mottled type. However, following this, fresh eggs with this unusual shell formation were still found in nests in the marsh. On June 25, a nest of seven fresh eggs of the same mottled pattern was found. Obviously, there had been at least two females in the marsh which laid this type of egg. If it is assumed that there were no others, the two females laid a minimum of 20 eggs or an average of 10 eggs each, a figure very similar to that derived from the total number of parasitic eggs counted in the marsh.

Judging from egg color, size, and shape, at least four and possibly five or six eggs may be deposited in one nest by an individual female. The fact that no more than three of the mottled eggs were found in any one nest and that nests containing them were widely separated in the marsh may have been atypical behavior due to the disturbance of the investigator. But it seems likely that a small number of eggs per nest is usual and results from the hesitancy of the parasite to face the defensive actions of the host. Aggressiveness of the host may well increase with each parasitic intrusion and probably increases with the broodiness. Such a pattern would

not only limit the number of eggs laid per nest, but would tend to cause a parasite to deposit her eggs at the time when the host is at her nest very little--the egg laying period. Thus the aggressiveness of the host, and lack of it in the parasite, are probably important to survival of eggs and in development of the parasitic mode of reproduction.

Number of females parasitizing one nest

In view of the fact that redhead nests have been found which contained 30 eggs (present study), 39 (Williams and Marshall, 1938), 50 (Wingfield, 1951), 74 (Gallop, in litt., Figure 10), or even 87 eggs (Nelson, 1943), it would be of great interest to learn how many females lay in one nest. Some measures of this were obtained through the records of the number of females captured per trap. In the ten effective trap nests, the following numbers of females were taken: 1, 1, 1, 2, 3, 3, 4, 6, 8, and 13! If as many as thirteen hens lay in one nest, it is not difficult to see how huge dump nests are formed. When a trapped female had not laid, her egg could be felt in the oviduct. She was probably on a preliminary exploring trip and would have laid if she found the nest satisfactory. Redheads continued to lay in deserted nests, both those with and without traps, but they did not lay in nests after eggs were broken and foul smelling. What determines the suitability of nests for laying is uncertain but there seemed a tendency for parasitic females to lay in active nests, an important factor in egg survival.

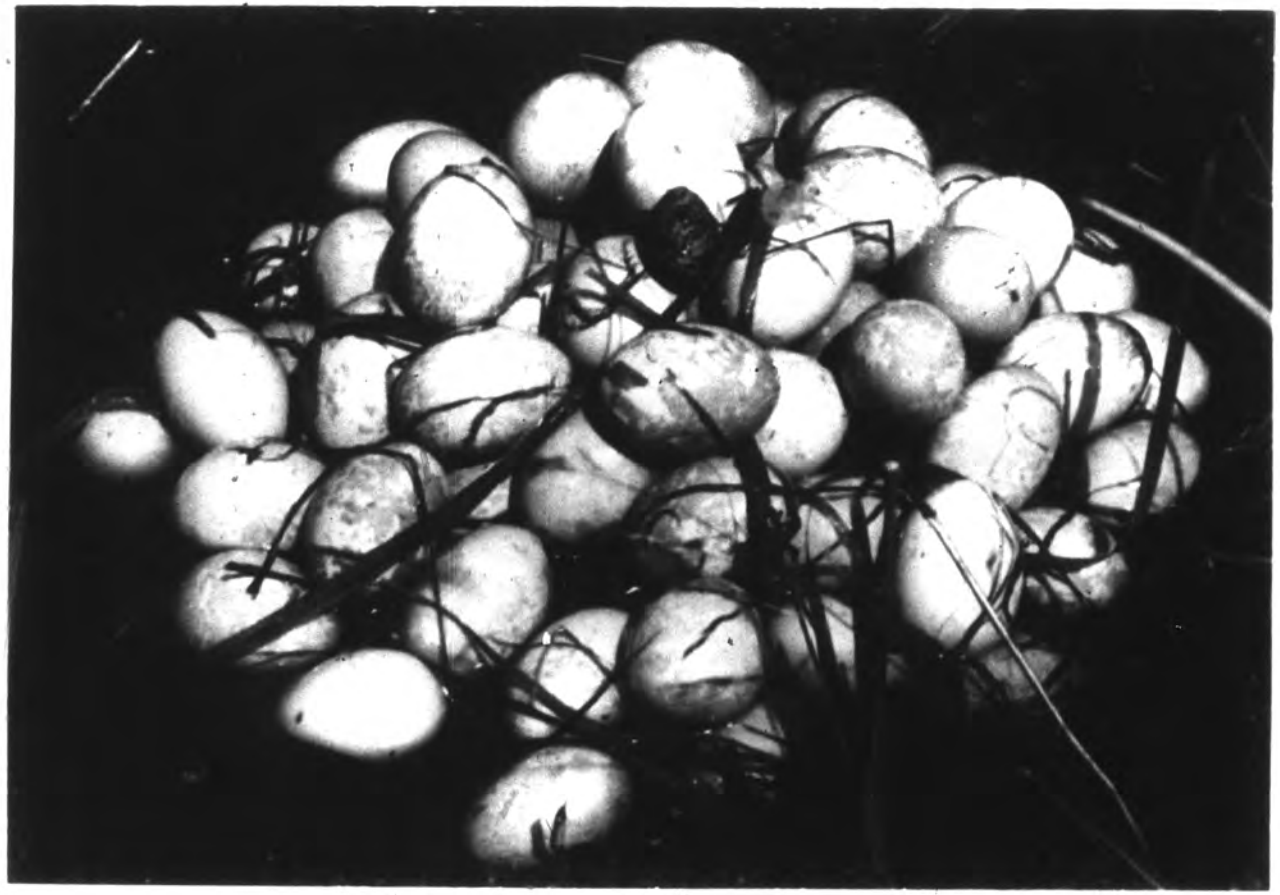


Figure 10. "Dump nest" at Whitewater Lake, Manitoba, containing 74 redhead eggs and one of the black tern. Eggs were piled up and photographed by B. Gallop, Canadian Wildlife Service.

The relation of laying to the host's incubation

That parasitism is less well developed in the redhead than the honeyguide, cuckoo, or cowbird is further shown by the fact that redheads commonly lay in nests after the host has started incubation; thus the eggs are destined to be left in the nest after the host's eggs hatch. The following tabulation shows the percent of parasitic redhead eggs laid prior to the time the host started incubation (as determined by the field candler).

Host	Area	Number of Parasitic Eggs	Percent Laid After Incubation Started
Cinnamon teal	Knudson	107	77
Mallard	Knudson	358	61
Canvasback	Delta, 1952	41	44
"	" 1953	110	50
"	" 1954	132	50

It is apparent that less than one-half the eggs laid have any chance of survival because they will be incubated for fewer days than necessary. There is no evidence that the incubation period of the redhead is any shorter than that of its close relative, the canvasback. A few well incubated parasitic eggs may hatch from the heat of the sun after the host leaves with her brood but no records of this were obtained in the present study or by Hochbaum (1944:91).

Yolk eating by trapped females

One female trapped in the Knudson Marsh in 1955 had yolk on her bill and the shells of a broken egg were found in the nest. It was apparent that the female had eaten the yolk and

part of the shell--probably after having broken it accidentally. Yolk was detected on the mandibles of six of 42 hens trapped. An example of a mallard egg partly eaten by a redhead is shown in Figure 11. There is no evidence of breakage other than the hole made by the bill. Very probably this behavior was due to the abnormal conditions of confinement in the trap; at least no evidence of egg eating by redheads was found in other nests. However, this is an obvious way in which the egg-eating habit of parasitic birds in general may have been developed. During the present study, it was found that incubating redhead females would eat egg remains during the hatching period (Figure 12). Poulsen (1953) and Tinbergen (1953:157) have shown that gulls will eat their own eggs if they are accidentally broken. Such action presumably rids the nest of debris which might attract predators or mat the plumage of ducklings. Because egg breakage is most likely to occur during battles between the host and a parasitizing hen, the normal reaction of the parasite (or the host) would be to eat an egg broken in this way. It is conceivable that this has survival value.

Age of the parasitizing female

Gudmundson (1932) suggested that parasitism in Icelandic eiders occurred when an old female returned to her previous year's nest site and found it occupied by a young hen. In such a case, he thought that the old female laid in the nest and that both females incubated the same eggs. Conversely, it

Figure 11. Mallard egg from which a trapped redhead ate the yolk.

Figure 12. Incubating redhead female eating shell of hatched egg.

may be that yearling birds (without nesting experience) are the principal parasites.

Unfortunately, age is not easily determined in breeding female redheads. During studies of known-age captives, the writer learned that some yearling females retain traces of juvenile plumage in the venter, rump, and lower back. In addition, the undertail coverts of yearlings were tannish gray, while those of adults were white with dark brown patches. The face of the yearling was more mottled with dark brown feathers. All characteristics were relative, however, and only occasionally was the combination of them clear enough to distinguish age with assurance. Among the 42 hens captured on nests, 14 were believed to be adult, and 22 yearlings (six unknown). While some of these determinations may be open to doubt, the evidence clearly indicates that both age groups were present.

Because such a high percentage of the redhead population is known to be parasitic (as discussed below), late nesters are assumed to have been parasitic earlier in the season. Two such late nesting females in the Delta Marsh were found to be banded birds of known age; both were yearlings released from the hatchery the previous year, that had migrated and returned to nest within 200 yards of the point where reared.

Physical condition of the parasitic female

As a measure of physical condition, females were weighed when captured. These data are presented in a scattergram in Figure 13. They show a general downward trend in weight

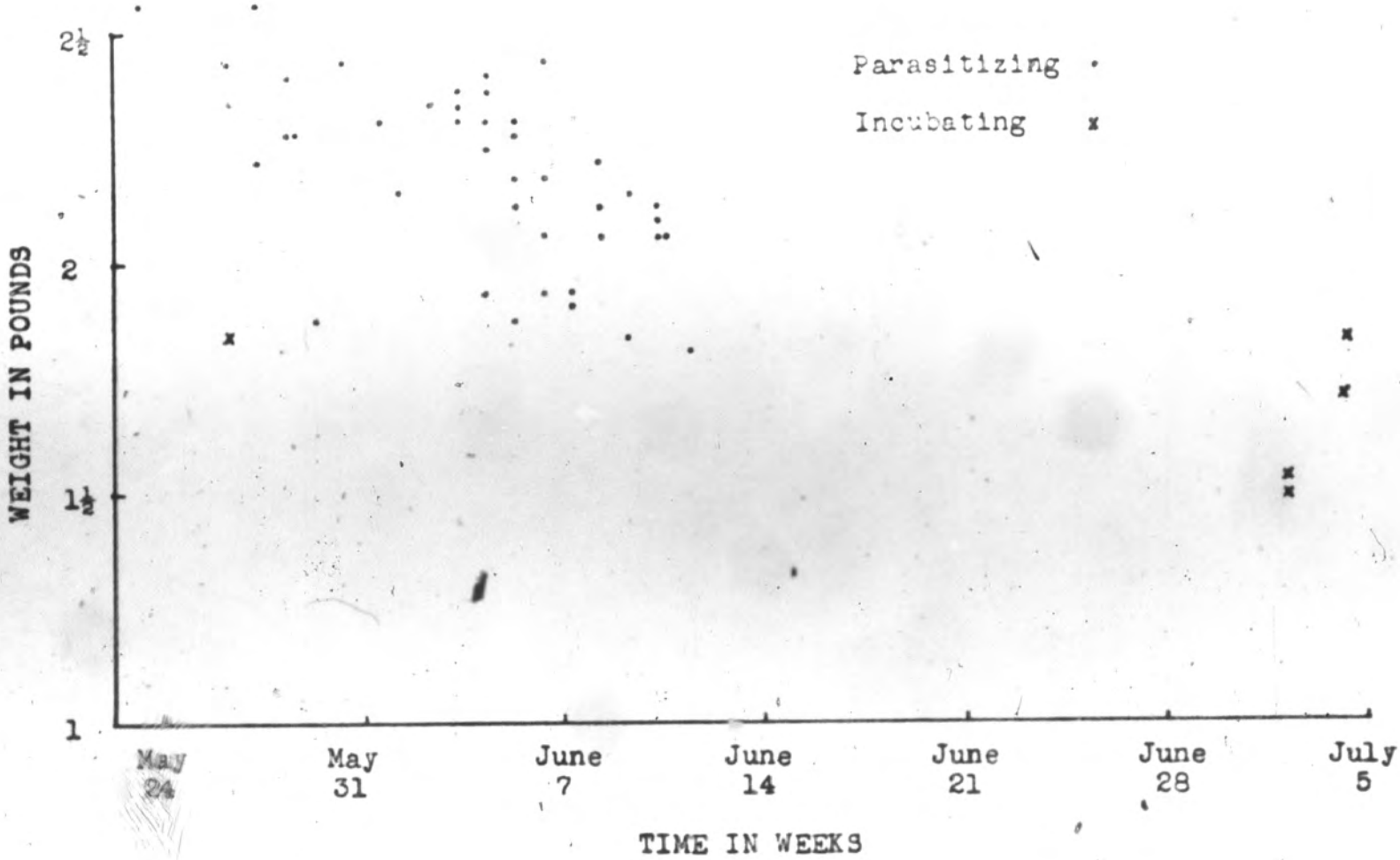


Figure 13. Body weights of parasitizing and incubating redhead females, Knudson Marsh, Utah.

throughout the laying period. One female, recaptured five days after she was first trapped, had lost six ounces. For comparison, the weights of five females trapped during incubation are also presented. A greater loss in weight is apparent in incubating than parasitizing females, presumably because incubating birds have less time to spend feeding.

Although Stresemann (1934), Tucker (1943), and Bailey (1952) state that no clear-cut brood patch is found in Anatidae as is present in other groups of birds, Stresemann (op. cit.) noted Jackson's (1915) description of a special nest down which developed on the belly and was plucked by the female. Obviously, a loss of breast down sufficient to supply the abundance of down found in some nests must leave a bare area. This was clearly seen in incubating female redheads captured in the present study. The patch was well formed by the ninth day of incubation and is probably present earlier. It is apparent that a nesting hen, or a female which had recently deserted, should have a brood patch. The fact that none of 42 redheads captured parasitizing nests had a brood patch shows that they were not nesting at the time of parasitizing nor had they done so previously.

REACTIONS OF THE HOST

Defense of the nest

The host may react to the parasitic intrusion of the redhead in a variety of ways. If she is on the nest when the

parasite arrives, she threatens and pecks at the intruder. Such battles were observed by Hochbaum (1944:91) at the nest of a captive canvasback and by McKinney (1954) at a wild canvasback's nest. A similar observation was made during the present study.

A female canvasback, which had just been trapped and marked, was very broody and was returning to her nest in spite of the fact that she knew of the investigator's presence in a blind only 40 feet away. Meanwhile, a pair of redheads landed in a small pool of water about 50 feet from the nest. In passing through the pool on her way to the nest, the canvasback threatened the redhead on first sight--directing her attention more toward the male than the female! After preening, probably as a displacement activity, she returned to her nest. About 30 minutes later, the redhead moved toward the nest (thus she arrived there 50 minutes before she attempted laying). The canvasback again threatened the intruder with the posture illustrated in Figure 14. This seemed to have little effect on the redhead which immediately climbed onto the base of the nest. She was met with bill peckings but these too did not deter her. Flapping her wings to keep balance, the redhead climbed to the edge of the nest. After about two minutes at the nest in an unsuccessful effort to get on the eggs, she left. This was probably due to the presence of a trap on the nest and the observer's blind nearby rather than to the aggressiveness of the host. Apparently she did not lay her egg.

Figure 14. Threat posture of incubating female redhead toward passing blue-winged teal male.

Acceptance of foreign eggs

The success of the parasitic egg depends on whether or not it is accepted by the host. Very commonly eggs are found outside the bowl of canvasback and redhead nests (Figure 15). Are they lost from the nest during battles between host and parasite or are they intentionally pushed from the nest by the host, as in songbirds (Swynerton, 1918, Baker, 1942)? Because the chances of witnessing either event were meager, eggs of various kinds were added to the nests of hens laying and incubating. Tests of this type have been used to study egg recognition by gulls (Nobel and Lehrmann, 1940, Tinbergen, 1953:157) and by ducks (Poulsen, 1953, Sowls, 1955:103). In the present study, tests of recognition of unlike eggs were of chief importance.

These tests showed that only the most conspicuous eggs seem to be recognized and ejected (Table II). Eggs very similar to those of the host, such as redhead eggs in canvasback or mallard nests, are accepted at any time during the nesting period. Eggs conspicuously different in either size or color are either ejected or buried if they have been added during the egg-laying period of the host but are accepted during the host's incubation period. Their acceptance during incubation is due to the fact that the brooding drive is then stronger and does not imply lack of recognition by the incubating female. This was clearly shown when a conspicuously marked chicken egg (Figure 5) was added to a redhead nest which already

Figure 15. Redhead nest showing eggs thrown out of the nest during struggles between the nesting and parasitizing hens and broken by a predator the next day.

TABLE II

EGG ACCEPTANCE TESTS

Nature of foreign egg	Host species	Results	Stage of nesting
Spotted Chicken	Canvasback	Ejected	Laying
" "	"	"	"
" "	"	Pushed from bowl	"
" "	Cinn. teal	Deserted	"
" "	Canvasback	Accepted	1-3 da. incub.
" "	Redhead	Accepted; later buried	12 da. incub.
" "	"	Pushed to side of bowl	20 da. incub.
Plaster	Mallard	Partially buried	Laying
Cinnamon teal	Redhead	Accepted	7 da. incub.
Canvasback	Canvasback	Accepted	Laying
7 Mallard	Mallard	Accepted; stopped laying	"
Redhead	Canvasback	Accepted	"
"	"	"	"
"	"	"	12 da. incub.

contained three ruddy duck eggs and six eggs of the host. The hen examined the egg closely (Figure 16a) but accepted it (Figure 16b) after a few seconds spent preening at the edge of the nest. A week later, however, when the water level rose, the hen raised the eight redhead eggs, leaving the chicken egg and the ruddy eggs buried beneath. Discrimination is not always perfect for often eggs of the host are buried as well. Thus emergency nest building may account for some buried eggs but others seem intentionally covered (Spencer, 1953, Sowls, 1955: 103).

From the above tests, it must be concluded that the resemblance of redhead eggs to those of mallard and canvasback usually prevents their being ejected or buried by these hosts. Nor are redhead eggs ejected by a redhead female host. Rather, eggs found outside nests must be attributed to accidental loss through battles and through normal nest care movements. These losses are none the less a direct result of the parasite.

Perhaps some of the eggs found outside nests are laid there by the parasite when the host is very aggressive and the parasite cannot force her way onto the nest. The likelihood of this was shown by the laying of females which were unable to enter traps because other hens were trapped in them. Such behavior might explain the presence of eggs found three to six feet from nests.

Figure 16a. Female redhead examining spotted egg in her nest.

Figure 16b. Female redhead settling on the nest containing the spotted egg.

Desertion

Another response of the host to the intrusion of parasitic eggs and the battles which may occur between birds, is desertion. Desertion is most likely to occur early in the nesting period when the nesting female's attachment to the nest is not great. Thus Sowls (1955:98) found that nearly 100 percent of mallard nests found with fewer than five eggs were deserted because of his intrusion, and half of similar pintail nests were abandoned. Later in the nesting period, broodiness increases and the bird's attachment to the nest is greater.

In the present study broodiness was measured by the distance of the observer from the nest when the female flushed. Candling provided the stage of incubation which was then correlated with flushing distance. These data are presented in Table III and show that hens are less prone to leave the nest as incubation progresses. The data are based only on first visits to the nest because birds reacted differently to the observer's later approaches: some learned what would happen and left the nest sooner, while others did not. The data for redheads and canvasback in the Delta Marsh are too meager to show the relationship but the data for redheads, mallards, and cinnamon teal in the Knudson Marsh better illustrate the comparatively lesser attachment of the redhead for her nest. This weak attachment to the nest is well known by all persons who have worked in marshes where the redhead breeds; the female is often so shy that she slips from the nest long before

TABLE III

AVERAGE FLUSHING DISTANCE IN FEET, BASED ON OBSERVER'S FIRST VISIT TO NEST. NUMBER OF FEMALES FLUSHED IN PARENTHESES

Species	Stage of the nesting cycle				
	Laying	1-6 da.	7-12 da.	13-18	19-Hatching
Delta Marsh					
Canvasback	145 (12)	85 (8)	92 (3)	40 (1)	44 (5)
Redhead	148 (7)	102 (9)	85 (4)	33 (2)	--
Utah Marshes					
Redhead	81 (11)	127 (15)	72 (11)	67 (10)	54 (6)
Mallard	31 (42)	21 (23)	19 (23)	14 (23)	12 (10)
Cinnamon teal	14 (15)	16 (10)	15 (8)	20 (4)	14 (2)

the investigator reaches it, and her attendance can be detected only by the warmth of the eggs.

Another measure of the brooding drive is nest attentiveness (Kendeigh, 1952). Although no quantitative measurements have been made, the canvasback is well known for her fidelity to the nest, leaving it only once or twice a day for a few minutes. Using a nest recorder, Low (1945) found that redhead hens left the nest from three to 26 times per day, with an average of six times per hen.

The fact that the redhead is less broody than other species makes it less tolerant of disturbances. This is easily seen in times of rising waters; the redhead may attempt to build up her nest but more often deserts, while the canvasback successfully maintains hers. Thus the redhead, and the ruddy duck which is similar to the redhead in parasitic tendencies and weak broodiness, suffer severe nest losses during flooding (Williams and Marshall, 1938, Low, 1941, 1945).

Desertion losses are also apparent when the redhead serves as host to its parasitic associates. However, it is difficult to determine the exact cause of desertion of an individual nest, for parasitized nests are commonly found which have also undergone flooding and predation. Desertion was most often caused by parasitic intrusions and flooding and secondarily by predation. In any case, the nest loss is related to the innately weak nesting habits of the species.

The effect of this lack of broodiness can be measured by examining some nest desertion rates reported in the literature (Table IV). These tabulations do not include data from the present study because trapping affected desertion rates. The table shows that desertion rates of the redhead and ruddy duck far exceed those of other species. A still higher loss would be shown if the exact cause of nest failure could be more accurately determined. Many of the losses attributed to flooding probably resulted from desertion due to weak attachment to the nest. The most parasitic species--the redhead and the ruddy duck--are those most affected by parasitic intrusions and other disturbances to their nesting.

Host's reaction to parasitic young

Just as passerines feed and brood the young cowbird without apparent concern or recognition, the duck serving as host to parasitic redheads shows no concern over the difference in the ducklings. In some cases (Figure 17) she has no ducklings of her own species. Canvasbacks, mallards, cinnamon teal, and gadwall have been observed with redhead ducklings in their brood. The actions of the hen were never observed to differ from those of hens with a normal brood. Similar unconcern was noted by Collias (in litt.) when he forced ducks and chickens to hatch and brood ducklings of various species.

Once the young are three or four weeks old, however, there does seem to be recognition by the ducklings of their own

TABLE IV

A COMPARISON OF DESERTION RATES OF WATERFOWL AS REPORTED IN THE LITERATURE

	Redhead	Ruddy	Mallard	Cinnamon teal	Shoveller	Gadwall	Pintail
Williams & Marshall, 1938 (egg losses)	38%	30%	30%	11%	11%	9%	9%
Miller & Collins, 1954 (nest losses)	15%	24%	8%	10%	8%	6%	2%
Wingfield, 1951 (egg losses)	57%	28%	7%	25%	-	-	-

Figure 17. Mallard hen with three redhead ducklings. No mallard eggs hatched because of inadequate incubation of the large clutch.

kind. When feeding undisturbed and occasionally when swimming from place to place, redhead and canvasback ducklings were observed to segregate by species. Often there appeared to be aggressiveness between the two groups. Collias (in litt.) observed that redheads were always dominant over canvasbacks in hand-reared ducklings of all ages, but Erickson (1948) presented data which suggested that redheads had a higher mortality than did canvasbacks in mixed broods. Perhaps young redheads may desert mixed broods when their aggressiveness develops, resulting in greater apparent mortality in redheads.

FACTORS AFFECTING THE DEGREE OF PARASITISM

Environment

The percent of nests parasitized and the number of parasitic eggs found per nest may vary between areas and years. The causes of these variations are difficult to appraise because one may mask the effect of another. One of the most interesting reasons suggested is the influence of such environmental factors as cover and water fluctuations on the number of eggs laid parasitically.

Nesting cover. Stoddard (1931:27) first suggested that intraspecific parasitism in bob-white quail was due to a shortage of adequate cover. Williams and Nelson (1943) were likewise impressed with the importance of cover for redhead nests and suggested that the lack of nest sites, as well as an inherent weakness in the redhead, was responsible for parasitism.

If a shortage of nesting sites is a factor inducing parasitism, it should be more evident in a hole-nesting species like the wood duck and the goldeneye. Thus in Massachusetts, McLaughlin and Grice (1952) found that when the number of artificial nest sites remained constant but the population increased, the percent of compound nests also increased. Thus where nest sites are limited to special niches, and their abundance limits the number of birds that can nest in an area, compound clutches may result from two or more females competing for the same site This is especially true because females may return and use the same nest box on successive years (J. Rogers, in litt.). This relationship cannot be termed parasitism, however, because it is a conflict of two females with strong attachment for the same nest and not a reduced attachment of a female to her nest which makes her deposit eggs elsewhere. If two hens are equally broody and thus tolerant of the other's presence, both may incubate the same eggs (Bellrose, 1943). The contest of two females over a nest site is essentially what Gudmundson (op. cit.) believed to be the cause of compound nests among eiders. Competition over nest sites in a colonial nester such as eiders may be as important in inducing parasitism as it seems to be in wood ducks.

In a non-colonial species which constructs nests, cover quality or nest site preference is difficult to relate to parasitism. To analyze the importance of cover quality, a comparison was made between parasitism and nesting conditions in the

Knudson Marsh in 1950 (Wingfield, 1951) and in 1955 (present study). In the first period, hardstem bulrush, which is the preferred nesting cover of the redhead, was so dense and tall that it was impossible for a man to walk through it (Low, in litt.). By 1955, after several years of drought, the bulrush and other nesting cover was only a few feet tall and was trampled by cattle, yet the degree of parasitism was not greater than in 1950 but slightly less. In 1950, 70 percent of the mallard nests and 79 percent of the cinnamon teal nests contained an average of 5.5 and 5.5 per parasitized nest, while in 1955 only 68 percent and 53 percent of mallard and cinnamon teal nests, respectively, contained 4 and 5.5 eggs per parasitized nest. However, the redhead population was reduced from 500 pairs in 1950 to 95 pairs in 1955, a change which is difficult to relate to the amount of preferred cover per bird.

That seasonal variation in cover is unimportant is shown by the fact that the redhead, like other ducks, usually uses old plant material for its nest and nest canopy in spite of its late nesting period. The following table shows the number of redhead nests in which any green plant material was found:

Delta Marsh	1952	1 of 12	nests
" "	1953	5 of 15	"
" "	1954	11 of 23	"
Knudson Marsh	1955	9 of 42	"
Ogden Bay Refuge	1955	19 of 23	"
Total		45 115	

Green material rarely constitutes a third of the volume. The percentage varies with plant growth conditions and probably

with the phenology of the season, but the bulk of the nest material is always old. Thus redheads which are able to find adequate nesting cover in June should be able to do so in early May. From the above data, there appears to be no good evidence that lack of dense cover for nesting influences the degree of parasitism.

Water fluctuation. Low (1941, 1945) found a correlation between water fluctuations, nest failure, and the degree of parasitism by ruddy ducks and redheads. He found that parasitism increased when water levels rose or fell rapidly and suggested that such fluctuations increased nest desertion and parasitism. These changes were shown intraspecifically in the number of nests parasitized and the number of eggs per nest, and interspecifically in the number of redhead nests parasitized by the ruddy duck. Water level control was therefore stressed as a means of managing for higher nest success and lower rates of parasitism. Support for Low's theory was found in the data of Marcus Nelson (1943). He found that the percentage of nests parasitized by redheads was higher in a unit where water levels fluctuated greatly (24 percent) than in an area of little fluctuation (six percent). These data were later confirmed by Noland Nelson (in litt.). However, it is apparent that the redhead made up a higher percentage of the breeding population in the area with uncontrolled water levels. Nolan Nelson agrees with the writer that this disproportionate number of redheads in the two areas influenced the degree of parasitism.

No evidence was found during the present study to indicate that water fluctuations were an important influence on the degree of parasitism. In 1953, after the period when most redheads had started nesting, the water level rose six inches in about two days but no increase in parasitism was noted. It was concluded that if parasitism was increased by nest losses caused from flooding, it occurred only early in the nesting period. However, in comparing three years of observations at Delta, no evidence for this was found. From 1952 to 1954, the water level of the Delta Marsh increased nearly four feet. In 1954 the marsh was joined with Lake Manitoba and during high winds severe water fluctuations occurred throughout the nesting period. The failure of these water fluctuations to increase parasitism is shown by the following data:

Year and water conditions	No. of Canvasback nests	Percent parasitized	Aver. No. redhead eggs per parasitized nest
1952			
Few minor fluctuations	17	100	6.5
1953			
Great fluctuations, 6"	23	100	5.9
1954			
Severe fluctuations, 6-11"	8	88	4.2

In the Knudson Marsh water levels occasionally fluctuated as much as three inches per day but, because of the low water, these fluctuations were below the level of the nesting vegeta-

tion and no nests were endangered or lost to flooding. Yet parasitism was severe. This agrees with the high degree of parasitism found by Wingfield in 1950 which occurred in spite of the fact that water levels were essentially stable.

Finally, it is apparent from Figure 18 that the peak of parasitism preceded the period of greatest nest initiation. This pattern was observed each year of the Delta studies but is best illustrated by data from the isolated Knudson Marsh. It is obvious that parasitism precedes nesting of the redhead and thus nest losses could not have caused parasitism. Further evidence that parasitism precedes nesting is found in the fact that none of the females trapped parasitizing nests showed evidence of a brood patch.

Disturbance. To learn the significance of human disturbance, a comparison of initiation dates of redhead nests in the Knudson Marsh and the Ogden Bay Refuge was made. The latter area was essentially undisturbed while the investigator was in Knudson Marsh nearly every day of the breeding season. Data from both areas are shown in Figure 18 and reveal no evidence that human disturbance influenced the time of redhead nest initiation. Moreover, the high degree of parasitism at Ogden Bay occurred in the absence of human disturbance.

From the foregoing, there is no evidence that factors such as cover quality, water fluctuations, or disturbance, affect the number of eggs laid parasitically by the redhead.

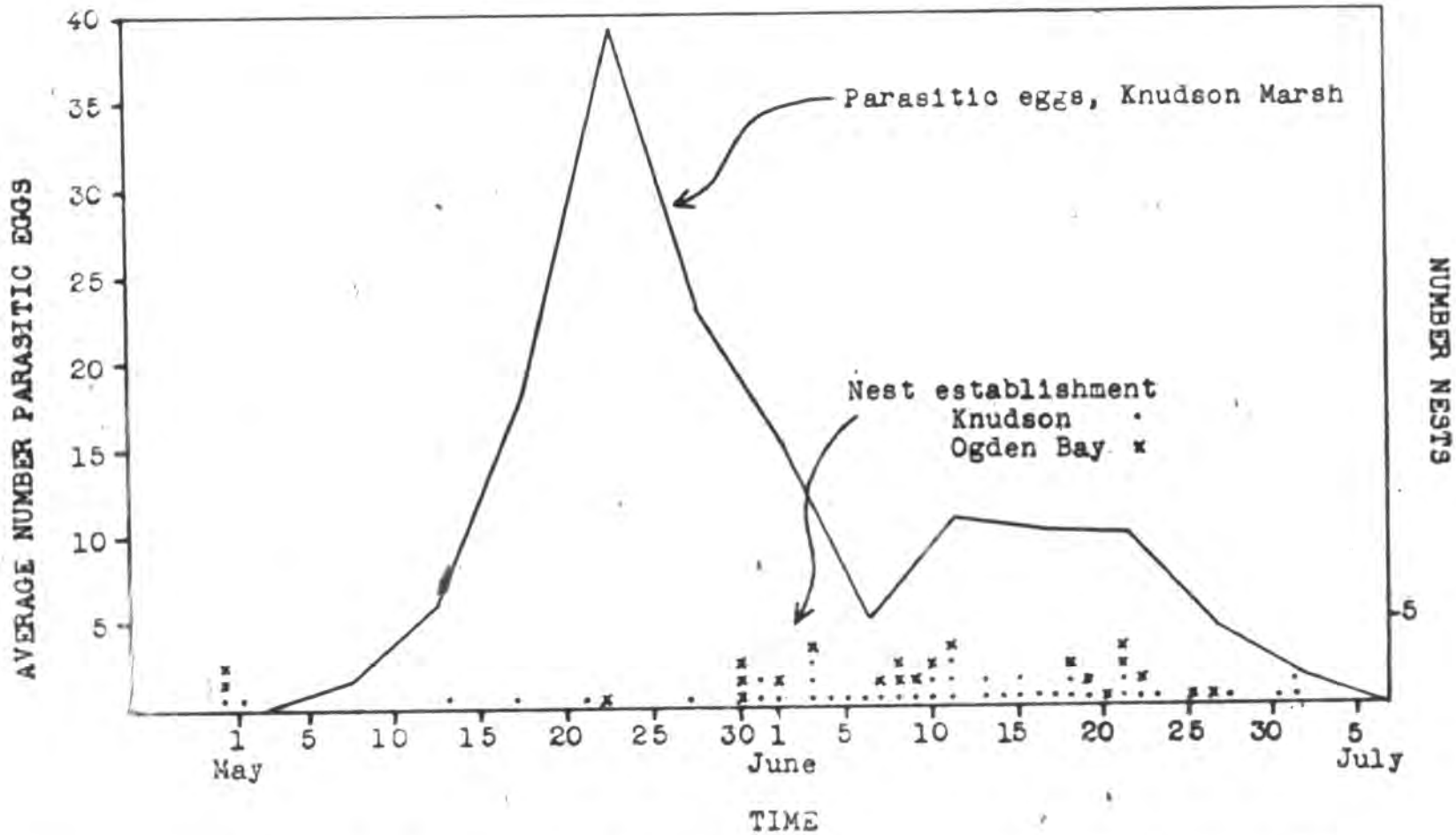


Figure 18. Relation of redhead parasitism to redhead nest initiation in Utah.

On the basis of present evidence it seems that the parasitic tendencies of species like the redhead and ruddy duck are inherent and not subject to measurable modification by the physical environment.

A number of contemporary investigators feel that redhead populations vary from year to year in their tendency to nest; that in some years they settle down and are highly successful in nesting while in others they are highly parasitic and do little nesting. Only a long-term study of population density the percent nesting, and the degree of parasitism in an isolated area can determine this with greater accuracy. Another unanswered question is whether concentrated nesting in preferred habitat increases the amount of parasitism or merely the opportunities for observation.

Habitat preference. King (1954) related parasitism by cowbirds to habitat preference of both the parasite and host. This relationship is also clear for waterfowl. Differences in degree of parasitism observed by Nelson (1943) in two study areas resulted chiefly from the fact that a unit with controlled water level was dominantly upland and preferred by dabbling ducks while the uncontrolled unit was marshy and more preferred by the redhead. A similar pattern of ecological preference is apparent in the Delta Marsh. Deep marsh species like the canvasback are heavily parasitized while field nesting dabblers are rarely affected. The

redhead apparently makes no effort to stray from its preferred habitat to parasitize nests.

Within the redhead's niche, certain areas may be preferred for courtship, loafing, and feeding, as well as nesting. If these areas are limited in number, a concentration of birds results. This effect was noticed in the Knudson Marsh where only a few deep channels and patches of water were suitable for feeding and courtship. Nests of any species located near these areas tended to receive great numbers of parasitic eggs. Nests farthest from the water's edge tended to be least parasitized.

Time

The chronology of nesting of the host and laying by the parasite is also important. Hochbaum (1944:91) noted that ruddy duck parasitism was restricted chiefly to other ruddy ducks because few other species nested as late. Both Erickson (1948a) and Wingfield (1951) observed that the earliest nesting ducks avoided parasitism because the redhead was not yet laying. That such relationships are not entirely responsible for varying degrees of parasitism among species is made apparent by comparing the nest initiation dates of teal and mallards with the temporal distribution of parasitic egg laying (Figure 19). Although the peak of the period of parasitism coincides more nearly with the laying period of teal than

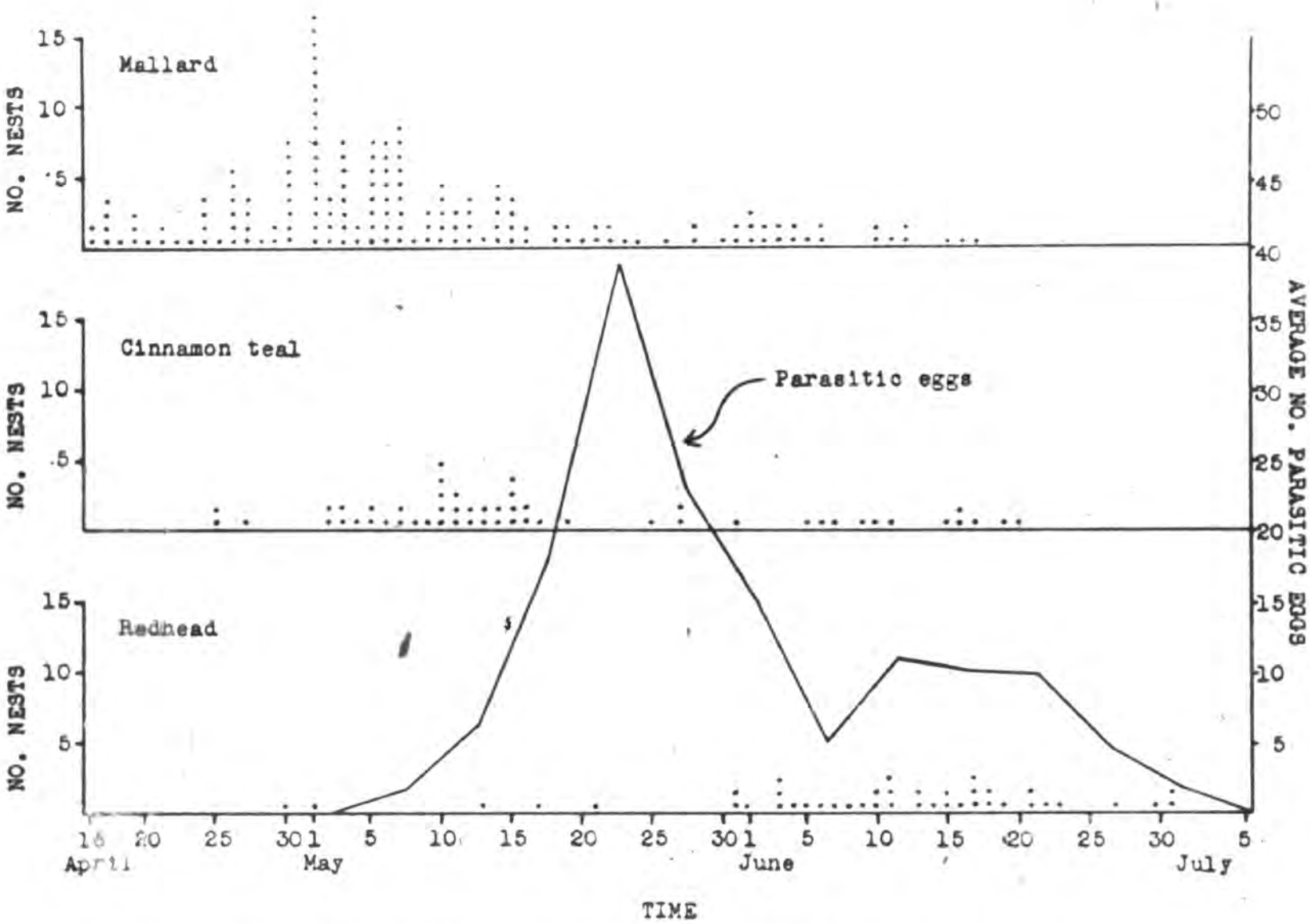


Figure 19. Relation of redhead parasitism to nest initiation in the Knudson Marsh.

of mallard, the mallard received the higher degree of parasitism.

Population density

One important factor influencing the degree of parasitism has not been discussed: the effect of the relative abundance of parasites and hosts. This relationship was first investigated by Nice in 1937. She observed that the percentage of song sparrow nests parasitized by cowbirds increased from 24 to 77 during the seven years of her study. Throughout this period her song sparrow population remained stable but the cowbird population increased. From Hicks' (1935) data she calculated that a ratio of one female cowbird to 12 hosts resulted in 35 percent of the nests being parasitized. Her own data gave close agreement, and hence she concluded that the degree of parasitism was in part a function of the host:parasite ratio.

Bennett (1938a:47-67) and Stokes (1954) have given evidence that the degree of inter- and intraspecific parasitism by pheasants varies directly with population density. Stokes compared data from various parts of North America and found that nest abandonment (due to intraspecific parasitism) was proportional to density.

McLaughlin and Grice (op. cit.) found that the rate of nest desertion in wood ducks was density dependent but the influence of the shortage of nest sites was difficult to evalu-

ate. As mentioned previously, degree of parasitism by redheads reported by Nelson (op. cit.) was also density dependent.

In the present study, host:parasite density relations could only be determined in the Knudson Marsh because it was impossible to estimate populations in the Delta Marsh. Population data are shown below; redheads are included because they also serve as hosts.

Species	Estimated population	Percent of nests parasitized	Estimated population	Percent of nests parasitized
Redhead	500 pairs	*	92 pairs	*
Mallard	450 "	70	125 "	68
Cinn. teal	300 "	79	60 "	53
Totals	1250 pairs	71	277 pairs	65
Ratio of redheads to hosts:	1:2.5		1:3	

(*Intraspecific parasitism cannot be accurately determined and is not included.)

The 20 percent increase in hosts per parasite resulted in a decrease of only six percent in the percentage of nests parasitized. There was no difference in the number of redhead eggs laid per mallard nest in the two years but there was an increase of 1.5 eggs or 37 percent per cinnamon teal nest. Thus no relationship is apparent between the change in host-parasite ratio and the percent of nests parasitized or the average number of eggs laid per parasitized nest.

Further attempt to determine the significance of the relative density of host-parasite was made by use of the aver-

age number of parasitic eggs laid in both parasitized and unparasitized nests. The average number of redhead eggs laid in mallard and teal nests decreased from 4.2 in 1950 to 3.4 in 1955--a decrease of .8 egg per nest or 19 percent, a close agreement with the 20 percent increase in number of hosts available.

The accuracy of this measure hinges on the assumption that the average number of eggs laid by the parasitic redhead is constant from year to year. To test this assumption, a comparison was made of the two years' data by multiplying the number of eggs laid per nest by the number of hosts available per parasite. For 1950 this was 10.5 (4.2 x 2.5) and in 1955 10.2 (3.4 x 3). Thus there is remarkably close agreement in the average number of eggs laid per parasite in these two years despite the fact that there had been a great change in habitat and population density.

While some biases are involved in estimating the host-parasite ratio on the basis of estimated populations, such a ratio based on nests would be far more biased because the percentage of the population which nest differs with the species. An increased host-parasite ratio causes an apparent increase in the number of eggs laid per female but figures derived in this manner still closely agree: 19.7 eggs per female in 1950 and 18.9 in 1955.

PARASITISM AND THE NORMAL NESTING OF THE REDHEAD

Chronology of parasitism in relation to nesting

Low (1945) suggested that parasitic egg laying in the redhead primarily occurred prior to nesting or following nest destruction. He favored the latter idea because he found a direct relationship between the rate of nest loss and the degree of parasitic egg laying. However, by comparing the dates of nest initiation for the redhead, canvasback, mallard, and cinnamon teal obtained in the present study (Figures 19 and 20), it may be seen that the redhead is a much later nester than the others. As shown previously, the peak of redhead parasitism precedes the peak of redhead nest initiation and the few early nest losses among redheads could not account for the degrees of parasitism found. Most conclusive was the finding that among the parasitizing females trapped, marked, and released, two were later found to have constructed nests of their own--thus proving that parasitic females do nest and rear their own brood.

Further study of the relation of nest initiation dates of redheads to the chronology of parasitism in the Knudson Marsh shows that the earliest females to lay were not parasitic because they began nesting before parasitism was found (Figures 18 and 19). Only four nests, or six percent of the total observed in Utah, were attributed to these early laying, non-parasitic females. A similar pattern was apparent

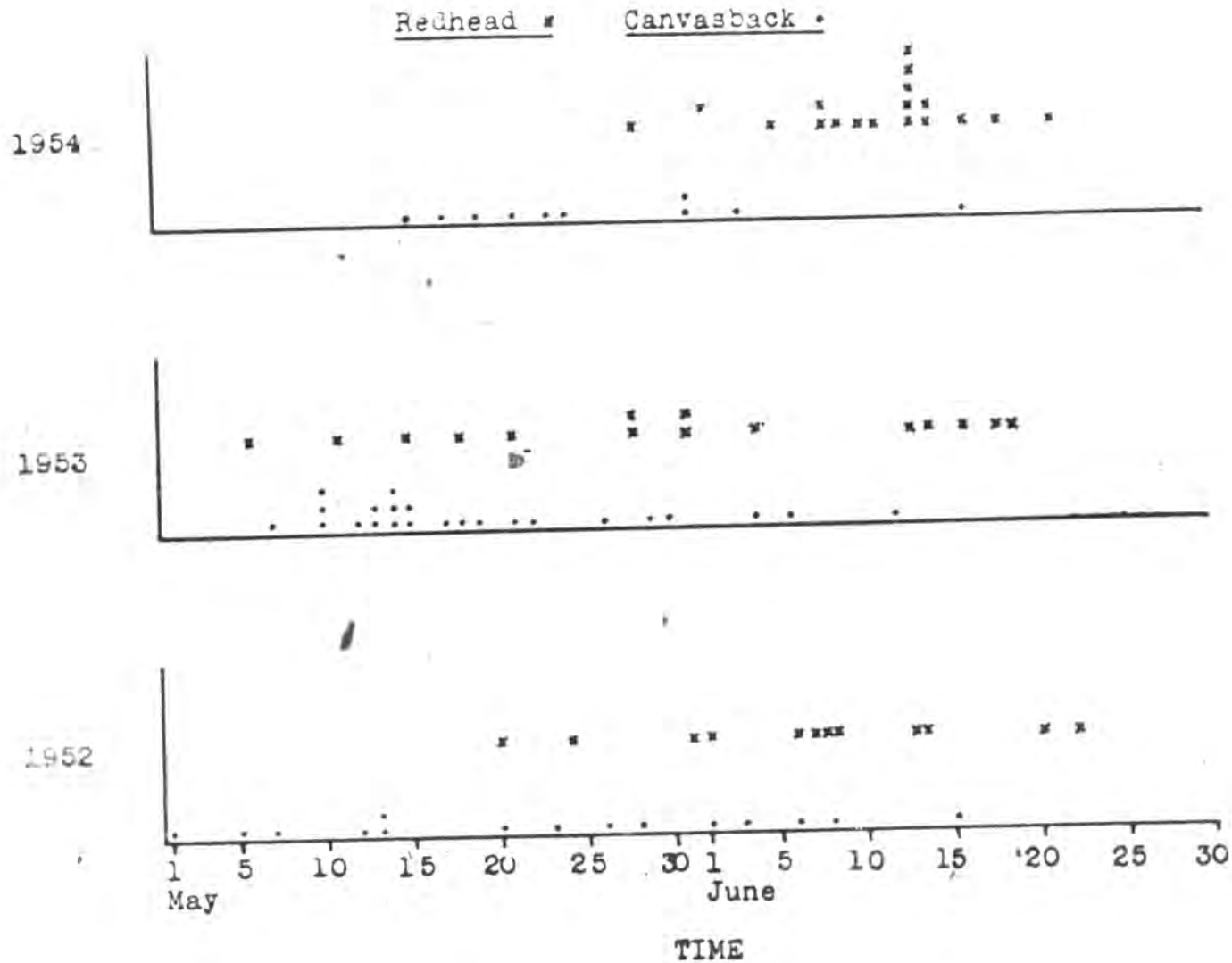


Figure 20. Chronology of nest initiation of redheads and canvasbacks in the Delta Marsh.

in the Delta Marsh. These early nesting redheads built better nests and were more broody and tolerant of parasitic and human intrusion; this tolerance was much lower among later nesters. Peter Ward (in litt.) observed that early nesting redheads were found in all years in the Delta Marsh and that they built excellent nests with an abundance of down. One interesting record of this type of nester was noted in 1955 at the Knudson Marsh. Because of the low water level, redheads made trails across mud flats to get to their nests (Figure 21a). The path of one such early nesting female was within three feet and in full view of an unparasitized mallard nest. The mallard nest had been initiated first, yet the redhead walked past it daily to lay but did not parasitize.

It is also apparent that parasitism did not cease at the peak of redhead nest initiation. Either some redhead females were completely parasitic (did not nest), or parasitized and nested simultaneously. The latter seems unlikely because the onset of broodiness is known to inhibit laying in doves and most other birds (Bates, Riddle, and Lahr, 1937).

Present evidence indicates that some redheads do not nest. During the three years of the study in the Delta Marsh, redhead females were commonly observed loafing with groups of males late in the nesting season after the peak of redhead nest initiation had passed. Had these females failed in nesting and not renested, or had they not attempted to

Figure 21a. Trail of redhead hen across mud flat from her nest to open water.

Figure 21b. Redhead nest in clump of hardstem bulrush with trail of down leading from nest.

nest? The answer is apparent in the following comparison of estimated breeding populations and the number of nests found in the Knudson Marsh in 1955:

	Estimated population	Number of nests found
Redhead	90-95 pairs	46
Mallard	125 "	173*
Cinnamon teal	60 "	56

(*Includes many renestings: see Figure 19.)

Thus only one-half of the redhead females appear to have attempted nesting. There is little question about the accuracy of the redhead population estimate or the number of nests observed. In addition to the 42 hens trapped and marked, an additional 25 unmarked females were flushed from nests. The percentage of nests found in relation to those constructed was considered high because of the clumped nature of the vegetation and the conspicuous light down of the redhead (Figure 21b). Even if one-third of the nests were overlooked, the data would indicate that one-fourth of the population did not attempt to nest.

In the Knudsón Marsh, 10 to 15 redhead females accompanied by males were often observed in the later part of the nesting season when most hens were incubating. Some of these hens were paired but there was no longer any intense courtship and the males were well into eclipse plumage. Two of the females in this group had previously been marked when parasitizing nests. Numerous females were seen early in July

among post-breeding flocks of 25 to 400 male redheads at Ogden Bay Refuge in Utah and at Lake Winnipegosis, 100 miles north of the Delta Marsh. It is very unlikely that such females would nest after joining large flocks late in the breeding season.

Thus the evidence indicates that a large cohort of the redhead population does not nest but is strictly parasitic. It is probably these birds that parasitize throughout the breeding season. It is probable that the strictly parasitic redheads lay 18 or 20 eggs and that the semiparasitic birds which later nest, lay fewer parasitically. In this latter group there may be all degrees of parasitism preceding nesting, thus accounting for the broad and late peak of nest initiation for which this species is noted.

Within one species there appear to be three types of nesting behavior: normal nesters, semiparasites, and complete or obligate parasites. From general observations, it is the opinion of the writer that the same pattern exists in the ruddy duck.

Nests and nest sites

When the semiparasitic redhead hen begins to nest, her constructing abilities show no inferiority (Figure 22a). Indeed, she constructs a nest second in quality only to the ruddy duck--another semiparasite!

The use of old nests for rearing young has been con-

Figure 22a. Redhead nest suspended in hardstem bulrush over three feet of water. Ox-bow Marsh near Brigham, Utah.

Figure 22b. Redhead egg in nest in early stages of construction. Delta Marsh.

sidered by some workers as a stage in the development of parasitism. Two examples of this were found in the present study. In one case, a redhead used an old nest in which a mallard had just hatched her young. In the other case, a redhead hen was found beginning incubation in a teal nest. Original ownership of the nest was indicated by teal down and a teal egg in the twelfth day of incubation. Thus both nest parasitism and egg parasitism occur within the same species.

Nest construction may begin simultaneously with laying, as indicated in Figure 22b, or presumably a day or two before, as noted in the canvasback by Hochbaum (1944:47). In dabbling ducks, the nest building is likewise closely attuned to laying and the eggs may be laid in a scrape in the ground and nest material added later (Ibid.:88, Sowls, 1955:93). Hochbaum also found dropped eggs of dabbling ducks in vegetation during the period of early nest building. No dropped redhead eggs were found in the present study but Low (1945) found a few on muskrat houses.

Clutch size

One of the most difficult problems in the study of semiparasitic species is the determination of the real clutch size because of the severe intraspecific parasitism. This is apparent in the average clutch figures presented by various writers (Table V). Special care was taken in the

TABLE V

AVERAGE CLUTCH OF THE REDHEAD AS REPORTED IN THE LITERATURE

Authority	Area	Number of nests	Average clutch size
Bennett, 1938b	Iowa	21	8.9
Bizeau, 1951, Steel, 1952	Idaho	75	9.1
Furniss, 1938	Sask.	3	9.3
Low, 1945	Iowa	115	9.8
Williams & Nelson, 1943	Utah	918	10.5
Erickson, 1948a	Oregon	70	11.4
Wingfield, 1951	Utah	151	13.5
Miller & Collins, 1954	Calif.	27	13.8

TABLE VI

SIZE OF UNPARASITIZED CLUTCHES OBSERVED IN THE PRESENT STUDY

Delta, 1953, 1954	6, 6, 8, 8, 9	Average 7.4
Knudson, 1955	5, 6, 6, 7, 7, 7, 7, 8, 8, 9, 9, 9	Average 7.3

present study to evaluate each clutch found. The best data were obtained from clutches of late nesters after parasitism was no longer intense. Parasitic eggs were distinguished by use of the field candler, distinctive size, color, and shape, and breakage or loss from the nest. The data in Table VI (page 101) represent, as nearly as possible, normal unparasitized clutches. It is these small clutches that have been considered renests by other workers. That late nests may be first clutches of semiparasitic hens is shown by the clutches of six and seven eggs laid by two females trapped earlier while parasitizing. The clutch size of early nesting hens could not be obtained but would be expected to be larger.

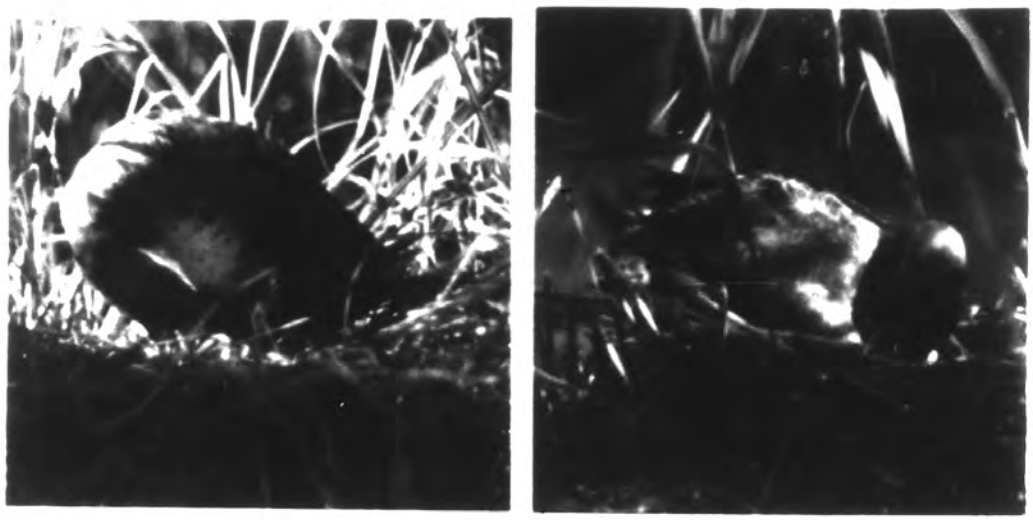
With the exception of early nesting, non-parasitic redheads, the occurrence of renesting is unlikely because the peak of nesting does not come until June and a renesting peak would not be anticipated until July. No nests were found to have been established after June. Seven incubating females were trapped and marked but none was seen again.

Behavior during incubation

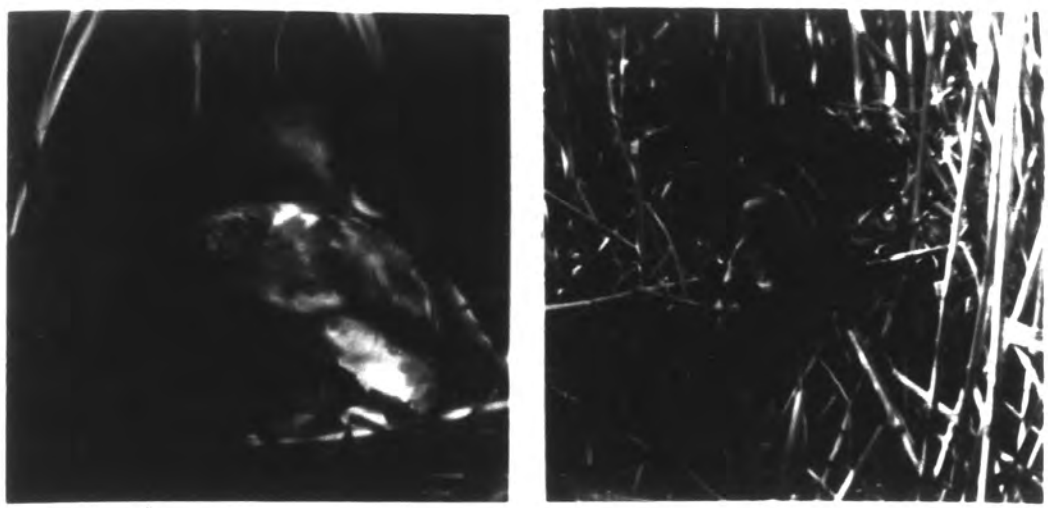
The nest maintenance and incubation behavior in the mallard and other dabbling ducks has been studied by McKinney (1951-52, 1953) and Sowls (1955:94-95) and in the Canada goose by Balham (1955). McKinney also made observations on the canvasback. To learn whether the incubation behavior of the semiparasite differed from that of "normal" species such as the

mallard and canvasback, five redhead nests were observed intensively from a blind at various stages of incubation. Early nest building and egg laying could not be watched because of the redhead's weak attachment to the nest at that time. Unlike other species, these hens frequently deserted nests because of the presence of a blind, at any stage of incubation. The best observations were made on two females which nested in the Delta Marsh after having been reared in the hatchery and released the previous summer. They were apparently more tolerant of human intrusion. The movements described by McKinney were all observed and are described briefly below, using his terminology.

When a hen arrives to incubate, she frequently climbs directly on the eggs but sometimes first preens at the edge of the nest. This may be a displacement activity (Armstrong, 1947:106) resulting from a conflict of the drives to incubate and flee. The breast and lower abdomen are preened by side to side movement of the bill (Figure 23a) and occasionally by nibbling; there is no plucking of breast feathers. Before taking her position on the eggs, the hen stands over them and pokes them with her bill (Figure 23b), causing rotation of the eggs. Then she places her belly on the eggs and settles into position by pushing alternately with her feet (Figure 23c). This movement serves to flatten the eggs into position as well as turn them. McKinney believes this flattening is also due to paddling--a quick movement of the feet detected



a b



c

Figure 23. Behavior of incubating redhead hen.

e

f

g

h

Figure 23 (cont.). Behavior of incubating redhead hen.

only by a side-to-side rolling of the body. Paddling probably also serves to insert the ruffled breast feathers around the eggs. The hen then performs the turning movement and shifts to a new position, sometimes a quarter-turn, sometimes a full-turn. She then repeats the sequence of poke, settle, paddle, and turn. Once established, she may pull in nest material from the base of the nest (Figure 23d) or from above (Figure 23e) and place it at the edge of the nest near her breast, occasionally patting it toward her with lower mandible (Figure 23f). When the material overhead does not break pulling results in the formation of a canopy (Figure 22a).

While watching a hen during a period of rising water level, I saw very intensive poking and pulling. Because the nest was in an unusual site under the canopy of trees, she had little vegetation close by and when all within reach that could be broken free had been used, she went to the edge of the nest and reached as far as possible for more material (Figure 23g). Finally she left the nest and moved to vegetation ten feet away. Picking up stems, she tossed them backwards over one shoulder (Figure 23h). A hen canvasback was also observed to make this same movement and it was reported in swans by Selous (1933:86). He noted that such material was never carried directly to the nest. Such tossing of material at various points around the nest puts it in reach of later pulling from the edge of the nest. Pulling up and tossing may form an opening in the vegetation which serves as a path to open water.

Pulling at the edge of the nest builds up the base of that structure and pulling from within moves material to the top of the nest. Patting moves it close to the bird and, with the settling movement of the feet, shapes the edge of the nest bowl. Poking then results in a movement of nest material from the edge of the nest to center of the bowl--thus increasing the height of the nest and eggs. Further evidence that poking is a nest building as well as an egg turning movement is provided by the observation that the poke movement may begin at a point where there are no eggs.

The function of the poke movement was tested experimentally in a nest made of whitetop grass. Material at the edge of the nest was dyed bright green and the following day some of it was found worked into the nest bowl. The amount of grass moved depends on the amount of poking. Excessive dampness of the nest and eggs probably stimulates nest building activity and results in a raising of the nest above the water level.

The nature, sequence, and function of the incubation and nest maintenance movements are the same as in other species in which they have been carefully observed.

Behavior of the hen during the periods of hatching and caring for young

At the time of hatching, one female was observed to carry the first egg shell away from the nest and out of sight.

She then ate the second shell and its membranes (Figure 12) and part of a third. The remaining shells were left in the nest and crushed by the weight of the hen. Another female carried the shell of the first hatched egg only to the edge of the nest where she sank it in water. Parts of shells were eaten from eggs hatched subsequently but none was completely consumed.

Hochbaum (1944:92) first reported the carrying of shells by ducks and Sowls (1955:103-108) observed it several times and induced it by adding shells to active nests. He found this behavior associated with the cleaning of nests after partial predation. However, he reported no such behavior during the hatching period.

The redhead is a quiet bird during incubation but just prior to hatching, a low "kuk-kuk-kuk" is occasionally heard. This is possibly stimulated by the sound of the ducklings in the eggs or by their first movements under her. It is the call which imprints the young to follow the hen (Collias, 1950; Fabricius, 1951).

The redhead's care of the young just after hatching seems much like that of other ducks. The following observation made in the Delta Marsh illustrates the pattern. A nest had been under observation intermittently for 25 hours and four young had hatched. At 8:00 A.M., the female appeared restless, flapped her wings, preened, gave the "kuk-kuk-kuk" call, and left the nest. Three young followed; the fourth

(probably the youngest) remained in the nest. The female hesitated, called again, and returned to the nest where she covered the remaining eggs with nest material. Then she left again, followed by all four ducklings. They remained within 30 yards of the nest, swimming for 27 minutes before returning to the nest where the hen brooded the young. An hour later, the hen left the nest and began tossing nest material; she was followed by two young. The two young in the nest gave distress calls and jumped into the water. Their second excursion took them up to 50 yards from the nest, during which time the female occasionally gave the following call. They returned after 27 minutes and the young remained in the water while the hen preened on the nest. She again gave the following call and the young came near and climbed onto the nest where they too preened (Figure 24a). The hen brooded them (Figure 24b) and they remained on the nest throughout the night (Figure 25). They left the nest at about 7 o'clock the following morning when the young were, at most, 47 hours old. At 8:00 P.M. that evening the brood was not observed on the nest but a duckling was seen nearby. A stem of cane was placed upright in the nest and was found knocked down the next morning; presumably the brood returned to the nest for the second night after hatching, possibly because no other dry roosting site was available.

After the hatching period, the female's brooding drive wanes. It is well known that redheads more commonly desert

Figure 24a. Preening of hen and young after swimming.

Figure 24b. Brooding posture of redhead hen

Figure 25. Redhead hen and young

their broods than any other species except ruddy ducks. Hochbaum (1944:99, 1946b) related this brood desertion to the onset of the post-breeding molt. In general, dabbling ducks nest earlier than do diving ducks and therefore have more time to care for broods before the onset of the molt. Redhead broods observed at Delta after late July were almost always without females (Table VII). However, early nesting redheads also desert their broods, suggesting that brooding of the young, as other breeding behavior, is weak in this species.

Another measure of the strength of the brooding drive is the injury-feigning ability (Armstrong, 1947:90-105) which is commonly found in ducks (Bennett, 1938a:54, Hochbaum, 1944: 105). The redhead is again the poorest of parents. Dabbling ducks will feign well even prior to hatching but the redhead will sneak away. The redhead rarely feigns except with newly hatched young but, as Hochbaum (loc cit.) stated, ". . . even this is poorly acted." The ruddy duck does not feign at all but takes flight. Feigning behavior in dabbling ducks persists until the young are nearly ready to fly, while in redheads the hen will flee--if she has remained with the young until then. While it may be said that feigning behavior in all divers is less intense than in dabbling ducks, it is not solely because divers nest late. The scaup, which nests during the same period as the ruddy duck, is a broody bird during

TABLE VII

RELATIONSHIP OF TIME TO THE REDHEAD HEN'S ATTENDANCE OF BROODS

DELTA MARSH, 1952 AND 1953

Date	Broods observed	Number with hen
June 15 - 21	1	1
June 22 - 30	4	3
July 1 - 7	2	1
July 8 - 14	4	4
July 15 - 21	8	6
July 22 - 31	10	4
August 1 - 7	3	1
August 8 - 14	7	1
August 15 - 21	12	1
August 22 - 31	1	0

nesting (Munro, 1938) and also feigns well when with young (Munro, 1941).

Thus while the onset of molt may influence brood desertion in the redhead, innate lack of broodiness also seems important. Either cause is directly related to the breakdown of nesting habits in the redhead; the late nesting season is due to pre-nesting parasitism and weak broodiness is related to its semiparasitic behavior.

THE EFFECT OF PARASITISM ON THE HOST AND ON THE PARASITE: AN EVALUATION

The host

Reduced clutch size. In the course of this study, it was found that the number of eggs laid by a duck in its own nest was reduced by the presence of redhead eggs laid parasitically. This may be attributed to the fact that ducks are indeterminate layers. By experimental modification of clutch size, two types of laying have been found. These were termed determinate and indeterminate by Cole (1917). The former is characteristic of doves and the latter of gallinaceous birds and waterfowl. Poulsen (1953) and other workers have shown that these laying patterns are not always clear-cut and may depend on the exact time in the laying cycle when clutch size is modified. Among determinate layers like ducks, additions of parasitic eggs to the clutch will have a depressing effect on ovulation. This is demonstrated by the data in Table VIII

TABLE VIII

EFFECT ON CLUTCH SIZE OF HOST OF PARASITIC EGG LAYING BY THE REDHEAD

Species	Average clutch size in unparasitized nests	Average clutch size in parasitized nests	Authority
Canvasback	9.9 (7)*	7.7 (47)	Erickson, 1948
Canvasback	8.0 (1)	6.6 (38)	Present study
Cinnamon teal	8.6 (14)	6.6 (35)	Wingfield, 1951
Cinnamon teal	10.1 (14)	8.3 (22)	Present study
Mallard	9.4 (63)	9.2 (223)	Wingfield, 1951
Mallard	8.3 (40)	7.2 (91)	Present study

(*number of nests observed.)

TABLE IX

COMPARATIVE EGG SUCCESS IN PARASITIZED AND UNPARASITIZED SUCCESSFUL NESTS

Species	Unparasitized	Parasitized	Authority
Canvasback	91%	77%	Erickson, 1948
Canvasback	-	59%	Present study
Mallard	92%	90%	" "
Mallard	6% less in parasitized		Wingfield, 1951
Cinnamon teal	89%	94%	Present study
Cinnamon teal	2% less in parasitized		Wingfield, 1951

which includes counts of the host's eggs found outside as well as within the nest.

The degree to which clutch size is affected depends on the stage of laying at which the eggs are added. In waterfowl, egg laying and nest building occur simultaneously; in songbirds, nest construction begins two to twenty days before laying (Wallace, 1955:164). Parasitic waterfowl have less opportunity to find nests in the nesting cycle than do cowbirds and cuckoos; therefore, redheads more commonly lay after incubation starts than before. Nevertheless, the number of eggs laid by the hosts suffering heavy parasitism may be reduced by two. While this seems to have little effect on the total number of young reared per nest, fewer ducklings of the host are produced.

Egg and nest losses. After the eggs are laid, parasitic intrusions may reduce clutch size in several ways. Some are lost from the nest either as a result of struggles between host and parasite or during normal nest movements when the clutches are very large. Among canvasbacks in the Delta Marsh, 22 percent of all eggs found during the three years of the study were under water around the nest. From redhead nests, Williams and Marshall (1943) reported a 13 percent loss of eggs, Wingfield (1951) one percent, and in the present study, three percent. Losses of cinnamon teal and mallard eggs were less than two percent in any of the studies. Possibly eggs lost from shallow nests of dabbling ducks are

retrieved by the hen. The very high loss from canvasback nests may be attributed in part to the greater degree of parasitism on this species.

Egg losses also occur by breakage during nest battles; most are only cracked but their hatchability is lost.

Finally, many losses occur because the host female can not incubate properly more than one layer of eggs. Large clutches invariably contain many eggs with dead embryos.

These three types of egg losses are lumped in all computations of egg success and may be determined by comparing the success of eggs in parasitized and unparasitized successful nests (Table IX, page 115). Little effect is noticeable in mallards or teal but canvasbacks suffered severe losses.

Egg losses may also be measured by comparing the average number of eggs hatched per nest in parasitized and unparasitized canvasback nests. Data from the present study and from Erickson (1948a) are presented in Table X. Lesser production in parasitized nests is again apparent.

The reaction of the host to continued parasitic intrusions may be desertion, the effect of which does not appear in egg loss calculations as shown in Table IX. For this reason, a comparison of nest success data is presented in Table XI. Again, the mallard seemed unaffected but the canvasback and the cinnamon teal showed losses due to parasitism.

In summary, parasitism lowers the reproductive success of the host by reducing clutch size and increasing egg and

TABLE X

HATCH OF CANVASBACK EGGS IN UNPARASITIZED AND PARASITIZED SUCCESSFUL NESTS

Unparasitized		Parasitized	
Average number canvasback eggs per nest	Average number eggs hatched per nest	Average number canvasback eggs per nest	Average number hatched per nest
Present study:			
8	-	7.2	4.2
Erickson, 1948:			
8	7.3	7.8	6

TABLE XI

COMPARATIVE SUCCESS OF PARASITIZED AND UNPARASITIZED NESTS

Species	Unparasitized	Parasitized	Authority
Canvasback	-	69% (35)*	Present study
"	57% (15)	46% (59)	Erickson, 1948
Cinnamon teal	44% (18)	26% (23)	Present study
" "	41% (34)	32% (107)	Wingfield, 1951
Mallard	66% (38)	68% (72)	Present study
"	64% (98)	66% (223)	Wingfield 1951

(*Number of nests observed.)

nest losses. The significance varies with the species and the degree of parasitism. Clutch size may be reduced 20 percent. It appears that parasitism in the order of 60 to 70 percent of the nests and four to six eggs per nest must occur before egg and nest losses are measurable. Further increases in parasitism probably result in rapid increases in nest losses. Parasitism of these extreme magnitudes has been found in only a few small areas. Although Williams and Nelson (op. cit.) found as many as 30 percent of duck nests parasitized in some areas of Utah, more than 5,000 nests throughout Utah showed only six percent contained foreign eggs. If this were true of other areas, which seems likely, parasitism is probably not of great significance.

The effect of parasitism on species like the mallard and perhaps the cinnamon teal could not be great because they have extensive breeding areas not overlapping geographically with that of the redhead. However, the effect of redhead parasitism on the canvasback is probably more serious because they occupy the same breeding range. In large marshes, where redheads tend to concentrate, it is quite possible that there is a density dependent relationship between redhead and canvasback--parasitism prevents canvasbacks from being abundant when redhead populations are high. In pothole nesting habitat, where redheads are less numerous than in marshes, canvasback production is probably affected less. The significance

of redhead parasitism on the canvasback cannot be assessed adequately on the basis of present data.

The parasite - the redhead

In obligate parasites such as the cuckoo and cowbird, reproductive success depends entirely on the number of eggs which hatch and are reared by the host. This is not true of species in the developmental stage of parasitism which not only parasitize but also nest. Such a transitional stage is essential to maintain the population during the slow evolution of the obligate parasite. It is a period of trial, for only by the differential survival of the parasitically reared young will the behavior develop. The relative success of the parasitic and the normal nesting cohorts of the population are difficult to evaluate.

From evidence obtained in this study, only five to ten percent of the redhead population nests normally and early in the season. All the others apparently lay eggs parasitically at some time. More than half of these hens are semi-parasitic and nest after parasitizing, while the remainder are probably completely parasitic. On the average, the parasitic birds lay from 11 to 12 eggs parasitically. Canvasbacks hatch seven percent (Erickson, 1948) to as high as 25 percent (present study) of the redhead eggs deposited in their nests. Steel (1952) reported 21 percent were hatched by canvasback, ruddy, mallard, and scaup hosts. Mallard and

teal in the Knudson Marsh hatched six to seven percent of these eggs in 1950 (Wingfield, 1951) and nine percent in 1955 (present study). On the average ten to 15 percent of the parasitic eggs hatch, or only one egg per parasitic female. Still fewer reach maturity. While such figures seem small, it is interesting to recall that only 64 percent of the cowbird eggs studied in Nice's song sparrow nests hatched and but half that number were fledged. Yet the cowbird is an abundant species.

It is impossible to determine the number of parasitic redhead eggs which hatch in redhead nests.

The major part of the reproductive success of the redhead still depends on the results of normal nesting. It appears that only 50-60 percent of the population nests. They must raise sufficient young to compansate for the low productivity of the non-nesting segment of the population. Because of its innately weak reproductive habits, the productivity of the redhead is lower than that of most other ducks. The effective clutch, including parasitic eggs, is large: 10.8 eggs as calculated from 1,359 clutches reported in the literature (Table V). The hatch of these eggs (10,802) is 32 percent (Table XII). These calculations include what little renesting occurs. The lack of renesting behavior, plus weak brooding habits, are the factors which cause the low egg success.

From these data, it may be concluded that the average

TABLE XII

EGG SUCCESS AS OBSERVED IN REDHEAD NESTS,

AS REPORTED IN THE LITERATURE

	Number of eggs		Percentage of success	Authority
	1629		21.8	Wingfield, 1951
	5683		30.6	Williams & Nelson, 1943
	802		31.4	Erickson, 1948
	186		40.5	Bennett, 1938b
	1516		45.0	Low, 1945
	683		70.0	Bizeau, 1951, Steel, 1952
Total	10,802	Aver.	32.0	

nesting female hatches 3.4 ducklings each season. If there is a 30 percent mortality to the young prior to the fall migration (Low, 1945), about 2.3 young are reared per nesting female. Hickey (1952:80) concluded from his mortality studies that each female redhead would have to rear 3.6 young by the first of September each year if the population were to remain stable. If foster parents rear one young redhead for each parasitic redhead female, and an average of 2.3 young are reared by the 60 percent of the redhead females which nest, the average number of young produced per female in the entire population would be only 2.3. The 3.6 young calculated by Hickey as essential recruitment per female could only be obtained if egg success was at least 40 instead of 32 percent. This eight percent difference may easily be due to the presence of the investigators.

While leaving something to be desired, these figures point out the low reproductive success of the redhead, mostly attributable to the degenerative reproductive behavior. In view of this, the present population status of the redhead is not surprising. Its population is characterized by rapid changes not always fluctuating synchronously with those of other waterfowl (Hochbaum, 1946a) and its status is usually considered precarious by waterfowl biologists. In view of the present knowledge of its behavior, it is questionable that the redhead has ever enjoyed the relative abundance previously reported for other species before the days of pothole

drainage and market hunting.

The delayed nesting which results from parasitism means a late brood period (Hochbaum, 1946a; Weller, 1954). Thus the young do not fly until late and are inexperienced--some even flightless--at the opening of hunting seasons on the breeding grounds. This, coupled with the normal curiosity and gregarious tendencies of the species, accounts for its high first-year mortality rates (Williams, 1944, Hickey, op. cit.:73-82, Robbins, 1949, Brakhage, 1953). Thus the deleterious influence of the redhead's unusual mode of reproduction is apparent throughout the life cycle of the species.

CHAPTER V

DISCUSSION

There is little doubt that the redhead is a species in the developmental stage of parasitism. The study of its behavior provides an opportunity to appraise factors influencing the evolution of this mode of reproduction. It is still impossible to make any positive statement of the origin of parasitism among birds, but further paths of investigation are suggested by considering the status of parasitism in the redhead.

Of particular interest is the fact that both "egg" and "nest" parasitism occur within this species. Both of these types have been suggested as ways in which parasitism may have evolved. Three distinct types of nest behavior are found in different individual redheads: normal nesting, semiparasitism, and obligate parasitism. In no other species has this wide range of parasitic stages been found.

The development of parasitism is characterized primarily by a loss of parental or maternal behavior. Weakened maternal instincts are apparent in both the redhead and the ruddy duck. Instinctive movements such as those of nest-building are present but they are not properly synchronized with egg laying and thus parasitism results. Following parasitism, the female builds a nest but her attachment to it and to her young

is weak. Thus the redhead shows a deterioration of what is considered usual breeding behavior.

Many reasons have been offered by ornithologists for the development of parasitism. Darwin (op. cit.) suggested that the long interval between eggs was instrumental in the development of parasitism in cuckoos. Altum (1866) suggested that cuckoos were too busy wandering in search of food to rear their own young; Forbush (1929:425) thought that parasitism developed in cowbirds because they followed migratory bison and had no time to rear a brood. Friedmann (1949) suggested that over-development of the building phase of the nesting cycle of weaver birds caused improper synchronization of laying with nest construction. This idea was based on the work of Herrick (1907a, 1907b, 1910) who stated that parasitism resulted from lack of attunement of laying and nest-building, but he could offer no explanation for it. Allen (1925:203) suggested that the sight of eggs in a nest may be such a strong stimulus that it induced parasitism but Friedmann (1929a:349) did not concur, saying:

> However, I cannot agree with this suggestion as a possible origin of the parasitic habit unless it be accompanied or preceded by a marked reduction in the attachment of the bird to its own nest. Even if the sight of eggs in strange nests stimulated egg production in a bird that was not parasitic, its natural instincts would associate the resulting eggs with its own nest and the bird would probably lay them there. . . .

He later suggested (ibid.:352) that the loss of protective instinct in the male was the most important cause of the origin of parasitism. He believed that cowbirds showed greater

interest in nests in which to lay than in the establishment of a territory and a nest site of its own. The fact that the female had lost her instinct to protect the nest (a behavior related to the weakening of the brooding drive) was considered unimportant as long as the male retained his protective drive. Friedmann's theory implies that the loss of territorial behavior in the male directly affected the innate reproductive behavior of the female! It does not explain how the instinct to nest was lost by the female bay-winged cowbird--the most normal of the species he studied. Elsewhere Friedmann has stated (1929:353) that the female of this species is "shy and nervous when incubating" and "has little desire to protect them [the eggs] once they are laid." It seems apparent that a deterioration of the brooding drive in the female was of primary importance and that this deterioration caused the female to lay in other birds' nests and use old nests for rearing young.

The redhead is similar, for it, too, has no clear-cut territory. The only aggressive behavior is the male's defense of the female against other males, similar to that described by Condor (1949) in geese and Koskimies and Routamo (1953) in the velvet scoter. Some mechanism serves to disperse pairs over the breeding grounds but the behavior responsible is not conspicuous. It is difficult to claim a relationship between parasitism and the breakdown of territorial defense in the redhead because the closely related canvasback shows the same

lack of territoriality but is non-parasitic and a very broody species.

Davis (1940a) considered the modification of territorial behavior as influential in the development of social nesting habits in anis; he further noted that the anis were indolent in the care of nest and young. Thus, changes in the female's reproductive behavior probably preceded and influenced the change from nest defense by pairs to that by flocks.

Two theories were advanced by Friedmann (1932) as possible ways in which parasitism developed in ducks. The first was based on the fact that both ruddy ducks and mali fowl lay large eggs which were thought to hatch by heat from fermenting vegetable matter in the nest. Meyer and Stresemann (1928) doubted the significance of incubation by heat of fermentation but Frith (Pers. Comm.) has recently shown that it is essential in mali fowl. Meyer and Stresemann had suggested that these eggs hatched because of their ability to retain and generate heat. Friedmann thought that if this ability obtains for the black-headed duck, ruddy duck and redhead, it would enable these eggs to hatch if only partially incubated. Thus, eggs dropped in nests of other birds would be very successful and the parasitic habit would develop. However, no such adaptation has been proven for duck eggs and the basic assumptions of Meyer and Stresemann were not sound. The ruddy duck incubates its own eggs but it is so shy that it is rarely seen at the nest. At any rate, these speculations bring us no closer

to the real origin of parasitic laying.

Friedmann's second theory was that parasitic females are becoming more "male-like"--essentially non-broody like males. This theory seems more tenable for ducks. Not only are the male redheads and ruddy ducks non-broody, as are most ducks (Kendeigh, 1952), but the females are notably less so. In the fulvous tree duck, also prone to be parasitic (Table I), little work has been done but its late nesting habits and large clutches suggest that broodiness is also weak in this species.

The maternal or brooding drive results from the pituitary hormone, prolactin (Riddle, Bates and Lahr, 1935). This hormone stimulates incubation, stops laying, and induces flow of crop milk in doves (Riddle, 1937). Prolactin inhibits follicle stimulating hormone, causing ovarian atrophy and cessation of laying. (Bates, Riddle, and Lahr, 1937; Nalbandov, Hockhauser, and Dugas, 1945.) It has been shown that pituitary glands of brooding female chickens contain more prolactin than those of non-brooding hens (Byerly and Burrows, 1936) and gulls (Bailey, 1952), and that pituitary glands of more broody breeds of fowl contain more prolactin than those of the less broody races (Burrows and Byerly, 1936; Nalbandov et al., op. cit.). In fowl, poultrymen have been able to select for broodiness in some races and non-broodiness in others.

Although semiparasitic redheads show this lack of broodiness, their chief failing is the lack of synchronization of

egg laying and nest building. Because these phases of nesting are closely attuned in other waterfowl, it is to be expected that more eggs are laid prior to nest construction. Nest building has been associated in a general way with the time of most rapid development of the ovary (Howard, 1929: 12,25; Riddle, 1937; Schooley, 1937; Emlen, 1941), but little endocrinological work has been reported. Injections of testosterone in night herons (Noble and Wurm, 1940) and in canaries (Shoemaker, 1939) induced toying with nest material but this was certainly related to courtship rather than to nesting; only the uninjected controls nested in Shoemaker's experiments.

Even less is known of factors stimulating laying; it has been classified as spontaneous or non-spontaneous by Marshall (1939). Spontaneous ovulators, like the domestic fowl and cuckoos (Davis, 1942), require no elaborate courtship to induce laying, while non-spontaneous layers, like pigeons, must be stimulated by displays. The role of courtship in inducing laying is difficult to assess in any species, especially in waterfowl which pair on wintering areas prior to migration. Craig (1913) found that the sight of eggs in nests could induce ovulation in doves but further experimental evidence is necessary.

No suggestions have been made as to how all phases of breeding behavior are synchronized. It is apparent that a delicate balance exists between phases--anything affecting one

probably influences all. Collias (in litt.) suggested that prolactin may be significant, broodiness being increased with each egg laid. Laying then stops but the mechanism which first elicits nest building is unknown. Unfortunately, too little is known of the control of normal nest behavior to determine how changes have taken place in parasitic species.

In the absence of more adequate knowledge of the physiology of the nesting cycle, it appears that parasitism in the redhead and probably in other birds developed as a natural consequence of the deterioration of normal nest behavior. The immediate cause of this deterioration is still not apparent. The importance of external factors, especially visual and climatic, have not yet been determined. Parasitism may have arisen from variations in the synchronization of laying and nest building phases. In waterfowl, apparently, there is little survival value to constructing a nest in advance of the first egg; thus a short interval has evolved. Whatever the immediate cause may be, it has affected the nesting behavior as follows: First, nest building and egg laying lack attunement and early eggs are laid in other birds' nests (egg parasitism), rather than on the ground. The drive to build then develops and nesting follows parasitism. All degrees of parasitism may occur and some individuals may be motivated to nest earlier than others.

The second stage in the loss of nest behavior apparently is a reduction of the nest building instinct so that nests

of other birds are used for rearing young when parasitic laying ceases. This has been termed nest parasitism.

The final stage of deterioration of nesting behavior occurs when the hen fails completely to become broody or construct a nest and lays all her eggs parasitically (complete or obligate parasitism). Special adaptations for parasitism develop simultaneously--ability to deposit the egg in a few seconds and anatomical adaptations of the young to eliminate nest mates. Among all species of waterfowl that do not nest in holes, none has white down except the redhead and the ruddy duck (Broley, 1950)--both semiparasites. Because white down is conspicuous and may well contribute to predation rates, its presence in these species may be further evidence of their degeneration.

The degenerate pattern of reproduction is not only apparent in the redhead but also in cowbirds. The bay-winged cowbird may lay in the nests of other birds (Hudson, op. cit.: 113), but usually uses old nests for rearing its young and is shy at the nest. It also builds nests of its own (Friedmann, 1929a:351). Thus the pattern of nesting in this species seems very similar to that of the redhead. The smooth billed ani, though ordinarily communal in nesting, is not very broody and some individuals construct nests of their own (Davis, 1940a).

A small number of eggs laid in the nests of other species early in the season would probably have a high survival rate and perpetuate the non-broody strain. Because semipara-

sites nest and produce young having the same genetic make-up as the young resulting from eggs they laid parasitically, this trait is perpetuated and may be evolving rapidly. Observations do not permit speculations as to the rate of evolution of this behavior.

There is no assurance that parasitism will be as successful a means of reproduction in waterfowl as in other families. Several traits of the group seem to be deterents. The close attunement of laying and nest building in potential hosts gives the duck parasite less time to find a nest prior to incubation than parasites of passerine birds usually have. Neither the male nor the incubating female is sufficiently aggressive to prevent the intrusion of a parasitizing hen, and eggs laid then are not incubated long enough for them to hatch. This tremendous loss can make no contribution to the evolutionary development of parasitism. In addition, territoriality in ducks is often weak and does not include the nest (Hochbaum, 1944:58). This permits ducks to nest very close to one another and increases the chances of a nest being parasitized by several female redheads. Territoriality in the parasite, as found in cuckoos, prevents several females from laying in a nest and increases egg success. Such an adaptation seems essential if parasitism is to become obligate. Apparently the black-headed duck has succeeded in becoming an obligate parasite but it is not an abundant species.

Because of the unusual breeding habits of the redhead,

it is not an abundant species and probably has not been for many years. It does not adapt easily to modified conditions of nesting and, as a game species, may be easily decimated. As Hochbaum (1946b) aptly stated of its parasitic inclination: "It cannot be controlled, but it has a bearing on policy." The status of the redhead must be watched closely. Legislation providing deferred opening seasons to protect the young on the breeding grounds is vital (Wetmore, 1921, Williams, 1944, Hochbaum, 1946b). Because of the heavy kill of redheads in restricted areas, the closing of shooting seasons during low periods may be a feasible management technique for this species. It is a species from which ornithologists may learn much of the evolution of parasitism in future years.

CHAPTER VI

SUMMARY

1. Parasitic egg laying in waterfowl has been little studied: hence the present study of the redhead, one of the most frequently parasitic ducks, was initiated in 1952. Three summers were spent in the Delta Marsh in southern Manitoba and and one in the Knudson Marsh in Utah. Additional observations were made at Whitewater Lake, Manitoba and the Ogden Bay Refuge in Utah.

2. The major objectives were: (1) to record the behavior of the parasitic female, (2) to determine the effect of parasitism on the host and the parasite, (3) to examine the breeding biology of the species to learn something of how and why parasitism originated, and (4) to learn whether the degree of parasitism might be altered by management.

3. It was found that females located the nests they parasitized by searching in the vegetation and probably by following hosts or other parasites to a nest.

4. Parasitic hens did not lay in artificial nests constructed in the marsh. Neither empty nests nor those which held chicken eggs stimulated laying. Perhaps this indicates that the presence of the host is essential in leading the parasite to the nest.

5. The redhead is not a highly adapted parasite. It requires about four minutes to deposit an egg and may poke the eggs and turn on the nest like an incubating hen.

6. The male usually accompanies the parasitizing hen and waits within 25 to 200 yards.

7. Eggs are laid parasitically at all times of the day but more are deposited in the morning than in the afternoon.

8. The average number of eggs laid by each parasitic hen in the Knudson Marsh was estimated to be 10.8. Observations on two hens which laid eggs with distinctive shells substantiated this calculation.

9. As many as 13 hens were trapped parasitizing one nest but three to four was usual. This explains how clutches of as many as 87 eggs are formed. Thirty was the largest number of redhead eggs found in a nest in the present study.

10. More than one half of the parasitic eggs laid in the Delta and Utah Marshes were deposited after incubation started and thus were destined not to hatch.

11. Six of 42 females trapped parasitizing nests had on their bills yolk which they had eaten from eggs in the nest. This may have resulted from accidental egg breakage in the trap but suggests a way in which the egg-eating habit of cuckoos and cowbirds may have developed.

12. Both adult and yearling females were captured parasitizing nests: 14 were adult, 22 were yearlings, and 6 could not be determined.

13. Parasitizing females gradually lost weight throughout the laying period but loss was far greater among incubating females.

14. None of the 42 females captured while parasitizing had brood patches. Thus none had nested or were nesting at the time of capture.

15. If the host is on the nest when the redhead lays, she pecks the parasite but usually cannot deter it. The host commonly accepts parasitic eggs which closely resemble her own, but some are buried intentionally, others accidently. Desertion is a common reaction to parasitic intrusion and is most common in the non-broody, semi-parasitic, redhead and ruddy duck. Broodiness was measured by flushing distances and showed the drive to be stronger in cinnamon teal, mallard, and probably canvasback, than in the redhead. From the literature it may be seen that the redhead and ruddy desert their nests more readily than do other species.

16. No relationship was found between cover quality and the degree of parasitism.

17. The contention among other workers that changing water levels increase nest losses and parasitism was not supported in the present study. Parasitism was found to precede nest initiation; therefore nest losses could not affect its intensity.

18. There was no evidence that disturbance by the investigator influenced the time of nesting or the amount of parasitism.

19. Parasitism by redheads was limited to their preferred habitat. Species most heavily parasitized were those using the same types of nest cover. Nests located nearest redhead feeding and loafing areas were most likely to be parasitized.

20. The degree of parasitism was influenced by the chronology of nesting of the host and the parasite.

21. The most important factor influencing the degree of parasitism was found to be the ratio of hosts per parasite. When this ratio increased by 20 percent, there was a proportional increase in the average number of parasitic eggs per nest. Females averaged the same number of eggs in 1950 as in 1955 despite the tremendous decline in nesting cover and redhead density.

22. Parasitism precedes nest initiation in the redhead. Five to 10 percent of the females nested before parasitic eggs were found and thus were not parasitic. Some females must have been completely parasitic for parasitism continued throughout the nesting period. Only one half of the redhead population in the Knudson Marsh attempted nesting in 1955. Among 40 marked females trapped while parasitizing nests, two were later found nesting and two were seen among loafing pairs which apparently did not nest.

23. In addition to egg parasitism, nest parasitism was found in two cases when redhead used old nests.

24. Clutch sizes reported in the literature vary from nine to 14 because of intraspecific parasitism. Unparasitized

nests examined in the present study showed that the true clutch size ranged only from five to nine. Small clutches have been considered re-nestings by other workers but no evidence was found that re-nesting occurs in the redhead.

25. Behavior during incubation was found to be similar to that described for the mallard and canvasback and includes the following movements: poke, settle, paddle, turn and pull. The poke was found important in nest construction. Nest material was pulled free around the nest but never carried directly to it. Pulling added to the bulk of the nest and poking moved material under the eggs.

26. During hatching, the female may eat or carry away egg shells. Those left in the nest are crushed by the weight of her body. During this period alone she calls "kuk, kuk, kuk," apparently to imprint the young and thus establish the following reaction.

27. After the hatching period, the female's brooding drive wanes. Both the semiparasitic redhead and ruddy duck desert their broods earlier than do dabbling ducks and other diving ducks. Feigning behavior in the redhead is poor and is restricted to the newly hatched brood.

28. Parasitism reduced the number of eggs laid by the host by 20 percent and decreased both egg and nest success. But this does not occur until 60 to 70 percent of the nests are parasitized and four to six eggs are added per nest. Such a high incidence seldom occurs and the effect of parasitism on

waterfowl production could not be great. Because the breeding range and nesting habitat of the redhead and canvasback coincide, it is the latter species which suffers most from parasitism.

29. At its present stage of development, parasitism is no asset to the redhead: approximately half the population never nests. The success of parasitically laid eggs and normal nests is poor. In addition, the late nesting results in high mortality of young on the opening day of shooting.

30. The parasitic habits of the redhead are a natural consequence of the deterioration of maternal instincts. Parasitism probably arose as a result of natural variation in the synchronization of laying and nest building. Three stages follow this: egg parasitism, nest parasitism, and complete or obligate parasitism.

31. It is conceivable that reproduction by parasitism will not be as successful in waterfowl as in other groups. The fact that the territory does not include the nest allows ducks to nest close to one another and enables several parasites to lay in the same nest. Moreover, the aggressiveness of the host is not sufficient to prevent the redhead from laying while the host is incubating, and thus over half of parasitically laid eggs never hatch. Both of these characteristics reduce egg success and slow the evolution of parasitism.

32. Because the redhead is in the intermediate stages in the development of complete parasitism, its reproductive potential is low. As a game species, the status of the redhead

must be closely watched because overshooting might well be sufficiently detrimental to cause its extermination. Much can be learned from this species in years to come.

LITERATURE CITED

LITERATURE CITED

Abbott, G. A. 1902. A grebe colony. Bird Lore, 4:86-87.

Adams, S. 1908. Notes on the rhea or South American ostrich. Condor, 10:69-71.

Allen, G. M. 1925. Birds and their attributes. Marshall Jones Co., Boston, 338 pp.

Allen, R. P. 1932. Eggs of royal tern in laughing gull's nest. Auk, 49:219-220.

Altum, B. 1866. Warum brutet der Kuchik nicht selbst. Jour. fur Ornith. 5:165-171.

Armstrong, E. A. 1947. Bird display and behavior. Lindsay Drummond Ltd., London, 431 pp.

Arnold, E. 1894. My '94 outing trip in northwest Canada. Nidiologist, 1:168, 2:11-13, 23-25.

Arnott, D. 1890. A four-storied nest. Ornith. and Oologist, 15:98.

Bailey, H. B. 1887. The brown thrush laying in the nest of the wood thrush. Auk, 4:78.

Bailey, R. E. 1952. The incubation patch of passerine birds. Condor, 54:121-136.

Baker, E. C. S. 1922. Cuckoos, some theories about birds and their eggs. Bull. Brit. Ornith. Club, 42:89-112.

_____. 1923. Cuckoo's eggs and evolution. Proc. Zoo. Soc. Lond. 277-294.

_____. 1942. Cuckoo problems. Witherby Ltd., London, 207 pp.

Balham, R. W. 1955. The behavior of the Canada goose (Branta Canadensis) in Manitoba. Unpubl. Ph.D. thesis, Univ. of Mo., 229 pp.

Balsac, H. de 1926. Un cas de parasitisme chez le Rongequeue Ph. ph. phoenicurus (L.) Rev. Franc d' Ornith., 10: 137-138.

Barker, B. W. 1938. American eider and herring gull--mixed sets. Oologist, 55:136-137.

Barnhart, F. S. 1901. Evolution in the breeding habits of the fulvous tree duck. Condor, 3:67-68.

Barrett, C. L. 1910. The origin and development of parasitical habits in the cuculidae. Smithsonian Report:487-492.

Barrows, W. B. 1912. Michigan bird life. Michigan Agric. Coll., Lansing, 822 pp.

Baskett, T. S. 1947. Nesting and production of the ring-necked pheasant in north-central Iowa. Ecol. Monogr., 17:1-30.

Bates, R. W., O. Riddle and E. L. Lahr. 1937. The mechanisms of the anti-gonad action of prolactin on adult pigeons. Amer. Jour. Physiol., 119:610-614.

Bellrose, F. 1943. Two wood ducks incubating in the same nest box. Auk, 60:446-447.

Bennett, L. J. 1936. The ring-necked pheasant as a nesting parasite of other game birds. Iowa State Coll. Jour. Sci., 10:373-375.

_____. 1937. Canvasback breeding in Iowa. Auk, 54:534.

_____. 1938a. The blue-winged teal. Collegiate Press, Inc., Ames. 144 pp.

_____. 1938b. Redheads and ruddy ducks nesting in Iowa. Trans. N. Amer. Wildl. Conf., 3:647-650.

Bent, A. C. 1902. Nesting habits of the Anatidae in North Dakota. Auk, 19:1-12, 165-174.

_____. 1907. Summer birds of southwestern Saskatchewan. Auk, 24:407-430.

_____. 1923. Life histories of North American wild fowl. Part I. U. S. Nat. Mus. Bull. 126. 244 pp.

_____. 1925. Life histories of North American wild fowl. Part II. U. S. Nat. Mus. Bull. 130. 316 pp.

_____. 1940. Life histories of North American cuckoos, goatsuckers, hummingbirds, and their allies. U. S. Nat. Mus. Bull. 176. 506 pp.

Beresford, R. P. 1922. Curlews' eggs in wild ducks' nest. Irish Nat., 13:72.

Berger, A. J. 1951. The cowbird and certain host species in Michigan. Wilson Bull., 63:26-34.

Bizeau, E. G. 1951. Factors affecting waterfowl production at Grays' Lake, Idaho. Unpubl. M. S. thesis, Univ. Idaho. 123 pp.

Blain, A. W. 1954. Bob-white eggs in pheasant nest. Wilson Bull., 66:217.

Bleitz, D. 1956. Eggs of the California quail in the nest of a spotted towhee. Condor, 58:77-78.

Brackbill, H. 1952. A joint nesting of cardinals and song sparrows. Auk, 69:302-307.

Brakhage, G. K. 1953. Migration and mortality of ducks hand-reared and wild-trapped at Delta, Manitoba. Jour. Wildl. Mgt., 17:465-477.

Brewster, W. 1900. Notes on the breeding habits of the American goldeneye or whistler. Auk, 17:207-216.

Broley, J. 1950. Identifying nests of the Anatidae of the Canadian prairies. Jour. Wildl. Mgt., 14:452-456.

Bryant, H. C. 1914. A survey of the breeding grounds of ducks in California in 1914. Condor, 16:217-239.

Burrows, W. H. and T. C. Byerly. 1936. Studies on prolactin in the fowl pituitary I. Broody hens compared with laying hens and males. Proc. Soc. Exp. Biol. Med., 34: 841-844.

Buss, I. O., R. K. Meyer, and C. Kabat. 1951. Wisconsin pheasant reproduction studies based on ovulated follicle technique. Jour. Wildl. Mgt., 15:32-46.

Byerly, T. C. and W. H. Burrows. 1936. Studies of prolactin in the fowl pituitary II. Effects of genetic constitution with respect to broodiness on prolactin content. Proc. Soc. Exp. Biol. Med., 34:844-846.

Chance, E. 1921. A third season's observations on a cuckoo. Brit. Birds, 59:218-232.

_____. 1922. The cuckoo's secret. Sidgwick & Jackson, Ltd., London. 239 pp.

_____. 1940. The truth about the cuckoo. Country Life, Ltd., London. 207 pp.

_____ and H. W. Hahn. 1942. The European cuckoo and the cowbird. Bird Banding, 13:99-103.

Cole, L. J. 1917. Determinate and indeterminate laying cycles in birds. Anat. Rec., 11:504-505.

Collias, N. E. 1950. The socialization of chicks. Anat. Rec., 108:

Conder, P. J. 1949. Individual distance. Ibis, 91:649-655.

Dabbene, R. 1921. Huevos del pavdo (Heteronetta atricapilla), en el nido del Carso (Aramus scolopaceus). El Horneo, 2:227.

Daguerre, J. B. 1920. Observaciones sobre los patos "Metopiana peposaca" y "Heteronetta atricapilla." El Horneo, 2:61-62.

_____. 1922. Lista de aves coleccionadas y observados en rosas, F.C.S. El Horneo, 2:259-271.

_____. 1923. Parasitismo del pato, Heteronetta atricapilla. El Horneo, 3:194-195.

_____. 1924. Apentus sobre algunas aves de la Provincia de Buenos Aires. El Horneo, 3:248-252.

Darwin, C. 1898. Origin of species. Vol. I, Appleton & Co., N. Y. 365 pp.

Davidson, J. L. 1887. Birds laying their eggs in the nests of other birds. Auk, 4:263-264.

Davis, D. E. 1940a. Social nesting habits of the smooth-billed ani. Auk, 57:179-218.

_____. 1940b. Social nesting habits of Guira guira. Auk, 57:472-483.

_____. 1942. The phylogeny of social nesting habits in the crotophaginae. Quart. Rev. Biol., 17:115-134.

Dawson, W. L. 1923. The birds of California. South Moulton Co., San Diego. 2,121 pp.

Delacour, J. and E. Mayr. 1946. Supplementary notes of the family Anatidae. Wilson Bull., 58:104-110.

Dickey, D. R. and A. J. Van Rossem. 1923. The fulvous tree-ducks of Buena Vista Lake. Condor, 25:39-50.

Durango, S. 1940. Om häckningsparasitiska tendenser hos nagra andfaglar. Fauna och Flora, Haft 3:

Elton, C. 1927. Animal ecology. Sidgwick and Jackson, Ltd., London. 209 pp.

Emlen, J. T. 1941. An experimental analysis of the breeding cycle of the tri-colored redwing. Condor, 43:209-219.

Erickson, R. C. 1948a. Life history and ecology of the canvasback (Nyroca valisneria Wilson), in southeastern Oregon. Unpubl. Ph.D. thesis, Iowa State College, Ames.

_____. 1948b. Life history and ecology of the canvas-back (Nyroca valisneria Wilson) in southeastern Oregon. Iowa State College Jour. of Sci. 23:30-32.

Fabricius, E. 1951. Zur Ethologie junger Anatiden. Acta Zoologica Fennica, 68:1-175.

Fannin, J. 1894. The Canada goose and osprey laying in the same nest. Auk, 11:332.

Ferry, J. F. 1910. Birds observed in Saskatchewan during the summer of 1909. Auk, 27:185-204.

Forbush, E. H. 1929. Birds of Massachusetts, Part II. Mass. State Board of Agric. 461 pp.

Friedmann, H. 1928. The origin of host specificity in the parasitic habit in the cuculidae. Auk, 45:33-38.

_____. 1929a. The cowbirds. Charles C. Thomas, Springfield, Md. 421 pp.

_____. 1929b. Social parasitism in birds. Smithsonian Report:363-382.

_____. 1931. Additions to the list of birds known to be parasitized by the cowbird. Auk, 48:52-65.

_____. 1932. The parasitic habit in ducks, a theoretical consideration. Proc. U. S. Nat. Mus., 80 Art. 18:1-7.

_____. 1934. Further additions to the list of birds victimized by the cowbird. Wilson Bull., 46:25-36, 104-114.

_____. 1948. The parasitic cuckoos of Africa. Wash. Acad. of Sci., Monog. No. one, Washington, D. C. 204 pp.

_____. 1949. The breeding habits of the weaverbirds. Smithsonian Report:293-316.

_____. 1955. The honey-guides. U. S. Nat. Mus. Bull. 208. 292 pp.

Fuller, R. W. 1953. Studies in the life history and ecology of the American pintail (Anas acuta tzitzihoa) in Utah. Unpubl. M. S. thesis, Utah State Agric. College. Logan.

Furniss, O. C. 1938. The 1937 waterfowl season in the Prince Albert District, Central Saskatchewan. Wilson Bull., 50:17-27.

Gibson, E. 1920. Further ornithological notes from the neighborhood of Cape San Antonio, Province of Buenos Aires. Ibis, (ser. II), 2:1-97.

Girard, G. L. 1939. Notes on life history of the shoveller. Trans. N. Amer. Wildl. Conf., 4:364-371.

Glover, F. A. 1956. Nesting and production of the blue-winged teal in Northwest Iowa. Jour. Wildl. Mgt., 20: 28-46.

Goodall, J. D., A. W. Johnson, and R. A. Phillippi. 1951. Las aves de Chile. Buenos Aires, Vol. 2. 445 pp.

Gross, A. O. 1938. Eider ducks of Kent's Island. Auk, 55: 387-400.

Gudmundsson, F. 1932. Observations made on Icelandic eider ducks. Beitrage zur Fortplanzungsbiologie No. 3/4. May and July.

Hahn, H. W. 1937. Life history of the oven-bird in southern Michigan. Wilson Bull., 49:145-237.

_____. 1941. The cowbird at the nest. Wilson Bull., 53: 209-221.

Hammond, M. C. 1941. Report of 1941 nesting studies at Lower Souris National Wildlife Refuge. Unpubl. report to U. S. Fish and Wildl. Serv. 6 pp.

Henry, C. J. 1940. Northern great plains region. Bird Lore, 42:469-470.

Herrick, F. H. 1907a. Analysis of the cyclical instinct of birds. Science, 25:725-726.

_____. 1907b. The blending and overlap of instincts. Science, 25:781-782.

_____. 1910. Life and behavior of the cuckoo. Jour. Exp. Zoo., 9:169-233.

Hickey, J. J. 1952. Survival studies of banded birds. Spec. Sci. Report, (Wildlife) 15, U. S. Fish and Wildlife Service, Washington, D. C. 177.

Hicks, L. E. 1935. A ten-year study of a bird population in central Ohio. Amer. Midl. Nat., 16:177-186.

Hochbaum, H. A. 1944. The canvasback on a prairie marsh. Am. Wildl. Inst., Washington, D. C. 201 pp.

_____. 1946a. Status of the redhead in southern Manitoba. Wilson Bull., 58:62-65.

_____. 1946b. Recovery potentials in North American waterfowl. Trans. N. Amer. Wildl. Conf., 11:403-418.

Howard, H. E. 1929. An introduction to the study of bird behaviour. Cambridge Univ. Press. 136 pp.

Hudson, W. H. 1920. Birds of La Plata. Vol. I. J. M. Dent and Sons, London and Toronto. 244 pp.

Jackson, A. C. 1915. Notes on the moults and sequence of plumages in some British ducks. Brit. Bird, 9:34-42.

Job, H. K. 1898. The enchanted isles. Osprey, 3:37-41.

_____. 1899. Some observations on the Anatidae of North Dakota. Auk, 16:161-165.

_____. 1902. Among the waterfowl. Doubleday, Page and Co. 224 pp.

Jourdain, F. C. R. 1925. A study on parasitism in the cuckoos. Proc. Zool. Soc. of London:639-667.

Kendeigh, S. C. 1952. Parental care and its evolution in birds. Ill. Biol. Monog., 22:1-356.

King, J. R. 1954. Victims of the brown-headed cowbird in Whitman County, Wash. Condor, 56:150-154.

Koskimies, J. and E. Routamo. 1953. Zur Forphlanzugsbiologie der Samtente Melanitta f. fusca (L.) 1: Allegemeine Nistökologie (The breeding biology of the velvet scoter, with Engl. summ.). Riistatieteellisia Julkaisuja, Paper on game research 10. 105 pp.

Lack, D. 1946. The life of the robin. H. F. & G. Witherby Ltd., London. 224 pp.

Leopold, F. 1951. A study of nesting wood ducks in Iowa. Condor, 53:209-220.

Leverkuhn, P. 1891. Fremde eider im nest. R. Friedlander, Berlin. 212 pp.

Löve, A. and D. Löve. 1955. Vegetation of a prairie marsh. Bull. Torrey Botanical Club, 81:16-34.

Low, J. B. 1941. Nesting of the ruddy duck in Iowa. Auk, 58:506-517.

_____. 1945. Ecology and management of the redhead, Nyroca americana, in Iowa. Ecol. Monogr., 15:35-69.

_____ and M. Nelson. 1945. Recent records of breeding waterfowl in Utah and southern Idaho. Condor, 47:131-132.

Macoun, J. and J. M. Macoun. 1909. Catalogue of Canadian birds. Publ. 973, Canadian Dept. Mines, Geol. Surveys Branch. Ottawa, Ont. 761 pp.

Makatsch, W. 1934. Ueber die phylogenetische Entwicklung des Brutparasitismus. Beitr. Fort. der Vogel, 10:61-65.

_____. 1937. Der brutparasitismus der Kukucksvogel. Quelle and Meyer, Leipzig. 152 pp.

Matthews, L. H. 1939. Visual stimulation and ovulation in pigeons. Proc. Roy. Soc. London, 126 B:557-560.

McKinney, F. 1951. Incubation and hatching behaviour in the mallard. Severn Wildfowl Trust. 5th Ann. Rep.:68-70.

_____. 1953. Studies on the behaviour of the anatidae. Unpubl. Ph.D. thesis, Bristol University.

_____. 1954. An observation on redhead parasitism. Wilson Bull., 66:146-148.

McLaughlin, C. L. and D. Grice, 1952. The effectiveness of large scale erection of wood duck boxes as a management procedure. Trans. N. Amer. Wildl. Conf., 17:242-259.

Meyer, O. and E. Stresemann. 1928. Zur kenntnis der entwicklung von Megapodius and Oxyura im Ei. Orn. Monatsber, 31:65-71.

Meyer, R. K., C. Kabat, and I. O. Buss. 1947. Early involutionary changes in the post-ovulatory follicles of the ring-necked pheasant. Jour. Wildl. Mgt., 11:43-49.

Miller, A. H. 1946. Social parasites among birds. Sci. Monthly, 42:238-246.

Miller, A. W. and B. D. Collins. 1954. A nesting study of ducks and coots on Tule Lake and Lower Klamath National Wildlife Refuges. Calif. Fish and Game, 40:17-37.

Munro, J. A. 1938. Lesser scaup duck defending nest. Wilson Bull., 50:238.

_____. 1941. Studies of waterfowl in British Columbia: greater scaup duck, lesser scaup duck. Can Jour. Res., D 19:113-138.

Nalbandov, A. L., M. Hockhauser and M. Dugas. 1945. A study of the effect of prolactin on broodiness and on cock testes. Endoc., 36:251-258.

Nelson, M. C. 1943. Studies of waterfowl areas (Utah). P. R. Quart., 3:203-204.

Nelson, N. F. 1955. Factors in the development and restoration of waterfowl habitat at Ogden Bay Refuge, Weber County Utah. Utah Dept. Fish and Game, Salt Lake City. Federal Aid Publ. 6, 87 pp.

Nice, M. M. 1937. Studies in the life history of the song sparrow, I. Trans. Linn. Soc. 4:1-247.

Noble, G. K. and D. S. Lehrman. 1940. Egg recognition by the laughing gull. Auk, 57:23-43.

_____ and M. Wurm. 1940. The effect of testosterone propionate on the black-crowned night heron. Endoc., 26:837-850.

Odum, E. P. 1953. Fundamentals of ecology. W. B. Saunders & Co., Philadelphia. 384 pp.

Peck, G. D. 1911. Reminiscences of the wood duck. Oologist, 28:35-36.

Pemberton, J. R. 1925. Parasitism in the roadrunner. Condor, 27:35.

Phillips, J. C. 1923-26. A natural history of the ducks. Houghton Mifflin Co., Boston.

Poulsen, H. 1953. A study of incubation responses and some other behavior patterns in birds. Vidensk. Medd. fra Dansk naturh. Foren., 115:1-131.

Raney, E. C. 1939. Robin and mourning dove use same nest. Auk, 56:337-338.

Riddle, O., R. W. Bates, and E. L. Lahr. 1935. Prolactin induces broodiness in fowl. Amer. Jour. Physiol., 3:352-360.

_____. 1937. Physiological response to prolactin. Cold Spgs. Harbor Symp. on Quant. Biol. 5:218-228.

Ritter, W. E. 1938. The California woodpecker and I. Berkeley, Univ. of Calif. Press. 340 pp.

Robbins, C. S. 1949. Migration of the redhead, in "Migration of some North American waterfowl," by J. W. Aldrich et al. Spec. Sci. Report (Wildlife) 1, U. S. Fish and Wildl. Serv., Washington, D. C. 49 pp.

Rockwell, R. B. 1911. Nesting notes on the ducks of the Barr Lake Region, II. Condor, 13:186-195.

Rodriquez, D. 1918. Costumbres del "Pato picazo." El Horneo, I:185-187.

Rothchild, M. and T. Clay. 1952. Fleas, flukes, and cuckoos. Collins, London. 304 pp.

Sampson, W. B. 1901. An exceptional set of eggs of the wood duck. Condor, 3:95.

Schooley, J. P. 1937. Pituitary cytology in pigeons. Cold Spgs. Harbor Symp. Quant. Biol., 5:165-179.

Selous, E. 1933. Evolution of habit in birds. Constable & Co., London. 296 pp.

Serventy, D. L. and H. M. Whittell. 1951. Birds of western Australia. Paterson Brokensha Pty. Ltd., Perth, W. A. 364 pp.

Shields, A. M. 1899. Nesting of the fulvous tree duck. Bull. Cooper Ornith. Club, 1:9-11.

Shepardson, D. I. 1915. The house finch as a parasite. Condor, 17:100.

Shoemaker, H. 1939. Effect of testosterone propionate on behavior of the female canary. Proc. Soc. Exp. Biol. Med., 41:299-302.

Sowls, L. K. 1949. A preliminary report on renesting in waterfowl. Trans. N. Amer. Wildl. Conf., 14:260-275.

_____. 1955. Prairie ducks. Wildl. Mgt. Inst., Washington, D. C. 193 pp.

Spencer, O. R. 1943. Nesting habits of the black-billed cuckoo. Wilson Bull., 55:11-12.

Spencer, H. E., Jr. 1953. The cinnamon teal (Anas cyanoptera Vieillot), its life history, ecology, and management. Unpubl. M. S. thesis, Utah State Agric. Coll. Logan.

Steel, P. E. 1952. Factors affecting waterfowl production at Grays' Lake, Idaho. Unpubl. M. S. thesis, Univ. of Idaho. 157 pp.

Stoddard, H. L. 1931. The bobwhite quail. Scribner's Sons, N. Y. 559 pp.

Stokes, A. W. 1954. Population studies of the ring-necked pheasant on Peelee Island, Ontario. Tech. Bull. (Wildl. Series 4) Ontario Dept. Lands and Forests. 154 pp.

Stresemann, E. 1927-34. In Aves, Kukenthal-Krumbach Handb. Zool. 7 Bd. 2. Halfte.

Strong, R. M. 1912. Some observations on the life history of the red-breasted merganser. Auk, 29:479-488.

Swynnerton, C. F. M. 1918. Rejections of birds of eggs unlike their own with remarks on some of the cuckoos problems. Ibis, 6 (10th ser.):127-154.

Taber, R. D. 1949. A new marker for game birds. Jour. Wildl. Mgt., 13:228-231.

Tinbergen, N. 1953. The herring gull's world. Collins, London. 255 pp.

Tucker, B. W. 1943. Brood-patches and the physiology of incubation. Brit. Birds, 37:22-28.

Voohus, K. H. 1947. Hot broed parasitism van de Kroonend (Netta rufina). Levende Nat. Amsterdam, 50:99-102.

Wallace, G. J. 1955. An introduction to ornithology. Macmillan Co., N. Y. 443 pp.

Ward, E. 1942. Phragmites management. Trans. N. Amer. Wildl. Conf., 7:294-298.

Weller, M. W. 1954. Growth rate and plumage development of the redhead duck (Aythya americana). Unpubl. M. A. thesis, Univ. Mo. 86 pp.

_____. 1955. Eggs galore. Mo. Conserv., 16:12-13.

_____. 1956. A simple field candler for waterfowl eggs. Jour. Wildl. Mgt., 20:111-113.

Wetmore, A. 1920. Observations on the habits of birds at Lake Burford, New Mexico. Auk, 37:221-412.

_____. 1921. Wild ducks and duck foods of the Bear River Marshes, Utah. U. S. Dept. of Agric. Bul. 936. 20 pp.

_____. 1926. Observations on the birds of Argentina, Paraguay, Uruguay, and Chile. U. S. Nat. Mus. Bull. 133. 448 pp.

Weydemeyer, W. 1931. An unusual nest of the ruddy duck in Montana. Wilson Bull., 43:62.

_____. 1933. Occurrence and nesting of the redhead in Montana. Auk, 50:210-211.

Willett, G. 1906. Peculiarities of ducks in nesting. Condor, 8:75.

_____ and A. Jay. 1911. May notes from San Jacinto Lake. Condor, 13:156-160.

Williams, C. S. and W. H. Marshall. 1938. Duck nesting studies, Bear River Migratory Bird Refuge, Utah, 1937. Jour. Wildl. Mgt., 2:29-48.

_____ and M. C. Nelson. 1943. Management of the redhead duck in Utah. Unpubl. Report to U. S. Fish and Wildl. Serv., Washington, D. C.

_____. 1944. Migration of the red-head from the Utah breeding grounds. Auk, 61:251-259.

Wilson, A. S. 1923a. Notas biologicas sobre algunas aves de Santa Fe. El Horneo, 3:84-89.

_____. 1923b. Huevos de pato en un nido de Chimango. El Horneo, 3:192.

_____. 1926. Lista de aves del sur de Santa Fe. El Horneo, 3:355-363.

Wingfield, B. H. 1951. A waterfowl productivity study in Knudson Marsh, Salt Lake Valley, Utah. Unpubl. M. S. thesis, Utah State Agric. Coll.

Wolf, K. E. 1952. Some effects of fluctuating and falling water levels on waterfowl production. Unpubl. M. S. thesis, Utah State Agric. Coll.

_____. 1953. Grebe-duck nesting parasitism. Auk, 70:84.

APPENDIX

APPENDIX

NOMENCLATURE OF BIRDS AND PLANTS IN THE TEXT

Birds[1]

Ani, smooth-billed	*Crotophaga ani*
Bittern, American	*Botaurus lentiginosus*
Bufflehead	*Bucephala albeola*
Chimango or cara cara	*Polyborus cheriway*
Coot, American	*Fulica americana*
Cowbird, Argentine	*Molothrus bonariensis*
, bay-winged	*Acelaioides badius*
, North American	*Molothrus ater*
, screaming	*Molothrus rufo-axillaris*
, shiny	*Molothrus bonariensis*
Cuckoo, black-billed	*Coccyzus erthrophthalmus*
, European	*Cuculus canorus*
, guira	*Guira guira*
, koel	*Eudynamis honorata*
, yellow-billed	*Coccyzus americanus*
Dove, mourning	*Zenaidura macroura*
Curlew	*Numenius arquata*
Duck, black-headed	*Heteronetta atricapilla*
, blue-billed	*Oxyura jamaicensis australis*
, fulvous tree	*Dendrocygna bicolor*
, rosy-billed	*Netta peposaca*

Pochard, common	*Aythya ferina*
, red-crested	*Netta rufina*
, white-eyed	*Aythya nyroca*
Quail, bob-white	*Colinus virginianus*
, California	*Lophortyx californica*
Rail, sora	*Porzana carolina*
Redhead	*Aythya americana*
Redstart	*Phoenicurus phoenicurus*
Rhea	*Rhea americana*
Roadrunner	*Geococcyx californianus*
Robin, American	*Turdus migratorius*
, European	*Erithacus rubecula*
Scaup, common	*Aythya m. marila*
, greater	*Aythya m. marila*
, lesser	*Aythya affinis*
Scoter, velvet	*Melanitta f. fusca*
, white-winged	*Melanitta fusca deglandi*
Screamer, crested	*Chauna chavaria*
Shelduck	*Tadorna tadorna*
Shoveller	*Anas clypeata*
Sparrow, English	*Passer d. domesticus*
, song	*Melospiza melodia*
Teal, blue-winged	*Anas discors*
, cinnamon	*Anas cyanoptera*
, green-winged	*Anas crecca carolinensis*
Tern, black	*Chlidanias nigra surinamensis*

Tern, royal	Thalasseus m. maximus
Thrasher, brown	Toxostoma r. rufum
Widgeon, American	Anas americana
Widow bird	Anomalospiza spp.
Wood duck	Aix sponsa
Woodpecker, California	Balanosphyra formicivora

Plants[2]

Bulrush, alkali	Scirpus paludosus
, hardstem	Scirpus acutus
, Olney's three-square	Scirpus Olneyi
Cane	Phragmites communis
Cattail	Typha latifolia
Glasswort	Salicornia spp.
Greasewood	Sarcobatus vermiculatus
Saltgrass	Distichlis strica
Whitetop grass	Scolochloa festucacea

---

[1] Scientific names of birds from following sources:

Peterson, R. T. 1941. A field guide to western birds. Houghton Mifflin Co., Boston. 240 pp.

_____. 1947. A field guide to the birds. Houghton Mifflin Co., Boston, 290 pp.

_____, G. Mountfort, and P. A. D. Hollom. 1954. A field guide to the birds of Britain and Europe. Houghton Mifflin Co., Boston. 318 pp.

Scott, Peter. 1950. Key to the waterfowl of the world. Severn Wildfowl Trust, Glos., England.

[2] Scientific names of plants from following sources:

Holmgren, A. H. 1948. Handbook of vascular plants of Northern Wasatch. Holmgren, Logan, Utah. 202 pp.

Love, Askell, and Doris Love. 1954. Vegetation of a prairie marsh. Bull. Torrey Botanical Club, 81:16-34.