1948

Life history and ecology of the canvas-back, Nyroca valisineria (Wilson), in southeastern Oregon

Ray Charles Erickson

Iowa State College

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UMI®
LIFE HISTORY AND ECOLOGY OF THE CANVAS-BACK,
NYROCA VALISINERIA (WILSON), IN SOUTHEASTERN OREGON

by

Ray Charles Erickson

A Thesis Submitted to the Graduate Faculty
for the Degree of
DOCTOR OF PHILOSOPHY
Major Subject: Economic Zoology

Approved:
Signature was redacted for privacy.

In Charge of Major Work
Signature was redacted for privacy.

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Dean of Graduate College

Iowa State College
1948
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INTRODUCTION

During the last two decades the emphasis in wildlife investigations has shifted from extensive research on broad groups of species or ecological communities of plants and animals to intensive studies of single species and the co-actions of these species with their environment. By this method, inconspicuous, but sometimes important, relationships have been revealed. Such details often escape detection in researches of broader scope.

When the field work herein reported upon was commenced in 1942, no published material based on an intensive nesting study of the canvas-back, *Aythya valisineria* (Wilson)^a^, was available. Consequently, the first year's research sought to obtain information on the breeding habits of the canvas-back. In this preliminary investigation extensive parasitism of canvas-back nests, principally by redheads, *Aythya americana* (Eyton), was found to be the most important, direct factor bringing about an extremely low nesting success of the canvas-back.

Interest in the conditions under which parasitism of canvas-back nests was most prevalent inspired two additional years of field research. Thus, while the life history and

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^a^Common and scientific names follow the nomenclature adopted by the following authorities: birds, American Ornithologists' Union (1931); mammals, Bailey (1936); and plants, Peck (1941).
ecology of the canvas-back continued to be of primary concern, special attention was directed toward learning more about interspecific relationships.

Field work on this problem was pursued on the Malheur National Wildlife Refuge and adjacent marshland, Harney County, Oregon during the following periods: April 4 to August 24, 1942; March 28 to September 13, 1946; and March 25 to September 11, 1947. The findings of the study are presented to provide additional information that may be of value in the development of future waterfowl management practices.
HISTORICAL REVIEW

Although the canvas-back has occupied a prominent place in North American waterfowl literature since early in the nineteenth century, many of the contributions on this species, dating from the writings of John James Audubon and Alexander Wilson, have merely quoted or reiterated in slightly modified form the works of these pioneer American ornithologists. Into another category falls the host of brief notes on occurrence, food habits and behavior.

Since 1920, however, three writers have presented a more complete picture of the life history of the canvas-back. Bent (1923) and Phillips (1923) thoroughly reviewed the existing literature and added unpublished observations. Hochbaum (1944) contributed importantly on the habits and motivating influences among canvas-backs and other ducks, including an attempted substantiation of "territoriality," at the Delta Duck Station in Manitoba.

In the early literature the canvas-back was confused with the European pochard (*Nyroca ferina*). It was first described as a separate species, *Anas valisineria*, by Alexander Wilson (1814). The species name was derived from Vallisneria, the generic designation for wild celery, which is an important item of the canvas-back's diet in some parts of the eastern United States during certain seasons. In 1922 Fleming proposed the genus "Nyroca, Latinised form of the Russian word
Nirok or Nyrok, meaning a diving duck . . . " (Kortright 1943, p. 241). Gray (1844) placed the canvas-back in this genus. The American Ornithologists' Union (1931) has listed *Nyroca valisineria* (Wilson) as the accepted identity of the canvas-back. A more complete history of the synonymy of the canvas-back has been given by Phillips (1923).

Detailed descriptions of the various plumages are given by Wilson and Bonaparte (1876), Coues (1884), Bent (1923), Phillips (1923), Forbush (1925), Hochbaum (1944) and other authors. Both sexes of the canvas-back, under most circumstances, are readily distinguished from a near-relative, the redhead, by the comparatively greater size, longer neck and wedge-shaped profile of the head. The pattern and color of plumage are additional marks of identification. Most of the head and neck of the breeding male is cinnamon-chestnut with blackish foreparts, whitish back, sides and belly, and black upper rump and tail. The female has a buffy-brown head and neck, darker on the crown, the rest of the body being a more slaty-brown with whitish vermiculations on the back. The iris is vermilion in the adult male and brown in the adult female. The legs and feet of both sexes are yellowish-blue to slaty-blue, being lightest on the toes.

The plumage of full-grown juveniles is quite similar to that of the adult female, but the back in both sexes is of a lighter color. The more reddish neck and lighter back
of the full-grown juvenile male may be used to distinguish it from the juvenile female at close range. The juvenile male retains the brown eye up to the time it is able to fly. Within two months thereafter, the iris changes to a ring of orange-vermilion. The iris in juvenile females remains brown.

The canvas-back is strictly a New World species and its breeding and wintering ranges lie within North America. The breeding range is exceedingly extensive, overlapping that of the redhead to the north and west. The redhead nesting range, however, extends farther to the south and southwest.

Dufresne (1942) reported small populations of canvas-backs breeding in Alaska. Forsild (1943) indicated that one was seen at Aklavik, Northwest Territories, Canada by C. H. D. Clarke on July 20, 1942. W. E. Stevens, while stationed at Aklavik, observed a female canvas-back with three ducklings less than a week old on a small lake located 68 degrees 18 minutes North latitude and 134 degrees 58 minutes West longitude on July 21, 1947 (Letter of July 22, 1947). Possibly the only more northerly breeding record was provided by MacFarlane (1908) who stated that canvas-backs were nesting in some numbers near Fort Anderson to the east and slightly north of Aklavik.

Various writers have recorded the canvas-back as breeding in the vicinity of Great Slave Lake (MacFarlane 1908,
Preble 1908). The greatest abundance of nesting canvasbacks occurs to the south of Great Slave Lake, probably in northern Alberta (Phillips, 1923), and is very common on Lesser Slave Lake, Peace River, the delta of the Athabaska and western end of Lake Athabaska (Preble 1908, Macoun 1909, MacFarlane 1908). It is not uncommon in the western two thirds of Manitoba, and is generally but sparingly distributed throughout southern Alberta and Saskatchewan. In British Columbia during the breeding season it is found mainly on the Fraser River and northward of 54 degrees North latitude (Brooks 1907). The same writer (1903, 1920) added that this species was common in the Cariboo region.

In the United States, McClanahan (1940) mapped the original principal breeding range to include all of North Dakota, Montana, Wyoming, Idaho, South Dakota. The rest of the southern periphery of the range passed through the western third of Minnesota, southeastern tip of South Dakota, northwestern third of Nebraska, northwestern two thirds of Colorado, a bit of northern New Mexico, northeastern half of Utah, northern edge of Nevada, northeastern tip of California and eastern halves of Oregon and Washington. The same publication showed a greatly reduced present breeding range in which northeastern North Dakota, eastern South Dakota, Nebraska sandhill region, Bear River marshes of Utah, and scattered localities in Washington, Oregon,
Idaho, Montana, Colorado and Minnesota were represented.

Some additional remarks on distribution of the canvas-back seem advisable. Two nesting records for Iowa (Bennett 1937, Provost 1947) together with sight records of broods in lakes near Ruthven, northwestern Iowa, may represent the southeastern limits of its present nesting range.

Felger (1900) reported the first record of canvas-backs nesting in Colorado, finding two nests on June 20 and another on July 4, 1900. Rockwell (1911, p.192, 195) studied duck nesting conditions on the same area, Barr Lake, during the breeding seasons of 1906 to 1908 and reported finding one canvas-back nest on a muskrat lodge during the first year for what he believed to be the first Colorado nesting record for this species. The authenticity of Rockwell's record is questioned for he reported that "The cavity was fairly well lined with white down, quite a quantity of which was scattered about the entrance of the burrow . . . female was surprised not far from the nest . . . ." Later he described a ruddy duck (Erismatura jamaicensis rubida) clutch with two " . . . Canvas-back's or Redhead's . . . ." eggs. In view of the white, scattered down in the "canvas-back" nest, the fact that the canvas-back female was not seen on or at the nest and in view of the writer's admission that he was unable to decisively identify the foreign eggs in the ruddy duck's nest as of either the canvas-back or redhead, Rockwell's observation cannot be considered a
reliable nesting record for north-central Colorado. On
the contrary, the photographic illustration of the nest
in question, showing especially the fluffy, white-appearing,
scattered down, when contrasted with the nest of the canvas-
back with its brownish-gray, compact down, gives evidence
that the nest was that of a redhead.

Wetmore (1920) reported seeing canvas-backs on Lake
Burford, New Mexico during the breeding season, and Nordhoff
(1922) mentioned seeing them nesting in Colfax County in
the same state. Villada (1891-1892) stated that the species
was a resident of the Valle de Mexico. These may have been
crippled or sick, non-breeding individuals.

Low (1945) made canvas-back brood observations in
northern Utah and southeastern Idaho, and Refuge Manager
Herbert H. Dill, in conversation with the writer, reported
a number of breeding pairs occupying the Ruby Lake National
Wildlife Refuge in the south part of Elko County, north-
eastern Nevada in 1946.

On August 3, 1946 Jewett (1947) saw a female canvas-
back with nine downy young on a small pond in the old Tule
Lake bed on Tule Lake National Wildlife Refuge, Siskiyou
County, in northern California, probably the first authentic,
published record of nesting of the species in this State,
although this had long been suspected.

In Oregon, Captain Charles Bendire (1877) found the
canvas-back to be a common breeding bird near Bear Creek
in the Blue Mountains and Woodcock (1902) found it nesting near Haines in the northeastern section of the State. In correspondence with Brewer (1875), Bendire did not include the canvas-back in his Malheur Lake notes for April 16 and 28, 1875. Willett (1919) recorded the redhead as an abundant breeder on Malheur Lake but made no mention of the canvas-back.

Although long-time residents indicated that from their earliest memory the canvas-back had been a common migrant on Malheur Lake, its presence as a breeding species was not established until 1936 when the first brood was seen. The first canvas-back nests were found in 1938 by Dr. C. A. Sooter who revealed these facts to the writer in conversation. Totals of 11 canvas-back nests in 1938 and six in 1939 were found by Dr. Sooter and associates who kindly gave duplicates of 14 of the nest history records to the writer for study.

In the State of Washington Dawson and Bowles (1909) reported that the canvas-back nests rarely on the east side of the Cascades.

From a large number of published and unpublished sources, Phillips (1923) has presented the wintering range of the canvas-back from which these notes, with indicated additions, were obtained. On the Atlantic Coast it ordinarily winters from Delaware southward, being common the Potomac River, James River and the upper Chesapeake, and large numbers
frequent Currituck Sound in North Carolina. Farther south on the Atlantic Coast, records become increasingly rare, although they have been seen near Lakeland, Florida (Elliot 1936), near Royal Palm Hammock in the lower part of the Florida peninsula, and even in the Bermudas. It rarely is a "... winter visitor to Cuba ... doubtful occurrence in Jamaica." (Bond 1940, p. 18).

Inland in the eastern United States, canvas-backs may winter in the vicinity of Lakes Erie and Ontario, and in New York, while a few remain in Kentucky, southern Illinois and Arkansas. Pearson (1917), quoting McIlhenny, reported seeing 40,000 canvas-backs in Louisiana, and that the birds winter regularly along the shores of the Gulf States. In Texas the canvas-back varies from a common to abundant winter resident. Substantial numbers pass the winter in New Mexico and Arizona (Hargrave 1939). Records are also available on wintering of the canvas-back in Montana, Colorado, Utah and Nevada.

On the Pacific Coast, canvas-backs frequent the seacoast and lower river channels of southwestern British Columbia (Brooks and Swerth 1925) and coastal Washington (Dawson and Bowles 1909). Jewett and Gabrielson (1929, p.14) related that they were "One of the most familiar of our fall and winter ducks on the Columbia River and adjacent sloughs ... " in Oregon. They winter almost throughout California, but mainly along the coastal bays and estuaries and to the north and east of
San Francisco.

Nordhoff (1922, p. 65) has suggested a possible route followed by canvas-backs in proceeding from California into Mexico. The

... southward migration of Canvasbacks leaves the coast at about the latitude of San Luis Obispo, and from that point follows the mountain lakes south. Many of them winter in the lakes of the San Pedro Martir Mountains, Lower California, but one never sees them on either coast of the peninsula. The records of a club like Bolsa Chica show how rare the "Cans" are along the southern coast of California, and yet on the grounds of the San Timoteo Gun Club, near Banning, Riverside County, one used to bag two Cans for one of every other kind of bird!

The distribution of wintering canvas-backs in Mexico is very incompletely known. The United States Bureau of Biological Survey (now, Fish and Wildlife Service) (U.S.D.A. 1937, p. 5) reported 30,000 birds including "... some 1,000 canvasbacks and about 600 redheads ..." on Lake Apam, State of Hidalgo, but no canvas-backs were seen on Lake Tlahualillo, State of Coahuila, where they were present in 1936. On Tamiahuo Lagoon, State of Vera Cruz, "Some 2,000 canvas-backs were noted 20 miles south of Tampico." Probably the most southern records for the North American mainland were specimens taken at Duenas and at Swan Isle, Guatemala.

Among Pacific islands on which canvas-backs have been encountered, probably as strays, are Clipperton Island (Beck 1907), Hawaii (Perkins 1903), the Marshal Islands (Reichenow 1901) and Yamashima (1931) has even recorded an
individual in Japan.

In the belief that most canvas-backs breeding in or passing southward through Oregon do not cross the Rockies to winter in the states to the east and southeast, the discussion of migration will include only Alaska, Canada, the United States west of the Rocky Mountains and Mexico.

According to Phillips (1923, p. 125) "... the females and young are the first to start south in the autumn." Hochbaum (1944) asserted that the canvas-back left punctually in the middle of October and returned to the Delta Marshes in Manitoba during the latter half of April. Freble (1908) listed the species as being of regular occurrence at Willow River, near Fort Providence, Northwest Territories, and to be rather common in autumn in the Vancouver district of British Columbia. Dawson and Bowles (1909) reported that the canvas-back was not commonly seen in migration through eastern Washington, but was rather common during the winter on the west coast. A count of canvas-backs in southwestern Washington placed the first record in October and the last in March, the peak occurring during February (Beer 1945).

In Oregon, Gabrielson and Jewett (1940, p. 157) found

... that the vanguard of the Canvas-backs arrives in September (earliest dates, September 20, Multnomah County, and September 25, Harney County), but the species does not become common until November. These ducks remain on the Columbia River and on the coastal bays and lakes through the winter until early May (latest record is May 5, Tillamook County).
We have found the greatest concentrations on Tillamook Bay, where in January and February we have frequently seen rafts estimated to contain more than 5,000 birds.

The canvas-back in California is a "... fairly common winter visitant to lakes of interior and salt lagoons along coast. Arrives in late October and leaves mostly in March," according to Willett (1933, p. 34). Grinnell and Wythe's (1927, p. 52-53) remarks are in fairly close agreement:

"Early arrivals reach us during the first part of October and some birds remain until the first part of April (last, the 22nd); most plentiful from late November to early March." They usually do not appear before November in Mexico, but most of them arrive on the Pacific Coast during November and December, Phillips (1923) reported.

The continental abundance of any species of waterfowl is difficult to appraise from published reports, for there is a tendency for observers to publish more readily notes on unusually large concentrations. In spite of these qualifications, the fact is evident that the present continental population of canvas-backs is far below that of the days of Wilson and Audubon.

In the last hundred years and probably for many preceding centuries waterfowl, as a group, have shown periodical gains and losses due to a large variety of influences not yet well understood. During the same period, however, various species' numbers have not necessarily varied in parallel
fluctuations. Phillips (1923) believed that except for a large decrease in the Chesapeake Bay area the canvas-back until recently had been maintaining its numbers quite well, and that this species had responded more favorably to protection than any other duck.

A more pessimistic picture was provided by Elliot (1893) who believed the canvas-back eventually would be crowded into a completely arctic nesting habitat. Allan Brooks (1907) saw no canvas-backs on the Fraser River in British Columbia prior to 1894, but reported it as common there since 1896.

In the Sandhill Region of Nebraska, Oberholser and McAtee (1920) found that both the canvas-back and redhead had increased towards the end of the first score of years in the twentieth century. On March 25, 1925, Oberholser (1925) observed an estimated 100,000 canvas-backs in a single raft in Broad Creek below Washington, D.C. where he had been making observations for several years, believing that the species was more abundant than it had been for perhaps half a century. There probably was little decline during the following year when the same writer (1926, p. 209) indicated that the canvas-back "... more abundant than any other single species, reached its peak on February 13, when it was estimated that there were 105,000 individuals present throughout 45 miles of the river ... south of Washington," D.C.
Following a possible 1925-6 "high" the numbers decreased until a "low" was reached during 1933 to 1936. Weydemeyer and Marsh (1936) recorded the canvas-back as being abundant in 1933, common in 1934 and found only 50 in 1935 on Lake Bowdoin, Montana. Reporting on the 1937 population as compared with the 1936 numbers, the Bureau of Biological Survey (U.S.D.A. 1938, p. 4) indicated that "... in the Athabaska Delta, a gratifying increase was noted for most species, and for the canvasback in particular," and at the same time announced an observed increase in the Atlantic flyway. In contrast with the preceding statement, Linsdale (1938) found their numerical status was disproportionately reduced, especially in interior California, during 1936.

The canvas-back appeared to continue its recovery through 1939 and Biologist Peters noted a distinct improvement in its numbers on the Atlantic flyway (U.S.D.I. 1940). Coincidental with favorable water conditions throughout most of its nesting range, together with the wartime reduction in hunting pressure, the canvas-back reached its greatest abundance in more than a decade in 1944 and 1945. In 1946 drought throughout much of the Canadian breeding grounds together with increased hunting pressure may have been instrumental in bringing about another severe reduction in most waterfowl. During the fall hunting season of 1947, in spite of greatly improved summer water conditions on the
breeding grounds, the waterfowl decline continued to be evident in most parts of the country.

The literature on the general habits and life history of the canvas-back for the years preceding 1923 has been admirably reviewed by Bent (1923) and Phillips (1923). The records of these and other authors will again be mentioned when such reference is pertinent to the text. A review of hunting methods employed in obtaining canvas-backs is also deemed unnecessary in view of treatment of this subject in the works of the two authorities mentioned above. A list of local names of the canvas-back has been prepared by McAtee (1923).
THE RESEARCH AREA

Malheur National Wildlife Refuge

The Malheur National Wildlife Refuge (Fig. 1) is located in the Harney Basin of Harney County in southeastern Oregon. The principal water bodies and adjacent marshland of importance to migratory waterfowl on the refuge (Malheur, Mud and Harney Lakes) were set aside as a Federal Bird Refuge on August 18, 1908 by order of President Theodore Roosevelt (Gabrielson and Jewett 1940). Other land has since been acquired including most of the Blitzen Valley in 1935 and the Double-0 Ranch Unit in 1941, so that the present total area is about 175,000 acres, or over 270 square miles. Although all of the land within the refuge fences is now closed to hunting some property is still in private ownership, especially parts of the Malheur Lake basin. The Federal Government gradually is obtaining complete control of these holdings through land purchases and condemnation suits, either by direct negotiation or through litigation.

The Harney Basin includes about 5,300 square miles of rather high, semi-arid country in southeastern Oregon. It is new, geologically, ranging from basaltic outcroppings and older siliceous extrusives of the Miocene, to the valley fill and other alluviation of Recent age. Except for
Fig. 1. Malheur National Wildlife Refuge, Harney County, Oregon.
buttes and other rocky eminences, the entire refuge rests within this valley fill zone.

The basin contains a low, central area comprised of playas and lake beds, alluvial plains and lava fields, with a higher surrounding area of erosion plains of greater altitude and more dissected upland. Occupying the lowest part of the central plain, Malheur and Harney Lake basins cover 125 square miles and range from 4080 to 4095 feet above sea level. The upland attains heights of 9,600 feet in the Blue Mountains north boundary and 9,400 feet in the Steens Mountains to the south.

Most of the Basin is drained by the Silvies River from the north and the Donner und Blitzen River from the south. The seasonal discharge of each stream fluctuates widely between a heavy spring run-off and little or no fall flow. Both rivers enter Malheur Lake, which with water levels of 4,092.50 feet or greater, drains westward through Mud Lake and into Harney Lake, the last having no outlet.

Water surfaces in this arid section are subject to heavy evaporation and transpiration. Because the average yearly precipitation in the lower basin is only 8.6 inches, most of which falls in winter as snow, the lake levels are responsive for the most part to winter, montane precipitation. Consequently, the lakes have been subject to much fluctuation in surface area, ranging from 125 square miles during good run-off years to no water during extreme, sus-
tained drought (Piper, Robinson and Park 1939).

The maintenance of surface acreages of nearly all other impounded water on the refuge is influenced by the annual flow of water from the surrounding slopes and mountains in the spring. With a good supply of water, as in 1942, about 75 per cent of the refuge can be inundated. In a dry year such as 1947, probably less than 35 per cent of the refuge land may be under water. The proportion of flooded land to dry land also has great seasonal variation, for large marshes that are dry in fall and winter following haying in late summer, may be under 12-30 inches of water during the waterfowl nesting season.

The recent drought of 1931-1934 dried Malheur Lake completely, and excellent cereal crops were raised on the fertile bottom in 1934. During the recovery of the lake in 1935, fennel-leaved, or sago, pondweed (Potamogeton pectinatus) and dormant hardstem bulrush (Scirpus acutus)\(^a\) came back in abundance. With the return of better water years, the lake level gradually rose and water again flowed from the Malheur Lake Basin into the Harney Lake Basin.

Arising in the Blue Mountains northwest of the City of Burns, the Silvies River descends to an alluvial plain where its waters fan out and are employed in extensive irrigation of about 61,000 acres. In this way the water by evaporation and transpiration is greatly increased over the \(^a\)Hardstem bulrush (Scirpus acutus Muhlenberg), considered a valid species by the present writer, has been "lumped" with softstem bulrush under Scirpus validus Vahl by Peck (1941).
loss which had occurred previously in the natural state.
In years of heavy spring freshets from the mountains, irrigating enterprises do not utilize all of the water and much of it flows past the grainfields and hay meadows in the Burns area into Malheur Lake. When the run-off is moderate to small, the discharge dwindles or ceases during the late spring or early summer.

The Donner und Blitzen River and its tributaries arise on the western slopes of the Steens Mountains and continue to the south shore of Malheur Lake by way of the Blitzen Valley. A more complete description of this important source of water and the enclosing valley will be given later.

The only other streams of consequence to the refuge are Silver Creek and Warm Spring Creek which receive water from a western part of the Harney Basin. These creeks are intermittent within the boundaries of the refuge in the Double-O Ranch Unit and Harney Lake Unit. Most of the Silver Creek water is used in irrigation while Warm Spring Creek is the principal source of water for Double-O Ranch Unit impoundments. Both creeks merge in marshland west and slightly north of Harney Lake during high water, and enter the lake near this point.

Of the four main lakes found on the refuge, Boca Lake is the only major body of open water in the Blitzen Valley. This lake is located in the east part of Unit 3 and serves
the dual purpose of a reservoir of emergency water for lower impoundments and an excellent feeding and brood-rearing area for waterfowl. It was deepened by the construction of a substantial dike running north-south across the west side of a natural concavity in the adjacent upland, impounding water to depths of at least 14 feet, the greatest known depths to be found on the refuge with the possible exception of those immediately upstream of diversion dams in the central canal.

The remaining three lakes, Malheur, Mud and Harney, are shallow, saucer-like playas of widely oscillating shorelines accompanying changes in lake depths of even a few inches. Records of water levels taken from staff gauges located at the mouth of the Donner und Blitzen River and at the outlet from the spring of 1938 to the present, are available for study. From these records and from testimony of persons having lived in the area for many years, the recent history of Malheur Lake levels was obtained.

A scattering of lake records date from 1826 during the travels of Peter Skene Ogden in Oregon to more recent surveys of Captain George Currey and his troops and Major Enoch Steen in 1864, and to other reports published during the 20th Century. The most complete summary to date which has supplied many useful reference suggestions for this section has been recorded by Piper, Robinson, and Park (1939). The above literature testifies that the three lakes have been
subject to great changes in area throughout the past century, varying from high-water expanses of 125 square miles in some years to little or no water during extreme drought.

The most recent, completely waterless period for Malheur Lake commenced in 1931 when "... all the tules [hardstem bulrush] were dormant owing to complete dessication of the lake . . ." (Piper, Robinson and Park 1939). The lake remained dry until 1935 when it began to fill again, reaching full capacity by 1942 when the study was commenced. The highest water level recorded on the Malheur Lake staff gauge located at the mouth of the Blitzen River during the period embracing the years of the investigation was 4,095.24 feet above sea level on April 24, 1943, and the lowest was 4,090.90 feet above sea level on September 15, 1947.

The preceding discussion has been devoted to a general description of some physical features of the Malheur Refuge. The following sections will concern a general faunal and floral review of the research area together with specific descriptions of the various administrative units of the refuge and adjacent marshes northward toward the city of Burns. Areas on which few or no canvas-backs were seen during the study will receive very brief treatment.

The Malheur Refuge and remainder of the Harney Basin floor lie within the extreme arid division of the Upper Sonoran Life Zone by the Merriam Classification (Bailey 1936).
Some mammals common to this climate and topography are the pronghorned antelope (Antilocapra americana oregona), Rocky Mountain mule deer (Odocoileus hemionus macrotis), Oregon jack rabbit (Lepus californicus wallawalla), Oregon cotton-tail (Sylvilagus nuttallii nuttallii), sagebrush chipmunk (Eutamias minimus pictus), Oregon ground squirrel (Citellus oregonus), Nevada wood rat (Neotoma lepida nevadensis), Peale's meadow mouse (Microtus montanus montanus), Rocky Mountain muskrat (Fiber zibethicus osoyoosensis), Nevada beaver (Castor canadensis baileyi), yellowhaired porcupine (Erethizon epixanthum epixanthum), kangaroo rats (Perodipus spp.), mountain coyote (Canis latrans letes), Arizona weasel (Mustela longicauda arizonensis), Western mink (Lutreola vison energumenos), California badger (Taxidea taxus neglecta) and Snake River Valley raccoon (Procyon lotor excelsus).

A total of 53 species and subspecies of mammals have been reported from the Malheur Refuge.

An extremely diversified avifauna occupies the refuge during the migration and nesting seasons. Of 228 species and subspecies of birds recorded on the Malheur Refuge, including a drake European widgeon (Mareca penelope) sight record made by the writer in 1946, 133 are definitely known to nest there. Some nesting birds typical either of the arid upland or aquatic habitat are the following: eared grebe (Columbus nigricollia californicus), Western grebe (Aechmophorus occidentalis), white pelican (Pelecanus ery-
thoracicus), Farallon cormorant (Phalacrocorax auritus albociliatus), Treganza's heron (Ardea herodias treganzai), Western least bittern (Ixobrychus exilis hesperis), various swans, geese, and ducks (Anseriformes) to be mentioned later, Western red-tailed hawk (Buteo borealis calurus), Swainson's hawk (B. swainsoni), prairie falcon (Falco mexicanus), duck hawk (F. peregrinus anatum), sage hen (Centrocercus urophasianus), Sandhill crane (Grus canadensis tabida), long-billed curlew (Numenius americanus americanus), Western willet (Catoptrophorus semipalmatus inornatus), avocet (Recurvirostra americana), black-necked stilt (Himantopus mexicanus), Wilson's phalarope (Steganopus tricolor), California gull (Larus californicus), Western mourning dove (Zenaida macroura marginella), Montana horned owl (Bubo virginianus occidentalis), Western burrowing owl (Speotyto cunicularia hypugaea), Pacific nighthawk (Chordeiles minor hesperis), Western belted kingfisher (Megaceryle alcyon caurina), Say's phoebe (Sayornis saya saya), dusky horned lark (Otocoris alpestris merilli), Northern cliff swallow (Petrochelidon albilors albifrons), American magpie (Pica pica hudsonia), American raven (Corvus corax sinuatus), Western crow (Corvus brachyrhynchos hesperis), Western marsh wren (Tylomolgytes palustris pleius), sage thrasher (Oreoscoptes montanus), Western robin (Turdus migratorius propinquus), California shrike (Lanius ludovicianus gambeli), Western warbling vireo (Vireo gilvus swainsoni), Nevada
red-wing (*Agelaius phoeniceus nevadensis*), pale goldfinch (*Spinus tristis pallidus*), Nevada savannah sparrow (*Passerculus sandwichensis nevadensis*) and Modoc song sparrow (*Melospiza melodia fisherella*).

Thirty-one species of Anseriformes have been recorded as visitors to the refuge, 14 of which nest there. Nesting species are: common Canada goose (*Branta canadensis canadensis*), common mallard (*Anas platyrhynchos platyrhynchos*), gadwall (*Chauliolum streperus*), baldpate (*Mareca americana*), American pintail (*Dafila acuta tzitzioha*), green-winged teal (*Nettion carolinense*), blue-winged teal (*Querquedula discors*), cinnamon teal (*Q. cyanoptera*), shoveller (*Spatula clypeata*), redhead, canvas-back, lesser scaup duck (*Ayroca affinis*), ruddy duck and American merganser (*Mergus merganser americana*).

Non-nesting visitors are: whistling swan (*Cygnus columbianus*), lesser Canada goose (*Branta canadensis leucopereia*), cackling goose (*Branta canadensis minima*), white-fronted goose (*Anser albirostris albirostris*), lesser snow goose (*Chen hyperboreoa hyperborea*), Ross's goose (*Chen rossi*), European widgeon, wood duck (*Aix sponsa*), ring-necked duck (*Ayroca collaris*), greater scaup duck (*N. marila*), American golden-eye (*Glaucionetta clangula americana*), Barrow's golden-eye (*G. islandica*), buffle-head (*Charitonetta albeola*), white-winged scoter (*Melanitta deglandi*), surf scoter (*M. perspicillata*), and hooded merganser (*Lophodytes cucullatus*).
In addition to the preceding may be given the trumpeter swan (Cygnus buccinator) juveniles introduced as pinioned captives from the Red Rock Lakes Refuge of Montana which are not yet of breeding age.

One of the most conspicuous features of the plant life on the Malheur Refuge is the abrupt change from arid upland forms to marginal and aquatic communities. Sagebrush (Artemisia tridentata) grew in well-drained, fertile upland of high porosity, commonly found in the higher portions of the refuge. Usually occupying lower situations of greater alkalinity and often with more soil moisture, greasewood (Sarcobatus vermiculatus) was dominant on the lower plain, especially throughout the playas and in the low ground adjacent to ponds in parts of the Blitzen Valley.

Intermediate between the sagebrush and greasewood, and often interspersed with them, were bud sage (Artemisia spinescens), shadescale (Atriplex confertifolia), hop sage (Grayia spinosa), and gray tetrady mia (Tetradymia canescens). Downy brome-grass (Bromus tectorum) shared most of the upland, excepting in alkaline situations, and giant rye-grass (Elymus condensatus) grew especially abundantly with the conspicuous, yellow-flowered rabbit-brush (Chrysothamnus spp.) in places with more moisture than the typical sagebrush habitat.

The principal remaining, non-aquatic habitat can be listed as ballast areas including dikes, levees, roadsides
and other disturbed soil situations. The most common ballast plant species included hoary nettle (Urtica holosericea), orache (Atriplex argentea, A. patula), goosefoot (Chenopodium album), Russian thistle (Salsola kali tenuifolia), hare's-ear mustard (Conringia orientalis), flixweed (Descurainia sophia), yellow-flowered peppergrass (Lepidium perfoliatum), penny-cress (Thlaspi arvense), other mustards (Cruciferae), sweet clover (Melilotus spp.), thistles (Cirsium spp.), horseweed (Erigeron canadensis), poverty weed (Iva axillaris), blue lettuce (Lactuca pulchella) and goldenrods (Solidago occidentalis, S. serotina).

On the banks along borrow pits, canals and other watercourses of the refuge, willows (Salix caudata parvifolia, S. exigua luteosericea) often grew in long, dense thickets. Alders (Alnus sp.) occurred mostly along the canals and streams of Unit 1. The wide margins of the playa lakes and sloping edges of many valley ponds characterized by seasonal flooding, much evaporation and high alkalinity were occupied by desert saltgrass (Distichlis stricta) meadows. Below the saltgrass belt in moist situations of lower alkalinity, squirrel-tail barley (Hordeum jubatum) flourished, vast fields of this conspicuous grass encircling and invading Malheur Lake and Mud Lake basins following recession of water levels during 1946 and 1947.

The remaining plant descriptions concern wet meadow, marsh, pond and lake species. More specific treatment will
be given this aquatic and submarginal vegetation in later discussions of habitat. Except where the land had been disturbed, most aquatic habitat showed a gradual slope below the saltgrass zone and usually much wet meadow and slough occurred marginally.

Alkali rye-grass (*Elymus triticoides*) often grew both above and below the saltgrass strip while redtop (*Agrostis alba*), reed canary-grass (*Phalaris arundinacea*), slough grass (*Beckmannia Syzigachne*), meadow barley (*Hordeum nodosum*), foxtail grass (*Alopecurus spp.*) and bluegrass (*Poa spp.*) occupied wetter situations of lower alkalinity. Below the meadow grass belt, sedges (*Carex spp.*) dominated and then yielded in lower situations to the more coarse emergents having species able to survive submergence during a large part or all of the growing season. Such species were broad-leaved cat-tail (*Typha latifolia*), broad-fruit bur-reed (*Sparganium eurycarpum*), water plantain (*Alisma plantago-aquatica*), arrowhead (*Sagittaria spp.*), manna-grass (*Glyceria spp.*), common reed (*Phragmites communis*), spikerushes and needlerush (*Eleocharis spp.*), bulrushes (*Scirpus spp.*), rushes (*Juncus spp.*) and smartweeds (*Polygonum spp.*).

The principal submergent and floating-leaved hydrophytes of the lakes, ponds and canals were muskgrass (*Chara sp.*), riccia (*Riccia fluitans*), pondweeds (*Potamogeton spp.*), waterweed (*Anacharis canadensis*), duckweeds (*Lemna spp.*, *Spirodela polyrhiza*), smartweeds (*Polygonum spp.*), Western
yellow pond-lily (Nymphaezanthus polysepalus), hornwort or coontail (Ceratophyllum demersum), water buttercups (Ranunculus spp.), water starwort (Callitriche spp.), marestail (Hippuris vulgaris), water milfoil (Myriophyllum sp.) and bladderwort (Utricularia sp.).

Donner und Blitzen Valley Units

Arising on the gradual, west slope of the Steens Mountains, the main Donner und Blitzen River originally meandered northward down the rimrock-enclosed Blitzen Valley plain through a myriad of marshes. Most of this river system within the refuge boundaries now is canalized and a series of dams, impoundments and the Boca Lake reservoir give greater control of the river flow.

By means of the main diversion dam found at the head of the valley (Fig. 2) much of the water of the trunk stream is headed into the east and west canals which, respectively, parallel the east and west margins of the upper four valley units. From these lateral canals a series of valley impoundments receives water throughout most of the season. Surplus water leaves these ponds and sloughs through spillways and valve-controlled outlets, continuing to lower impoundments or flowing directly into the central canal. Thus, the central canal carries surplus water down the valley to Malheur Lake and receives water from unit impoundments throughout much of its length, usually in quantity
Fig. 2. Main diversion dam on the Donner und Blitzen River, Harney County, Oregon

to permit local migration of trout (Salmonidae) up- and downstream. A more or less continuous flow of water through the impoundments serves the additional features of preventing excessive stagnation and maintaining desirable water levels in the valley ponds and marshes.

A small tributary, Krumbo Creek, enters the central canal in Unit 5 and the valley water flow then continues through a narrow gorge below which another alluvial plain extends to the southwest shore of Malheur Lake. Another water-control structure in Unit 6, termed the Grain Camp Dam, again builds up a "head" of water, permitting irrigation of adjacent grain and hay lands and diverting of water into another west canal for use in Units 8 and 10, while
a varying discharge of water continues down the central canal until blocked by Busse Dam in the northeast part of Unit 8.

Just below Grain Camp Dam, the lower Diamond Valley portion of the refuge provides an additional source of water, Kiger Creek and McCoy Creek supplying water to marshes, canals, impoundments and grain fields in Units 7 and 9. Surplus water passes through successive impoundments or back into the central canal.

Having progressed the entire length of the Blitzen Valley, the Donner und Blitzen River enters Malheur Lake northeast of the refuge headquarters buildings. Unlike that of the Silvies River, the discharge of the Donner und Blitzen River does not cease completely during any season of the year except possibly during the most extreme drought. It flowed continuously throughout the seven-year period embracing the investigation, although reduced to little more than a trickle at times.

Detailed descriptions of all areas of the refuge were deemed unnecessary since some, including brushland, were rarely occupied by canvas-backs during any phase of the investigation. Included in this unoccupied class were Units 1, 2 and 5. The first two units at the head of the Blitzen Valley contained relatively isolated, nearly-closed sloughs or small ponds occupied mainly by puddle ducks and a few redheads. Although Unit 5 contained one large, open
pond margined by dense emergent vegetation, canvas-backs were never seen thereon, though mallards, pintails, shovelers and cinnamon teal reared broods there. All three of these units had heavy growths of willows margining the streams and canals interspersed in Units 1 and 2 by park-like hay meadows forming favored mule deer yards. Unit 6 water was found mainly in canals and contained a few canvas-backs during migration.

From the standpoint of migration utilization and production of the canvas-back, Units 3, 4, 7, 8, 9, 10 and 11 were the only Blitzen Valley units of importance in the study. Of these, 3, 8 and 9 contained large, permanent and temporary ponds while the other units maintained pond levels only during the spring migration and summer season, being drained for haying and grazing after the middle of July in most years.

The levels of most of these ponds were maintained fairly constantly during the nesting season and thus provided a definite contrast in stability with the changes in water level of Malheur Lake which induced extensive oscillations of the shoreline each year. No temporary water bodies on the Malheur Refuge occupied by nesting canvas-backs were subject to violent depth fluctuations following filling in the spring. The permanent ponds of Units 3, 8 and 9 were controlled by valves and spillways which easily carried off excess water.
The valley ponds were of two principal types: the permanent ponds which had levels varying from a few inches to about two feet during the entire year; and temporary or seasonal ponds which were filled to desired levels prior to or during the first part of the canvas-back nesting season. The water supply for the temporary ponds usually became exhausted by the end of the nesting season due to transpiration, evaporation and seepage, or else water was diverted or drained from the ponds when haying was begun in July and August in adjacent meadows, so that levels went progressively lower in late summer and early fall. Many of these ponds, especially in lower Unit 10 and 11, were without water until the following spring but some retained a reduced volume of water in lower situations. Since limited space does not permit descriptions of all types of habitat occupied by canvas-backs at Malheur, brief descriptions of representative ponds of permanent and temporary nature are given.

Perhaps the best example of a permanent type of pond was one located near the south end of Unit 8 (Fig. 3) which will be referred to as the Buena Vista pond in later discussion. The north end of this pond, shown to the right of center in the photograph, was deepest and was bounded by a dike and road on the west, north and east sides. The area of the interspersed emergent vegetation and open water of this pond was approximately 320 acres with a southwardly
Fig. 3. "Permanent type" Buena Vista impoundment.

extending marsh of about 300 acres. The principal emergent vegetation of the semi-open part of the pond was hardstem bulrush, broad-fruitied bur-reed and broad-leaved cat-tail. The bulrush appears in the photograph as small, dark clumps margined near the water-line with lighter bands; cat-tail has a lighter shade of gray and occurs as larger stands in shallower parts of the pond on the left side of the photograph; and bur-reed stands, similar in shade to bulrush but with no light band near the water-line, are visible in the extreme upper right side of the pond.

The marshy appendage of this pond was believed to have been occupied by no canvas-backs during the study and was dominated by bur-reed and cat-tail throughout the central
area, with few scattered stands of common reed, and margined with sedges (Carex) which gave way peripherally to such grasses as manna-grass, redtop, foxtail grass, slough grass and reed canary-grass.

The submerged aquatic vegetation in this permanent pond consisted principally of water milfoil and water buttercup (Fig. 4), with lesser quantities of sago pondweed. In the deeper borrow pit along the north dike, heavy growths of coontail occurred. The depth of water in areas grown with milfoil-buttercup ranged between one and three feet, while pure stands of coontail were found in three to eight feet of water.

Fig. 4. Dense milfoil-buttercup growth replacing sago pondweed in Buena Vista pond.
Most ponds in the Blitzen Valley less than 320 acres in surface area were of the temporary or seasonal type. They differed from the permanent ponds in their larger, more continuous stands of bulrush, cat-tail and bur-reed; in wider vertical range in distribution of emergent vegetation; and, especially, in the low incidence or absence of the water milfoil-buttercup community in the open water. One of the best examples of this type was an 80-acre pond and associated section of marsh (Fig. 5) located in the north half of Unit 9. This pond and marsh, excepting about one-half acre of water surface in the deepest part, was almost dry in late fall and winter during each of the three years of the study. In the small, deeper remnant remaining

Fig. 5. Unit 9 "temporary type" impoundment popular as canvas-back nesting and brood-rearing area.
persisted the only milfoil growth to be found in this impoundment. Temporary ponds inhabited by migrating or nesting canvas-backs were found in every unit of the valley except Units 1, 2 and 5, while permanent ponds serving canvas-backs (Boca Lake can be included in this category) were found only in Units 3, 8 and 9.

Malheur Lake and Mud Lake

Since Malheur Lake (Fig. 6) provides the major part of canvas-back-occupied migrating and breeding habitat of all refuge waters during favorable water-years, it merits the detailed description necessary to a more complete understanding of the factors which control its depth, area,
vegetation and utilization by waterfowl. Throughout the following discussion reference has been made to Table I which lists monthly extremes in water levels of Malheur Lake during the April-September season of 1942, 1946 and 1947, and to Fig. 7 which provides a graphic study of (1) vertical ranges in Malheur Lake levels during the three seasons of study, (2) vertical ranges in elevation of zoned, emergent plant communities, and (3) approximate water-surface acreages of Malheur Lake and Mud Lake at various lake levels.

As a result of water flowing away into Mud Lake, transpiration, evaporation and seepage, Malheur Lake levels tended to lower as the season progressed each year. Surface-water run-off from adjacent upland during March and April sug-

Table I. Malheur Lake Levels in Feet Above Sea Level During the Canvas-back Breeding Seasons of 1942, 1946 and 1947

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Fig. 7. Relation between water levels, emergent vegetation zoning and water-surface area in Malheur Lake Basin, Oregon during April-September, 1942, 1946 and 1947.
mented by water from melting snow in the higher parts of the Steens Mountains and Blue Mountains, provided substantial relief from the agents of water loss in 1942, so that the lake became deeper during the spring and reached the greatest level for the three years of the study of 4094.31 feet above sea level on June 7. After this date the mountain run-off continued to decrease and no longer could offset the factors of lake water loss. Consequently, the lake level gradually lowered to 4093.66 feet a.s.l. during August, giving a vertical lake-level range of 1.15 feet during the five months (no gauge readings were available for September, 1942).

As a consequence of continued water loss with light fall and winter precipitation on the refuge, in adjacent upland and in the mountain drainage following the high-water year of 1945, the lake did not recover in the spring of 1946. Beginning that season at 4093.44 feet a.s.l., the level rose only to 4093.60 feet on May 9 marking the "high" for the season. From this date the level steadily subsided and shorelines constricted quite rapidly because of the shallow, pan-like structure of the lake basin. By the middle of September, the lake level stood at 4091.92 feet a.s.l. Paralleling the decrease in depth, the total area was reduced from approximately 63,000 acres on June 7, 1942 to about 31,000 acres on September 11, 1946.

A slight recovery during the winter of 1946-7 raised
the water level to 4092.80 feet a.s.l. during February and March, 1947. The highest level recorded for the 1947 breeding season was 4092.78 feet on April 19. From this date the lake level steadily subsided to 4090.84 feet in late September, the lowest gauge reading for the three years of the investigation and also the lowest since February, 1941. During the 1947 season, the lake area was reduced from 45,000 acres to 19,000 acres. The total reduction in depth of Malheur Lake from 4094.81 feet to 4090.84 feet a.s.l. between 1942 and 1947, a difference of 3.97 feet, resulted in a decrease in surface area of about 44,000 acres or a loss of nearly 70 per cent of the June 7, 1942 surface acreage.

These gradual but drastic changes in depth, area and shoreline of Malheur Lake were reflected not only in a changed flora but also in a change of availability of certain plant species for food and cover requirements as shown in Fig. 7. During the 1942 nesting season, all aquatic plant communities were inundated to varying depths, and even the saltgrass marginal belt was flooded during May and June when levels exceeded 4094.50 feet a.s.l. The vegetation zones given vertically in the middle of the figure were not characterized by unequivocal boundary delineation, but occasionally varied under conditions imposed by the mechanics of plant succession. Character of the soil substratum, alkalinity, wave action, muskrat utilization,
and possibly other undetermined or less obvious influences all may have acted as modifiers of vegetation zonation.

Considerable overlap of vegetation zones existed in some situations, but from oft-repeated depth measurements of water among representative emergent vegetation stands in the lake and adjacent marshes during the three years of this study, the elevations given were established and substantiated. In spite of the wide fluctuations in marginal inundation, the plant communities occupying those situations failed to show any apparent changes. The most noticeable change took place among the hardstem bulrush growth in the deeper portions of Malheur Lake. In 1942 this bulrush was too sparse to support canvas-back nests but with lake levels reduced more than two feet in 1946 and 1947, the bulrush grew more thriftily, being at least four times as dense in those situations. An attempted explanation of the ecological factors responsible for this constancy of zonation does not lie within the limited province of this thesis, but depth measurements made each year in every cover type during varying lake levels left no doubt of its existence.

On the left side of Fig. 7 the ranges of Malheur Lake levels have been given for the three years' nesting periods. The levels show a decline each succeeding year characterized by a low level early in the season which was followed by a substantial gain only in 1942, followed by the usual subsidence after the middle of July. The absence of much run-off
water from the mountains in the last two years of the study provided no recovery from the April low levels and consequently the lake was very low when the study was terminated in 1947.

The lake levels fluctuated both seasonally and yearly. The influence of these changes in the availability of canvas-back nesting cover becomes apparent by studying Fig. 6. Depths of water existing on a given date in any plant community may be obtained by extending a horizontal line from the brace enclosing the plant community through the section representing current lake levels. The vertical difference, expressed in feet, between the point on the water-level curve and the elevation of the plant community, constitutes the current water depth.

The approximate acreages of plant cover also can easily be determined from this figure. For instance, the bur-reed-cat-tail community is seen to occupy elevations of 4092.50 feet to 4093.50 feet a.s.l. By extending these limits horizontally to the right until they intersect the curved line representing the water-surface area, the lower limit touches a point below approximately 42,000 acres while the upper limit intersects the line about midway between 50,000 and 55,000 acres, or about 52,500 acres. By subtracting 42,000 from 52,500, the approximate acreage of the bur-reed-cat-tail community, 10,500 acres is obtained. Total water-surface acreages of the Malheur Lake during any period of
the breeding season of 1942, 1946 or 1947 may quickly be determined by extending the desired point of the lake level curve on the left side of the figure horizontally until it intersects the water-surface area curve on the right side of the figure. The current lake-surface acreage is then found by reading the numerical value directly above the intersected point on the water-surface curve.

All plant communities listed were inundated to some degree in June, 1942 when the shoreline advanced well into the desert saltgrass zone. During 1946, however, the shoreline never reached the saltgrass and barely covered the lower parts of the zone including the spikerushes. By the end of this season, even the bur-reed-cat-tail community was out of water.

In 1947, the bur-reed-cat-tail community was partly flooded in April and the first week of May, after which it remained out of water. By the end of August, 1947 the shorelines had contracted to such an extent that all communities except the sparse hardstem bulrush of 1942 were out of water, and even the sparse bulrush stands had increased in density until they resembled the heavy 1942 bulrush stands which were growing in shallower water.

The principal open water areas of Malheur Lake during 1942-7, meanwhile, were reduced in average depth from over three feet in May-June, 1942 to about 11 inches in September, 1947. This lake-level subsidence had a profound effect on
the quality of submergent vegetation from year to year. In 1942, excellent stands of sago pondweed were encountered in nearly all muskrat-opened channels or other interspersed clearings among the dense bulrush cover, occupying about one third of the lake area. The deeper third of the lake occupied by sparse bulrush and open water was principally grown with water milfoil, with lesser quantities of sago pondweed and coontail. During August and September, 1946 much of the pondweed was exposed by receding shorelines. As the range in lake levels for 1947 shows, this zone was again covered in early 1947, but again gradually became exposed until the pondweed zone, together with the bulrush stands which had been dense in 1942, were completely out of water during the last week of August, 1947. Parts of the "pondweed zone" had already been exposed by June 21 of the same year when black-necked stilts (Fig. 8) and avocets were found nesting on the bulrush-strewn mud flats previously supporting excellent pondweed stands.

Because of its deeper-water location, most of the water milfoil retained at least some degree of submergence throughout the study. This growth appeared as a purplish-red blanket covering the lake during 1946-7 when viewed from a distance in late May and June, but by August much of this vegetation was becoming exposed on mud flats or lay putrefying in shallow water, acquiring a brown color when drying.

Mud Lake was a small body of water lying at the extreme
Fig. 8. Black-necked stilt at nest on mud flat left exposed by recession of Malheur Lake shoreline.

western tip of the Malheur Lake Basin (Fig. 1) and was almost completely free of emergent vegetation. The principal submergent hydrophytes present in order of abundance were water milfoil, sago pondweed and coontail. This lake was heavily utilized by migrant canvas-backs during 1942 and 1946 and will be discussed further in the section on migration. The acreage of this small lake was constantly changing from a 1942 area of about 1200 acres to dryness in August, 1947.

Harney Lake Unit

Reference has already been made to this vast alkali bowl which plays the role of a sump for the watershed of
the Harney Basin. The only emergent vegetation substantial enough to support nests of ducks on this lake occurred as a few clumps of hardstem bulrush near the mineral springs on the extreme southeast side of the lake basin. Canvasbacks and redheads made little use of this lake, except during migration. Although no soundings were taken during the study, contour lines on refuge maps indicate that during high water, depths greater than ten feet may be reached.

Except for a negligible increment from surface run-off, this lake received most of its water from Mud Lake when the latter body reached elevation levels of about 4093 feet a.s.l. or greater, and from the Silver Creek drainage via impoundments and canals of the Double-O Ranch Unit. Since Mud Lake received water from Malheur Lake only when the latter's levels exceeded 4092.50 feet a.s.l., it can readily be seen that during the high water levels of 1942 exceeding 4094 feet on Malheur Lake, much water was able to pass through the small Mud Lake into Harney Lake. Judging from the record of Malheur Lake depth gauge readings during 1943, 1944 and 1945, a discharge from Malheur Lake could have passed into Harney Lake during each of these three intervening years, although during the exceedingly high water level of March-May, 1943, the inflow must have been by far the greatest. The last two years of the study witnessed a shrinking of the shoreline of this lake, and no water was received through the Malheur-Mud Lake system.
A depauperate growth of sago pondweed occurred along the southwest shoreline, but no other submergent vegetation was found. As the shoreline receded each summer, outer limits of the lake basin were exposed as brilliantly white margins of crystallized salts, or "alkali slicks" as they were termed locally. No plants were seen to grow on these exposed shores after the water recession.

No definite band of marginal vegetation existed along the shoreline although a few rushes (Juncus) occurred about seeping springs. Above the high-water mark, alkali- and salt-tolerant greasewood was thriving. A colony of about 2,500 nesting pairs of California gulls and a few pairs of Caspian terns (Hydroprogne caspia imperator) occupied a sandspit on the lake during 1946. No other nesting waterfowl were in evidence on Harney Lake.

**Double-O Ranch Unit**

The low, playa lands surrounding part of Harney Lake extended northward to include the Double-O Ranch Unit ponds and canals. Very little improvement work has been accomplished on irrigation devices or water-control structures in this unit since its purchase by the Government in 1941, so these structures are in need of extensive repair and continuous maintenance. Except for stable, thermal, spring-fed ponds, most of these water bodies fluctuate widely. The area provides nesting facilities for
most species of puddle ducks present on the refuge, and Canada geese, and some redheads also nest in the bulrush clumps on the permanent ponds. Suspected canvas-back nesting was substantiated by a brood seen there in 1942. One of the foremost values of this unit is its utilization by migrating lesser snow geese which congregate in large flocks on the shallow ponds and nearby hay meadows.

Non-Refuge Ponds and Marshland

The work accomplished on the canvas-back study at the Malheur Refuge was supplemented by migration, nesting and brood observations made on marshes immediately adjacent to the refuge and northward towards the City of Burns. The marshes adjoining Malheur Lake are a part of the system described under the discussion of that basin. The marshes south and southeast of Burns are more closely comparable with some parts of the Blitzen Valley, for their principal source of water is the Silvies River which arises in the Blue Mountains. These marshes form part of a large irrigated flood plain, and any benefit of this area to ducks, geese and swans appeared incidental rather than intentional.

On the "Burns marshland" occurred the heaviest spring migration concentrations of lesser snow geese and white-fronted geese. The "flash-flooding" of haylands and small grain fields each spring provided fine resting and feeding
grounds for waterfowl, and several hundred canvas-backs were seen frequently on the deeper water during migration. Probably as many as thirty pairs remained to nest in marshes and along the canals in this area, and several broods were seen each year along the State highway southeast of Burns.
THE CANVAS-BACK INVESTIGATION

During the first year of the study field work was commenced April 4 and terminated August 24, 1942, with primary attention to the breeding habits of the canvas-back. The investigation was interrupted by World War II, but was subsequently pursued from March 28 to September 13 in 1946 and from March 23 to September 11 in 1947.

Each year, observations were begun on the research area prior to the time that the main body of migrating canvas-backs were passing northward through the refuge, and the first autumn migrants had arrived by the time observations were terminated. The data collected have been supplemented by notes of competent refuge observers, especially for the early part of the spring migration, fall migration, hunting season and winter, and records of weather and lake levels were available from refuge files.

Equipment and Techniques

In spite of the large size of the research area, familiarity with even the more remote units was acquired rapidly through daily reconnaissance and frequent reference to refuge maps. While working in the field, careful notes were taken on all observed phases of waterfowl activities,
with special concentration on the canvas-back, redhead and
duddy duck. Water levels and depths, weather conditions,
aquatic vegetation, available food and duck mortality were
closely watched. These data were recorded in a small,
loose-leaf notebook and later were typewritten and filed
subjectively. Though this procedure entailed additional
time and effort, it served the dual purpose of expediting
later reference and aiding memory of specific incidents.

Most observations while afoot were made in marshes and
shallow ponds or from willow thickets bordering ponds, and
from boat or canoe on various bodies of water. Of the two
methods of water transportation, the canoe was the more
versatile. It provided relatively rapid travel whether by
manual or motor propulsion. The light weight permitted
easy portaging to a few remote ponds, while the shallow
draft and comparatively narrow beam enabled navigation
through shallow marshes and narrow channels.

Light-weight sportsman's rubber boots were worn during
the first few weeks of the study, but they quickly wore out
in contact with the coarse, emergent vegetation, so heavier,
stiffer boots were substituted. After June 15 each year,
the water became warm enough to permit wading without boots.

The boat motor was used only on Malheur Lake. Its
greatest value lay in facilitating rapid travel over the
open areas of the lake as well as through the myriad of
labyrinthic channel systems among the hardstem bulrush, and was used throughout the first year's work. After June in 1946 and during all but a few weeks of the 1947 season, water levels were so low that the motor could be effectively employed only in certain parts of the lake, for dense submersent vegetation quickly fouled the propellor. The noise of the motor was a disadvantage in preventing much close observation, but was helpful in rousing nesting females during nest-searching.

For the purpose of obtaining accurate measurements of various nests and associated nesting habitat features, as well as keeping records on the progress of all nests, diving duck nest history forms were mimeographed on durable, water-resistant, bond paper. These were carried on each trip into the field during the nesting season. Fig. 9 exhibits the nest history form used during the study.

Upon discovering a nest, a number was assigned and all blank spaces in the upper third of the nest history form, plus the spaces in the column for the first visit, were filled. Information on the progress of the nest was recorded under given captions during successive visits. On the visit following termination of the nest history, the bottom third of the form was completed. In addition to recording information during the first visit, a small, waterproof, paper tag showing the assigned nest number was attached firmly and inconspicuously to a willow wand or to substantial
DIVING DUCK NEST HISTORY FORM

Nest Number __________________ Species __________________

Location ____________________________

Vegetation Cover: Species __________________ Proportions __________________

Size of Stand density __________________ Green Veg. %

Nest: Outer diameter __________________ bowl diameter __________________ bowl depth ______________
bowl floor over water __________________ vertical thickness of nest at clutch completion __________________ ramps __________________ cupola

Observer's disturbance __________________ depth ______ distance to take-off area ______

Water body: Type __________________ depth ______ distance to take-off area ______

Male waiting site: Type __________________ distance ______ direction ______

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Date __________________

Hour of day __________________

Distance female flushed (yds.) __________________

Eggs: Laid by owner __________________

Laid by intruder(s) __________________

Temperature (warm or cold) __________________

Covered (0,1,2,3) __________________

Nest visible down (0,1,2,3) __________________

green plant materials (%) __________________

concealment (0,1,2,3) __________________

Date of nest

Successful: Date __________ Condition of nest

Unsuccessful: Date __________ Condition of nest

Abandoned: Cause __________________

Destroyed: Cause __________________

Other fate __________________

Eggs Laid by Owner __________________

Eggs Hatched __________________

Eggs not hatched left in nest embryos undeveloped embryosalve undeveloped, found in water, destroyed embryosalve undeveloped, removed, fate

Undetermined fate __________________

Owner __________________

Intruder(s) __________________

Additional comments: __________________

Fig. 9. Diving duck nest history form used during the canvas-back study in southeastern Oregon.
vegetation in the vicinity of the nest. Tags were placed at least 50 yards from and out of sight of incubating females. The information recorded under "Location" included the exact location of the nest tag and the distance and compass bearing of the nest from the tag.

Throughout the spring and summer seasons, additional items of equipment were employed. A Bausch and Lomb 7x, 35 binocular proved to be the most useful field glass for ordinary purposes in waterfowl study, while a 3½ x 4½ Speed Graphic camera with accessories was satisfactory for obtaining photographs under most conditions. A pocket compass was carried in the field at all times. Other equipment used included a portable plant press, insect net, hardware-cloth dredge net, glass vials for alcoholic, biological specimens, and a vernier caliper for egg measurement.

Vehicles were available for travel throughout the refuge during parts of the 1942 study and during 1946 and 1947. Many valuable observations were made from an automobile, for most ponds in the Blitzen Valley and Double-O Ranch units were bordered by dike roads, and waterfowl appeared much less disturbed by the appearance of an observer in a vehicle than when traveling afoot. Cole Island Dike, traversing the eastern third of Malheur Lake, and roads adjacent to Mud Lake and Harney Lake offered additional points of vantage for the study of waterfowl, especially during migration and brood-rearing.
Other techniques employed in the study of migration, nesting, juvenile-rearing and postnesting activities of the canvas-back will be described in their respective discussions.

Weather and Habitat Conditions

Weather and the general condition of the habitat were found to influence the behavior of the canvas-backs. It seems advisable at this point, therefore, to report in detail on general and specific weather conditions as they related to habitat changes on the research area.

The semi-arid climate of the Harney Basin usually does not permit growth of crops without irrigation. Snow may fall on the valley plain during all months except July, August and September, but falls on the mountains during any month of the year. The daily and seasonal range in temperature is very wide, relative humidity is low, evaporation is rapid and the proportion of cloudless days is high. Though strong winds are common throughout the year especially from March to June, they rarely, if ever, reach the velocity of a tornado.

The average length of the frost-free period at Burns is 118 days, the latest frost of the spring occurs about May 24, and the earliest killing frost of autumn on September 19. Freezing temperatures may occur in any month.
of the year. Records of the Harney Branch Experiment Station, located about 22 miles north of refuge headquarters and six miles east of Burns, show that the monthly average evaporation of water in inches from a six-foot pan have been as follows: for April, 3.8; May, 6.3; June, 7.4; July, 9.3; August, 8.1; September, 5.2; October, 2.8, averaging 42.9 inches for the seven-month period, or over 5.5 times as much water loss as the total, average, yearly precipitation.

Average wind velocity records given in miles per hour for the same locality during the months of January through December are as follows: 2.8, 3.3, 4.5, 5.4, 5.5, 4.6, 4.1, 3.5, 3.5, 3.4, 3.0 and 2.9, giving an annual average velocity of 3.9 miles per hour.

The following discussion of climatological phenomena is principally concerned with weather and habitat conditions present during the three seasons of the investigation. Before May 1, during the canvas-back migration and prior to the period of intense nesting, weather and habitat conditions largely determined the local distribution of migrating and resident waterfowl. The ice usually went out on Malheur Lake during the last half of February or the first week in March, although some of the more shallow valley ponds were ice-free somewhat earlier. Cold spring- and warm spring-fed ponds supplied limited open water the year round, and they were usually occupied by coots, mallards.
and pintails during the winter. A few canvas-backs also wintered at Malheur in the winter of 1941-1942. Grain fed to captive trumpeter swans in one of the ponds at refuge headquarters attracted these temporary boarders and as other open water appeared and the nesting season progressed the number decreased, although a few came in for night feeding throughout the spring, summer and fall months.

A wide variation in diurnal and nocturnal maximum and minimum temperatures existed throughout the season each year, maximum daily ranges being 40 degrees, 48 degrees and 56 degrees Fahrenheit, respectively, for the three years. March was the coldest and July was the warmest month of the March-to-September period. Precipitation was usually heaviest in winter and lowest during July and August. Precipitation for the seven-month period of 1942, 1946 and 1947 totaled 4.20, 3.51 and 5.51 inches, respectively. Most moisture fell in the form of rain, but snow was recorded at the refuge headquarters weather station in April.

Latest freezing temperatures were encountered each year on the following dates: May 13, 1942; June 24, 1946; and June 30, 1947. Maximum temperature for the three years were 96 degrees Fahrenheit on July 4, 1942, 99 degrees on July 21, 1946, and 93 degrees on July 14, 17 and 21, 1947. July and August had the greatest number of cloudless days and March had the most cloudy days. Climatological information for the period March through September, 1942, 1946 and
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</tr>
<tr>
<td></td>
<td>1946</td>
<td>86.1</td>
<td>46.1</td>
</tr>
<tr>
<td></td>
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<td>83.1</td>
<td>43.6</td>
</tr>
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<td></td>
<td>1946</td>
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<tr>
<td></td>
<td>1947</td>
<td>78.0</td>
<td>36.9</td>
</tr>
<tr>
<td>Month</td>
<td>Year</td>
<td>Temperature</td>
<td>Inches precipitation</td>
</tr>
<tr>
<td>-------</td>
<td>------</td>
<td>-------------</td>
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</tr>
<tr>
<td></td>
<td></td>
<td>Mean max.</td>
<td>Mean min.</td>
</tr>
<tr>
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<td>69.5</td>
<td>39.2</td>
<td>54.3</td>
</tr>
<tr>
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<td>72.0</td>
<td>38.4</td>
<td>55.2</td>
</tr>
<tr>
<td>1947</td>
<td>72.7</td>
<td>38.0</td>
<td>55.3</td>
</tr>
<tr>
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</table>
Fig. 10. Correlation of daily temperature ranges with canvas-back nest inceptions on Malheur Refuge during the nesting seasons of 1942, 1946 and 1947.
1947, has been summarized in Table II.

Weather conditions of March, April and May in general were similar during 1946 and 1947 when the peak of nest inceptions occurred coincidentally with a warm latter half of April and May. In 1942, however, after three weeks of unseasonably warm weather in the first three weeks of April, comparatively low temperatures, characterized by a short maximum-minimum temperature range, prevailed until about the end of the second week in May. After this date temperatures for all three years were more nearly alike. Fig. 10 presents a record of daily temperature ranges of April-July with correlated estimated dates of known nest inceptions for 1942, 1946 and 1947.

The prevailing wind direction during most months of the year was from west-northwest, but was subject to daily and even hourly changes. Strong winds were common during March and April, usually from the northwest quarter, while storms bringing precipitation during the spring and summer usually were from the southwest.

In 1942 heavy spring winds, together with high water levels and the activities of muskrats, caused the rapid disintegration of most bulrush stands in central Malheur Lake. As fast as the culms became dislodged they were drifted about the lake, usually lodging along the southeast shore where they formed a wide barrier mat of decaying vegetation. The barrier varied from a few feet to over 200 yards in
width and extended for more than six miles along the west side of Cole Island Dike. Along with the drifted vegetation muskrat lodges, often crowned by active Canada goose nests, were swept across the open water and became part of the barrier. Such transplanted goose nests invariably were abandoned by the nesting pair, but muskrats, possibly other than the original tenants, continued to use the lodges. Velocities of the more violent storms in 1942 were estimated to be between 25 and 35 miles per hour. During these windy periods nearly all waterfowl sought cover, but a few American coots (Fulica americana americana) and an occasional ruddy duck could be seen on open water in even the roughest weather.

With shallower water and reduced area, together with fewer high winds, very little bulrush cover and no observed muskrat lodges during 1946-7 were swept away in Malheur Lake. There was little evident effect of wind and waves on nesting in the Blitzen Valley ponds and marshes because of the comparatively small size of open water areas and shallowness of the water.

The Prenesting Period

Spring migration

The Malheur National Wildlife Refuge is located in the Great Basin about midway between the east and west borders.
on the Pacific Flyway. The canvas-back, as well as many other species of waterfowl, has frequented this section of the country over a long period. DeMay (1941) reported finding remains of waterfowl, of which mallard, canvas-back, pintail and coot were most abundantly represented, in Pleistocene deposits at Lower Klamath Lake in northern California.

While Malheur Lake was becoming free of ice during late February and the first week in March, mallards began to appear on the open pools. American pintails reached the refuge only slightly, if at all, later than the mallards, and Canada geese followed shortly thereafter.

The first canvas-backs appeared early in March and became abundant by March 15 on Malheur and Mud Lakes, but usually were not common in the Blitzen Valley until late in March. The main migration of redheads was about three weeks later than that of the canvas-back, and they did not become common until about April 1. The lesser scaup migration period usually embraced the flights of canvas-back, redhead and ring-necked duck, the last species being most common just before the peak of the canvas-back abundance early in April.

The lesser snow goose and white-fronted goose migration peaks came during March, and the earlier canvas-back migrants were often seen feeding in shallow, open expanses of Malheur Lake in their company. The heaviest flights of
whistling swans usually passed through Malheur during the last two weeks in March. On March 26, 1947 an estimated 5,000 whistling swans were seen feeding in a large, shallow section of Malheur Lake east of Cole Island Dike, accompanied by about 6,000 canvas-backs, some of which fed on plant materials brought to the surface by the swans. Although this swan-canvas-back feeding association was not commonly seen, the two species often mingled on all swan feeding areas.

All species of ducks, geese and swans regularly seen as migrants and residents at the Malheur Refuge at some time during the three-year investigation were found with the canvas-back in a more or less incidental or casual association. The canvas-back usually tended to associate with others of its own kind, and most observations found them during migration as singles, pairs, or in groups up to several hundred individuals. These larger groups, however, remained loosely dispersed over feeding and resting water areas, except during blustery, cold weather of March and early April when they tended to favor lee shores or semi-open clearings and channels among emergent vegetation. In this way, 500 or more canvas-backs could be distributed over 200 acres to two square miles of lake surface, interspersed with a large number of coots and many species of ducks and geese feeding, courting, preening, and resting.

As might be expected, the diving ducks generally oc-
occupied the open, deeper water while the shoal-water, river, or puddle ducks remained along the shores or margins of emergent vegetation. Of the latter group, however, bald-pates were most commonly seen among the diving ducks in open water beyond dabbling depth, apparently subsisting in large part on material floating to the surface as a result of the feeding activities of diving ducks and coots.

Some mallards and pintails also fed in shallow, open water during favorable weather, but the majority of them remained in marginal situations. On Malheur Lake, shovelers were most abundant adjacent to or on flattened bulrush mats surrounding large expanses of open water, while cinnamon and blue-winged teal remained on ponds, sloughs, streams or the semi-open water of Malheur Lake, spending most of the day sunning on banks, muskrat lodges or floating vegetation mats.

Other waterfowl apparently occurring incidentally among migrating canvas-backs were eared grebe, Western grebe, pied-billed grebe (*Podilymbus podiceps podiceps*), white pelican and Farallon cormorant. No visible friction was witnessed between the migrating canvas-backs and other waterfowl.

Although some flights of canvas-backs were observed arriving or departing during the day, most diurnal flight movement was local and consisted of irregular changes in feeding areas individually or in small groups, or of court-
ship flights composed usually of one female and one or more males. Diving ducks, including the canvas-back, did not engage in dawn and dusk flights between resting and feeding areas, as reported by Low (1945) for the redhead in Iowa. Both feeding and resting were accomplished on the open water of the refuge, and migrating canvas-backs avoided water which had much emergent vegetation or which was small in area.

Most of the arrivals and departures took place during the night, producing a variation in the number of individuals present from day to day. Small flocks of three to 12 canvas-backs were occasionally seen heading northeast in direct flight from Malheur Lake during the evening, increasing their altitude upon leaving the lake basin to heights of 200 feet to about 1,000 feet above the ground. On the basis of the direction of their flight these birds probably were en route to more northerly breeding grounds.

A general perusal of the literature containing information on canvas-back migration through the Pacific States discloses the probably route followed by this species. This general route has its southernmost limit in southern Mexico (and Guatemala, rarely) and extends from New Mexico, Arizona and California through Utah, Nevada, western Montana, Idaho, Oregon and Washington into British Columbia and the Prairie Provinces of Canada.

Whether the resident population of canvas-backs at
Malheur was derived principally from the early, intermediate or late migrants was not known. The nesting areas of the Blitzen Valley seemed subject to a steady increase in nesting pairs as migration progressed, but this valley attained its summer "quota" while a large number of migrants still occupied the open water at Malheur and Mud Lakes. Thus, it would seem that the residents tended to be early rather than late arrivals.

The flight speed of canvas-back seemed greater than for most species of ducks, but the record listed by Munson (1930) of at least 72 miles per hour when chased by airplane must be very near its limit. Observations of the progress of flying canvas-backs over measured courses in the Blitzen Valley found their velocity, taking air movement into consideration, to be between 40 and 50 miles per hour in direct flight, averaging about 46 miles per hour. In each of the four instances, the timed individuals were lone, adult males in breeding plumage. In faltering flight over marsh, pond, or lake the velocity was often reduced to an estimated air speed of 30 miles per hour. Aroused from a resting attitude in the water of canals and borrow pit ponds along refuge roads, canvas-backs reached air speeds of slightly more than 35 miles per hour within approximately 100 yards, as measured with an automobile speedometer.

In flight, the canvas-back progressed with rapid, apparently labored wing-beat, extending the long neck and head
forward below the longitudinal axis of the rest of the body. When coming in to alight, the head and neck remained extended forward horizontally, and the rest of the body hunched into a more vertical position. Just before contact was made with the water the legs were extended down and forward with broad, webbed feet spread, and the wings beaten along a more horizontal plane to reduce momentum. The canvas-back then tobogganed into the water against the wind if one was blowing.

Most of the feeding was done from dawn to about ten a.m. and from about three p.m. until darkness, but intermittent feeding was carried on throughout the day and during light, cloudless nights. While feeding, all waterfowl on the lake acted as mutual sentinels. If any showed uneasiness, this unrest was quickly transmitted throughout the group, although the individuals more distant from the disturbance usually were least disturbed, to outward appearances, by it. The omnipresent coot was a factor of consequence in rousing other waterfowl upon the approach of an intruder.

Occasionally golden eagles (*Aquila chrysaetos canadensis*) hovered at altitudes of several thousand feet over feeding and resting ducks. This raptor was quickly noticed and identified, the entire group flushing and milling around in the air in apparent fear, but re-alighting and continuing to feed when the eagle had passed. The ducks appeared to have remarkable perceptive powers, showing no alarm at the
sight of high flying turkey vultures (Cathartes aura sep-
tentronicsis) requiring a binocular for identification by
the observer, but they immediately arose when an eagle flew
over at such heights as to be barely visible to the human
eye.

An estimate of the total number of canvas-backs utilizing
the facilities of Malheur Refuge during migration was sub-
ject to the possibility of a high percentage of error because
of the vastness of the area, the large number of waterfowl
involved, local movements of waterfowl and, most important
of all, the impossibility of determining the period of resi-
dence at the refuge of each migrant. Recording the numbers
of birds seen daily on representative water areas through-
out the migration season appeared to be the best method for
finding the daily influx of canvas-backs at Malheur and
formed the basis of computations in Fig. 11.

Migration records for the three springs agreed in passage
of the main body of canvas-backs during the period March 20
to April 20. In the spring of 1942 only one recognizable
peak occurred on April 9 and 10, numbers of migrants rapidly
increasing from less than one hundred individuals on March 5
to nearly 12,000, then making a rapid but gradual return to
a low resident population after May 1.

The 1946 and 1947 spring migrations were different
from the 1942 spring migration in two main ways: (1) They
were characterized by an earlier "minor peak" and a later
Fig. 11. Estimated spring migration canvas-back populations on the Malheur National Wildlife Refuge, Oregon during 1942, 1946 and 1947.
"major peak"; and (2) the total number of canvas-backs passing through the refuge was markedly reduced. In 1946 the first main wave of migrant canvas-backs passed through the Malheur Refuge on March 28 and the second and largest wave appeared on April 9. In 1947, corresponding waves were observed on March 26 and April 7. The estimated total number of canvas-backs passing northward through the refuge during each of the three years was, respectively, 18,000, 16,000 and 15,500, subject to the latitude of error previously mentioned.

Most late spring migrants during 1942 had left Malheur by April 30, although a few lingered through the first week of May. In 1946 and 1947, the end of migration occurred about one week earlier. Warm weather was correlated with accelerated migration from the refuge, while with cold weather the reverse was true. Consequently, in migrations accompanied by warm weather, passage through an area was rapid and lesser concentrations of waterfowl resulted. During the cold weather, the ducks arriving at the refuge delayed their departure, resulting in gross, non-rhythmic fluctuations of populations.

In his Iowa study of the redhead, Low (1941) reported a correlation between a rise in temperature and departure of migrants. Hochbaum (1944, p. 14) stated that the canvas-back and other ducks usually came to and departed from the Delta Station marshes with a south wind, and that the canvas-
back did not arrive on the Delta Marsh until "... the thaws of mid-April ... brought open water and promise of good weather ahead."

Data presented in Fig. 11 taken at face value could be misleading, for although the bars representing periods of the 1946 migration are consistently longer than corresponding 1947 bars, the total number of migrating canvas-backs was only slightly less in 1947. Apparently the reduction of lake surface and loss of valuable feeding grounds was responsible for the smaller number present during most of the 1947 migration, for water bodies having remained relatively unchanged throughout the study, such as Boca Lake and an isolated bay of Malheur Lake, received increased utilization. The daily population fluctuations on representative bodies of water in 1947, however, indicated a more rapid turn-over in non-resident individuals so that although the number of ducks present at any given time was usually lower than in 1946, the total number of spring migrants was quite similar for the last two years of the study.

Distribution of migrating canvas-backs on the three playas lakes of the refuge appeared to be governed by (1) presence and depth of water, (2) interspersion of emergent hydrophytes and water, (3) species and availability of submergent hydrophytes, (4) size of water body, (5) air movement, (6) temperature, (7) sources of intrusion, and (8) sex of canvas-backs in the air and on the water. The first three
were considered of primary importance, for each was capable of becoming a limiting or excluding factor. The remaining five were of secondary importance in governing canvas-back distribution.

(1) Canvas-backs never were observed to alight on or feed on land, but were witnessed feeding in water too shallow to accommodate their displacement and loafing on land out of water. An example of this type of situation was found at the outlet of Malheur Lake where canvas-backs occasionally were seen walking in water less than two inches deep, apparently feeding on seeds and other drift lying in a semi-floating mass along the margins of the pond. Providing the other extreme of depth of migration water bodies for the refuge, the west side of Boca Lake in Unit 3 was used by migrating canvas-backs and other diving ducks which fed and rested over water depths of 14 feet. The majority of canvas-backs were found on water exceeding two feet in depth.

(2) Interspersion of emergent plants also was instrumental in determining the presence and abundance of migrant canvas-backs. Entirely closed sloughs were completely shunned. If scattered vegetation exceeded about 50 percent of the lake or pond area, it usually was occupied by few or no canvas-backs. Preferred water surfaces usually ranged from lakes and ponds completely free of, or with marginal vegetation, to surfaces less than one fourth vegetated (Fig. 12).
Fig. 12. A shallow, open-water part of Malheur Lake occupied by canvas-back migrants.

(3) The species and availability of plants, principally submergent ones, were limiting factors even in the presence of favorable (1) and (2). Examination of popular migrant resting or feeding areas almost invariably disclosed an abundance of food in the form of sago pondweed and hardstem bulrush achenes on the bottom, or a growth of water milfoil, coontail or muskgrasses. Of the above foods, pondweed beds seemed most sought after.

Although canvas-backs would alight on water largely barren of potential foods, they usually did not remain long before moving on to other sections. This frequently occurred on the relatively barren expanses of saline Harney Lake,
where canvas-back arrivals often settled down far out in the large lake, but soon swam to marginal situations where other individuals of this species were obtaining a meager fare from the slightly less saline, spring-diluted water along the lake shore where a sparse stand of sago pondweed could be found in summer.

In 1942 and 1946, Mud Lake contained excellent stands of pondweed with lesser proportions of water milfoil and coontail accompanying water depths ranging to four feet or possibly slightly more. During and following the dry 1946 season, the lake level rapidly subsided, and by March 1947 Mud Lake's greatest depth probably did not exceed 30 inches and averaged less than 20 inches.

Bottom sampling showed an abundant supply of sago nutlets but apparently the reduced depth lessened utilization of this lake by canvas-backs, for rarely were more than a hundred present on it any single day in 1947, while more than a thousand occupied the lake on some days during the height of the 1942 and 1946 spring migrations. The canvas-backs were replaced, however, by a substantial increase in puddle ducks which favored the shallow water. In 1947, most migrating canvas-backs were seen along the east side of Malheur Lake, and especially east of Cole Island Dike prior to April 12.

(4) The size of water bodies frequented by migrating canvas-backs varied, but none of the smaller ponds or flooded
borrow pits were occupied by many migrant canvas-backs at any time. As already mentioned, the expanses of Malheur Lake and Mud Lake were occupied by the majority of the canvas-backs passing through the refuge, and only the larger ponds of the Blitzen Valley (Fig. 15) and Double-O Ranch Unit seemed to contain non-residents. Ponds having less than ten acres of open water usually were bypassed unless they occurred as part of a larger, nearby system.

(5) and (6) Air movement, or wind, and temperature can be best discussed together. Soft to moderate winds up to eight miles per hour seemed to affect very little the
distribution of canvas-backs, even when the temperatures were below the freezing point. When the winds became stronger, and especially if sustained for several hours in the presence of low temperatures, most canvas-backs present approached the lee situations along marginal plant cover or shore. Calm, warm weather found canvas-backs well-distributed over the lakes, but cold, blustery squalls caused them to raft and later move to protected places among scattered bulrush stands.

(7) Human intrusion was of little apparent significance because of the isolated nature of the refuge. In ponds bordered by roads, such as those at Buena Vista in Unit 8, canvas-backs remained on the sides farthest from these thoroughfares, though they showed little evident apprehension at the approach of a vehicle. Canvas-backs and other ducks would flush quickly at sight of an eagle, but would soon return to the same place when the predator had passed. Coyotes and other mammals received little more than passing attention. Along with eagles, man afoot inspired the greatest amount of apparent distress to canvas-backs.

(8) The sex of canvas-backs on lakes and ponds appeared to be an element influencing the decision of flying individuals to alight or continue flying. Drakes singly or in small groups flying falteringly over water containing canvas-backs often settled near females, and after alighting,
swam toward them to join courting parties or to be repelled by other candidates. When a female arose in courtship flight or merely to leave the area, a number of drakes nearly always followed her, so that lone female canvas-backs in the air were very uncommon.

**Sex ratios**

The unequal sex ratio seen elsewhere among diving ducks was apparent among the spring migrant canvas-backs, as well as among other diving ducks, in southeastern Oregon. During the three seasons, 7,619 canvas-backs were counted and sexed. Counts of the sexes were not made when the less conspicuous females may have escaped notice because of distance, lighting, wind and waves or other visual obstructions. The results of these censuses are found in Table III.

The variation in average ratios for the three canvas-back migration seasons was slight, ranging from 1.42 males to a female in 1942 to 1.63:1 in 1947. These ratios may represent fairly accurate sex proportions of canvas-backs passing through the refuge. The data seem to indicate that a greater proportion of males appeared early in migration followed by a recession of this numerical advantage as the season progressed, perhaps due to the passing of unmated males on to more northern breeding grounds and/or the later arrival of many mated pairs and unmated females at Malheur Refuge.
Table III. Canvas-back Sex Ratios During Spring Migrations of 1942, 1946 and 1947 in Southeastern Oregon

<table>
<thead>
<tr>
<th>Period</th>
<th>1942 Males per female</th>
<th>1942 Number sexed</th>
<th>1946 Males per female</th>
<th>1946 Number sexed</th>
<th>1947 Males per female</th>
<th>1947 Number sexed</th>
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<tbody>
<tr>
<td>March 24-27</td>
<td>2.24</td>
<td>479</td>
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<td></td>
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<tr>
<td>28-31</td>
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<td>2.27</td>
<td>327</td>
<td>1.75</td>
<td>239</td>
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<tr>
<td>April 1-4</td>
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<td>111</td>
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<tr>
<td>5-8</td>
<td>2.14</td>
<td>160</td>
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<td>422</td>
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<td>794</td>
</tr>
<tr>
<td>9-11</td>
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<td>427</td>
<td>1.24</td>
<td>215</td>
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<tr>
<td>12-14</td>
<td>1.52</td>
<td>267</td>
<td>1.32</td>
<td>468</td>
<td>1.39</td>
<td>416</td>
</tr>
<tr>
<td>15-18</td>
<td>1.24</td>
<td>477</td>
<td>1.33</td>
<td>77</td>
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<tr>
<td>19-22</td>
<td>1.71</td>
<td>141</td>
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<td>238</td>
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<tr>
<td>23-26</td>
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<td>231</td>
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<td>99</td>
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<td>2353</td>
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<td>2995</td>
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<tr>
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<td></td>
<td>1.52</td>
<td></td>
<td>1.83</td>
<td></td>
</tr>
</tbody>
</table>

| April 27-30a | 2.26 | 306 | 1.73 | 60 | 1.84 | 91 |
| Totals       | 2120 |     | 2413 |   | 3086 |   |

*aFigures for this period include males on waiting sites.
The figures for April 27-30 again show a marked increase in the proportion of males. These figures presumably were a result of a large number of males, either being seen on waiting sites, or previously having parted company with the female some time after the onset of incubation. Also, many females may have been inspecting nesting cover prior to nesting and were out of sight among the emergent plant cover while the male remained in open water. Since these last numbers do not constitute a true census, they have not been included in the computation of ratios among migrating canvasbacks, and they obviously do not represent the actual ratio of breeding individuals at Malheur. They were included in the table mainly to illustrate an evident, possible source of error in census techniques based only numbers of ducks observed late in migration in the nesting range of a given species.

On the basis of these findings, one would not expect, ordinarily, to find a similar disproportionate number of males late in the migration season on non-nesting areas, but the periodic ratios should show a progression toward numerical equality of sexes. On the Delta marshes, another breeding canvas-back habitat, Hochbaum (1944, p. 14) found "The first small vanguard of Canvasbacks to reach Delta are paired birds, while the wave of migrants which follows consists largely of unpaired groups." Limited observations by refuge personnel during the early part of March at Malheur
are not in agreement with this statement, for they found that the first groups to arrive contained about three times as many males as females and less than ten per cent were paired.

As the migration season advanced the proportion of paired to unpaired individuals increased through April 26 (Table IV). Following this date paired females became less conspicuous and males on waiting sites gave indications of a much lower percentage of paired individuals than actually existed, as shown during the April 27-30 period in the table. Fig. 14 presents a record of progressive increase and sharp terminal drop in the proportion of paired to unpaired canvas-backs on the Malheur Refuge throughout the observed portion of the migration period (March 24 through April 30) during the three years of study. As shown in the figure, nearly 70 per cent of the migrant canvas-backs during the peak of migration at Malheur Refuge were paired.

Of 95 adult canvas-backs banded during the spring and fall migrations from 1935 to 1945, inclusive, 65 males and 30 females were captured, yielding a male:female ratio of 2.17:1. This ratio was least disproportionate during the years following 1940. Of interest was the fact that among nine banding returns from recovered birds shown in a later table (Table XXXI), six were males and three were females, approximating the male:female ratio of the 95 banded canvas-backs, giving slight evidence of non-selective mortality of sexes through hunting.
Table IV. Relation of Canvas-back Pairing to Advancement of the Spring Migration Season in Southeastern Oregon

<table>
<thead>
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<th>Period</th>
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<th>1946</th>
<th>1947</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>Total %</td>
<td>Total %</td>
<td>Total %</td>
</tr>
<tr>
<td></td>
<td>Counted Paired</td>
<td>Counted Paired</td>
<td>Counted Paired</td>
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<tr>
<td>March 24-27</td>
<td></td>
<td></td>
<td>479</td>
</tr>
<tr>
<td>28-31</td>
<td>327</td>
<td>48</td>
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<td>April 1-4</td>
<td>111</td>
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<td>9-11</td>
<td>427</td>
<td>67</td>
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<tr>
<td>12-14</td>
<td>267</td>
<td>70</td>
<td>468</td>
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<td>15-18</td>
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<td>221</td>
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</tr>
<tr>
<td>27-30</td>
<td>306</td>
<td>59</td>
<td>60</td>
</tr>
</tbody>
</table>

85
Fig. 14. Pairing progress among spring migrant canvas-backs on Malheur Refuge, Oregon during 1942, 1946 and 1947

Among records of canvas-back sex ratios in the literature, the following data from other regions are given for comparative purposes. McIlhenny (1934), during 22 years of banding at Avery Island, Louisiana, found a ratio of 4.5 males to each female. The same author (1940) later reported a lower ratio of 1.74:1. Both records were taken from canvas-backs captured in banding traps. In Iowa Low (1941) found a male:female ratio of 2.04:1 among 800 canvas-backs
seen during 1938, 1939 and 1940.

Erickson (1943) reported a sex ratio of migrating canvasbacks in Minnesota during March 26 to April 17, 1938 to 1940, of 2.05:1, and during the period of March 18 to May 15 of the same three years, a ratio of 1.26:1. The count on which these ratios were based involved only 147 individuals, but the ratios agree well with the findings at Malheur. Because very few canvas-backs remained to nest in Minnesota, it may be expected that few conspicuous males attending nesting females would be present to increase the numerical inequality of the sexes with the onset of nesting in April and May. Erickson's overall ratio averaged 1.77:1.

At the Delta Station in Manitoba, Hochbaum (1944) found at least two drakes for each female canvas-back during the four years 1939 to 1942. For southeastern Washington, Beer (1945) reported sex ratios of 1.96:1, 2.61:1 and 1.30:1 for January, February and March, respectively. Like Erickson's (1943) findings, these ratios show a large, early-season disparity between sexes of the canvas-backs, indicating that the early migrants were mostly males. In the same report, Beer (1945, p. 122) "... found that the ratio was more unbalanced in large flocks than in smaller groups" and was the "... most unbalanced of any of the common ducks in this area."
Courtship and mating

Among the canvas-backs arriving on the Malheur Refuge during the spring migration, some already were paired. The proportion of paired to unpaired individuals increased with the advance of the season among migrating as well as resident canvas-backs. Preliminary courtship apparently began on the wintering grounds and was well advanced among some of the ducks during their northward flight through Oregon. Hochbaum (1944, p. 19) noted captive canvas-backs going through one courting posture after another in non-competitive manner in autumn.

On bright sunny days in late September and early October, after adult drakes have donned their new breeding dress, displays of captive Redhead and Canvasback males in the Delta pens are almost as frequent as during the spring courtship period. Hochbaum continued (1944, p. 20) "These occasional actions apparently are not related to the development of the gonads, as they may occur at any time during the period of sexual inactivity."

These so-called "courtship displays" apparently do not merit such designation, for neither the stimuli nor the results of true courtship exist. These attitudes seem to be nothing more than nervous responses to non-sexual stimuli, for certain postures associated with spring and summer courtship among adult canvas-backs were noted among unattended juveniles one-third grown, the latter showing apparent
anxiety when approached too closely. They exhibited the
*neck-stretch* shown in Fig. 33c.

Competitive courtship among canvas-backs on Cayuga
Lake, New York was witnessed during the latter part of
February and early March by Allen (1931). Hochbaum (1944,
p. 22) reported that J. Donald Smith, in unpublished manu-
script, saw on Lake Christina, Minnesota

"... no pairs among the earliest arrivals dur-
ing the first week of April, 1942. By April 9,
however, approximately 10 per cent of the popula-
tion on this lake was paired, and by April 16
paired birds made up 65 per cent of the migrant
gatherings."

It is assumed that such matings were preceded by true com-
petitive courtship.

In his chapter on courtship, Hochbaum (1944) presented
his observations and description on this phase of the life
history of the canvas-back in considerable detail, with
numerous notes on the activity of captive birds. It is not
deemed necessary to repeat many of these observations, but
the following discussion involves descriptions of court-
ship activities observed in Oregon which either differed
from Hochbaum's findings or suggested other interpretations.

Hochbaum (1944, pp. 23-24) describes four attitudes or
poses exhibited by courting canvas-back drakes. They are:
(1) the "head-throw" in which the head is thrown sharply
backward until the crown touches the back and then is re-
turned to the usual erect position; (2) the "neck-stretch"
in which the head is raised to a lofty position with the tip of bill elevated; (3) the "sneak" posture in which head and neck are extended anteriorly on or above the water; and (4) the "threat" position with head held low in the position of a "crouch." The courting maneuvers of sexually active females were reported to be limited to the neck-stretch display. At Malheur Refuge, female canvas-backs frequently assumed the threat posture just before driving off drakes in courting parties. This attitude appeared to be one of intimidation with both males and females. The courting of all canvas-backs, however, followed closely the general pattern described by Hochbaum.

The voice of the courting canvas-back has been described by Bent (1923), Phillips (1923), Allen (1931), Hochbaum (1944) and many others. Bent (1923, p. 190), from notes furnished by Dr. Arthur A. Allen, described an ick, ick, (pause) cooo sound uttered by the drakes. With the first two notes,

... the back of the neck swells and the feathers rise as though a gulp of air were being swallowed. Immediately, however, it seems as though exhalation occurred with the bill closed, accompanied by a low cooo like a muffled bark or distant moo of a cow and not so very different from the ordinary grunting note of the male bird when alarmed. Accompanying this note the chin swells out for an instant with a curious swelling about the size of an ordinary marble.

Very frequently this note was accompanied by the head-throwing performance ... the ick, ick notes being given when the head was thrown back, and the cooo when the head was brought forward again,
the swelling on the chin being noticeable as the head assumed the normal position. This head-throwing performance was practically the same as has been described by Doctor Townsend for the golden-eye and has been observed by me frequently while watching redheads and scaup ducks as well.

The calls of the males were answered by the females with a low, guttural cuk cuk . . . males then began swimming . . . sometimes with their heads close to the water after the fashion of the mallards, sometimes calling as already described, and frequently jerking their heads so that the occiput struck the back. Occasionally one of the males would approach a little closer to the females and then one of the females would lower her head and chase him away . . .

The cu-cu note has been further described by Hochbaum (1944) as being cu-coj a sort of "split-note." The present writer found it to be a tri-syllabic uh-yoo'-uh, requiring about one-half second to complete, the first two utterances made with rising inflection, and the last, an extremely soft, muffled murmur. The entire expression was similar to the distant mooing of a cow mentioned above by Allen, or resembled a sound which might be obtained by pressing and pushing a moistened finger across a windowpane.

In producing the notes, the male dropped his head and bill down and slightly rearward from one to three inches, the vocal pouch filling. The sound was common among actively courting males, and often was produced in apparent anxiety by paired males when the female seemed reluctant to flush at the approach of an observer. A slightly similar, cat-like me-yoo was frequently emitted by paired drake redheads feeding with the captive trumpeter swans in a small
pond when the enclosure was approached.

Two other vocal utterances by captive canvas-back drakes were heard. A lead-poisoned drake in April, 1942, when approached produced a wheezing note very similar to the three-syllable courting note but threw head and upper neck farther forward as the last syllable was heard. This seemed to be a fear reaction or intimidation response, for if the hand were extended toward the bird, the drake responded with a quick nip.

Another drake during his period of eclipse in the fall of 1947, produced only a low, wheezy, growling note whenever disturbed. It showed none of the pugnacity of the breeding-plumaged, lead-poisoned drake, but did adopt another posture out of water which combined the attitudes of the threat and sneak, and appeared to be an instinctive, fear-inspired reaction. In this stance, the body was inclined toward a more upright position with the head and neck fully extended forward and upward at an angle somewhat less than 45 degrees above the horizontal, while both feet were planted well apart.

The cuk cuk sound of courting female canvas-backs reported by Allen (Bent, 1923) was not heard in the present study. The only voice by this sex was a low, reedy, hoarse whaaa aaaa aaaa, never in courtship associations, but often uttered by females making a return flight over the nest after having been flushed while incubating.
The elements of a courting party were a sexually aroused female and two or more attendant males. The female was always the focus of excitement. Most actions originated by the female received nearly identical response from the courting drakes. In an active courting party, males ranged from one to more than 20 and averaged 6.37 males to each female.

During the competitive courting females at first made permanent selection of no single male, but appeared to encourage the attentions of certain candidates while resisting the advances of others. Shortly this situation would change and females accepted the company of another male. None of these temporary partnerships terminated in copulation in the immediate presence of the courting group, although the drakes frequently approached the female laterally or from behind. Never were females seen diving to escape courtship pursuit, although they often fed intermittently under the water surface while engaged in courting. Upon its reappearance among the attending drakes, the female often offered the neck-stretch which almost simultaneously was returned by the drakes.

The following field note dated April 16, 1947 described the activities of a courting party seen on the north side of Malheur Lake during the height of migration. The water was over four feet in depth and a luxuriant growth of sago pondweed flourished on this area later in the season.
A courting party of one female and seven male canvas-backs was constantly moving about among a large assortment of other ducks and coots, the drakes deployed in an irregular ellipse about the female. Driving first at one, then another, the female showed little apparent discrimination in these attacks. The drakes also chased each other, then quickly returned to attend the female, indulging in the neck-stretch and head-throw. After each rush at a nearby male, or upon return to the surface after a feeding dive, the female quickly made the neck-stretch, and some of the males responded.

Three other males abandoned a female to approach the courting group, but did not take an active part in the courting. Their interest seemed to wane for they soon returned to their female and fed and preened. The courting progressed in the first group while they swam aimlessly for more than 700 yards. Toward the end of the incident, the female ceased courting, preened for a few minutes, then rested with head lying on back among the scapulars. The males also preened, fed and rested nearby.

Courting often became very ardent, the males closing in about the female which dodged their attempts to cover, lunged away, ran on the water or even took to the air with the drakes in close pursuit. In flight, the female usually led, and the males flew in no uniform deployment, but would alternately approach the female from behind, nip gently at its tail and flanks, then fall back as others gained a position advantage. Other than the rush of wind through the pinions, no sound was heard from the female during these flights. Alighting again on the water, courting or feeding, resting and preening was resumed.

The type of habitat most frequently occupied by mated, courting canvas-backs not yet nesting contained an increased
proportion of vegetation to open water, compared with areas previously occupied by migrating birds. A food supply was a primary requirement, for mated pairs spent the entire day and night in the same locality prior to nesting and did not leave to feed. In the Blitzen Valley, semi-open ponds containing scattered stands of hardstem bulrush (Fig. 15) were most likely to contain courting and mated resident pairs, for all valley ponds with bulrush had moderate depths of water favorable to the growth of submergent vegetation used as food by canvas-backs.

During late March and the first half of April, courting was common during all hours of daylight, but greatest activity was observed between eight a.m. and ten p.m. Cold, blustery squalls resulted in temporary cessation of courting, although the courting parties usually remained intact and apart from the other ducks present. With the return of calm, warmer conditions, courting was resumed with increased intensity. When warm, fair weather dominated during late April, May, and early June, the greatest activity among courting parties occurred from seven a.m. to ten a.m. and from three p.m. to six p.m. The five-hour mid-day period was devoted principally to preening and resting with sporadic courting. Feeding, however, was carried on intermittently throughout the hours of intense courtship.

A temporary type pond located near the Blitzen Canal in Unit 8 was populated with many canvas-backs during the
height of the nesting season from May 15 to June 15 just after the peak of nest inceptions each year. The pond had a labyrinth of meandering channels margined by Baltic rush (*Juncus balticus*) and contained a thrifty growth of sago pondweed (Fig. 16).

These birds were predominantly drakes which had abandoned incubating mates, while a smaller number of scattered pairs were usually present. The number of pairs dwindled with the increase of single males. The great number of canvas-backs counted on a single visit was 31 single males, one single female (nesting), and six pairs for a total of 44 canvas-backs on May 30, 1946. After the middle of June,
the drakes rapidly disappeared, and none was seen again during the season on this pond after June 22.

Any unattached female canvas-back was repeatedly accosted by courting males. When the female was receptive to the advances of the males, a courting party resulted. When the female did not return the neck-stretch or exhibit other interest in the actions of the drakes, they soon moved to other females or courting groups. In this way, sexually active females were assured of male attendance.

Prior to and following the establishment of more permanent pairing bonds copulation among canvas-backs was occasionally seen, mainly between the hours of eight a.m. and
four p.m. The earliest date on which this act was seen was April 1, but it probably occurred during migration to the area from the wintering grounds. On the above date, a female canvas-back which had been courted by 15 drakes finally began to exhibit apparent favor toward one. Receiving this encouragement, the drake immediately became very pugnacious towards the other males, assuming the threat posture and driving in short dashes at the nearest of them. The female joined in these attacks.

Soon the two began to drift away from the group, indulging in the neck-stretch as they went. When slightly over ten yards distant from the other drakes, the female prostrated itself in the oestral position, sinking until only bill, crown and a small part of the back were visible. The drake immediately covered the female, grasping the occipital feathers in its bill, the female sinking out of sight, though in some instances the female's head remained above water. The male remained astride for about 10 seconds and then dismounted as the female bobbed to the surface.

Immediately thereafter, both ducks engaged in vigorous preening, washing themselves by quickly immersing the head, neck and foreparts of the body, then rising in the water and flapping the wings as the water ran down the back. Soon the drake abandoned its erstwhile partner to join another courting group of one female and five males, while the female continued to wash and preen, later joining a mixed
group of canvas-backs.

When the female finally accepted a mate for the season, both individuals underwent a change in habits. The male became very aggressive and possessive, refusing to permit other drakes or female canvas-backs to approach them. The male always remained between the female and any source of danger or intrusion, and would battle any number of its species in short or more sustained drives across the water, returning immediately thereafter to swim closely alongside the mate. At times the female joined in driving off other males, and in other instances seemed completely oblivious of the drake's efforts.

On three occasions in 1946, two pairs of canvas-backs were seen to exchange mates temporarily. The following description of one such exchange was fundamentally similar to the other two incidents. Three mated pairs of canvas-backs were seen in a pond of the Blitzen Valley. Two pairs began to converge, the two males continuing to advance toward each other in the threat posture, while the females remained aloof. As if by mutual consent, the drakes compromised and exchanged partners, approaching the temporary mates in threat attitude. The newly formed "pairs" swam aimlessly for about ten minutes, the females resting, but swimming away with head on back when the strange male attempted copulation. Then the males again, as if by additional agreement, returned to their original mates. A similar exchange
by the same ducks was made five minutes later.

A mated drake usually was the victor in most tussles with intruder males or females, but a few exceptions were noted. In one instance, two mated pairs were resting in a pond of Unit 8 when another drake suddenly appeared from among some bulrush clumps. Swiftly it swam between the pairs, chasing first one and then the other male to a distance of about 20 yards. Both females appeared willing to accept its company and to repudiate their previous associates.

While the interloper was swimming with one of the females, the female's mate drove headlong into the neck of the intruder and a vigorous tussle ensued, each endeavoring to peck and tread, or otherwise submerge, the other. In about 15 seconds, the original mate made a hasty retreat. The interloper than resumed its position with the female for several minutes. When the intruder finally swam back among the bulrush clumps, the original mate returned to the female. No explanation could be found for this intrusion and subsequent departure of the aggressive drake. In another instance, however, an intruding male exhibiting the neck-stretch and head-throw was driven away by the combined efforts of two canvas-back pairs. In even the most vigorous battles, the greatest apparent physical damage to any participant was the loss of a few feathers.

Visible friction was not limited to intraspecific en-
gagements, but involved other species of ducks as well. In an encounter of a mated drake canvas-back with the female of a pair of redheads which had lingered nearby, the canvas-back drake drove at the female redhead and chased it for about 15 yards, then returned to the mate.

In flight, mated pairs would nearly always fly with the male following the female while unmated canvas-backs in the formation did not adhere so strictly to this practice. When a mated pair of canvas-backs flushed, the male almost invariably waited until the female began to patter across the water, then promptly followed (Fig. 17).

Fig. 17. Canvas-back pair flushing on Malheur Lake, female leading.

Sometime the female seemed to exhibit greater curiosity or concern than its mate and would not flush until the ob-
server approached to within 50 yards or even less. The male showed great apparent anxiety at the delayed departure, swimming nervously around the female, and often lunging with open bill, grasping the female's flank feathers, tail or back. On only three occasions were males seen to flush before their female mates.

When a pair was attended by another male or female, either of the single ducks flushed first, followed by the mated female, and finally, by the mated drake. Among the Anatinae, the females usually flushed first, but confusion often resulted when the females failed to flush with the males. The latter would then re-alight and wait again to flush with their mates. This uncoordinated flushing was seen rarely among canvas-backs. In one instance, a redhead female flushed, accompanied by a canvas-back. Apparently quickly noting the error, the drake returned to his mate on the water and they flushed together.

The Nesting Period

The time elapsing between appearance of a mated pair on a pond and subsequent nesting varied from less than a week to nearly two months. During this time both members were seen daily feeding, resting or courting in a limited part of the pond or lake. When the water became choppy in heavy winds, they often climbed out of water and rested on
bulrush mats, low islets or other prominences barely above the waves. The sight of pairs in definite locations from day to day not only expedited an accurate census of resident breeding pairs but was a very important clue to the location of nests. Later, when the solitary male was seen, the female was believed to be engaged in nesting activities nearby, and a systematic search of the vegetation often disclosed a nest.

**The nesting season**

On the basis of information obtained from observing nests during the three years of the study, durations of the nesting seasons, including the period between laying of the first canvas-back egg in the first known nest to hatching of the last duckling in the last nest, were respectively, 117 days, 94 days and 74 days. The extreme dates embracing the nesting seasons each year were April 10 to August 4, 1942, April 6 to July 8, 1946 and April 20 to July 2, 1947.

The egg-laying period of observed nests during each of the three years was as follows: April 10 to July 15, 1942, a period of 97 days; April 6 to June 15, 1946, or 71 days; and April 20 to June 9, 1947, or 51 days. The hatching period of observed nests during each of the three years was July 8 to August 5, 1942, or 29 days; May 24 to July 8, 1946, or 46 days; and May 24 to July 2, 1947, or 40 days.
The above periods of nesting, including egg-laying, incubation and hatching, attained greater significance and accuracy when supplemented by field observations on canvas-back broods. In order to obtain the earliest and latest estimated dates of hatching, the earliest and latest hatched broods were noted in the field. By subtracting the approximate age, in days, of the brood approximate dates of hatching were obtained. On the basis of these field observations, the nesting periods of the canvas-back were, respectively, for the three years: entire nesting season, 118, 132 and 86 days; egg-laying season, 98, 99 and 86 days; and egg-hatching season, 61, 97 and 52 days.

Dates of egg-laying for the three nesting seasons, based on both nest and brood observations were April 10 to July 15, 1942, March 22 to June 28, 1946 and April 20 to June 11, 1947. Dates of hatching for each season were June 5 to August 5, 1942, April 26 to July 31, 1946 and May 24 to July 14, 1947. Total nesting seasons for each year were from April 10 to August 5, 1942, March 22 to July 31, 1946 and April 20 to July 14, 1947.

Resident populations

Compared with the number of canvas-backs which annually passed through Malheur National Wildlife Refuge and other parts of southeastern Oregon, the number remaining to nest was small. In 1942 an estimated 18,000 canvas-backs occupied
the refuge at some time during the spring migration. Of this number only 460 paired canvas-backs and 104 additional drakes, just 3.13 per cent of the total spring migrants, remained on the refuge as potential breeders, the rest presumably moving to more northern breeding grounds.

In 1946 and 1947, although the total numbers occupying the refuge during spring migration showed decreases of only 2,000 and 2,500 canvas-backs, respectively, from the 1942 figure, the breeding populations exhibited proportionately greater declines. The 1946 resident breeding population was estimated to be 128 pairs with 52 surplus drakes (1.9 per cent of the migrants), and in 1947 only 97 pairs and 42 extra drakes (1.5 per cent of the migrants) remained on the refuge.

The above population figures were derived from frequent inventories of waterfowl throughout the refuge lakes, ponds and marshes. Canvas-back pairs were daily observed and records kept of their exact location. The pairs remained quite apart from other canvas-backs as the time approached for the female to nest. Consequently, nesting canvas-backs were widely dispersed over the refuge, and locational identity of the pairs was facilitated.

In view of the predisposition of mated canvas-backs to occupy semi-open ponds near prospective nesting cover prior to the onset of nesting, together with the sparse population, estimates of resident pairs were believed to have been quite
accurate. The motility and gregariousness of the "super-
numerary" drakes, however, rendered estimates of their numbers
subject to greater error. These estimates were further
complicated by the difficulty or impossibility of distinguish-
ing between previously mated drakes and non-breeding ones
later in the season. Canvas-back population estimates for
Malheur Refuge administrative units, together with numbers
of nests found per unit, during 1942, 1946 and 1947 have
been listed in Table V.

The decrease in number of migrant canvas-backs using
the refuge during successive years of the study apparently
reflected the general continental decline in most species
of diving ducks. It does not follow, however, that the
numbers of canvas-backs remaining to nest corresponded with
the continental numerical status. Breeding populations de-
clined each year on the refuge and adjacent areas as a whole,
but this reduction was not proportional for all parts of
the refuge (Table V).

Units 1, 2, 5, 6 and Harney Lake can be eliminated from
consideration of these changes since they were not occupied
by breeding canvas-backs during the investigation. Exclud-
ing the Malheur Lake (Unit 12) figures from the refuge popu-
lations during the three years gives censuses of 170, 188
and 199 individuals for 1942, 1946 and 1947, a range of only
29 canvas-backs. In the same three years, the Malheur Lake
populations were estimated to be 394, 120 and 37 individuals,
Table V. Distribution of Adult Canvas-backs and Location of Discovered Nests on Malheur Refuge during the Nesting Seasons of 1942, 1946 and 1947.

<table>
<thead>
<tr>
<th>Unit of Refuge</th>
<th>1942 Nests</th>
<th>1946 Nests</th>
<th>1947 Nests</th>
<th>Pairs found</th>
<th>Pairs found</th>
<th>Pairs found</th>
<th>Tot. Refuge Can. Pop. incl. unmated drakes</th>
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a range of 357 canvas-backs. These figures demonstrate that while the populations advanced in other parts of the refuge during each succeeding year of the study, the number of residents on Malheur Lake showed a tremendous decline. Thus, the reduced lake population was principally responsible for the overall reduction in the Malheur Refuge breeding population during the last two years of the study, and the residential numbers in the ponds and marshes of the Blitzen Valley (Units 1 through 11) increased slightly during the two last nesting seasons.

Because the canvas-back population increased steadily in the Blitzen Valley during the three years while the numbers on Malheur Lake dropped critically, environmental influences were analyzed for reasons bringing about this disproportionate habitat occupancy. The greatest change in populations occurred on Malheur Lake, and therefore it was believed that the habitat changes in Malheur Lake could have been important considerations.

Subsidence of Malheur Lake levels has been discussed in the description of the research area, presented in Table I and graphically demonstrated in Fig. 7. As shown in the figure, during the May and June height of the nesting season, lake levels averaged about 1.3 feet lower in 1946 than in 1942, and about 1.1 feet lower in 1947 than in 1946, a total of 2.4 feet difference between the 1942 and 1947 nesting season levels. The figure further shows a
decrease in lake area from the May-June, 1942 average of 62,000 acres to 38,000 acres in May-June, 1947, a total reduction of 24,000 acres or 39 per cent of the lake surface.

As the water-surface area curve in Fig. 7 demonstrates, when water levels are reduced to less than 4092.50 feet above sea level only bulrush remains as nesting cover over water on Malheur Lake and all shallower-growing vegetation is out of water. The substantial stands of bulrush which were the principal nesting cover of canvas-backs in 1942 on Malheur Lake were in undesirably shallow water during the last two years of the study. In this way, only a reduced part of the total lake vegetation, the sparse bulrush-open water areas of 1942, remained in suitable depths of water in 1946, and in 1947 water became very shallow even in the deeper parts of Malheur Lake.

The water levels existing in April seemed to be the main factor determining the number of migrant canvas-backs remaining on any given breeding habitat. The high levels of 1942 on Malheur Lake entertained the greatest number of nesting canvas-backs, while the successively lower levels of 1946-7 showed parallel losses in population numbers. The major ponds of the Blitzen Valley, which fluctuated little during the three years, also showed less fluctuations in breeding populations. Correlation of proportionately larger, local populations with an earlier supply
of water was evident in some of the temporary ponds of the Blitzen Valley, adding further support to the idea that early water conditions largely determined the number of canvas-backs which would remain as potential breeding birds.

The Blitzen Valley (Units 1 through 11) contained totals of 67 canvas-back pairs in 1942, 83 in 1946 and 82 pairs in 1947. Although this numerical variation may not be important, the number of paired resident canvas-backs increased in the last years in spite of reduced water acreages in the valley. A movement of Malheur Lake erstwhile residents, in the face of lowering water levels, to the stabilized valley ponds with the onset of nesting might explain these population increases. This belief was further supported by observation of a more constant breeding population of canvas-backs in nesting habitat of Malheur Lake during the 1942 nesting season, while in 1946 and 1947, post-migration canvas-back populations dwindled to a scattered few after the beginning of nesting season during May, while the valley resident populations, coincidentally, gained slightly, but in lower proportion.

Nestling associates

Inasmuch as the canvas-back occupied a variety of habitat ranging from the semi-open water of Malheur Lake in feeding and loafing, to land-nesting situations on Cole Island Dike and river banks, pond margins and in marshes
of the Blitzen Valley, it was not surprising that this breeding habitat was shared with an ample variety of associating species of birds. Rarely did nesting canvas-backs show evident disharmony with other waterfowl. Although evidence of strife between canvas-backs and certain ducks, notably redheads, was observed during the courtship phase of their life history at Malheur, this interspecific belligerence was not apparent among nesting canvas-backs, except during parasitic intrusion at the nest.

The following species of waterfowl occupied habitat used by the canvas-back during the nesting seasons of 1942, 1946 and 1947: Western grebe, pied-billed grebe, white pelican, Farallon cormorant, Treganza's heron, American egret (Casmerodius albus egretta), Brewster's egret (Egretta thula brewsteri), black-crowned night heron (Nycticorax nycticorax hoactli), American bittern (Botaurus lentiginosus), Western least bittern, white-faced glossy ibis (Plegadis guarauna), whistling swan, common Canada goose, common mallard, gadwall, baldpate, American pintail, green-winged teal, blue-winged teal, cinnamon teal, shoveller, wood duck, redhead, ring-necked duck, lesser scaup duck, buffle-head, ruddy duck, American merganser, marsh hawk (Circus hudsonius), sandhill crane, Virginia rail (Rallus limicola limicola), sora rail (Porzana carolina), American coot, long-billed curlew, Western willet, avocet, black-necked stilt, Wilson's phalarope, Franklin's gull (Larus franklini), California
gull, ring-billed gull (*L. delawarensis*), Forster's tern (*Sterna forsteri*), Caspian tern, black tern (*Chlidonias magra surinamensis*), short-eared owl (*Asio flammeus flammeus*), Western marsh wren, Western yellow-throat (*Geothlypis trichas occidentalis*), yellow-headed blackbird (*Xanthocephalus xanthocephalus*) and Nevada red-wing.

All of the preceding birds, with the exception of buffleheads and ring-necked ducks occurring as late migrants, regularly nested on Malheur Refuge.

**Behavior during nesting**

With the approach of nesting among mated pairs, gregariousness and competitive courting were supplanted by tendencies toward isolation or at least modified to association with other pairs of canvas-backs and non-displaying individuals. This has been termed the period of nuptial courtship by Hochbaum (1944). He believed nuptial courtship achieved mutual stimulation and served as a challenge to intruders. At this stage of courtship the drake offered only the neck-stretch to its mate although the other displays were given to intruders.

In the more secluded nesting areas, canvas-backs spent a large share of the day alternately feeding, preening and resting, and frequently did not indulge in courting procedures, except when approached by others. In resting, the partners floated side by side or a few feet distant, head
thrown on back and facing any wind strong enough to cause wave action. When one member of the pair fed while the other rested, the resting member followed the feeding individual with occasional swimming strokes while its head remained on its back, eyes closing sleepily a few seconds, then opening briefly. When surprised by an intruder while resting out of water on blustery days, canvas-backs promptly entered the water to swim away or to flush.

While the female was attending the nest, the male remained on open or semi-open water in the vicinity. On Malheur Lake and in the larger ponds of the valley, drakes usually remained in the open water near the nest, but mates of females nesting in a semi-closed marsh or small ponds frequently co-occupied common waiting sites. One quarter-acre pond in a meadow adjacent to the large Buena Vista pond consistently contained nine drakes during part of one season, while in the large nesting pond nearby only two drakes were seen. Approximately nine female canvas-backs were nesting in the large pond, most of them laying eggs or incubating, and presumably still attended by the drake. The two drakes occupying the nesting pond usually remained within two hundred yards of their respective nesting mates, while mates of some drakes residing on the small pond were over 600 yards distant.

The mates of the two drakes on the nesting pond joined them from time to time during the day on the drakes' waiting
areas. Drakes on the small waiting pond occasionally flushed, flew to the nesting pond and alighted. The female usually joined the mate shortly thereafter. Other females were seen leaving the nest and flying to the waiting pond. When a female arrived a drake always detached itself from the others and immediately joined the female. The remaining males seemed to withdraw to one side, leaving about half of the pond to the pair. When any of the drakes strayed toward the part of the pond occupied by the pair, the mated drake immediately went through the neck-stretch maneuver in approaching the intruder and would drive it back toward the other drakes.

This display of intolerance should not be confused with "defense" of "territory" for the aggressiveness of the drake was obviously conditioned by stimulation of the mate's presence. Prior to the female's arrival the male had been, to all outward appearances, merely one of a number of drakes at a waiting site. After the female appeared, the drake established a sphere of intolerance in the small pond and threatened other drakes which attempted to approach them. When the female returned to the nest, the male attached itself to the group of waiting drakes, showing none of the previous intolerance. Upon the arrival of another female from the nesting pond, another waiting drake went through the same aggressive action, while the previously intolerant drake was crowded to one side with the other drakes. In this
way, the same general area was successively occupied by each of the pairs. The size of the occupied area was not static but seemed to vary with the female’s location in the waiting pond. In each case, the dominance of the male disappeared upon the departure of its mate, the other males soon spreading out uniformly over the surface of the waiting site pond.

In only one instance were two pairs seen on the small pond at the same time. However, the second pair flushed before the drake of the first pair became aggressive. Frequent observations of the nesting activities and intolerances of shoal-water ducks, principally of cinnamon teal, shovellers, mallards and gadwalls at waiting sites, revealed an antagonism based on maintenance of the isolation of the female from intraspecific intrusion during the early part of the nesting period. Unless each analysis of aggressiveness of males at waiting sites takes into account both antecedent events and succeeding action accompanying such acts, interpretation of momentary observations of aggressiveness of “territorial” drakes may stray far from the truth.

From the foregoing, together with other supplementary evidence collected during the study, it was evident that existing views on "territoriality" among waterfowl do not apply to canvas-backs or certain other waterfowl at Malheur. Instead, the frank skepticism expressed by Provost (1947, p. 103) in his interpretation of the "... so-called 'de-
fence' . . . behavior as simple intolerance or aggressiveness manifested under the conditioning influence of a physiological state" is favored.

Males at waiting sites were good indicators of the presence of nesting females in the vicinity. When the nest was approached, the male occasionally flushed and flew over the nesting cover, further advertising the location of the nesting mate. The females then often swam from the nest, flushed and joined the male in the air. In addition to the use of the waiting site as a place for the female to feed, rest and associate with the male while off the nest, it also provided a sentry post with better visibility than was possible within the vegetation at the nests. The waiting site was selected by the male following choice of a nesting site by the female. When the waiting sites were drastically altered through changes in water levels or enclosure by marginal submersent vegetation, the drakes moved to other sites where the females joined them during resting periods.

The length of time that the male remained with the mate after nest construction appeared to have been influenced by the length of time required to complete the clutch. With the onset of incubation, the male and female were seen together on the waiting site or in the vicinity of the nest, but sexual union was not witnessed after incubation had commenced, though the male was seen perfunctorily and un-
successfully attempting coition with the unresponsive mate.

Usually within a week after the female began to incubate, the male no longer remained at a regular waiting site, though it still may have frequented the same general area. Meanwhile, the female spent more time on the nest, and during nesting or feeding periods, associated less with the drake. One drake, believed to have been the mate of a female nesting in a small, shallow pond, remained in the vicinity until about a week before the eggs hatched, sometimes accompanied by another drake. Most drakes, however, abandoned their mates' nesting areas within seven to ten days after the onset of incubation. Females abandoned by mates after the onset of incubation were not known to have renested after the incubated nest proved unsuccessful. Thus, the female's reproductive potential for the season diminished as the female's attraction for the male waned.

Nest site selection. Prior to the time of nesting the female spent several parts of each day moving among emergent plant cover while the male remained in the loafing or feeding area. This prenesting reconnaissance was also accomplished in flight when the pair flew falteringly over potential nesting cover. Occasionally the female dropped down among the vegetation of marshes and the male either followed or else flew to nearby open water. To all appearances, the male took no active part in selection of the nesting site, although the proximity of the waiting site may have been a
factor in the final choice by the female. Although the exact time of any nest site selection was not observed, inspection of plant cover by potential nesting females occurred during most hours of the day with a decrease in this activity during midday.

There is much difficulty in trying to generalize on the type of nesting situations preferred by female canvasbacks, for the nests were found in most types of emergent vegetation and water depths. One was found on land several feet from water in 1942. Judging from successive utilization of certain cover during each year of the study it seemed evident that either a large proportion of the females may have been previous occupants of a given nesting area and had returned to the former nest location, or that recognition of a suitable nesting situation was a faculty enjoyed by most females of the species.

The oft-quoted example of Lincoln's (1934) barnyard-nesting mallard gives some support to the idea of animal successive utilization of a nesting site, and other evidence in the literature indicates that such a habit may exist. Among terrestrial nesting species on Cole Island Dike in Unit 12, the placement of nests in 1947 seemed to follow only a random pattern in relation to the location of nests during the preceding year. In a large pond of Unit 8 during 1947, nests were built within 20 yards of 1942 nest locations, but considering the rapid turnover of duck popula-
tions indicated by banding studies, that more than a very few 1942 refuge nesting canvas-back females survived to nest in the same area in 1947, five years later, seems unlikely.

The hypothesis that the females have a common ability to recognize suitable nesting sites seems to offer a more logical explanation for continued nesting occupancy of restricted areas by canvas-back females throughout the years when habitat remains relatively unchanged. Termination of the use of a nesting habitat by canvas-backs when conditions within the habitat were altered provides additional support for this belief.

The most important considerations in vegetative cover utilization were presence of water and interspersion of cover and water. Pure bulrush together with mixed communities of bulrush-cat-tail, bulrush-bur-reed and bulrush-sedge contained 62 (84 per cent) of the 74 canvas-back nests found; 12 nests were found in a variety of other cover types (Table VI). The discussion of nest measurements and nesting habitat may explain some of the factors which encouraged utilization of the various types of plant cover.

Care of nests and eggs. Final selection of a nest site was indicated by the start of nest-building, a responsibility assumed entirely by the female. That the precise location of the nest was made with a view to materials at hand was doubtful. More logical are Herrick's (1935, p. 160)
beliefs that

Birds, as a rule, must adapt themselves to their environment so far as building materials are concerned; and though some may travel far for the materials of their choice, they commonly take what their immediate neighborhood affords.

Some canvas-back nests found in bulrush cover had, as chief materials of construction, soft bur-reed culms which had to be dragged or carried more than two yards.

Table VI. Comparison of Nest Success in Pure and Mixed Bulrush Cover with Nest Success in Other Plant Communities on Malheur Refuge During 1942, 1946 and 1947

<table>
<thead>
<tr>
<th>Nesting cover</th>
<th>Total Nests 1942</th>
<th>Total Nests 1946</th>
<th>Total Nests 1947</th>
<th>Successful Nests 1942</th>
<th>Successful Nests 1946</th>
<th>Successful Nests 1947</th>
</tr>
</thead>
<tbody>
<tr>
<td>Hardstem bulrush</td>
<td>25</td>
<td>15</td>
<td>22</td>
<td>3</td>
<td>9</td>
<td>13</td>
</tr>
<tr>
<td>(pure stands and</td>
<td>73%</td>
<td>73%</td>
<td>96%</td>
<td>12%</td>
<td>60%</td>
<td>59%</td>
</tr>
<tr>
<td>mixed communities)</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>All other nesting</td>
<td>7</td>
<td>4</td>
<td>1</td>
<td>2</td>
<td>4</td>
<td>1</td>
</tr>
<tr>
<td>cover</td>
<td>22%</td>
<td>21%</td>
<td>4%</td>
<td>29%</td>
<td>100%</td>
<td>100%</td>
</tr>
</tbody>
</table>

The materials chosen in building the nest did not seem always to be the best suited for this purpose. The use of bur-reed in bulrush cover over deep water necessitated more rapid addition of nest materials in order to keep the structure afloat, whereas utilization of available bulrush fragments would have, by their increased volume, buoyancy and comparatively greater resistance to water-logging, enabled
the female to maintain her nest with much less effort.

The stiff cat-tail stalks never were used by nesting females, but the more pliable cat-tail leaves furnished good nest-lining. Since canvas-back nests in cat-tail were found in shallow water, the nest rested on the ground. With this increased support, less rapid addition of even such absorbent, non-buoyant materials as cat-tail leaves was required to keep the eggs above water.

Bur-reed was another source of material which soaked very readily, but since it grew in shallow water usually less than two feet in depth, the nest structure rested on the ground and settled very slowly. In building a nest in bur-reed, the soft plants were sheared or torn off at or below the level of the water and incorporated into the nest, often leaving it quite exposed in the center of a clearing. The female used such clearings in flushing when startled. If not surprised by the intruder, the female usually swam away from the nest.

During the early part of the nesting season each year, only dead vegetation was available for use as nesting materials, for the current growth of the coarse, emergent plants did not appear above the water surface until after the middle of April, and did not equal the previous-year's growth in height until after June 1 in bulrush. The percent of composition of green plants in canvas-back nests, therefore, increased with the advance of each season.
Per cent utilization of green materials in nest construction and maintenance lagged behind the proportions of green plants in dead and green bulrush cover. This further illustrated the tendency of canvas-backs to select the more pliable, water-softened, dead culms as building materials, and to avoid the stiffer, green plants. This preference is shown in Table VII to be true also for broad-leaved cattail, to some extent. Growing bur-reed and Baltic rush were very pliable (Fig. 18), and generally their per cent of utilization was only slightly lower than the per cent of green plants in green-dry cover.

Fig. 18. Canvas-back nest in Baltic rush plant cover with nearby culms incorporated into nest structure. Nest rested on ground in ten inches of water.
Table VII. Relation of Green and Dead Composition of Plant Nesting Cover to Seasonal Utilization by Female Canvas-backs on the Malheur Refuge, Oregon

<table>
<thead>
<tr>
<th>Plant Species</th>
<th>Number of Nests</th>
<th>Average per cent of green plants or green plant material in nesting cover: in nest structure</th>
<th>TOTALS</th>
</tr>
</thead>
<tbody>
<tr>
<td>Hardstem bulrush</td>
<td>April-May</td>
<td>10 7 18 13 34 18 11 3 3 20 5</td>
<td></td>
</tr>
<tr>
<td></td>
<td>June-July</td>
<td>8 3 1 67 53 20 38 3 0 60 26</td>
<td></td>
</tr>
<tr>
<td>Mixed veg. containing bulrush</td>
<td>April-May</td>
<td>1 2 2 0 40 18 0 5 5 25 4</td>
<td></td>
</tr>
<tr>
<td></td>
<td>June-July</td>
<td>6 3 1 75 42 20 53 3 0 60 33</td>
<td></td>
</tr>
<tr>
<td>Broad-fruited bur-reed</td>
<td>April-May</td>
<td>1 1 50 75 60 0 63 30</td>
<td></td>
</tr>
<tr>
<td></td>
<td>June-July</td>
<td>2 80 68 80 68</td>
<td></td>
</tr>
<tr>
<td>Mixed veg. containing bur-reed</td>
<td>April-May</td>
<td>1 1 80 10 60 0 45 30</td>
<td></td>
</tr>
<tr>
<td></td>
<td>June-July</td>
<td>1 75 75 75 75</td>
<td></td>
</tr>
<tr>
<td>Baltic rush</td>
<td>April-May</td>
<td>1 1 20 75 25 75 20 25</td>
<td></td>
</tr>
<tr>
<td></td>
<td>June-July</td>
<td>1 75 10 75 10</td>
<td></td>
</tr>
<tr>
<td>Broad-leaved cat-tail</td>
<td>April-May</td>
<td>1 1 5 5 5 5</td>
<td></td>
</tr>
<tr>
<td></td>
<td>June-July</td>
<td>1 75 10 75 10</td>
<td></td>
</tr>
<tr>
<td>Wild mustard</td>
<td>April-May</td>
<td>1 75 50 75 50</td>
<td></td>
</tr>
<tr>
<td></td>
<td>June-July</td>
<td>1 75 75 75 50</td>
<td></td>
</tr>
</tbody>
</table>

<table>
<thead>
<tr>
<th></th>
<th>TOTALS</th>
</tr>
</thead>
<tbody>
<tr>
<td>1942 1946 1947</td>
<td>32 19 23 49 44 18 32 7 2 38 18</td>
</tr>
</tbody>
</table>
Information on physical features of canvas-back nests and pertinent habitat features obtained from the diving duck nest history forms are found in Table VII. The construction of nests within any given species of plant cover showed great uniformity throughout the study, but in a variety of species of plants, nest measurements showed wide variations. Consequently, nest measurements have been listed according to plant cover types.

Of 74 canvas-back nests found during the study, 47 rested in hardstem bulrush, 15 in vegetation containing bulrush and other emergent species, four in broad-fruited bur-reed, three in mixed vegetation containing bur-reed, two in Baltic rush, two in broad-leaved cat-tail and one on land in mustard (Cruciferae).

The distance from nests to situations in which the female could easily flush ranged from water adjacent to the nest to 75 feet distant and averaged 11.7 feet, but nearly all nests were situated in such a manner as to permit the female to swim away from the nest structure. The average distances to flushing situations were greatest in cat-tail and least in bur-reed. When abruptly disturbed at the nest female canvas-backs flushed directly from the nest structure. Only one of these take-offs was successful, the other two females crashing back into the cover near the nest. The female flushing successfully had launched herself directly into a strong wind and after initial difficulty was able to
Table VIII. Physical Features of Canvas-Back Nests and Nesting Habitat on Malheur Refuge, Oregon

<table>
<thead>
<tr>
<th>Nest and nestling habitat measurements</th>
<th>Bulrush with Hardstem bulrush</th>
<th>Bur-reed with Bur-reed species</th>
<th>Baltic rush</th>
<th>Cat-tail</th>
<th>Wild mustard</th>
</tr>
</thead>
<tbody>
<tr>
<td>Total no. of nests</td>
<td>47</td>
<td>15</td>
<td>4</td>
<td>3</td>
<td>2</td>
</tr>
<tr>
<td>Distance from nest to flushing area (ft)</td>
<td>Max. 75.0</td>
<td>60.0</td>
<td>30.0</td>
<td>20.0</td>
<td>30.0</td>
</tr>
<tr>
<td></td>
<td>Min. 1.0</td>
<td>0.0</td>
<td>1.0</td>
<td>6.0</td>
<td>0.0</td>
</tr>
<tr>
<td></td>
<td>Avg. 10.4</td>
<td>13.5</td>
<td>9.7</td>
<td>13.7</td>
<td>15.2</td>
</tr>
<tr>
<td>Water depth at nest (in.)</td>
<td>Max. 54.0</td>
<td>42.0</td>
<td>20.0</td>
<td>18.0</td>
<td>15.0</td>
</tr>
<tr>
<td></td>
<td>Min. 3.0</td>
<td>1.0</td>
<td>7.0</td>
<td>6.0</td>
<td>10.0</td>
</tr>
<tr>
<td></td>
<td>Avg. 23.6</td>
<td>17.7</td>
<td>12.3</td>
<td>10.3</td>
<td>12.5</td>
</tr>
<tr>
<td>Height of nest bowl above water (in.)</td>
<td>Max. 8.0</td>
<td>4.0</td>
<td>5.0</td>
<td>3.0</td>
<td>4.0</td>
</tr>
<tr>
<td></td>
<td>Min. 0.0</td>
<td>1.0</td>
<td>3.0</td>
<td>2.0</td>
<td>3.0</td>
</tr>
<tr>
<td></td>
<td>Avg. 3.4</td>
<td>2.7</td>
<td>4.0</td>
<td>2.7</td>
<td>3.5</td>
</tr>
<tr>
<td>Nest bowl depth (in.)</td>
<td>Max. 6.5</td>
<td>6.0</td>
<td>5.0</td>
<td>6.0</td>
<td>6.0</td>
</tr>
<tr>
<td></td>
<td>Min. 2.0</td>
<td>3.0</td>
<td>4.0</td>
<td>4.0</td>
<td>3.5</td>
</tr>
<tr>
<td></td>
<td>Avg. 4.4</td>
<td>4.2</td>
<td>4.5</td>
<td>5.0</td>
<td>4.7</td>
</tr>
<tr>
<td>Nest bowl diameter (in.)</td>
<td>Max. 10.0</td>
<td>9.0</td>
<td>8.0</td>
<td>9.0</td>
<td>8.5</td>
</tr>
<tr>
<td></td>
<td>Min. 5.0</td>
<td>5.5</td>
<td>7.0</td>
<td>7.0</td>
<td>8.0</td>
</tr>
<tr>
<td></td>
<td>Avg. 7.6</td>
<td>7.5</td>
<td>7.7</td>
<td>8.0</td>
<td>8.2</td>
</tr>
<tr>
<td>Thickness of nest structure (in.)</td>
<td>Max. 25.0</td>
<td>20.0</td>
<td>18.0</td>
<td>10.0</td>
<td>18.0</td>
</tr>
<tr>
<td></td>
<td>Min. 5.0</td>
<td>1.0</td>
<td>10.0</td>
<td>8.0</td>
<td>12.0</td>
</tr>
<tr>
<td></td>
<td>Avg. 10.4</td>
<td>9.8</td>
<td>13.3</td>
<td>9.3</td>
<td>15.0</td>
</tr>
<tr>
<td>under bowl (in.)</td>
<td>Avg. 0.5</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Time (hr.)</td>
<td>Ave.</td>
<td>Min.</td>
<td>Max.</td>
<td>Measured Temperature</td>
<td>Other</td>
</tr>
<tr>
<td>-----------</td>
<td>------</td>
<td>------</td>
<td>------</td>
<td>----------------------</td>
<td>-------</td>
</tr>
<tr>
<td>14.0-5</td>
<td>19.6</td>
<td>19.6</td>
<td>20.0</td>
<td>20.4</td>
<td>24.0</td>
</tr>
</tbody>
</table>

TABLE VIII (continued)
continue in flight. One of the unsuccessful flushing females could not get up through dense cat-tail cover, and the other unsuccessful female, flushing down wind in a moderate breeze lost altitude and plunged into bulrush cover. Nest take-offs were undertaken only in extreme emergencies, but never when the female received warning of the approach of the observer. Late in incubation, however, the female showed a greater reluctance to leave and occasionally delayed flushing until the last moment.

The fact that diving ducks experienced greater difficulty than shoal-water ducks in flushing directly from nesting cover appeared to be the important factor in selection of nest sites near vegetation-free water. Since hardstem bulrush provided a type of cover which furnished an ample supply of nesting materials up to the edge of the clump or stand, the nest could be placed a minimum distance from open water in these communities. Communities of sedges, bur-reed and cat-tail tended to become too sparse toward deeper water, requiring the female to build the nest farther back in this type of cover where materials were adequate, thereby increasing the distance to flushing areas.

In the Blitzen Valley, most canvas-back nests were found in two general types of plant cover: dense clumps in open or semi-open, deeper ponds such as the east half of the Buena Vista pond (Fig. 19), or in semi-open, shallower marsh in the edges of moderately dense stands of bulrush margined
Fig. 19. Clump-type vegetation, mainly hardstem bulrush, contained most canvas-back nests in semi-open, deeper ponds.

Fig. 20. Bulrush-spike rush marsh was second most important canvas-back nesting habitat in the Blitzen Valley.
by spikerush (Fig. 20). Spikerush cover usually was sparse enough to permit flushing of diving ducks, while the bulrush furnished a good nesting substrate. Deer and stock trails through sparse, low vegetation, such as spikerush, provided flushing lanes.

Water depths at nest sites ranged from zero to 54 inches. As would be expected, greatest average depths of 23.6 inches were found in hardstem bulrush communities, and the least average depths occurred at nests in mixed vegetation containing bur-reed. The only exception to the preceding was one nest located on the side of a dike well above and a few feet away from water.

The depth of water seemed less important than vegetation-water interspersion. The significance of specific water depths in nest-site selection by females was not believed to be great, as demonstrated by the large range in depths at known nests.

The height of the nest bowl above water was an important measurement, for it not only indicated the degree of vulnerability of the clutch to flooding by waves or rising water levels, but also gave evidence concerning the age of the structure and attentiveness of the nesting female. As with the other measurements, these were made or estimated for nests during the onset of incubation. One nest bowl located eight inches above the water surface in bulrush represented the maximum, and another nest in the same type
of cover had the bowl floor at water level with some of the eggs barely resting in water. Nests located in bur-reed and cat-tail cover had the greatest average bowl heights above water (four inches), being of the type which rested on the ground.

Nest bowl depths ranged from two inches to 6.5 inches, both extremes being found in bulrush. Nest bowl diameter extremes of five and ten inches were also found in bulrush. In general, both of these extremes usually conformed with the size of the clutch, and both measurements ordinarily increased during each nest history, so that initially small, shallow, nest bowls developed into more ample receptacles by hatching time.

The maximum outside diameter of any canvas-back nest at the water line was 35 inches in a bulrush nest. The minimum diameter was found in a 12-inch nest in bulrush-cat-tail cover. The majority of nests were between 18 and 24 inches in outside diameter.

The thickness of the nest structure under the bowl was another criterion of the age of floating or partly floating nests because materials were constantly added by the attending female throughout their nest histories. This attention was less evident in nests with foundations resting on the bottom since they soaked and settled more slowly with less need for adding materials. The thickness of nest structures ranged from 27 inches in a cat-tail nest to one half
inch in the nest in mustard.

Nest canopies or cupolas of vegetation were found over about half (53 per cent) of the nests. These structures possibly served some protection but seemed incidental rather than intentional in location of the nest, for they often were used by the occupant in building up the nest, especially when other materials were not readily available. In this way, especially in bur-reed, all vegetation within a two- or three-yard radius was pulled or sheared off, leaving the nest in the center of a small clearing. Thus, no persisting canopies were found on nests located in bur-reed or Baltic rush.

Ramps constructed on the sides of nests aided passage of the female between nest and water and were found in 65 (88 per cent) of the nests. The ramps extended downward from the rim of the nest into the water and were built of interwoven vegetation similar to but usually coarser than the material used in the nest, and usually were kept in constant repair. The ramps communicated with one or more channels leading to a flushing area or else led directly to open water. They varied from a fraction of a foot to five feet in length and from four to 20 inches in width, being widest at the junction of ramp and nest. Nine canvasback nests (12 per cent) had no ramps, 28 nests (38 per cent) had a single ramp, 32 nests (43 per cent) had two ramps and five nests (7 per cent) had three ramps.
The plant materials comprising the bulk of the nest structure were more coarse than those used in forming the bowl, and were crudely interwoven to form a foundation for the rest of the structure. Somewhat finer-textured materials were used to fashion the upper contours of the nest and bowl. Rarely were eggs deposited before nest-building was begun. In one known instance, the female laid an egg on a floating mat of bulrush, then built a nest around it and the succeeding eggs.

The bowl of the nest was usually very small while the first few eggs were being laid, but it was enlarged to accommodate additional eggs in the clutch. A total of 43 eggs was found in the bowl of one canvas-back nest in 1942. The bowl and upper parts of the nest were formed by the female while on the nest. Even while incubating the female continued to improve the nest's appearance and serviceability.

The channels between nest and flushing area often contained floating vegetation which was removed occasionally for nest-building purposes. When the supply of materials near the nest was exhausted, the channels were kept clear, but when the nest was well supported and settled more slowly vegetation debris accumulated in the channels, along with duckweeds (Lemnaceae). Canvas-backs did not seem intentionally to keep the channels open, but rather open channels seemed to be a result of the female's quest for nesting materials.
While the first eggs of the clutch were being laid, the female spent a varying time in attendance at the nest, laying an egg and continuing nest construction. Eggs were deposited until the bowl was fairly full, some eggs resting on others. By the time that the last few eggs had been laid, the clutch was neatly arranged along the bottom and sides of the nest bowl in a single concave layer which conformed to the shape of the female's body.

When the female remained on the nest for an extended period of time to continue construction or to deposit an egg, the rest of the eggs were partly warmed, but the unincubating female never was found to remain long enough to completely warm them. Consequently, non-incubated nests could be distinguished from incubated ones by feeling the eggs for warmth. If the lower side of the eggs was cold, excepting with those freshly laid, the nest was not yet being incubated. If the eggs were uniformly warm or only slightly warm, or if the upper side of the clutch was partly cooled indicating the female had been off the nest for an extended period, the clutch was being incubated.

Comparative temperatures of eggs were determined by touching them to a part of the face above and behind the eye where external temperatures remained quite constant. Eggs feeling colder than this area of the human face were listed as cool and those feeling as warm or warmer were indicated as being warm. Sun-warmth was occasionally a consideration
in determining whether a nest was being incubated, especially when the female had previously left the nest without covering the eggs. In sun-warming of eggs, as in pre-incubation warming of eggs by the female the upper sides were usually warmer than the lower sides.

The first few eggs to be laid sometimes reposed in such a flimsy nest structure that some of them lay partly in water. Partial immersion in water did not seem to be detrimental to the viability of the eggs as long as they were not being incubated, and if half or more of the egg remained out of water. Lippincott and De Puy (1923) found that apparently normal chicks of the domestic fowl (Gallus gallus) may be hatched from eggs which lie in a half-inch of warm, distilled water during the first 18 days of incubation. Presumably the lower temperature of lake or pond water was the lethal feature causing death of embryos in inundated, incubated canvas-back eggs at Malheur.

Prior to most voluntary departures from nests, female canvas-backs carefully covered the eggs, uncovering them again upon their return. At first, moist or dry plant fragments were dragged over the eggs (Fig. 21) but after three or four eggs had been laid, the female began to strip down feathers from its breast for lining the nest bowl, and during the later days of egg-laying and incubation a soft, downy blanket was available for covering the eggs (Fig. 22).
Fig. 21. Canvas-back nest containing unincubated clutch covered by moist bulrush fragments during absence of female.

Fig. 22. Canvas-back nest in bulrush on Malheur Lake showing dark, downy lining. Musk rat-sheared culms indicate previous year's (1946) lake level.
The covering over the eggs during the absence of the female served at least two functions: the eggs were more effectively obscured or camouflaged from the view of other waterfowl and predators, and the blanket provided fine insulation from heat loss or gain. The frequent use of moist plant fragments during egg-laying may have aided in keeping the eggs cool through evaporation. Phillips (1923) reported that the New Zealand Scaup (*Aylyra novaehollandiae*) covered its incubated eggs with wet duckweed, possibly protecting them from the hot rays of the sun.

Canvas-back down feathers consist of a short shaft from which many plumose barbs, one to two centimeters in length, arise. The barbs and barbules are clove-brown to lighter in color, the proximal portions of the barbs graduating into lighter shades to smoky-white, the entire feathers giving an appearance of dark tufts with lighter centers (Fig. 18). In a canvas-back nest, the downy lining appeared as gray-brown in contrast with the fluffier, whitish down found in nests of the redhead (Fig. 23). Having longer barbs, redhead down was more showy and less compact in appearance, and was more easily blown from the nest by wind, aiding somewhat in redhead nest discovery.

Although two females were known to delay incubation until all eggs had been laid, most of them began to incubate during the laying of the last two or three eggs of the clutch. Often the first day or two of incubation seemed to
be undertaken with some lack of direction, for eggs which had been completely warmed were found cool on the following day, after which the eggs were kept warm constantly.

Down was most abundant during the first ten days of incubation. Gradually it disappeared and by hatching time many nests were nearly or entirely without visible down. Some down was blown out of the nest by the wind or carried away by Western marsh wrens for nest-building (Fig. 24). Utilization of down feathers from duck and goose nests by
Western marsh wren nest contains canvas-back down feathers, probably from canvas-back nest 20 feet distant. Lesser duckweed (Lemna minor) covers water surface.

Marsh wrens was most frequent in areas where cat-tail did not grow, such as in central parts of Malheur Lake and in the larger ponds of the Blitzen Valley. In small ponds and marshes, cat-tail "fuzz" was most frequently used for nesting lining by marsh wrens. A few contour and down feathers of the canvas-back were found in a white-faced glossy ibis nest. Most of the down, however, was buried among the nest materials as vegetation was constantly added to the nest.

The rate of loss of down was almost directly propor-
tional to the rate at which new plant materials were added to the top of the nest. In floating nests which required frequent and constant maintenance, nests often were without down by the end of the first week of incubation. Most nests with bases resting on the soil had down visible throughout their histories, and the single nest resting on land out of water retained nearly all of the initial downy lining. As the supply of visible down in some nests decreased toward hatching time, the female again continued to use dry plant fragments in covering the eggs while absent from the nest.

The apparent devotion or attachment for the nest increased daily though the female usually did not show as much anxiety as most other local nesting ducks when the safety of nest and eggs was threatened. With the approach of an observer, the female usually flushed and flew away in alternately high and low flight, occasionally returning to make an aerial inspection of the intruder. Sometimes the female, with or without the mate, circled back and flew past the nest from ten to 50 feet above the water uttering its low, twangy call. No nesting canvas-backs were seen to feign injury in order to lure away intruders, but females with broods frequently employed this ruse.

In order to learn more about female attendance at the nest, flushing data from nest histories of females known to be nesting were examined. These data have been listed in Table IX. The figures indicate that females were most
Table IX. Analysis of Nest Attendance by Female Canvasbacks on the Malheur Refuge, Oregon during 1942, 1946 and 1947.

<table>
<thead>
<tr>
<th>Period of day (8 a.m.-8 p.m.)</th>
<th>On or off nest</th>
<th>Pre-incubation period</th>
<th>Incubation period</th>
<th>18 days</th>
<th>Total visits</th>
</tr>
</thead>
<tbody>
<tr>
<td>8:00-9:59</td>
<td>on</td>
<td>3</td>
<td>2</td>
<td>1</td>
<td>4</td>
</tr>
<tr>
<td></td>
<td>off</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>10:00-11:59</td>
<td>on</td>
<td>6</td>
<td>2</td>
<td>4</td>
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<td>3</td>
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<td>4</td>
</tr>
<tr>
<td></td>
<td>off</td>
<td>1</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>2:00-3:59</td>
<td>on</td>
<td>1</td>
<td>7</td>
<td>6</td>
<td>10</td>
</tr>
<tr>
<td></td>
<td>off</td>
<td>2</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>4:00-5:59</td>
<td>on</td>
<td>1</td>
<td>1</td>
<td>1</td>
<td>4</td>
</tr>
<tr>
<td></td>
<td>off</td>
<td>2</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>6:00-7:59</td>
<td>on</td>
<td>1</td>
<td>1</td>
<td>1</td>
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<tr>
<td></td>
<td>off</td>
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<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Totals</td>
<td>on</td>
<td>13</td>
<td>18</td>
<td>14</td>
<td>27</td>
</tr>
<tr>
<td></td>
<td>off</td>
<td>4</td>
<td>2</td>
<td>7</td>
<td>6</td>
</tr>
</tbody>
</table>

frequently found at the nest during the morning hours of eight to 11. Nests were not visited earlier than eight o'clock a.m. because of the extremely low nocturnal temperatures, even during midsummer, and the existing danger of cooling incubated eggs before the return of flushed females. During the remaining hours of the day, especially after two o'clock p.m. and until about six in the evening, the nests were more frequently found unattended.
There was no apparent difference between the pre-incubation and incubation periods of nest attendance, but the fact that attended nests were more likely to be discovered than unattended ones could have distorted the figures in the pre-incubation period. Consequently, first visits to nests were not included in this tabulation. Prior to incubation, females usually remained very near the nest during morning, but toward late afternoon the females rejoined their mates to feed and rest throughout the night, returning to the immediate vicinity of the nest early the following morning.

A female flushed by an observer, usually returned to the nest much sooner than when leaving voluntarily to feed or rest. In three timed returns of flushed birds, the maximum period of absence was 40 minutes, the minimum was 14 minutes and the average, 28 minutes. When leaving voluntarily, canvas-back females were known to have been absent for as long as three and one-half hours on a warm day though they usually were gone less than an hour. On cold, windy days they left the nest less frequently and returned more quickly.

In an analysis of nest attendance by female birds, Huggins (1941, p. 148) used recording potentiometers and a portable galvanometer, with copper constantan thermocouples in birds' eggs. He found that "... when the bird returns to the nest after being chased off the first
attentive period is extremely long."

In an Iowa study of the redhead, Low (1945) found no definite rhythm of incubation and rest periods either during the day or night. Using a device adapted from the itograph of Kendeigh and Baldwin (1930) which was designed to record departures and returns of nesting birds, Low reported nesting redheads left the nest as many as 26 and no fewer than three times during a single 24-hour period, averaging 6 departures per day. He found daily temperatures to be of consequence in the periods of nest attendance, and that renesting females spent fewer hours on the nest and left more frequently than initial nesters.

Canvas-backs left the nest more readily upon being disturbed than any other resident duck except the ruddy duck. The distance at which females flushed from the observer varied from less than a yard to more than 200 yards, but most of them flushed at from ten to 50 yards. Table X gives average flushing distances of nesting canvas-back females showing correlation with the period of the season and the period in the nest history. In general, the period in the nest history was the most important factor determining the average distance of flushing. The advance of the season seemed less important.

In only three instances did females flush directly upward from the nest structure itself. This extreme exertion was accompanied by defecation on the nest and eggs as
Table X. Average Flushing Distances of Nesting Canvas-backs on Malheur Refuge, Oregon during 1942, 1946 and 1947

<table>
<thead>
<tr>
<th>Period in nest history when flushed</th>
<th>Period</th>
<th>Pre-incubation</th>
<th>1-8 days</th>
<th>9-17 days</th>
<th>18-25 days</th>
<th>Average flushing distances</th>
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<tbody>
<tr>
<td></td>
<td></td>
<td>period</td>
<td>incubation</td>
<td>incubation</td>
<td>incubation</td>
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<tr>
<td>April 16-30</td>
<td>1-30</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td>1-30</td>
</tr>
<tr>
<td>May 1-15 1a-50 b</td>
<td>12-41</td>
<td>3-40</td>
<td>1-2</td>
<td>17-35</td>
<td></td>
<td></td>
</tr>
<tr>
<td>May 16-31</td>
<td>7-62</td>
<td>13-28</td>
<td>9-41</td>
<td>6-28</td>
<td>35-32</td>
<td></td>
</tr>
<tr>
<td>June 1-15</td>
<td>2-40</td>
<td>5-41</td>
<td>4-8</td>
<td>6-25</td>
<td>13-34</td>
<td></td>
</tr>
<tr>
<td>June 16-30</td>
<td>4-24</td>
<td>5-32</td>
<td>1-20</td>
<td>4-33</td>
<td>17-25</td>
<td></td>
</tr>
<tr>
<td>July 1-15</td>
<td>2-40</td>
<td>1-15</td>
<td></td>
<td>4-25</td>
<td></td>
<td></td>
</tr>
<tr>
<td>July 16-31</td>
<td>2-30</td>
<td></td>
<td></td>
<td>2-30</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Totals</td>
<td>16-43</td>
<td>39-34</td>
<td>17-32</td>
<td>17-21</td>
<td>97-33</td>
<td></td>
</tr>
</tbody>
</table>

a Number of birds flushed
b Average distance birds flushed from observer
shown in Fig. 25. This foul-smelling deposit was usually not in evidence for more than two days after the hasty departure. In each of the above cases of delayed flushing from the nest, the clutch hatched within the following three days, indicating the females were much more reluctant to leave the nest late in incubation. In Fig. 25 one egg is already seen to be pipped, and this nest hatched during the 36 hours after the disturbance.

Female canvas-backs turned the eggs frequently, and marks made with a wax crayon usually were nearly or completely obliterated in less than a week, presumably due to friction with the bill, body and feet. No special effort
was believed to have been made by the nesting female to keep the eggs clean, and they soon became stained by nest materials and the female's damp body when returning to the nest.

As a result of various types of intrusion and other psychological factors, female canvas-backs abandoned nests in which they had laid eggs or incubated. When this abandonment or desertion occurred prior to completion of the clutch, the female still was believed to have been a potential nester. With egg-laying completed and if incubating, the possibility of a desertion and subsequent renesting effort seemed very remote, for after deserting incubated clutches females were often seen frequenting the scenes of their earlier attempts at nesting, having previously parted from their mates as incubation occupied much of their time. These females occasionally joined other paired groups of canvas-backs, but were neither courted nor repelled by mated or unmated males. Eventually they left the nest locality, presumably to go into the post-nuptial molt.

When a nest containing only a few cold eggs was abandoned, another nesting attempt could usually be anticipated in the near vicinity of the first. This was an especially frequent occurrence during 1942 when the nesting success was low. In attributing the later "Companion nest" to be a result of the efforts of the previously deserting female, two sources of time and space evidence were considered.
First, the renesting had to follow the desertion. Secondly, the very low canvas-back nesting densities and tendencies of females toward isolation from others of their species during nesting reduced the possibility of another female commencing nesting with the first female's drake still in attendance nearby.

In general, late renests showed less workmanship and smaller clutches than initial nests or early renestings, but it is admitted that identification of a structure as an initial nest or a renest simply on the basis of materials or construction was not possible. Rather, an intimate acquaintance with the numbers and movements of the somewhat limited and dispersed population, together with evidence obtained at the nest, aided in identifying renesting attempts.

The amount of time elapsing between desertion of a nest by a female canvas-back seemed to vary in the light of field observation of isolated females in areas of some exceedingly low canvas-back nesting densities (less than one female in a half-section of pond and swamp) on the Malheur Refuge. A number of females apparently proceeded from earlier attempts without a break in egg-laying when the earlier attempt consisted of one to three or four unincubated eggs. Such renests seemed to entail compensatory egg-laying, for these renesting females laid clutches that approached in number of eggs the size of interpreted, initial, final
clutches. Thus, the importance of the loss of the earlier attempts, from a production standpoint, was decreased or nullified. When renesting of a female followed an earlier attempt in which most of the clutch had been laid, the time required for "... renewing of her reproductive efforts...", as shown by Errington 1942, p. 170, appeared much greater. This assumption was based on observation of isolated females remaining near the sites of earlier failures with mates for more than a month before appearance of another nest in the immediate vicinity.

Analysis of the data on nest inceptions in 1942 (Fig. 10), the year of low initial success and heavy renesting, may reveal information concerning the amount of time elapsing between first nesting attempts and later renestings. These data are again presented in Fig. 26 for easier reference and interpretation. Twenty-nine of the 32 canvas-back nests found that year may be grouped as follows: I, May 1-6, four nests; II, May 12-24, eight nests; III, June 3-10, six nests; IV, June 16-21, seven nests; and V, June 28-July 2, four nests. The other three nest inceptions occurred in isolated positions outside the five groups, including one dated April 10, another dated June 13 between groups III and IV, and the last dated July 14, nearly two weeks after the last date for group V.

The first two groups embraced by the dates May 1-24 were believed to have included most initial nesting attempts while the last three groups, begun during the period from
Fig. 26. Canvas-back nest inception periods during 1942 on the Malheur Refuge, Oregon.

June 3 to July 2 were thought to have represented renestings by canvas-backs following one or more initial failures. The period of no inceptions between May 6 and May 16 was reflected by a similar break in nest inceptions between June 10 and June 16, about five weeks later. The reason for the May 6 to May 12 discontinuity in nest inceptions was not definitely known although it may have been influenced by certain weather conditions during the period of interpreted initial nesting attempts.

The information presented in Fig. 26 appears to suggest that between four and five weeks usually elapsed between the time of abandonment of one nest and inception of
a renesting attempt by the same female. For example, group I was followed by the renesting inceptions of group III about 34 days later, and group II was followed by group IV about 31 days later. Group V may possibly represent another concentration of renestings of the I-III series, occurring about 28 days after group III. If group V constitutes a valid renesting group, there is indication that as the season progresses, the time between the earlier nest and inception of successive renests tends to decrease. This is indicated in the intervals of 34 days between groups I and III, 31 days between groups II and IV, and 28 days between groups III and V. The validity of group V may be questioned for towards the end of the season continuation of periodic inceptions of renesting attempts among most resident female canvas-backs might not be expected. The data, however, agree with field observations in every respect.

The low nest success of 1942 was correlated with a large proportion of females renesting, while the high nest success of 1946 and 1947 was correlated with few females making more than one attempt at clutch formation. The addition of foreign eggs by other female ducks (and in one case, by a coot) increased the nest maintenance tasks of the canvas-back host. Sometimes the female deserted the nest immediately after a foreign egg appeared in the nest, but on other occasions seemed to accept them without evident disturbance.
As the quantity of eggs increased so that the nest bowl could no longer accommodate them, some fell or were pushed over the side of the nest into the water and usually sank to the bottom. Thereafter, the female abandoned the nest or remained to lay or to incubate the remaining eggs. The eggs lost over the side were both host and intruder, and in five 1942 nests, only redhead eggs remained in the bowl at the termination of the nest histories. Consequently, canvas-back females hatched broods entirely composed of redhead ducklings.

Another response of the female canvas-back to intrusive ovipositing was the building of a new bowl over one or more earlier bowls. Erickson (1942, pp. 65-66) reported that:

In three instances, females were found to make more than one attempt at clutch formation in the same nest after parasitism or raven (Corvus corax simanus) predation. Under those circumstances during egg-laying by the female canvas-back, female redheads often contributed eggs to the original nest contents. Occasionally this was not tolerated by the true owner which covered the incomplete clutch with plant fragments constructing another bowl above and usually to one side of the original bowl. In one nest the female went through this procedure three times while the nest gradually settled in the water due to saturation and decomposition of nest materials and the extra weight of additional clutches, so that the lower three incomplete clutches, each containing both canvas-back and redhead eggs, were completely submerged. By addition of nest materials, the upper bowl of the nest was kept above the water and eggs eventually hatched.

The egg composition of the nest was as follows: First (bottom) clutch, six canvas-back and 17 redhead eggs; second clutch, five canvas-back and three redhead eggs; third clutch, three canvas-
back and one redhead egg; and fourth (successful) clutch, two canvas-back and eight redhead eggs, a total of 16 canvas-back eggs and 29 redhead eggs.

... Each clutch of eggs was well-separated from successive clutches by a firm layer of nest material which formed the floor of the succeeding bowl. In this way, clutch sequence was easily determined.

The above-described canvas-back nest was reminiscent of a four-storied nest of the yellow warbler (Dendroica aestiva) found near London, England, reported by Arnott (1890). In each of the lower three bowls of the warbler nest was found a cowbird egg, while the fourth or upper bowl contained two warbler eggs.

In the large clutches of canvas-back and intruder eggs some eggs must have been lost into the water through no deliberate act of the host or intruding female. However, eggs were ejected forcibly from the nest for they sometimes were found on the bottom in the water as much as three feet to one side of the nest. These nests often showed signs of scuffling. Hochbaum (1944, p. 91) reported witnessing such scuffling between a captive female canvas-back and a wild female redhead at the nest of the former.

A wild female Redhead, sometimes accompanied by her drake, sometimes alone, came every morning to slight near the nest of a captive Canvasback. Her first visit was when the Canvasback nest held four eggs. The redhead waited near until the owner departed; then she sat on the captive's nest to drop her egg. On several occasions the Canvasback hen returned to find the intruder sitting. There followed pitched battles between the two hens, until, after several such encounters, all of the eggs were rolled into the water, and the nest, quite torn apart, was abandoned by owner and intruder.
Such an occurrence was never witnessed by the present writer, but the condition of some nests after desertion had taken place indicated that similar melees were not uncommon in 1942.

As a result of such activity at the nest or of the large number of eggs present, the shells of some were cracked. In spite of odors from the broken-shelled eggs which were very offensive to the human nose, the females continued incubation without removing the spoiled eggs.

The length of time that a female remained in attendance at unsuccessful nests varied from one to 37 days (Table XI) and from 31 to 42 days for successful canvas-back nests, averaging, respectively, 15.7 and 33.5 days. These periods of nest attendance dated from the time that the first egg was deposited, to termination of the nest history by destruction, desertion or until the brood left the nest with the female. During the 1942 season of heavy parasitism, the period of attendance for successful nests was over two days more than the average for the three years among successful nests. In the same year, the parasitism factor seemed to cause earlier abandonment of unsuccessful nests as indicated by average attendance periods of 14.5 days for 1942 and 17.7 days during 1946-7.

Parasitized nests were found more quickly after inception than unparasitized nests. Nest histories of active nests prior to discovery in 1942 were shortest with 3.1 days,
Table XI. Duration of Canvas-back Nest Histories on the Malheur Refuge, Oregon during 1942, 1946 and 1947

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<thead>
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<tr>
<td></td>
<td>Min. 33</td>
<td>31</td>
<td>31</td>
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<tr>
<td></td>
<td>Avg. 35.6</td>
<td>5</td>
<td>33.3</td>
<td>13</td>
<td>32.9</td>
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<tr>
<td>Unsuccessful nests</td>
<td>Max. 37</td>
<td>29</td>
<td>34</td>
<td></td>
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</tr>
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<td>Min. 1</td>
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<td>1</td>
<td></td>
<td></td>
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<tr>
<td></td>
<td>Avg. 14.5</td>
<td>27</td>
<td>17.7</td>
<td>6</td>
<td>17.7</td>
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<tr>
<td>Canvas-back nests(^a) prior to discovery</td>
<td>Max. 25</td>
<td>37</td>
<td>29</td>
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<tr>
<td></td>
<td>Min. 1</td>
<td>1</td>
<td>1</td>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td>Avg. 8.1</td>
<td>25</td>
<td>14.4</td>
<td>16</td>
<td>10.3</td>
</tr>
<tr>
<td>Interpreted unsuccessful final canvas-back nests</td>
<td>Max. 37</td>
<td>29</td>
<td>34</td>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td>Min. 11</td>
<td>15</td>
<td>8</td>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td>Avg. 21.3</td>
<td>13</td>
<td>23.7</td>
<td>4</td>
<td>19.8</td>
</tr>
<tr>
<td>Unsuccessful nesting attempts probably followed by re-nesting</td>
<td>Max. 19</td>
<td>9</td>
<td>6</td>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td>Min. 1</td>
<td>2</td>
<td>1</td>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td>Avg. 8.2</td>
<td>14</td>
<td>5.5</td>
<td>2</td>
<td>4</td>
</tr>
</tbody>
</table>

\(^a\)Does not include nests in which evidence of the start of egg-laying or hatching was obscure.
longest in 1946 with 14.4 days, and intermediate in 1947 with 10.3 days. As will be discussed later, the average number of intruder eggs per canvas-back nest was greatest in 1942, least in 1946 and intermediate in 1947.

One might expect that as the investigator became familiar with nest-finding techniques and with the research area, the nests would be more quickly and more easily located. In this study, however, durations of nests prior to discovery were shortest in the first year of field work, possibly indicating a greater unrest or nervousness among nesting female canvas-backs, coincidental with the heavier nest parasitism. This unrest may have aided nest searching by the earlier departure of females from the nest at the approach of the observer. Such a factor obviously would find less application with systematic nest searching in all plant cover.

Nest durations interpreted to represent the final, unsuccessful efforts of the canvas-back female for the season lasted an average of 20.9 days, while abandoned nests believed to have been followed by renesting averaged 8.7 days.

Nest Fates

Terminations of nest histories were included in two categories: unsuccessful or successful. Unsuccessful nests were those in which no eggs hatched while in successful
nests, one or more eggs hatched. The term "hatch" is here defined as the complete emergence of the duckling from the egg shell. Nests in which no ducklings hatched were considered unsuccessful.

Unsuccessful nests

On the more completely managed waterfowl nesting areas, according to Kalmbach (1939), nesting success tends to be higher and more constant from year to year than on unmanaged areas. Management may be completely upset, however, by violent climatic conditions, unexpected predation, and possibly by other less obvious population depressants about which little is known. The parasitic habit of some birds may be placed in the last category, for during the 1942 nesting season, parasitic intrusion was believed to have been the principal, direct cause for the failure of more than half the nests found, while untoward climatic conditions and predation were relegated to minor roles. The possibility that climate or the conditions of the habitat may be manifested indirectly in displays of promiscuous egg-laying, with consequent low nesting success, should be kept in mind.

During the three years of the investigation, a total of 42 canvas-back nests (57 per cent) were unsuccessful (Table XII). Over half of these unsuccessful nests (27) were included in the 1942 season, while only six and nine unsuccessful nests, respectively, were found in 1946 and 1947.
Table XII. General Summary of Canvas-back Nest Fates on Malheur Refuge, Oregon.

<table>
<thead>
<tr>
<th></th>
<th>1942a</th>
<th>1946a</th>
<th>1947a</th>
<th>Totals</th>
</tr>
</thead>
<tbody>
<tr>
<td>Total canvas-back nests</td>
<td>32</td>
<td>19</td>
<td>23</td>
<td>74</td>
</tr>
<tr>
<td>Successful nests</td>
<td>5(16)</td>
<td>13(68)</td>
<td>14(61)</td>
<td>32(45)</td>
</tr>
<tr>
<td>Unsuccessful nests</td>
<td>27(84)</td>
<td>6(32)</td>
<td>9(39)</td>
<td>42(57)</td>
</tr>
<tr>
<td>Abandoned due to:</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Nest parasitism</td>
<td>21</td>
<td>2</td>
<td>4</td>
<td>27</td>
</tr>
<tr>
<td>Muskrat activity</td>
<td>1</td>
<td></td>
<td></td>
<td>1</td>
</tr>
<tr>
<td>Sheep carcass</td>
<td>1</td>
<td></td>
<td></td>
<td>1</td>
</tr>
<tr>
<td>Wind and wave action</td>
<td>1</td>
<td></td>
<td></td>
<td>1</td>
</tr>
<tr>
<td>Human intrusion</td>
<td></td>
<td>2</td>
<td>2</td>
<td>4</td>
</tr>
<tr>
<td>Undetermined factor</td>
<td>1</td>
<td></td>
<td></td>
<td>1</td>
</tr>
<tr>
<td>Totals</td>
<td>25(93)</td>
<td>2(33)</td>
<td>6(67)</td>
<td>33(79)</td>
</tr>
<tr>
<td>Destroyed by:</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>American raven</td>
<td>2</td>
<td>3</td>
<td>3</td>
<td>8</td>
</tr>
<tr>
<td>Mustelidae</td>
<td>1</td>
<td></td>
<td></td>
<td>1</td>
</tr>
<tr>
<td>Totals</td>
<td>2(7)</td>
<td>4(67)</td>
<td>3(33)</td>
<td>9(21)</td>
</tr>
</tbody>
</table>

aPercentages are in parentheses.

All unsuccessful nests were listed under two major subheadings: abandoned and destroyed. Thirty-three nests were abandoned during the three nesting seasons, constituting the bulk (79 per cent) of the 42 unsuccessful nests.
Destruction by predators accounted for nine nests for the three seasons, comprising the remainder (21 per cent) of the unsuccessful nests.

Interpretation of causes, and especially primary causes, of nest abandonment or destruction constitutes one of the most difficult (and often abused) accomplishments in wildlife nesting studies. More vague but pertinent evidence may be obscured by extremely obvious but irrelevant indicators. For this reason, diagnoses of nest fates are most accurate when supplemented with extensive knowledge of antecedent events in the nest history.

Part of the history of a successful 1942 canvas-back nest may be used as an example of some pitfalls in interpretation.

The nest contained seven, warm, redhead eggs when found on July 20, and was attended by a female canvas-back. That incubation was well advanced was evidenced by lack of much visible down in the bowl, the reluctance of the female to leave the immediate vicinity of the nest, incorporation of all nearby plant materials into the nest, and by the heavily stained color of the eggs. On July 24 the nest was revisited, and though the female was not seen, the eggs were found to be warm and uncovered, indicating that the female had slipped off unseen and probably was lurking in the vegetation nearby. The nest was in good condition with the floor of the bowl at least three inches above water. The last visit to the
nest was made on August 4 when the nest was found to be settling. Seven cold eggs in the flattened nest had been partly covered with muskrat feces and clipped bulrush culms (Fig. 27). Two apparent conclusions might be drawn from the above information: (1) the female canvas-back had appropriated and incubated a redhead nest and (2) muskrat activity at the nest had resulted in desertion of the nest prior to a successful hatch by the female. Neither of these conjectures were, in the light of other evidence, found to be completely true. The evidence was as follows:

![Fig. 27](image-url)
(1) Canvas-back down found below in the nest structure, coupled with an absence of redhead down, indicated that the nest originally contained eggs laid by the canvas-back and that the redhead eggs had been intruded when or after the canvas-back eggs had been pushed into the water. The fact that no canvas-back eggs were found on the ground below the nest indicated they were either destroyed by a predator or that they had floated away from the nest after having been incubated and pushed into the water.

(2) Close examination of the seven, soiled eggs showed three which seemed slightly cleaner than the other four. Upon breaking the eggs, the cleaner three were found to have had embryos less than a week old, three had embryos almost of hatching age and the other egg was very malodorous, indicating it was infertile or had contained an embryo which died early in development several weeks previously.

(3) The three eggs with embryos less than a week old were parasitically deposited in the nest following the July 24 visit, while the other four eggs must have been in the nest during the first visit by the writer.

(4) Among the seven eggs and partly buried in the disorganized nest structure were remains of three, hatched redhead eggs, indicating that the female had left the nest with three redhead ducklings. The remaining redhead embryos apparently did not hatch early enough to be included in the canvas-back's brood.
(5) Since the bulrush culms had been dragged over the remaining eggs, the nest probably had been abandoned at the time of the disturbance, the female leaving with three redhead ducklings.

The reconstructed nest history was believed to have proceeded as follows:

1. The nest was built and the eggs laid by a canvas-back female.

2. Redhead female(s) deposited eggs in the nest prior to or during the loss of the canvas-back eggs from the nest.

3. Three more redhead eggs were laid after July 24 but before hatching took place, totaling ten redhead eggs in the nest.

4. The clutch began to hatch, muskrat disturbances occurred, and the female left the nest with three redhead ducklings.

Fortunately, most nest histories were less involved than the preceding one. With the low per cent of unsuccessful nests during the last two years of the study, few nest failures required such involved interpretation.

Of the 42 unsuccessful canvas-back nests listed in Table XII, abandonment by the female of 33 nests resulted in failures. Almost four-fifths (25 nests) of these desertions occurred in 1942. The principal cause of desertions in 1942 was promiscuous egg-laying, mainly by redhead, and to a lesser extent, by ruddy ducks. The only
other species known to lay eggs in canvas-back nests at Malheur were an American pintail (?) in 1942 and an American coot in 1947. Only one egg of each of the last two species was found in canvas-back nests.

The per cent of failure was greater in parasitized than in unparasitized nests during all three nesting seasons, although because of the small sample of successful nests in 1942 it need not be considered representative.

During 1946-7 when the greater proportion of observed nests were successful the difference was more easily seen. This fact is especially obvious in the three-year totals of Table XIII where the per cent of unsuccessful nests having

| Table XIII. Incidence of Foreign Eggs in Relation to Nest Success of the Canvas-back on the Malheur Refuge, Oregon |
|--------------------------------------------------|----------|----------|----------|----------|
| Total canvas-back nests                          | 1942a    | 1946a    | 1947a    | Totalsa  |
| Nests without foreign eggs                       |          |          |          |          |
| Successful                                       | 32       | 19       | 23       | 74       |
| Unsuccessful                                     | 6        | 4        | 5        | 15       |
| Nests with foreign eggs                          |          |          |          |          |
| Successful                                       | 26       | 15       | 18       | 59       |
| Unsuccessful                                     | 15       | 4        | 6        | 25       |

*Percentages are in parentheses.*
no foreign eggs was 42.8, while in nests with intruder eggs the per cent of nest failures was 54.1.

In 1942, the abandonment of 21 of 25 nests was attributable to parasitism. The two abandoned nests in 1946 and four of six abandoned nests in 1947 were also believed to have resulted from parasitism. A total of 27 of 33 abandoned nests was believed deserted because of nest parasitism during the three years.

The remaining six abandoned canvas-back nests were unsuccessful for a variety of reasons. One nest (not the nest with muskrat interference mentioned previously) was deserted following the shredding of bulrush culms on the eggs and nest by muskrats. The putrefied carcass of a sheep floating against another nest in 1942 seemed instrumental in its desertion. On Malheur Lake, a canvas-back nest built on a floating mat of dead bulrush was abandoned following a night of heavy winds and large waves during which the nest was badly battered. This was the only known instance of nest desertion or destruction directly attributable to the elements. Although much care was taken to avoid disturbance of nest and female, two nests in 1947 were believed to have been deserted following intrusion by the observer, and one 1942 nest listed as deserted due to some undetermined reason may also have been the result of human intrusion.

The only species of birds or mammals known to have
destroyed canvas-back nests or eggs in this study were the American raven and weasel or mink. The raven was held accountable for eight destructions, and a mustelid predator destroyed one clutch in a nest located on the bank of the Donner und Blitzen River near the refuge headquarters. In destroying eggs, the raven usually carried them from the nest to some promontory such as a haystack, island or dike before devouring them. The mustelid predator, very probably a small mink, consumed the eggs in and near the nest bowl, leaving tracks in the nearby mud and what appeared to be marks of canine teeth on some of the eggshells. The coyote was an important predator on terrestrial nests, but the canvas-backs habit of placing its nest over water reduced vulnerability to these larger mammals.

Desertion or destruction of a canvas-back nest did not always imply unproductivity of the attending female for the entire season. When the interruption occurred prior to the end of egg-laying, the female often was able to nest again, sometimes with greater chances of success. In 1942, all nests commenced during the first half of the nesting season ended unsuccessfully, while all successful nests were begun during the last half of the season and appeared to have been renestings. During the other years, successful nests were more uniformly scattered throughout the season, although the successful nests in 1947 seemed to be mainly initial attempts; with the higher success in 1946 and 1947
the proportion of renestings was greatly reduced.

Successful nests

Nesting studies of waterfowl in various parts of the United States and Canada have revealed varying degrees of nest success, both for locality and year in which they were conducted. Kalmbach (1939) made an analysis of nest success based on the reported findings of 22 field studies involving more than 7,600 nests of 13 species of ducks and the Canada goose. In this report he stated (p. 599)

Although the average success percentage of 63 . . . is considered good for waterfowl under varied nesting conditions, it must be considered as only a moderate or low standard of success for long-established, well-managed areas . . . it is not unreasonable to set a standard of 70 per cent hatch of eggs as a reasonable objective on managed areas.

Among the studies of Kalmbach's review were nest success tabulations of 59 per cent for 282 duck nests and a success of 63 per cent for 240 Canada goose nests found on the Malheur Refuge and reported by Sooter in 1939. Regarding this data Kalmbach (1939, p. 598) remarked "Sooter's work on the Canada goose on Malheur Refuge in 1938 also indicates, as did his duck-nest studies, the dangers still encountered by waterfowl on a newly managed area." Low (1945) found nest success percentages for the redhead in Iowa in 1938, 1939 and 1940 to be, respectively, about 55, 74 and 43.
The only study with nest success data on the canvas-back available for comparison is that of Furniss (1938) in central Saskatchewan. Of 14 canvas-back nests found in 1935, 12 (85.7 per cent) hatched, and of 26 nests in 1937, 22 (84.6 per cent) were successful. Occurring just south of the region of principal abundance of nesting canvas-backs, these figures may represent a higher average nest success attained by a species in the heart of its breeding range under favorable nesting conditions.

In computing the "nesting" success of waterfowl, one method has been widely used. This has been determination of the per cent of nests hatching and application of this figure to the estimated total number of resident pairs on a given area, giving the average and total success of a species. It proceeds on three, main assumptions: that the per cent of success found in the study approximates a good cross-section of actual success throughout the area, that the census of total, resident pairs was reasonably accurate and that all resident pairs were breeding pairs. It does not consider the significance of possible renestings after earlier failures by a female.

In the true sense of the word, this technique of estimating success can be referred to only as nest success, not nesting success. Nest success implies only the per cent of nests which hatched, while nesting success indicates the per cent of breeding pairs or females which successfully
hatched part or all of a clutch of eggs. During years of low initial success, nest success may be also low, but may be given a substantial boost by renesting success later in the season. Consequently, nest success may be very misleading, and nesting success of observed nests is the important consideration in computing seasonal production for a given area.

Errington (1942, p. 179) has discussed this phase of "compensatory reproduction" among some of the higher vertebrate populations in detail, and warns against "... errors arising from neglect of compensatory trends in reproductive and loss rates." He also states (p. 165) "... species that readily renest throughout a long breeding season—may be, moreover, few in number, subject to pronounced if not lethal handicaps, or undesirable from special human viewpoints." These factors will be discussed in the section on production.

The nesting success estimate used in this study involves the success of all observed nests, and makes provision for improvement of observed nest success percentages by consideration of the probability of renesting by some females after a number of earlier failures. This technique of success computation proceeds on the same three assumptions as the first method. In addition, this method requires an estimate of the approximate number of observed nests believed to have been followed by renesting, and
assumes that unobserved renestings were attended by the same degree of success as renestings under observation throughout the period.

Of the 42 unsuccessful canvas-back nests listed in Table XIII, 19 (45.1 per cent) were believed to have been followed by renesting attempts, and 23 (54.9 per cent) were believed to represent final, unsuccessful attempts. For the three years of the study, 14 (51.9 per cent) of 27 unsuccessful nests in 1942, two (50 per cent) of four in 1946 and three (50 per cent) of six unsuccessful nests in 1947 represented attempts probably followed by renesting.

Of the observed canvas-back nests, five (15.6 per cent) of 32 hatched in 1942, 13 (63.4 per cent) of 19 hatched in 1946, 14 (60.9 per cent) of 23 hatched in 1947. During the three nesting seasons at Malheur 32 (43.2 per cent) of 74 canvas-back nests were successfully hatched. These are nest success percentages. Evidence at the nest permitted definite fate determinations of success or failure in all of the 74 observed canvas-back nests, so no nests were left with undetermined fates.

The data in the two preceding paragraphs furnish information necessary for an estimate of the canvas-back nesting success percentage (synonomous with per cent of females hatching one or more eggs) for each of the three years of the investigation. This estimate may be expressed in the simple algebraic formula
\[ S = \frac{H}{N - (R + U)} \]

where

- \( S \) = nesting success percentage
- \( H \) = nests with hatched clutches
- \( N \) = total nests observed
- \( R \) = unsuccessful nests probably followed by re-nesting
- \( U \) = nests with undetermined fates

In the above computation of nesting success, the reason for subtracting the sum of \( R \) plus \( U \) from \( N \) may require additional explanation. Since female canvasbacks laying in nests represented by \( R \) presumably nested again with as great or greater opportunities for success, and since \( U \) should have agreed with the general nesting per cent of success (although \( U \) was not represented in this study, it might well be involved in other similar studies where fates of all nests could not be determined), it was necessary to subtract \( R \) and \( U \) from \( N \) before dividing \( H \) by the difference. The difference between \( H \) and \( N - (R + U) \), of course, represents the number of observed, final, unsuccessful, nesting attempts. Although this figure is of consequence in determining the estimated number of unproductive females, unsuccessful nest figures are not needed for computation of the rate of nesting success.

To apply the formula to the Malheur canvas-back nest data for the three-year period where

\[ \begin{align*}
N & = 74 \\
H & = 32 \\
R & = 19 \\
U & = 0
\end{align*} \]
Thus, the actual nesting success percentage of observed nests was 58.2 for the three seasons. By employing the same formula in computing yearly success, the following nesting success figures resulted: 1942, 27.8 per cent; 1946, 76.5 per cent; and 1947, 70.0 per cent, in contrast with 15.6 per cent, 68.4 per cent and 60.9 per cent, obtained for the three years when renesting was not considered.

In applying the nesting success percentage to the numbers of breeding pairs previously given in Table VI (230 in 1942, 128 in 1946 and 97 in 1947) we find the estimated total number of successful, resident, female canvas-backs to have been 64 in 1942, 98 in 1946 and 68 in 1947, or 230 for the three years. These numbers compared very favorably with the estimated numbers of broods observed on the refuge later in the season each year of the investigation, for the number of successful females and number of broods produced are identities.

Conversely, the reciprocals of nesting success percentages agreed closely with the difference between the estimated total number of breeding pairs occupying Malheur Refuge and the estimated number of canvas-back broods divided by estimated total number of breeding pairs. These "double-checks" provided indicators of the degree of accuracy of this method of nesting success computation.
In view of these considerations, the above formula is offered as providing the most simple and reasonably accurate method of nesting success computation for studies of the present type. The use of the nesting success formula in determining waterfowl production will be discussed later.

This nesting success formula was devised for application mainly to nesting waterfowl which ordinarily bring off no more than one brood per year. It may not apply in far-north breeding grounds where short breeding seasons may preclude possibilities of successful renesting. It might well find use in studies of upland game birds which habitually produce only one brood each year, such as grouse (Tetraonidae), partridges and quails (Perdicidae), pheasants (Phasianidae) and wild turkeys (Meleagridae), but only when the investigator undertakes a nesting study which permits him to obtain knowledge of local populations and allows a reasonably accurate determination of the number of nests under observation that were followed by renesting. This technique obviates the necessity of complete reliance on brood census methods in order to obtain production figures, but reliable brood estimates in various size- or age-categories will serve as a valuable check of the accuracy of this method and of the earlier census of breeding pairs as well.
Eggs and Clutches

This section and a later one on nest parasitism are intimately associated. Under the present topic are discussed some of the findings of the study regarding eggs and clutches of canvas-backs and other associated ducks, while the later section on parasitism will attempt to provide a more philosophical discussion of this problem and its significance in the ecology of the canvas-back.

The following description of canvas-back eggs was taken from an unpublished breeding habits study of the canvas-back in Oregon undertaken during 1942 (Erickson 1942, pp. 62-65).

Color of canvas-back eggs, in the terminology of Ridgway (1912), varied from "water-green" and "greenish-glaucous" to "pale olive-buff", but the greenish color, though sometimes only slightly discernible, was usually present. By frequent contacts with the damp body of the incubating bird as she returned to the nest from resting or feeding, the eggs were soiled. When this soiled coating was washed off, the eggs again approached their former color. The luster of newly laid canvas-back eggs was dull in comparison with the lighter and more glossy redhead eggs occurring parasitically in the nests. Also, canvas-back eggs were of greater average size than redhead eggs.

Previous to or when desertion occurred, the eggs were often pushed out of the nest... Since incubation usually was not greatly, if at all, advanced, the fresh eggs sank to the bottom. After remaining in water a few days, the egg shell began to undergo partial dissolution and became permeated with numerous small holes. Upon drying, characteristic colors and gloss of the eggs became obscured by the chalky texture of the shell. This
factor, coupled with intergrading color and gloss characteristics of canvas-back and redhead eggs, infrequently complicated their identification when both were found in the water beneath a nest. In those few instances, reliance was placed on a combination of the above characters and other available evidence.

Sizes and proportions were obtained by the measurements of 100 canvas-back eggs from 15 canvas-back nests throughout the nesting period. Most measured eggs were from deserted nests. The four size extremes are shown in the following dimensions given in millimeters: 69.8 x 44.7; 57.8 x 41.7; 67.5 x 48.8; and 66.6 x 41.2. The range in length of eggs was 12.0 millimeters and the difference in width between the two extremes was 7.6 millimeters. The average egg measured 64.4 millimeters by 44.9 millimeters. Bent (1923, p. 194) gave proportions based on the measurements of 88 canvas-back eggs showing the following four extremes: "66.8 by 43.2, 63 by 45.8, 56.5 by 40.7, and 57 by 38.8 millimeters," averaging 62.2 by 43.7 millimeters.

The eggs were uniformly ovate to elliptic-ovate in longitudinal outline although one odd-shaped egg was very elongate, measuring 66.6 by 41.2 millimeters. There was no apparent significance between the size, shape or proportions of canvas-back eggs and hatching success, failure, or laying sequence.

Remarks by Hochbaum (1944, p. 49) concerning descriptions of redhead and canvas-back eggs agree with those of the writer.

The egg of the Redhead is cream or buff color. I have never seen a green one, but I have seen some Canvasback eggs that were buff, very nearly like those of the Redhead. Redhead eggs average slightly smaller, though a large one may be of greater size than a small Canvasback egg. The average measurements of 43 Redhead eggs is 58.8 by 43.2 millimeters, while 103 Canvasback eggs average 63.7 by 44.6 millimeters.

Kendeligh (1941, p. 246) found that the "... average weight of the egg in the house wren and the number laid per
set decrease during the breeding season," and that the
"... average weight of eggs is greatest when their forma-
tion occurs at moderate air temperatures during the three
days previous to laying and decreases when air temperatures
are either raised or lowered."

The average incubation period of canvas-back eggs, as
determined from observations of nests found before incuba-
tion had begun and watched closely until hatching occurred
was 25 days, with known extremes of 24 and 29 days. Five
canvas-back and five redhead eggs taken from abandoned nests
in 1942 and incubated under a domestic hen, extremes of
24.98 days and 25.25 days of incubation were required for
the canvas-back eggs. The redhead eggs began to hatch
several hours earlier averaging 24.58 days of incubation.
Under natural conditions, this difference in incubation
periods was not noticeable, so there probably was little,
if any, danger of canvas-back females with compound clutches
leaving nests with earlier hatching redheads and abandoning
their own progeny. The period of audible pipping prior to
hatching was from 20 to 45.5 hours. The average canvas-back
brood hatched within a 48-hour period after 24 days of incu-
bation.

The period elapsing between emergence of the first
duckling from an egg and departure of the last juvenile
from the nest among observed nests ranged from 18 to 45
hours. While emerging from the eggs, the duckling was moist
and it seemed to have little control over its neck. The natal down dried rapidly, shedding small, scale-like sheaths which had enclosed the downy barbs, and within an hour the duckling had a dry, fluffy appearance (Fig. 28). Ducklings having hatched earlier often hastened the drying process.

![Canvas-back Nest at Hatching](image)

Fig. 28. Canvas-back nest at hatching showing three, dry ducklings and one, moist individual just emerging from the eggshell. This nest also is shown in Figs. 25 and 30.

and plumage-dressing of the later arrivals by preening the down of their moist nest-partners. The "egg-tooth" present on the bill of hatched ducklings disappeared toward the end of the second day.

The ducklings remained in or very near the nest until
most or all of the eggs had hatched and then were escorted away by the parent. When the majority of eggs had hatched and a disturbance caused the female to leave the nest with the brood, the female was not known to return to attend the unhatched eggs. If the disturbance occurred near the beginning of hatching, however, the female returned later, staying until most of the pipping embryos had emerged. Then, before leaving, the female covered the remaining eggs in much the same way that they had been covered during off-nest periods earlier in the nest's history.

In this study, the term clutch implies any number of eggs deposited in one group in a nest or nest-like structure. Final clutch denotes a clutch believed to represent the female's last attempt at nesting for the season regardless of possible previous nestings, while incomplete clutch indicates the female owner of the nest had not yet laid its last eggs for the season. Compound clutch is used to designate a number of eggs deposited together representing the contributions of more than one waterfowl female. A compound nest is one which contains two or more clutches, also called multiple nest by some writers.

In agreement with the findings of Low (1945) with the redhead in northwestern Iowa, canvas-backs did not appear to follow any definite schedule of egg-laying at the same time each day, but oviposited during most hours of daylight. Clean, warm eggs were found with cooler, slightly soiled
ones upon several visits to canvas-back nests at varying hours, indicating that they had just been laid. Hochbaum (1944, p. 49) reported of the canvas-back at Delta that "Eggs are laid in the morning," and Bennett (1938) stated that egg-laying of the blue-winged teal usually took place between seven a.m. and 11 a.m.

The principal factor influencing the amount of time necessary for the completion of a clutch, excepting in cases of parasitic intrusion, was the number of eggs it contained at completion. In some clutches of six eggs or less, the female deposited one egg per day, but in larger clutches, one or two days sometimes passed with no egg additions to the clutch, indicating that the 27-hour ovulation cycle which applies to the domestic fowl may be duplicated by a somewhat similar cycle in ovulation of canvas-backs.

In a study of the Arctic tern (Sterna paradisaea), Lack (1938) reported that although egg-laying is primarily dependent on the condition of the gonads, a more immediate control is exerted through the nervous system by which nesting conditions, sudden cold and other factors can limit breeding.

In this canvas-back study cold blustery weather temporarily checked commencement of nests, and unseasonably warm weather accelerated nest-building. Possibly cold or
unusually warm periods could result in retardation or
cessation of egg-laying during certain parts of a season,
but the present data do not warrant such a conclusion.

Among the 74 canvas-back nests found during the study,
59 (80 per cent) contained eggs laid by other species of
waterfowl, and only 15 nests (20 per cent) were free of
this interspecific intrusion (Table XIV). During the three

<table>
<thead>
<tr>
<th>Year</th>
<th>Canvas-back nests without foreign eggs</th>
<th>Canvas-back nests with foreign eggs</th>
<th>Total canvas-back nests</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>Number</td>
<td>Per Cent</td>
<td>Number</td>
</tr>
<tr>
<td>1942</td>
<td>6</td>
<td>19</td>
<td>26</td>
</tr>
<tr>
<td>1946</td>
<td>4</td>
<td>21</td>
<td>15</td>
</tr>
<tr>
<td>1947</td>
<td>5</td>
<td>22</td>
<td>18</td>
</tr>
<tr>
<td>Totals</td>
<td>15</td>
<td></td>
<td>59</td>
</tr>
<tr>
<td>Averages</td>
<td>20</td>
<td></td>
<td>80</td>
</tr>
</tbody>
</table>

nesting seasons the per cent of canvas-back nests containing
foreign eggs varied from only 78 per cent to 81 per cent.

The greatest difference in parasitic egg-deposition was
not in the per cent of nests receiving foreign eggs, but in
the number of intruder eggs which canvas-back nests received.
Thus, in 1942 a total of 581 eggs were known to have been
laid in observed canvas-back nests, 380 (65.4 per cent) of which had been laid by intruding females, while only 201 (34.6 per cent) were laid by the nest owners (Table XV).

Table XV. General Numerical Summary of Eggs Laid in 74 Observed Canvas-back Nests on the Malheur Refuge, Oregon

<table>
<thead>
<tr>
<th>Year</th>
<th>Total Nests</th>
<th>Host Eggs</th>
<th>Intruder Eggs</th>
<th>Host and Intruder Eggs</th>
<th>Average number of eggs per nest</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td></td>
<td>Host</td>
<td>Intruder</td>
<td>Host and Intruder</td>
<td></td>
</tr>
<tr>
<td>1942</td>
<td>32</td>
<td>581</td>
<td>201</td>
<td>380</td>
<td>18.2</td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td>6.3</td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td>11.9</td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td>34.6%</td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td>65.4%</td>
</tr>
<tr>
<td>1946</td>
<td>19&lt;sup&gt;a&lt;/sup&gt;</td>
<td>179</td>
<td>135</td>
<td>44</td>
<td>9.9</td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td>7.5</td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td>2.4</td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td>75.8%</td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td>24.2%</td>
</tr>
<tr>
<td>1947</td>
<td>23&lt;sup&gt;b&lt;/sup&gt;</td>
<td>230&lt;sup&gt;c&lt;/sup&gt;</td>
<td>146</td>
<td>34</td>
<td>11.3</td>
</tr>
<tr>
<td>Totals</td>
<td>74</td>
<td>990</td>
<td>482</td>
<td>508</td>
<td>13.1</td>
</tr>
</tbody>
</table>

<sup>a</sup> Contains one nest with undetermined number of eggs not included in computation of average number of eggs for each nest.

<sup>b</sup> Egg data for three of the 19 nests were obscure so were omitted from computation of average number of eggs for each nest.

<sup>c</sup> One canvas-back egg and three redhead eggs in this figure were omitted from computation of average number of eggs for each nest since they were remnants of destroyed nests.

In other words, intruding females laid almost two eggs for every host egg in canvas-back nests. An average of 18.2 eggs were laid in each of the 32 nests, only 6.3 of which were canvas-back eggs. The remaining 11.9 eggs were laid by intruders.
In the nesting seasons of 1946 and 1947 the composition of clutches returned to what is believed to be more "normal" for canvas-backs at Malheur. The proportion of nests containing foreign eggs was about the same, but with few exceptions intrusive egg-laying was much less sustained. In 1946 only 44 of 179 eggs in canvas-back nests were laid by other species, and in 1947, 84 of 230 eggs were laid by intruding females.

The number of eggs laid in a nest ranged from one to 58, the latter consisting of ten canvas-back eggs and 48 redhead eggs laid in a nest in 1942. During the observed history of this nest, the greatest number seen in the bowl on any visit was 16 eggs, only four of which were canvas-back, and on the following visit, only ten intruder eggs remained in the nest. Returning the following week, the nest was found to have been flattened and was without eggs. Coots and possibly ducks had been using the remaining nest structure for a resting or brooding station as evidenced by feathers and droppings. Apparently the female canvas-back had forsaken the nest shortly prior to the second visit by the observer. A search of the bottom of the pond within a one-yard radius of the nest revealed 58 eggs.

Fifteen canvas-back nests during the three years of the study were not parasitized. Of this number, seven were being incubated and appeared to have been initial nesting attempts with an average of 9.9 eggs per clutch. This is
believed to be the average number of canvas-back eggs laid on the first attempt by undisturbed females. At the Delta Station "The average of 38 complete Canvasback nests was 10 eggs, exclusive of Redhead intrusions" (Hochbaum 1944, p. 49). At Malheur, the average number of eggs laid in all final, unparasitized nestings was 8.6 canvas-back eggs.

In 18 interpreted final, compound, canvas-back clutches in 1942, an average of 7.8 canvas-back eggs were laid; in 13 final, compound clutches in 1946 the average was 7.5 eggs; and in 16 final, compound clutches in 1947, an average of 7.9 canvas-back eggs was deposited. The average number of canvas-back eggs to the nest in the 47 final nests during the three years was 7.7. During the same years, respectively, averages of 17.8, 3.3 and 5.0 intruder eggs were deposited in the same 47 canvas-back nests.

These data indicate that parasitic egg-laying by other species did not inhibit the size of clutch formation by the canvas-back host, for in 1942 the extremely sustained parasitism of canvas-back nests was not reflected by a decline in the average number of host eggs laid per nest during the same year. Indeed, the average number of host eggs laid in the 18, compound, final, canvas-back clutches in 1942 was identical with the three year average of 7.3 canvas-back eggs. According to the above findings the host duck did not reduce the output of eggs, even when its nest was filled to overflowing with foreign eggs. Instead it
continued laying until, presumably, this potential was ex-
hausted or until desertion of the nest occurred. Bennett
(1938, p. 49), in regard to the terrestrial-nesting blue-
winged teal, stated "In parasitized nests the number of
pheasant eggs lowered the number of duck eggs deposited in
the nest."

On the other hand, in an indirect manner, nest para-
sitism increased the average number of host eggs laid per
nesting female. The females often indiscriminately ejected
eggs from their nests, including those they had laid, then
deserted or continued to lay or incubate. If a large pro-
portion of the eggs was expelled from the nest and the
females still had not, to employ a phrase used by Herrick
(1935, p. 104), "... laid enough eggs to arouse their
brooding instinct ...," they might continue to lay until
a suitable clutch would provide the proper "contact stimulus,"
or until their ovulating potential was exhausted. Perhaps
the location of teal nests on land in Bennett's (1938) study,
as compared with the aquatic nests of canvas-backs, may have
prevented many host or parasitic eggs from being lost from
the nest, and thereby provided the "contact stimulus" which
curtailed further production of eggs before the female teal
had laid an average-sized clutch of her own eggs.

In 40 compound clutches, no eggs of which were found
out of the nest, an average of 7.4 canvas-back eggs were
laid. In 18 compound clutches, all of which lost one or
more eggs out of the nest into the water, a greater average of 8.9 canvas-back eggs were deposited, indicating that the nesting female may be able to compensate, to a limited extent, for some of the eggs lost from a clutch.

Overlooking eggs lost into the water from floating or semi-floating nests is a possible source of error in nesting studies or certain diving ducks that might tend to minimize both the apparent sizes of clutches and the apparent degree of parasitic intrusion. For this reason, at the termination of each nest history, a careful search was made for eggs on the ground under and adjacent to the nest, as well as for floating eggs among the nearby vegetation. The greatest single yield of any such search was the 53 eggs mentioned earlier.

The canvas-back only rarely became promiscuous in its egg-laying habits for in 77 redhead, 4 ruddy duck, one lesser scaup, 134 puddle duck and over 3,000 coot nests, only one intruded canvas-back egg was found. That egg was deposited with a redhead clutch which hatched, the pipping canvas-back embryo having been left to die in the nest.

There was no evidence to indicate that much, if any, intraspecific nest parasitism occurred among canvas-backs in southeastern Oregon. This belief is supported by the paucity of records in the literature on promiscuity of the canvas-back. Hochbaum (1944, p. 49) stated that "In 56 complete Redhead clutches . . . I found only 3 which con-
tained Canvasback eggs; each of these held 4 Canvasback eggs.

In nature the percentage of hatching success rarely equals that of nest success because nearly always a varying proportion of eggs fail to hatch in successful nests. The number of eggs hatching divided by the total number of eggs laid in canvas-back nests gives the hatching success of eggs. Obviously, since the rate of hatching success rarely approaches the nest success which, in turn, usually does not approach the nesting success, the waste of eggs even under "normal" nesting conditions may be considerable. This waste is usually apparent with such upland game birds as quail and pheasants, and during some years among various birds, the egg waste proceeds in inverse ratio to nest success. With some parasitized duck nests this loss is suffered not only by the nesting female but even more so by the intruder. The foreign eggs are unproductive because they are often laid too late in the nest history to receive adequate incubation.

Early egg losses in unsuccessful nests may find partial compensation in renesting but only when the later attempts are successful. Egg losses in unsuccessful nests followed by later losses of clutches merely augment this egg waste.

A general summary of nest success showing the numbers of host and intruder eggs laid in both successful and unsuccessful canvas-back nests during 1942, 1946 and 1947 is
given in Table XVI. In interpreting these data, the eggs listed in the **successful** and **failed** columns apply only to the number of eggs deposited in successful nests and unsuccessful nests, respectively, rather than to success or failure of individual eggs. The object of this tabulation is to indicate the great number of eggs laid in canvas-back nests in 1942, the year of extensive parasitism, as contrasted with the relatively few eggs laid in seasons of less sustained parasitism. This difference is mainly the result of heavy parasitism during 1942 when the average number of intruder eggs per successful and unsuccessful nests, respectively, was 10.2 and 12.2 eggs. The variation in averages for canvas-back eggs laid in all nests during the three years was only 0.8 egg compared with the variation in averages of 9.6 parasitic eggs.

The relation of parasitic egg-laying to the advance of the nesting season for each of the three years has been presented in Tables XVII, XVIII and XIX. These tables show that during 1942 the successful nests were limited to the last half of a long season of nest inceptions; in 1946, the successful nests were rather uniformly scattered throughout a relatively short nesting season; and in 1947, the earlier inceptions were attended by relatively higher hatching success (see also record of nest inceptions in Fig. 10).

In general, the relatively lighter parasitism of canvas-back nests during the first two weeks of nesting in 1942 and
### Table XVI. General Summary of Nest Success Showing Numbers of Host and Intruder Eggs Laid in Successful and Unsuccessful Canvas-back Nests on the Malheur Refuge, Oregon

<table>
<thead>
<tr>
<th></th>
<th>1942 nests</th>
<th>1946 nests</th>
<th>1947 nests</th>
<th>All nests</th>
</tr>
</thead>
<tbody>
<tr>
<td>Total canvas-back nests</td>
<td>5</td>
<td>27</td>
<td>32</td>
<td>13</td>
</tr>
<tr>
<td>Total eggs</td>
<td>93</td>
<td>488</td>
<td>581</td>
<td>137</td>
</tr>
<tr>
<td>Average no. of eggs laid per nest</td>
<td>18.6</td>
<td>18.1</td>
<td>18.2</td>
<td>10.5</td>
</tr>
<tr>
<td>Canvas-back eggs</td>
<td>42</td>
<td>159</td>
<td>201</td>
<td>104</td>
</tr>
<tr>
<td>Avg. no. of canvas-back eggs laid per nest</td>
<td>8.4</td>
<td>5.9</td>
<td>6.3</td>
<td>8.0</td>
</tr>
<tr>
<td>Intruder eggs</td>
<td>51</td>
<td>329</td>
<td>380</td>
<td>33</td>
</tr>
<tr>
<td>Avg. no. of intruder eggs laid per nest</td>
<td>10.2</td>
<td>12.2</td>
<td>11.9</td>
<td>2.5</td>
</tr>
</tbody>
</table>
### Table XVII
Relation of Parasitic Egg-laying to Advancement of the 1942 Canvas-Back Nesting Season on the Malheur Refuge, Oregon

<table>
<thead>
<tr>
<th></th>
<th>April 1-15&lt;sup&gt;a&lt;/sup&gt;</th>
<th>May 1-15&lt;sup&gt;a&lt;/sup&gt;</th>
<th>May 16-31&lt;sup&gt;a&lt;/sup&gt;</th>
<th>June 1-15&lt;sup&gt;a&lt;/sup&gt;</th>
<th>June 16-30&lt;sup&gt;a&lt;/sup&gt;</th>
<th>July 1-15&lt;sup&gt;a&lt;/sup&gt;</th>
<th>Totals</th>
</tr>
</thead>
<tbody>
<tr>
<td><strong>Successful nests</strong></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Canvas-back eggs</td>
<td></td>
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<td></td>
<td></td>
<td></td>
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<tr>
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<tr>
<td>Intruder eggs</td>
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<tr>
<td>Total eggs</td>
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</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td><strong>Unsuccessful nests</strong></td>
<td>1</td>
<td>5</td>
<td>7</td>
<td>6</td>
<td>6</td>
<td>2</td>
<td>27</td>
</tr>
<tr>
<td>Canvas-back eggs</td>
<td>10</td>
<td>23</td>
<td>57</td>
<td>30</td>
<td>24</td>
<td>10</td>
<td>159</td>
</tr>
<tr>
<td></td>
<td>(10.0)</td>
<td>(5.6)</td>
<td>(8.1)</td>
<td>(5.0)</td>
<td>(4.0)</td>
<td>(5.0)</td>
<td>(5.9)</td>
</tr>
<tr>
<td>Intruder eggs</td>
<td>0</td>
<td>47</td>
<td>119</td>
<td>70</td>
<td>65</td>
<td>28</td>
<td>329</td>
</tr>
<tr>
<td></td>
<td>(9.4)</td>
<td>(17.0)</td>
<td>(11.7)</td>
<td>(10.8)</td>
<td>(14.0)</td>
<td>(12.2)</td>
<td></td>
</tr>
<tr>
<td>Total eggs</td>
<td>10</td>
<td>75</td>
<td>176</td>
<td>100</td>
<td>89</td>
<td>38</td>
<td>438</td>
</tr>
<tr>
<td></td>
<td>(10.0)</td>
<td>(16.0)</td>
<td>(25.1)</td>
<td>(16.7)</td>
<td>(14.8)</td>
<td>(29.0)</td>
<td>(18.1)</td>
</tr>
<tr>
<td><strong>All nests</strong></td>
<td>1</td>
<td>5</td>
<td>7</td>
<td>8</td>
<td>7</td>
<td>4</td>
<td>32</td>
</tr>
<tr>
<td>Canvas-back eggs</td>
<td>10</td>
<td>23</td>
<td>57</td>
<td>46</td>
<td>40</td>
<td>20</td>
<td>201</td>
</tr>
<tr>
<td></td>
<td>(10.0)</td>
<td>(5.6)</td>
<td>(8.1)</td>
<td>(5.7)</td>
<td>(5.7)</td>
<td>(5.0)</td>
<td>(5.3)</td>
</tr>
<tr>
<td>Intruder eggs</td>
<td>0</td>
<td>47</td>
<td>119</td>
<td>83</td>
<td>94</td>
<td>37</td>
<td>380</td>
</tr>
<tr>
<td></td>
<td>(9.4)</td>
<td>(17.0)</td>
<td>(10.4)</td>
<td>(13.4)</td>
<td>(9.2)</td>
<td>(11.9)</td>
<td></td>
</tr>
<tr>
<td>Total eggs</td>
<td>10</td>
<td>75</td>
<td>176</td>
<td>129</td>
<td>134</td>
<td>57</td>
<td>581</td>
</tr>
<tr>
<td></td>
<td>(10.0)</td>
<td>(15.0)</td>
<td>(25.1)</td>
<td>(16.1)</td>
<td>(19.1)</td>
<td>(14.2)</td>
<td>(18.2)</td>
</tr>
</tbody>
</table>

<sup>a</sup>Figure in parentheses represents average number of eggs for each nest.
Table XVIII. Relation of Parasitic Egg-laying to Advancement of the 1946 Canvas-back Nesting Season on the Malheur Refuge, Oregon

<table>
<thead>
<tr>
<th>Periods of nest inceptions</th>
<th>1-15&lt;sup&gt;a&lt;/sup&gt;</th>
<th>18-30&lt;sup&gt;a&lt;/sup&gt;</th>
<th>1-15&lt;sup&gt;a&lt;/sup&gt;</th>
<th>16-31&lt;sup&gt;a&lt;/sup&gt;</th>
<th>1-15&lt;sup&gt;a&lt;/sup&gt;</th>
<th>Totals</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>April</td>
<td>May</td>
<td>June</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Successful nests</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Canvas-back eggs</td>
<td>17 (8.5)</td>
<td>33 (8.3)</td>
<td>26 (8.6)</td>
<td>28 (7.0)</td>
<td>104 (8.0)</td>
<td></td>
</tr>
<tr>
<td>Intruder eggs</td>
<td>1 (0.5)</td>
<td>5 (1.2)</td>
<td>2 (0.7)</td>
<td>25 (6.2)</td>
<td>33 (2.5)</td>
<td></td>
</tr>
<tr>
<td>Total eggs</td>
<td>18 (9.0)</td>
<td>38 (9.5)</td>
<td>28 (9.3)</td>
<td>53 (13.2)</td>
<td>137 (10.5)</td>
<td></td>
</tr>
<tr>
<td>Unsuccessful nests</td>
<td>1</td>
<td>2</td>
<td>3&lt;sup&gt;b&lt;/sup&gt;</td>
<td></td>
<td>6&lt;sup&gt;b&lt;/sup&gt;</td>
<td>187</td>
</tr>
<tr>
<td>Canvas-back eggs</td>
<td>8 (8.0)</td>
<td>13 (9.0)</td>
<td>5 (2.5)</td>
<td></td>
<td>31 (6.2)</td>
<td></td>
</tr>
<tr>
<td>Intruder eggs</td>
<td>0 (0)</td>
<td>4 (2.0)</td>
<td>7 (3.5)</td>
<td></td>
<td>11 (2.5)</td>
<td></td>
</tr>
<tr>
<td>Total eggs</td>
<td>8 (8.0)</td>
<td>22 (11.0)</td>
<td>12 (6.0)</td>
<td></td>
<td>42 (8.4)</td>
<td></td>
</tr>
<tr>
<td>All nests</td>
<td>1</td>
<td>4</td>
<td>6&lt;sup&gt;b&lt;/sup&gt;</td>
<td>4</td>
<td>19&lt;sup&gt;b&lt;/sup&gt;</td>
<td></td>
</tr>
<tr>
<td>Canvas-back eggs</td>
<td>8 (8.0)</td>
<td>35 (8.8)</td>
<td>33 (8.3)</td>
<td>31 (6.2)</td>
<td>135 (7.5)</td>
<td></td>
</tr>
<tr>
<td>Intruder eggs</td>
<td>0 (0)</td>
<td>5 (1.2)</td>
<td>5 (1.8)</td>
<td>9 (6.2)</td>
<td>44 (2.4)</td>
<td></td>
</tr>
<tr>
<td>Total eggs</td>
<td>8 (8.0)</td>
<td>40 (10.0)</td>
<td>38 (9.5)</td>
<td>40 (8.0)</td>
<td>179 (13.2)</td>
<td>199</td>
</tr>
</tbody>
</table>

<sup>a</sup>Figures in parentheses represent average number of eggs for each nest.

<sup>b</sup>Undetermined number of eggs in one nest not included in per cent computation.
Table XIX. Relation of Parasitic Egg-laying to Advancement of the 1947 Canvas-back Nesting Season on the Malheur Refuge, Oregon

<table>
<thead>
<tr>
<th>Periods of nest inceptions</th>
<th>April 16-30d</th>
<th>May 1-15d</th>
<th>June 16-31d</th>
<th>June 1-15d</th>
<th>Totals</th>
</tr>
</thead>
<tbody>
<tr>
<td>Successful nests</td>
<td>9</td>
<td>2</td>
<td>2</td>
<td>1</td>
<td>14</td>
</tr>
<tr>
<td>Canvas-back eggs</td>
<td>(8.1)</td>
<td>(7.0)</td>
<td>(5.5)</td>
<td>(7.0)</td>
<td>97</td>
</tr>
<tr>
<td>Intruder eggs</td>
<td>(5.0)</td>
<td>(3.0)</td>
<td>(5.7)</td>
<td></td>
<td>48</td>
</tr>
<tr>
<td>Total eggs</td>
<td>(13.1)</td>
<td>(10.0)</td>
<td>(5.5)</td>
<td>(7.0)</td>
<td>(11.2)</td>
</tr>
<tr>
<td>Unsuccessful nests</td>
<td>1</td>
<td>6</td>
<td>2</td>
<td></td>
<td>9</td>
</tr>
<tr>
<td>Canvas-back eggs</td>
<td>(7.0)</td>
<td>(8.2)</td>
<td>(1.0)</td>
<td>(7.0)</td>
<td>49</td>
</tr>
<tr>
<td>Intruder eggs</td>
<td>(2.0)</td>
<td>(6.2)</td>
<td>(3.0)</td>
<td></td>
<td>36</td>
</tr>
<tr>
<td>Total eggs</td>
<td>(9.0)</td>
<td>(14.4)</td>
<td>(4.0)</td>
<td>(12.1)</td>
<td></td>
</tr>
<tr>
<td>All canvas-back nests</td>
<td>10</td>
<td>8</td>
<td>4</td>
<td>1</td>
<td>23</td>
</tr>
<tr>
<td>Canvas-back eggs</td>
<td>(8.0)</td>
<td>(7.9)</td>
<td>(4.0)</td>
<td>(7.0)</td>
<td>(7.3)</td>
</tr>
<tr>
<td>Intruder eggs</td>
<td>(4.7)</td>
<td>(5.3)</td>
<td>(1.0)</td>
<td>(4.2)</td>
<td></td>
</tr>
<tr>
<td>Total eggs</td>
<td>(12.7)</td>
<td>(13.2)</td>
<td>(5.0)</td>
<td>(7.0)</td>
<td>(11.5)</td>
</tr>
</tbody>
</table>

*a*Includes nest with obscure egg data omitted from per cent computations.

*b*Includes two nests omitted from per cent computations.

*c*Includes three nests omitted from per cent computations.

*d*Figures in parentheses represent average number of eggs for each nest.

1946 (less evident in the shorter 1947 season) was believed a result of the tendency of the redhead to nest later than the canvas-back. Otherwise, the tables show no apparent
relation between the average number of parasitic eggs laid in canvas-back nests and the advance of the nesting season.

After the completion of each nest history all eggs and eggshell remains associated with the nest were carefully examined. These remaining eggs and shell fragments of hatched eggs could be found down in the bowl mixed with nest materials and down feathers where they had been trampled by parent female and brood. The eggs and shell remains indicated the number of successful eggs, for in hatching, the shells were pipped at the larger end in circular pattern, an opercular section of the shell being pushed open by the duckling in emerging.

The unhatched egg and shell remains found in one successful canvas-back nest are shown in Fig. 29. When first found the nest had eleven canvas-back eggs. The shell fragments indicated ten ducklings hatched in the nest. Most nests had less complete evidence of hatching, for some shell fragments were often lost over the side of the nest into the water. In contrast with the more delicate linings of unsuccessful, slightly incubated eggs, linings of hatched eggs were tougher and darker in color, separating more readily from the shell as observed by Girard (1939).

Eggs remaining in the nest after the termination of the nest history were carefully examined and the embryos, when present, were assigned approximate ages. The ages of the oldest, canvas-back embryos in abandoned nests often
indicated the duration of the nest history before desertion, although embryos sometimes died during incubation because of chilling or possibly the inherent weaknesses or imperfections of the egg itself. In these cases consideration of this source of error was exercised. The ages of embryos in intruder eggs, taking the age of canvas-back embryos into cognizance, frequently gave evidence of the time in the canvas-back nest history when intrusion occurred, and were used in determining the influence of parasitism in the abandonment of some victimized nests.
Fig. 30. Nine canvas-back and two redhead ducklings had left this nest with parent canvas-back. Twelve, unhatched, redhead eggs (one not visible) remained in nest. Linings from hatched eggs lie on nest ramp.

The occurrence of embryonated or unembryonated eggs in abandoned and destroyed, as well as hatched, canvas-back nests has been summarized in Tables XX, XXI and XXII. An example of embryonated eggs left in a successful nest after departure of the female is illustrated in Fig. 30. This nest, shown also in Figs. 25 and 28, contained seven, warm canvas-back eggs when found. Eight days later two more canvas-back eggs and two redhead eggs were found in the nest, while 20 days later the nest contained nine canvas-back eggs and 14 redhead eggs. Of this clutch of
Table XX. Embryo Development of Eggs in Abandoned Nests of the Canvas-back on the Malheur Refuge, Oregon

<table>
<thead>
<tr>
<th>Year</th>
<th>Nests</th>
<th>Eggs</th>
<th>Abandoned nests</th>
<th>Host eggs</th>
<th>Foreign eggs</th>
</tr>
</thead>
<tbody>
<tr>
<td>1942</td>
<td>25</td>
<td>465</td>
<td></td>
<td>39</td>
<td>96</td>
</tr>
<tr>
<td>1946</td>
<td>2</td>
<td>12</td>
<td></td>
<td>5</td>
<td></td>
</tr>
<tr>
<td>1947</td>
<td>6</td>
<td>65</td>
<td></td>
<td>25</td>
<td>8</td>
</tr>
<tr>
<td>3-yr totals</td>
<td>33</td>
<td>542</td>
<td></td>
<td>64</td>
<td>109</td>
</tr>
</tbody>
</table>

Table XXI. Embryo Development of Eggs in Destroyed Nests of the Canvas-back on the Malheur Refuge, Ore.

<table>
<thead>
<tr>
<th>Year</th>
<th>Nests</th>
<th>Eggs</th>
<th>Destroyed nests</th>
<th>Host eggs</th>
<th>Foreign eggs</th>
</tr>
</thead>
<tbody>
<tr>
<td>1942</td>
<td>2</td>
<td>23</td>
<td></td>
<td>13</td>
<td>10</td>
</tr>
<tr>
<td>1946</td>
<td>4</td>
<td>30</td>
<td></td>
<td>10</td>
<td>8</td>
</tr>
<tr>
<td>1947</td>
<td>3</td>
<td>20</td>
<td></td>
<td>7</td>
<td></td>
</tr>
<tr>
<td>3-yr totals</td>
<td>9</td>
<td>73</td>
<td></td>
<td>17</td>
<td>29</td>
</tr>
</tbody>
</table>

Table XXII. Embryo Development of Eggs in Successful Nests of the Canvas-back on the Malheur Refuge, Ore.

<table>
<thead>
<tr>
<th>Year</th>
<th>Nests</th>
<th>Eggs</th>
<th>Successful nests</th>
<th>Unhatched host eggs</th>
<th>Unhatched foreign eggs</th>
</tr>
</thead>
<tbody>
<tr>
<td>1942</td>
<td>5</td>
<td>93</td>
<td></td>
<td>1</td>
<td>18</td>
</tr>
<tr>
<td>1946</td>
<td>13</td>
<td>137</td>
<td></td>
<td>12</td>
<td>5</td>
</tr>
<tr>
<td>1947</td>
<td>14</td>
<td>145</td>
<td></td>
<td>6</td>
<td>7</td>
</tr>
<tr>
<td>3-yr totals</td>
<td>32</td>
<td>375</td>
<td></td>
<td>19</td>
<td>30</td>
</tr>
</tbody>
</table>
23 eggs nine canvas-back and the two original redhead eggs hatched, leaving twelve unhatched redhead eggs in the nest of which 11 are visible in Fig. 30. All unhatched eggs contained embryos in varying stages of incubation from nearly mature embryos to eggs only slightly incubated.

The embryo development of eggs in successful nests was listed in Tables XX, XXI, and XXII under two categories, abandoned and destroyed nests. Under abandoned nests, as might be expected, the proportion of eggs with embryos usually was greater among host than among foreign eggs since the latter were introduced into the nest during all parts of the nest history from the time of nest inception to the time of hatching. In fact, redheads frequently laid eggs in canvas-back nests which had already hatched or been deserted until the nest either sank below the surface from the weight of the extra eggs and lack of constant repair of the nest (Fig. 31) or until the eggs began to spill out. Any eggs laid after the female canvas-back had abandoned the nest or left with brood were not included in tabulations for they were not considered part of the canvas-back's compound clutch.

In one instance, a redhead appropriated an unsuccessful canvas-back nest about a week after the female had abandoned it. The original eggs had been lost into the water. The redhead female built up the nest, laid its own clutch and finally produced a brood. This can not be considered an
Fig. 31. Canvas-back nest in hardstem bulrush abandoned and sinking in absence of maintenance by the owner.

act of intrusive egg-deposition, for the host female had already gone and the succeeding redhead female, except for occupying the same site in nesting, performed all other nesting duties itself. In one other case, a ruddy duck female appropriated a canvas-back nest after the host female had departed with the brood, but the second occupant's egg-laying was not followed by incubation or nest maintenance, the structure eventually sinking and immersing the eggs.
The great waste of eggs during the year of low success, 1942, as well as during the year of greatest nest success, 1946, is shown in Table XXIII. During 1942, only 39 eggs (6.7 per cent) hatched from a total of 581 canvas-back and intruder eggs deposited in 32 canvas-back nests. Of these 39 hatched eggs, only 23 (4.0 per cent of the total eggs) produced canvas-back ducklings, while 542 (93.3 per cent) eggs remained unhatched! Of these unhatched eggs, 178 were canvas-back and 364 were intruder eggs.

The impact of nest parasitism in depressing the biotic potential of the species was most effective in 1942, but in 1946 and 1947, though the egg waste still was considerable (72 eggs or 40.2 per cent and 133 eggs or 57.8 per cent, respectively), the hatching percentage of eggs was greatly improved. Compared with nest success percentages for each of the three years of the study of 15.6, 68.4 and 60.9, respectively, the egg hatching success of 6.7, 59.8 and 42.2 per cent showed a definite reduction as a result of unhatched eggs in successful canvas-back nests, mostly eggs of intruders.

The number and per cent of eggs hatched in observed, successful, canvas-back nests during the three seasons have been recorded in Table XXIV. These data show that even in successful nests the waste of eggs was considerable, though the canvas-back eggs in successful nests were more successful than foreign eggs in the same nests.
Table XXIII. Hatching Success of Eggs Laid in Canvas-Back Nests on the Malheur Refuge, Oregon

<table>
<thead>
<tr>
<th>Year</th>
<th>No. &amp; % of total eggs</th>
<th>Eggs in all nests</th>
<th>Hatched eggs</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td></td>
<td>Total</td>
<td>Host</td>
</tr>
<tr>
<td>1942</td>
<td>Number (32 Per nests) cent</td>
<td>581</td>
<td>201</td>
</tr>
<tr>
<td></td>
<td>1946 (19 Per nests) cent</td>
<td>179</td>
<td>135</td>
</tr>
<tr>
<td></td>
<td>1947 (23 Per nests) cent</td>
<td>230</td>
<td>146</td>
</tr>
<tr>
<td></td>
<td>3-yr Number totals (74 Per nests) cent</td>
<td>990</td>
<td>482</td>
</tr>
</tbody>
</table>

Having previously discussed the role of nest parasitism in resultant desertions by canvas-back females which caused such an extremely low nesting success in 1942, and during the other years to a lesser extent, attention is now called to another way in which intruded eggs may reduce the total number of canvas-back eggs that hatch during years of parasitic intrusion. The hatching of parasitic eggs in a given canvas-back clutch form a complementary as well as supplementary part of that clutch. To state this idea in a different way, the hatching of host and intruder ducklings at victimized, canvas-back nests finds a reduced average number of host progeny leaving such nests.
Table XXIV. Number and Per Cent of Eggs Hatched in Observed, Successful, Canvas-back Nests on the Malheur Refuge, Oregon

<table>
<thead>
<tr>
<th>Year</th>
<th>Eggs and Per Cent</th>
<th>Eggs in Successful nests</th>
<th>Eggs hatched</th>
<th>Average eggs hatched per nest</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td></td>
<td>Total</td>
<td>Host</td>
<td>Foreign</td>
</tr>
<tr>
<td>1942</td>
<td>Eggs</td>
<td>93</td>
<td>42</td>
<td>51</td>
</tr>
<tr>
<td></td>
<td>(5 successful Per cent)</td>
<td>100</td>
<td>45.2</td>
<td>54.8</td>
</tr>
<tr>
<td>1946</td>
<td>Eggs</td>
<td>137</td>
<td>104</td>
<td>33</td>
</tr>
<tr>
<td></td>
<td>(13 successful Per cent)</td>
<td>100</td>
<td>75.9</td>
<td>24.1</td>
</tr>
<tr>
<td>1947</td>
<td>Eggs</td>
<td>145</td>
<td>97</td>
<td>48</td>
</tr>
<tr>
<td></td>
<td>(14 successful Per cent)</td>
<td>100</td>
<td>66.9</td>
<td>33.1</td>
</tr>
<tr>
<td>3-yr</td>
<td>Eggs totals Avg.</td>
<td>375</td>
<td>243</td>
<td>132</td>
</tr>
<tr>
<td></td>
<td>(32 Per cent successful nests)</td>
<td>100</td>
<td>62.7</td>
<td>37.3</td>
</tr>
</tbody>
</table>
Information from this canvas-back investigation indicated that approximately the same proportion of canvas-back nests were victimized each year (Table XIV), but the average number of intruded eggs for each nest in different years showed wide variation (Tables XV, XVI, XVII, XX and XXIII). Nest records in the literature, e.g. Bent (1902, 1923), Phillips (1923), Hochbaum (1944) and Low (1945), provide evidence of the widespread occurrence of the parasitic habits of some diving ducks, with special reference to those habits of the redhead and ruddy duck. If the habit is a frequent or usual one with these two species throughout most of their range, this production depressant could be more important than might be realized.

In order to evaluate the influence of parasitic intrusion in reducing the number of canvas-back eggs hatching, a comparison of clutch success was made of successful, unparasitized nests with eggs hatched in successful, parasitized canvas-back nests. The results of this comparison have been presented in Table XXV.

Data on seven unparasitized and 24 parasitized, successful, canvas-back nests involving fates of 375 canvas-back and intruder eggs have been considered in Table XXV. Of 56 eggs in unparasitized nests, 51 (91.1 per cent) hatched. Comparable figures for all eggs in parasitized nests show a hatch of 60.2 per cent, this latter figure being depressed largely by the low success (37.1 per cent) of intruder eggs.
Table XXV. Comparison of Egg-hatching in Successful, Unparasitized, Canvas-back Nests with Egg-hatching in Successful, Parasitized, Canvas-back Nests on the Malheur Refuge during 1942, 1946 and 1947

<table>
<thead>
<tr>
<th></th>
<th>Successful nests</th>
<th>Parasitized nests</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>Unparasitized</td>
<td>Parasitized</td>
</tr>
<tr>
<td></td>
<td>nests</td>
<td>Totals</td>
</tr>
<tr>
<td>Total nests</td>
<td>7</td>
<td>24</td>
</tr>
<tr>
<td>Total eggs</td>
<td>56</td>
<td>319</td>
</tr>
<tr>
<td>Total eggs hatched</td>
<td>51</td>
<td>192</td>
</tr>
<tr>
<td>Per cent of total</td>
<td>91.1</td>
<td>60.2</td>
</tr>
<tr>
<td>eggs hatched</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Avg. no. eggs for each nest</td>
<td>8.0</td>
<td>13.3</td>
</tr>
<tr>
<td>Avg. no. eggs hatched</td>
<td>7.3</td>
<td>8.0</td>
</tr>
</tbody>
</table>

aDoes not include one 1947 unparasitized nest with incomplete data on eggs.

Compared with the success of 91.1 per cent of host eggs in unparasitized nests, however, canvas-back eggs in parasitized clutches exhibit a success of only 76.5 per cent, a difference of 14.6 per cent. This difference could not be attributed to a substantially smaller, average number of canvas-back eggs laid in each mixed clutch for that difference is only 0.2 egg.

Considering the fact that an average of eight canvas-back eggs were laid in each unparasitized nest and 13.3 eggs...
(7.8 host eggs and 5.5 intruder eggs) in parasitized nests, one might expect a relatively larger brood of host and intruder ducklings to leave parasitized nests. This was not found to be true, for the difference was only 0.7 duckling in favor of parasitized nests. Of the eight ducklings which left the average, parasitized, canvas-back nest, two were from eggs laid by intruding females, and only six canvas-backs were hatched in the average victimized nest. The difference between the average canvas-back production of the two types of nest, 7.3 hatching in unparasitized nests and 6.0 in parasitized nests, is believed to represent a result of parasitic intrusion in canvas-back nests at Malheur.

The average size of broods leaving parasitized nests was quite similar to the number of ducklings leaving unparasitized nests, however, because parasitic ducklings formed a complementary part of the brood. The ratio of canvas-back ducklings to redhead ducklings hatched in canvas-back nests was 1.44:1 in 1942; 4.35:1 in 1946; and 6.46:1 in 1947. Comparison of the species composition of compound broods leaving observed nests with the composition of canvas-back broods observed in brood-census work will be made under the section on production.

For several reasons, fewer canvas-back ducklings were believed to have hatched in the average, parasitized canvas-back nest. When many intruder eggs were added to the clutch, a number of host eggs, as previously mentioned, often were
lost, together with some intruder eggs, over the side of
the nest as the female continued to lay or incubate, the
female appearing not to discriminate between her own eggs
and those of intruding females. This egg loss was the
most important factor in reducing the number of canvas-
back eggs which hatched in parasitized nests. Thus, in
general, the greater the number of intruded eggs the fewer
canvas-back eggs hatched. In one successful 1942 nest
which had contained 16 canvas-back eggs and 29 redhead
eggs, only one canvas-back egg and five redhead eggs
hatched.

Larger clutches increased the tasks of nest maintenance.
In several instances, the female's efforts at upkeep did
not keep pace with parasitic intrusion and some of the in-
cubated eggs, including those of the canvas-back, in the
lower part of the nest bowl, were partly immersed and
chilled in the cool water, the embryos dying and thereby
decreasing the number of canvas-back juveniles leaving
the nest.

As a result of obvious physical limitations, females
were unable to successfully cover and incubate all eggs
in some large clutches. Thus, some of the eggs located
peripherally may easily have chilled during the low tempera-
tures at night.
Production

The appearance and number of broods present on the research area during and following the nesting season, correlated with earlier estimated breeding populations and success of known nests, were expressions of the nesting success of the canvas-back. Production, as employed herein, is construed to mean the total number of birds reaching flight age. Consequently, the annual reproductive increment can not be based merely on the estimated total ducklings hatched, for decimating factors during brood-rearing reduced the average sizes of broods in successive age-class groups.

Brood-rearing

The hazards in the life of a duckling commenced before it left the nest. Although an egg was considered successful when the duckling emerged from the shell, weak ducklings, or ducklings which hatched after the female had left the nest with the brood usually died of exposure during the cold nights prevalent at the moderately high altitude even during mid-summer. A few of these "orphans" may have joined other canvas-back or redhead broods, but in view of the fewness of canvas-back broods over a vast refuge area, together with the spread of the period of hatching, foster-
age of parent-less ducklings by other females probably saved few if any of the late-hatched birds. This belief was given limited support by a lack of observed canvas-back ducklings in the many redhead broods seen about the refuge, although some redhead females occasionally were seen with puddle duck progeny in their broods. Prolonged incubation and late-hatching produced weaker birds less able to cope with outside conditions even when attended by parents. Single ducklings found dead in the nest on three occasions in 1946 may have died under the feet of the female or from some physical imperfection. Low (1943) reported a deformity of a redhead duckling in which the legs were not attached normally.

The problems of post-hatching nest sanitation which confront altricial species were obviated by an early departure by canvas-back and other duck broods, so their nests were usually very clean-appearing after hatching, though varying amounts of eggshell fragments and unhatched eggs usually remained as evidence of success.

With observed canvas-back broods, the greatest motility was shown during the first week after hatching. This apparent restlessness seemed to continue until the brood arrived in a suitable area. There the growing ducklings would be observed from day to day. The distance which broods traveled during this early period of motility, based on observations of broods believed hatched in discovered
nests, ranged from 200 yards from the nest site to four miles. In the first instance, the small size of the pond in which the nest was located, together with the isolated nature of that water body, may have been the main factor preventing an exodus to a more distant brood-rearing location. When such habitat limitations were not in evidence, broods usually went much farther from the nest to locate in rearing areas.

The longest, known journey made by a canvas-back brood from nest to rearing site of four miles in Unit 10 appeared prompted by receding water. In this case, the female and brood of ten canvas-back ducklings and one redhead duckling followed the dwindling watercourse down the Blitzen Valley until they reached a three-acre, temporary pond where they were seen while growing to flight size (Fig. 32). The only time that this brood was absent from the pond between its arrival and eventual flight was for five days when the level of the pond was reduced 9-10 inches. The female and brood had promptly moved to a nearby pond. When the previous water level was restored by turning in additional water, the family returned.

The observed tendency of broods to disperse from their natal location may have served the purpose of reducing losses to predators possibly attracted to the locality during nesting, or of lessening the concentration of broods which would reduce competition for food in areas of high duck-nesting.
Fig. 32. Female with brood of nine canvas-backs and one redhead over half grown. Brood previously contained another duckling which disappeared when less than one fourth grown.

densities. This latter idea seems the more logical. No observations of strife between females with broods were observed to indicate that the cause of brood dispersal was intraspecific intolerance. The possibility of habitat inadequacy near the nest site prompting this departure appeared unlikely, for broods from other nests often frequented sites of previously hatched canvas-back nests, while the original tenants moved to more distant rearing locations.

Although the broods often remained in the ponds or section of the lake where hatched, they tended to move to
areas of more open water. Some canvas-back ducklings less than half grown were seen in the open water of Malheur Lake over a mile from the nearest cover, while on Boca Lake (Fig. 33), canvas-back broods could not be induced to seek cover along the shores when followed by canoe, but always sought to escape by diving, probably because the emergent cover growing peripherally on the lake occurred in very shallow water.

The movement of broods out of natal areas was sometimes impeded by various physical obstacles. Emergent vegetation
seemed little, if any, hindrance to the movement of canvas-back broods. One female nesting in the middle of a large bulrush-bur-reed marsh led its brood through one quarter mile of dense emergent plant cover to a more open pond. Upland was definitely believed to be a barrier to canvas-back broods when it reached elevations as to prevent sight of one pond by ducks on the water in another pond. Thus, in an extremely small, rectangular pond (Fig. 34) located on the opposite side of a dike from an excellent, large, rearing pond, a brood of canvas-backs remained over six weeks, not leaving until the water level began to subside. Other
instances of this reluctance to leave "visually isolated" brooding areas for what appeared to be better nearby ponds were witnessed each year. These obstacles were readily surmounted, however, when the water levels in brood-rearing ponds became low, and the parent and brood were required to find more permanent water.

No observed preference was shown for any specific type of plant cover, but canvas-back ducklings in emergencies would usually resort to the nearest emergent vegetation. Because bulrush, cat-tail and bur-reed grew in most brood-rearing ponds and permitted entrance of juveniles among the spaced culms, all three were readily utilized as escape cover. The fact that bulrush was most frequently used seemed to result from its abundance in most deeper ponds.

The female usually was quite deliberate in leading the brood away from a disturbance, in contrast with the frenzied maneuvers of most puddle ducks. When hard-pressed, the female usually took flight, or less often briefly feigned injury while the brood swam rapidly away, scurried on the water toward cover or dived. The female sometimes alighted nearby and appeared to try diverting attention of the observer by modest feigning, directing the escape efforts of the brood by low, nasal, vocal utterances not unlike those produced by females flying over discovered nests. Following disappearance of the observer, broods again could be seen in open water, within a half-hour after the disturbance, to
all outward appearances having forgotten about the interruption.

Rallying of broods was usually accomplished in three ways: by vocal direction of the female, by sight and sounds of other members of the brood, or through a combination of these actions. In dense cover, the female usually circled over the area where the brood had disappeared before realighting, possibly trying to see or hear members of the brood. The ducklings remained quiet for a few minutes while in hiding, then began to peep, softly at first but increasing in volume proportionately with the time spent away from the other ducklings. Soon, however, the brood again could be seen with the female, swimming in compact formation immediately behind the parent or straggled out in search of food. Ordinarily, the male took no active part in brood-rearing, although a few drakes were seen in attendance of females and broods. Under such circumstances, when the female and drake parted momentarily to feed or swim around obstructions, the brood almost invariably followed the female. No evidence indicated that the drake's presence with female and brood resulted from more than a casual interest of the male.

Canvas-back ducklings did not have to be taught to feed. One duckling found hatching in a previously deserted canvas-back nest was kept under observation for several days. Less than five hours after hatching it was seen jumping at flies and other insects within sight. During the first two weeks
the female helped the ducklings obtain food by tipping or
diving and bringing food items to the surface where the
ducklings quickly snatched them.

While feeding the juveniles fanned out in all direc-
tions from their parent. Observations of downy juveniles,
unchecked by stomach analysis, indicated that the food
during the first two weeks consisted largely of small in-
vertebrates found on or near the water surface. Soon be-
coming adept at diving, they began to feed on rootstocks,
tubers and other vegetative parts of submerged, aquatic
plants.

Two unattended juveniles, about one third grown, seen
in the valley pond shown in Fig. 16, were unusually tame,
allowing observation of their habits and actions virtually
at arm’s-length (Fig. 35) from the boat. When first en-
countered they were resting together, but at the boat’s ap-
proach, started swimming slowly away (Fig. 35a). As the
boat followed, they at first appeared uneasy, stretching
the wings and legs (Fig. 35b and d) and later, as an ex-
pression of apparent concern or fatigue, executed the neck-
stretch (Fig. 35c) in a manner similar to but less experi-
enced than the analogous courtship gesture of courting
adults.

Within five minutes the ducklings seemed to be much
less apprehensive of the boat and occupant. Approaching
water containing sago pondweed in depths more than six
feet, they cast quick glances to right and left, then dived in grebe-like manner. The water was clear enough to show their descent was beyond three feet. They remained below from five to 12 seconds, apparently swallowing most of the food while submerged. When the ducklings became widely separated while engrossed in feeding or when one duckling dived just before the other's emergence, the latter would peep softly, swim a short distance, then quickly dive again.

Moving to shallow water of less than 12 inches depth, the feeding habits were altered. Before diving or dabbling they peered into the water (Fig. 35e), then dived or merely tipped in very shallow water with legs and tail spread wide (Fig. 35f). Returning to a floating position with tail spread, they frequently began an alternate water-treading motion with the legs and feet at the rate of four or five strokes per second (Fig. 35g and h), apparently creating water currents which stirred up the silt or mud and thus exposed the pondweed roots and other coarser or more dense items of food. This habit is a common occurrence among feeding adult ducks, Canada geese and swans.

The ducklings were feeding mostly on the roots and shoots of sago pondweed, and so energetically were they engaged in feeding that they gasped and breathed heavily upon each return to the surface, audibly "chewing" and swallowing items which they had found. They were intolerant of crowding, the more rufous-headed duckling driving off the other
Fig. 35. Swimming, feeding, resting and fatigue attitudes of two parentless, juvenile canvas-backs.
when its feeding efforts were hampered. They were much more wary while loafing than while feeding, treading and diving within two feet of the boat's gunwale. When resting with head on back (Fig. 35d) they were more cautious, remaining about six feet distant from the boat with at least one eye open, paddling enough to maintain or increase the distance. The progress of growth to near-adult size of the two ducklings was followed to the time when they left the Unit 8 pond to join a group of 38 juvenile canvas-backs in a nearby Unit 9 pond shown in Fig. 5.

Feeding of broods was carried on during all hours of the day and some were seen feeding in the evening as late as nine p.m. Juvenile feeding was most active from seven to nine o'clock in the morning and from four to seven o'clock in the evening. The coldness of early morning, often below 50 degrees Fahrenheit even in mid-July (Fig. 10), seemed to delay extensive feeding until well after sunrise. By seven o'clock the air was usually quite warm and feeding was evident among all species of duck broods. When cold temperatures persisted throughout the entire day, feeding activity was less intense but of greater duration. Rain squalls accompanied by warm, strong winds did not seem to curtail the feeding of broods. Instead, the ducklings showed accelerated activity as they darted over the surface, presumably taking advantage of an "insect windfall."

At night, as well as during loafing periods in the day,
females were seen resting with their broods on small islands, flattened vegetation (Fig. 36), muskrat lodges, floating logs and other eminences out of but immediately adjacent to

Fig. 36. Lodged Baltic rush cover served as loafing platforms out of water for broods and for molting ducks as indicated by scattered feathers.

water. During the warmest part of hot summer days the female and brood remained in the shade of tall, emergent, plant cover, avoiding exposure to the sun by restricting feeding to the earlier and later cool parts of each day.

While attended by the female, broods of canvas-backs less than half grown showed a disinclination to band, but when unattended, they banded more readily. Banding was
evident late in the brood-rearing season, after most broods were parentless. Even while attended by the parent, juveniles of various broods often became mixed during the day but returned to their respective parents toward evening. Consequently, the best times for brood-censusing were from six to nine o'clock in the morning and five to seven o'clock in the evening when the identity of individual brood and parent was more distinct.

The tendency of canvas-back broods to band in the absence of parental care was less evident early in the brood-rearing season, possibly because of the greater need of parental warmth during low, nocturnal temperatures. Nearly all broods had attending females prior to the first week of July each year, including those juveniles nearly of flight size. Broods occurring on isolated ponds also retained their unity and distinctiveness much better than broods in large ponds or on Malheur Lake and Boca Lake.

When accosted in large ponds, the bands of canvas-back, redhead and ruddy duck juveniles remained in open water while other juveniles sought cover. In small ponds of one fourth acre or less the juveniles usually proceeded to nearby cover. Many small, shallow ponds in the Blitzen Valley were margined with spikerush (mainly Eleocharis palustris) which in turn was bordered with hardstem bulrush (Fig. 37). The intermediate cover of spikerush was sought during slight disturbances, but when major disturbances occurred, such as
appearance of a human near the pond, the ducklings swam through the spikerush into the hardstem bulrush.

Parents showed greatest apparent concern for their broods early in the season but this attention waned as the season advanced. By August, some broods having ducklings less than one quarter grown were commonly seen unescorted. The decrease in dependence of the young on the parent as the weather grew warmer also may have been instrumental in severing the filial ties.

The canvas-back parent did not readily adopt strange ducklings hatched in nests other than its own, in contrast
with the redhead which on one occasion was seen leading a line of 24 ducklings of at least four different ages and of two species. In another instance, a female redhead approaching and showing possible adopting actions toward a canvas-back brood was quickly driven away by the parent. Canvas-back ducklings, too, seemed reluctant to accept foster parents, and when permanent separation from the parent occurred, they rarely joined another escorted brood except when escaping during an intrusion by an observer.

Early in August many juvenile canvas-backs were on the wing and at this time smaller ponds of the valley which had previously contained broods were abandoned by them. Coincidentally with their disappearance in the small ponds, the populations of juveniles on larger, open ponds and on Boca Lake began to show increases, indicating that the juveniles were beginning to band. A few, adult females occasionally were present in these aggregations although they showed no interest in even the younger members of these flocks. The greatest concentration of nearly full-grown juveniles seen in the Blitzen Valley was found in a small pond of Unit 9 where a total of 39 young canvas-backs and an associating group of 120 redheads and ruddy ducks were seen on August 10, 1946 in less than three acres of open water densely grown with sago pondweed. Broods of several species of puddle ducks, totaling over 200 individuals were found nearer the shoreline of this pond.
Brood ponds were usually shallower, often had more dense growths of submergent vegetation and the per cent of emergent plant cover was often greater than on ponds where juveniles banded. Boca Lake, however, was an especially fine open body of water for brood-rearing and banding of all species of ducks nesting in that general area, frequently containing more than 500 broods during July and August in addition to many incoming, late-summer immigrant ducks. The greatest number of waterfowl seen on this lake during any single visit was from 40,000 to 45,000 ducks and coots in the first week of September, 1946. Of this aggregate, about 75 per cent were coots.

In view of the detailed descriptions of juvenile canvasbacks recorded by Phillips (1923), Bent (1923), Kortright (1943), Hochbaum (1944) and others, further elaboration seems unnecessary. One observation in this regard, however, seems of value. The iris in the eye of a juvenile canvasback drake captured on August 31, when it was barely able to fly, changed from the usual brown color to vermilion within three months.

Continuous observations upon individual canvas-back broods indicated that the juveniles began to make short flights soon after the tenth week of life. Bent (1923) reported the flight age to be between ten and 12 weeks while Hochbaum (1944) indicated that the first flight occurred between the age of nine and 11 weeks. After the
juveniles had begun to develop their flight feathers, they were seen frequently flapping their wings and often ran on the water flapping vigorously as if testing their pinions. What were believed to be exhibitions of early flight experience usually were very labored attempts to get into the air often followed by awkward landings. In later flights, young canvas-backs circled ponds or flew some distance away, but usually returned, in no regular formation.

Coincidentally with commencement of flight among juveniles on the valley ponds, the size of duckling rafts began to decrease as the flying juveniles moved to the larger bodies of water on the refuge, such as Boca Lake, Mud Lake and Malheur Lake. At the end of the 1947 brood-rearing season, many of the locally produced canvas-back juveniles were believed to have left the refuge for Mud Lake was completely dry, Malheur Lake was very low and the very few, full-grown, canvas-back juveniles seen there, together with those on Boca Lake, represented only a small part of the refuge production.

Annual reproductive increment

Previous discussion has included explanation of the techniques for estimating the total number of breeding pairs and nesting success percentages for the three years. Before the annual reproductive increment from canvas-back nests on the research area is computed, however, the details of
brood-census methods will be covered.

With the purpose of obtaining information on the number of broods, survival of ducklings and proportion of canvasback and parasitic ducklings in each family, brood counts were made throughout each brood-rearing season. The number of canvas-back and parasitic ducklings, approximate age, and exact locality were noted for each brood. In 1942 the estimated ages of broods were placed in three categories: Class I, less than three weeks old; Class II, from three to six weeks; and Class III, juveniles more than six weeks.

Regarding brood counts Erickson (1942, pp.103-105) reported:

... that the greatest juvenile mortality seemed to be between the first and sixth weeks of life when the broods were reduced an average of 1.7 individuals.

Subsequent work during 1946 and 1947 revealed that nearly all of the decrease noted between Classes II and III in 1942 resulted from separation of ducklings from the rest of the parental brood rather than from juvenile mortality. Consequently, in the present study, computations of production were based upon the number of ducklings surviving and reaching the second class. On the basis of this method, a greater number of surviving juveniles was believed to apply for the 1942 reproductive increment.

Near the end of the first year of the study, the merits of following closely the progress of individual broods towards maturity became apparent, the main shortcoming of the
previously described random-sample method of brood census being that as a result of the small number of broods present on the refuge, the few which were counted might easily not be taken at random, and therefore not be true samples. Thus, a very few, large or small broods seen frequently in conspicuous places could easily have distorted census records.

Consequently, the method used in 1942 was abandoned in 1946 and 1947 in favor of a system which required following closely the histories of as many specific broods as possible throughout the brood-rearing season each year. Since the broods spent most of the early and late parts of the day on open water, both habitat and their habits contributed to a more accurate census with the later-used technique. By this system an attempt was made to obtain representative brood samples during each week of the rearing season, so that reduced brood sizes late in the season hatching from smaller clutches would be considered in the determination of production as well as larger, earlier broods.

In order to follow the sequence of events in the life of a growing brood of ducks, some method or combination of methods was necessary in order to establish the identity of each brood seen in the field which would enable its recognition when again encountered. Identity of most broods was readily established from the application of part or all of the following items of evidence. The recognition of no brood could be based on any single item of this evidence.
When most of the checks were in agreement, however, the identity of the brood was established with reasonable certainty. These tools of identification were as follows:

(1) Time element. Broods hatching throughout the season could be segregated by periods when seen.

(2) Space element. Extremely low densities of nesting canvas-backs and resulting isolation of many broods aided recognition.

(3) Topography. Broods showed a reluctance to cross dikes, broad expanses of arid upland or drained marshland, and often were effectively confined in certain isolated ponds until of flight size or until compelled to leave by certain adverse, habitat changes.

(4) Observations on hatched nests. Numbers and ages of broods seen in the field could sometimes be correlated with progeny leaving previously hatched nests.

(5) Size or age of ducklings. The size of members of a brood was an extremely important criterion in establishing the identity of a brood. For example, a brood of six ducklings three-fourths grown on July 1 should not be confused with half-grown young seen on a later date.

(6) Numerical size of canvas-back brood. The variation in number of ducklings in each brood was evidence of reduction due to mortality or banding together of parentless ducklings.

(7) Species composition of the brood. The numbers of
both canvas-back and parasitic ducklings in a brood were very important, not only in identifying the brood, but in determining survival of the two species in the same brood.

(8) Relative immotility of broods after the initial period of movement. This feature has already been discussed and is closely linked with the space element. Localizing of the activities of a brood to a few acres of pond aided recognition to a great degree.

(9) Distinctive peculiarities in habits of adult and brood. In some areas where more than one brood was represented, certain females with broods followed a given escape procedure, the same response to the observer's appearance or showed the same degree of apparent fear or disregard of such observational intrusion.

The tendency of canvas-back broods to occupy the more open water areas of the refuge permitted a fairly representative census of broods throughout the rearing season each year. Because of this factor, and by virtue of the above methods of establishing brood identity, the proportion of local canvas-back broods believed to have been counted to broods produced during the three years was 39 per cent in 1942, 61 per cent in 1946 and 74 per cent in 1947. The low figure for 1942 may be explained by a lack of transportation facilities for visiting valley units more frequently during the brood-rearing season together with the greater difficulty of systematically inventorying broods on Malheur Lake.
and in valley ponds during that highwater year.

This method of brood study is believed to be much more accurate than the usual custom of trying to obtain random counts of representative sizes or ages, and consequent mortality in broods. The random-count method is most convenient in the majority of studies, but because many observed, canvas-back broods at Malheur could be recognized with a reasonable amount of certainty after having been seen previously, this method of brood-counting was preferred.

The data noted with each brood observation were: number of ducklings in brood, approximate age of brood, species composition of the brood if possible (this was usually undertaken with ducklings more than one fourth grown, because distinction between younger redhead and canvas-back ducklings was often very difficult or impossible under ordinary field conditions of brood observation), whether or not attended by the parent, exact locality where seen, and date on which the observation was recorded. Each brood was assigned a reference number. Whenever a brood was recognized in the field, its reference number was plotted on a map of the refuge, showing not only the distribution but also movements of the broods.

The number of recognizable broods encountered during 1946 was 42, and an identical number could be recognized in 1947. Some broods were located in ponds passed almost daily in field work and the brood shown in Fig. 32 was seen
more than 30 times during its development. A total of 133 brood observations was made in 1946 and 96 was made in 1947, averaging 2.7 observations per brood during the two years.

The brood data were listed under three age-class categories: I, newly hatched to four weeks (downy juveniles); II, four to seven weeks (ducklings past the downy stage to three fourths grown); III, over seven weeks old (more than three fourths grown). Under each of the three age-class groups, the brood counts were segregated according to species composition of canvas-back broods as follows: canvas-back ducklings, redhead ducklings and undetermined species. For each age-class group, however, data from any specific brood appeared only once, regardless of the number of times the brood was observed while of a specific age-class. For example, if Brood 24 was seen having six ducklings of undetermined species composition, age-class I on June 20, 1946 and was seen in age-class III on July 18 and July 20 with five ducklings, only two entries were made, one each under age-classes I and III. The columns for all categories were then totaled, the results appearing in Table XXVI.

During each year the per cent of redheads to the brood decreased with each succeeding age-class, while the reverse was true with canvas-back ducklings, possibly indicating that a differential mortality may exist among the two species within the brood, or more probably, that redheads tend to
Table XXVI. General Summary of the Species Composition of Canvas-back Broods on the Malheur Refuge, Oregon

<table>
<thead>
<tr>
<th>Age-class</th>
<th>No. of Individuals</th>
<th>1946a</th>
<th>1947a</th>
<th>1946-1947 Totalsa</th>
</tr>
</thead>
<tbody>
<tr>
<td>Age-class I (1-4 wks)</td>
<td>28</td>
<td>33 (71.7)</td>
<td>38 (84.4)</td>
<td>71 (78.1)</td>
</tr>
<tr>
<td>Canvas-back</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Redhead</td>
<td>13 (28.3)</td>
<td>7 (15.6)</td>
<td>20 (21.9)</td>
<td></td>
</tr>
<tr>
<td>Undetermined species</td>
<td>140</td>
<td>126</td>
<td>266</td>
<td></td>
</tr>
<tr>
<td>Average brood-size</td>
<td>6.6</td>
<td>6.1</td>
<td>6.35</td>
<td></td>
</tr>
<tr>
<td>Age-class II (4-7 wks)</td>
<td>14</td>
<td>30 (85.7)</td>
<td>37 (94.9)</td>
<td>67 (90.3)</td>
</tr>
<tr>
<td>Canvas-back</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Redhead</td>
<td>5 (14.3)</td>
<td>2 (5.1)</td>
<td>7 (9.7)</td>
<td></td>
</tr>
<tr>
<td>Undetermined species</td>
<td>52</td>
<td>56</td>
<td>108</td>
<td></td>
</tr>
<tr>
<td>Average brood size</td>
<td>6.2</td>
<td>5.9</td>
<td>6.05</td>
<td></td>
</tr>
<tr>
<td>Age-class III (over 7 wks)</td>
<td>14</td>
<td>65 (95.6)</td>
<td>23 (95.8)</td>
<td>88 (95.7)</td>
</tr>
<tr>
<td>Canvas-back</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Redhead</td>
<td>3 (4.4)</td>
<td>1 (4.2)</td>
<td>4 (4.3)</td>
<td></td>
</tr>
<tr>
<td>Undetermined species</td>
<td>7</td>
<td>29</td>
<td>36</td>
<td></td>
</tr>
<tr>
<td>Average brood size</td>
<td>5.4</td>
<td>5.3</td>
<td>5.35</td>
<td></td>
</tr>
</tbody>
</table>

*Per cent figures are in parentheses.*
leave the foster-parent canvas-back earlier than the young canvas-backs. Again, unfortunately, the data are too few to permit any conclusions.

Dividing the total broods by the total ducklings seen in each age-class gave the average size of broods for the given group. The average number of eggs hatched in each successful nest during 1946 and 1947, respectively, was 8.2 and 6.9 (Table XXIV). The two-year difference of 1.3 ducklings leaving observed canvas-back nests was reflected in the brood census results in Table XXVI which shows that the average size of broods in age-class I during the two years was 6.6 and 6.1 ducklings.

The difference between the average number of ducklings leaving observed canvas-back nests and the average brood of age-class I in the field (1.6 ducklings in 1946 and 0.8 ducklings in 1947) may have arisen from mortality following departure from the nest. Decimation of ducklings was also evident between age-classes I and II. Losses in broods already having survived for seven weeks were believed negligible. Based on continuous field observation of broods, the drop in number of ducklings in broods between age-classes II and III was explained by departure of ducklings from parent to join aggregations of nearly full-grown diving duck juveniles in the larger ponds, for coincidentally with the decrease in size of broods in age-class III, nearby groups of parent-less ducklings and numbers of single, un-
attended juveniles showed corresponding increases.

With knowledge of the approximate number of breeding pairs of canvas-backs on the refuge, their nesting success percentage, the per cent of canvas-back ducklings in canvas-back broods at hatching and the average number of juveniles reaching age-class II, the annual reproductive increment (A.R.I.) may be computed. This is done by multiplying the estimated number of breeding pairs on the refuge by their average nesting success percentage, by the per cent of canvas-back ducklings in canvas-back broods at hatching, by the average number of juveniles per brood reaching age-class II as follows:

1942 230 pairs x 27.8% x 59.0% x 5.2 juv. = 196 A.R.I.
1946 128 pairs x 76.5% x 81.3% x 6.2 juv. = 494 A.R.I.
1946 97 pairs x 70.0% x 86.6% x 5.9 juv. = 347 A.R.I.

The number of redheads hatched in canvas-back nests surviving to age-class II may be figured the same way by substitution of the per cent of redhead ducklings per canvas-back brood at hatching, i.e., the reciprocal of the canvas-back percentage. Thus, 123 redheads in 1942, 114 in 1946, and 54 in 1947 were contributed from the nesting efforts of the female canvas-backs at Malheur Refuge. The total increment from canvas-back nests for both species was 319 in 1942, 608 in 1946 and 401 in 1947. These findings, presented in Table XXVII, illustrate the complex array of inter-related factors which had to be considered before a reasonably ac-
curate estimate of yearly production could be obtained.

In 1942, the estimated number of potential breeding adults remaining on the refuge was 564 compared with a production of 196 surviving canvas-back juveniles, furnishing an adult:juvenile ratio of 1:0.56. With reduced nest parasitism and higher nesting success in 1946 and 1947, this ratio was more favorably changed to 1:1.97 and 1:1.70, respectively, i.e., for each adult canvas-back remaining on the Malheur Refuge during 1942, 1946 and 1947, 0.56, 1.97 and 1.70 canvas-backs were produced.

Table XXVII. Production Data for the Canvas-back on the Malheur Refuge, Oregon

<table>
<thead>
<tr>
<th></th>
<th>1942</th>
<th>1946</th>
<th>1947</th>
</tr>
</thead>
<tbody>
<tr>
<td>Estimated total canvas-back breeding population</td>
<td>564</td>
<td>308</td>
<td>236</td>
</tr>
<tr>
<td>Estimated number of breeding pairs</td>
<td>230</td>
<td>128</td>
<td>97</td>
</tr>
<tr>
<td>Total surviving juveniles from canvas-back nests</td>
<td>319</td>
<td>608</td>
<td>401</td>
</tr>
<tr>
<td>Total canvas-back surviving juveniles</td>
<td>196</td>
<td>494</td>
<td>347</td>
</tr>
<tr>
<td>Total redhead surviving juveniles</td>
<td>123</td>
<td>114</td>
<td>54</td>
</tr>
<tr>
<td>Canvas-back adult:progeny ratio</td>
<td>1:0.56</td>
<td>1:1.97</td>
<td>1:1.70</td>
</tr>
</tbody>
</table>
Mortality

The only observed mortality of juveniles consisted of three, newly hatched ducklings in 1946 and one found dead in the nest in 1947. Two of the 1946 casualties resulted from strangulation among the nest vegetation and the other one hatched late. The 1947 casualty was a redhead duckling that hatched in a weakened condition after the eggshell of a previously hatched canvas-back, which had covered the pipping end of the hatching redhead egg (Fig. 38) had been removed. No observed evidence of mortality from predation was seen, but the chance was small of finding a few victims over such a large area.

Fig. 38. Partly pipped redhead egg prevented from hatching by enveloping eggshell of previously hatched canvas-back duckling.
Predation. The habit of most canvas-back females of building their nests over water rendered them less vulnerable to strictly terrestrial predators such as marmots (Marmota) and ground squirrels. However, this aquatic location did not protect the nest and eggs from some other predators to be treated by groups in this discussion.

(1) Lower vertebrates. Several species of snakes were common on the refuge. Rattlesnakes (Crotalus) were encountered in the dry upland but were never seen in the marsh. Garter snakes (Thamnophis), bullsnakes (Pituophis) and blue-racers (Coluber) were common in the marsh and were sometimes seen swimming across open water of small ponds, but no predation could be attributed to them. Large predaceous fish were unknown in the area with the exception of black bass (Micropterus salmoides) in Malheur Lake and trout (Salmonidae) in the streams and canals of the Blitzen Valley.

(2) Birds. Potential predators on adult canvas-backs, eggs or ducklings included the black-crowned night heron, various hawks, falcons and eagles (Falconidae), coot, various gulls and terns (Laridae), owls (Strigidae) and magpies, crows and ravens.

In the only observed predation by a black-crowned night heron on a diving duck, the heron captured a two-week-old lesser scaup at a river dam and flew away with it in its bill, the downy duckling actively wriggling.

Swainson's hawks frequented telephone poles overlooking
ponds occupied by duck and coot broods in late summer. On several occasions, this predator was seen devouring freshly killed coots, and one was encountered with a warm, juvenile gadwall about one third grown. After capture, the prey was usually carried to the nearest pole and promptly decapitated.

Marsh hawks frequently coursed low over marsh vegetation but were not observed catching coots or ducks. One marsh hawk was flushed from a freshly killed juvenile redhead. The progress of marsh hawks over ponds could often be followed by watching the splashes of coots as they dived at the hawk's close approach.

The only observation of any falcon molesting a duck was an unsuccessful attempt by a duck hawk to capture a cinnamon teal in flight. In spite of the apparent fear shown by waterfowl upon the approach of eagles, no duck predation by these raptors was seen.

During most of the nesting season, the coot outnumbered all species of ducks by at least four to one on most refuge nesting habitat, and the ratio was greater in most open-water areas. No friction between coots and diving ducks was noted and a nesting canvas-back was seen to hatch a clutch within six feet of a coot nest.

California gulls were common on the refuge and these birds twice were seen unsuccessfully trying to capture juvenile coots, while on another occasion one California gull caught and swallowed two downy mallard ducklings from
a brood of seven which were being escorted across a stretch of open water by the parent. The adult mallard tried in vain to protect the brood by lunging at the gull, the latter evading the duck female and snatching a duckling from the closely clustered brood behind the parent. One duckling was consumed in mid-air and the other was swallowed after the gull had flown a short distance and alighted. By that time the mallard had led the brood into protecting rushes.

On another occasion, a California gull captured a pied-billed grebe not more than ten days old. The grebes dived as the gull approached and as one juvenile reappeared nearby, the gull caught it. This same technique might easily be employed in capturing juvenile canvas-backs. Although three species of terns were present, none was seen in any acts of waterfowl predation.

Montana horned owls and short-eared owls frequented canvas-back habitat. Owl pellets examined throughout the spring and summer each year showed heavy utilization of coots but no remains of canvas-back adults or juveniles.

Magpies were most common along the willow-bordered streams and canals of the Blitzen Valley and Double-O Ranch units but they were not witnessed pilfering waterfowl nests. The stomachs of crow nestlings were examined for eggshell fragments. Instead, they usually were filled with a large variety of insects, insect larvae, and fruits, principally squaw currants (Ribes cereum).
The American raven was the most serious predator on eggs of over-water nesting waterfowl at the Malheur Refuge. During spring, ravens around Malheur Lake obtained a large part of their fare from an abundance of dead muskrats, apparently victims of an undetermined form of epizootic. By the time that the Canada geese nested in abundance, however, few dead muskrats remained, and the raven abandoned the role of scavenger to include eggs in its diet. Goose eggs usually were consumed at the nest because of their size and weight, but duck eggs often were carried to some nearby land eminence, or if in the middle of the lake, to a muskrat lodge not far away. Unless disturbed during the act, ravens usually destroyed or consumed every egg. In carrying the eggs, the bill was either thrust into, and often through, the egg or else eggs were carried unbroken in the bill. When the nest was a substantial structure, the eggs usually were eaten where they lay.

Cole Island Dike in Unit 12 was a common rendezvous of ravens. From this structure they made periodic forays into Malheur Lake, and also plundered many terrestrial nests on the dike. Hundreds of duck and coot eggshells, showing typical raven handiwork, were found along the dike during the three years of the study. Less than one per cent of all eggshell remains were of the canvas-back. Many of the destroyed eggs may have come from nests previously deserted, so the importance of eggshell evidence from the production standpoint is difficult to evaluate. Eggs remaining in the
duck nest until they became foul usually were merely pecked open by ravens and left uneaten in the nest.

During the three nesting seasons, raven damage was believed responsible for the failure of eight canvas-back nests (10.8 per cent), including two in 1942, three in 1946 and three in 1947. Ravens also attacked four other canvas-back nests which had previously been deserted or destroyed. The stomach of one raven collected near Malheur Lake contained remains of a mallard duckling one fourth grown believed to have been picked up as carrion. No raven predation on living ducklings was witnessed.

(3) Mammals. The most prominent mammalian predator on the refuge was the mountain coyote. No canvas-back nests were known to have been destroyed by coyotes although they were seen systematically searching drying sloughs and edges of ponds and lakes for various forms of prey and carrion. Probably the greatest degree of vulnerability of canvas-back broods to coyotes occurred late in the summer when many of the smaller temporary ponds began to dry and the partly grown residents were compelled to seek deeper water. Traveling overland to the nearest water, the parent and brood would have been easy victims. However, because canvas-backs usually left ponds when the levels began to decline, they were able to swim away before the avenues of escape became completely dry. Mallard, shoveller, cinnamon teal and pintail broods often remained in ponds which had
lost all but two or three inches of water and were more exposed to a large variety of predators. Coyote scats and stomachs examined during all months of the study revealed no positive evidence of canvas-back predation.

Only one of the 74 canvas-back nests was believed destroyed by a mammal, excluding the one deserted as a result of muskrat activity, and that failure was attributed to predation by a large weasel or small mink. With its nest located on the bank of the Donner und Blitzen River, falling water levels compelled the female canvas-back to walk through the mud to water, leaving a trail to the nest for the predator to follow.

Badgers were found in most sections of the refuge and were responsible for localized damage to terrestrial waterfowl nests. Concentrated puddle duck nest predation on Cole Island Dike during 1947 was attributed to coyote, badger and raven predation. One raccoon was seen swimming across a large open pond through a formation of canvas-backs and redheads which paid very slight heed to this mammal. The raccoon then inspected each nearby clump of vegetation and finally curled up on a muskrat lodge to sleep. Skunks (Mephitis, Spilogale) were present but appeared to avoid the aquatic habitat in which most canvas-backs nested and reared their broods.
Diseases and parasites. The only known afflictions taking a toll of canvas-backs at Malheur Refuge during the study were lead-poisoning and botulism during the spring and late summer of 1942 as earlier reported (Erickson 1942, pp. 108, 109).

During the first two weeks of April, five dead and two sick male canvas-backs were found in or near the entrance of the Donner und Blitzen River into Malheur Lake. The two sick ducks were brought to the laboratory and given an alimentary flushing treatment by the use of a rubber syringe equipped with a rigid, 10-inch, tubular attachment.

The five dead canvas-backs were very emaciated, and the stomachs had green, semi-deteriorated linings. The sixth and surviving canvas-back was in fair flesh when found . . . but had difficulty in walking and swimming. After three weeks of care, this bird again possessed full control of its movements, even snapping its bill vigorously when the observer entered the enclosure. The other sick canvas-back, which was found in an advanced state of emaciation, had lost completely its control of the limbs, head and neck by the time of discovery. Failing to respond to treatment, it died the fifth day after being brought to the laboratory.

Stomachs of the six, dead, lead-poisoned canvas-backs contained a dominant proportion of coarse grit or small stones and a small quantity of seeds of hardstem bulrush, large-fruited bur-reed, pondweed (Potamogeton spp.), and water milfoil. No green plant matter was found during the examinations. Only one lead shot . . . reduced in size, was found.

In addition to canvas-backs, one male redhead, two male ring-necked ducks, one male and one female American golden-eye, two male lesser scaups, one male mallard, one male baldpate and twenty coots were found in the same area and appeared to have died from lead-poisoning. No suitable explanation for the heavy preponderance of males among these
casualties was evident. In proportion to the number of individuals present, canvas-backs exceeded all other species of ducks dying apparently as a result of this poisoning.

More waterfowl died from the effects of botulism than any other sickness on the refuge. During the botulism epizootic of 1942, between 2,000 and 3,000 waterfowl were estimated to have perished, while approximately 1,500 died in 1947. One sick mallard showed typical symptoms of botulism and a half-dozen ducks were found dead during the entire 1946 nesting season, but they may have been victims of some other ailment. The single, known canvas-back drake possibly having died of this sickness was found along Cole Island Dike in 1942. Dates of first appearance of sick ducks were July 20, 1942 and July 28, 1947, lasting through August and most of September both years.

For a brief description of the 1942 outbreak, reference is made to Erickson (1942, pp. 110, 111).

This important duck sickness accounted for only one dead male canvas-back found in the vicinity of Cole Island Dike on August 28, just 40 days after the first botulism-sick duck was found. Most dead ducks were found near the south end of the dike on Malheur Lake although a few were found in other units of the Refuge. The water at the south end of the dike contained much decaying plant debris lodged in drifts along the shore and in shallow water.

Canvas-backs were rarely seen near the outbreak area which may account for their very low mortality. However, sick or dead adult ruddy ducks and downy juvenile redheads were occasionally found. The deep-water feeding habits of most diving ducks kept them away from the shallow-water infection.
centers . . . Pintails, mallards, shovellers, cinnamon teal, green-winged teal, and baldpates all were abundantly represented in the mortality list.

The first botulistic duck, a cinnamon teal, was found on July 20 and the last occurrences were recorded during the first half of October.

Several conditions seemed to provide favorable conditions for the botulism outbreak. A vast barrier of hardstem bulrush culms drifted against the west side of Cole Island Dike was decomposing, providing organic pollution and anaerobic conditions apparently favorable to culturing of the organism during late July, August and September. Dying ducks augmented this organic pollution, and other outbreak foci appeared.

During the 1947 botulism epizootic, the area near the mouth of the Donner und Blitzen River in Malheur Lake was the center of abundance for sick ducks. The river water might have been expected to have been better oxygenated than the water of Malheur Lake and thus have been less suitable for propagation of the botulism organism. By acquiring a heavy, organic solute load during drainage of Blitzen Valley hayfields in July, the river water mixing with the previously stagnant water of milfoil-choked, mud-margined Malheur Lake may have provided an excellent outbreak culture medium.

Sooter (1937) and Low (1945) reported leeches (Thero-myzon occidentalis) infesting waterfowl in Iowa. A few small leeches were found on the feathers of juvenile and adult canvas-backs, but only in sick or dead waterfowl
did they occupy the oral and nasal cavities, apparently indicating that weakened waterfowl were more vulnerable to this infestation.

During the course of the investigation, bird fleas (Ceratophyllus) were found infesting some of the over-water nests of the canvas-back and redhead. The fleas were most abundant in late-season nests retaining the downy lining. In one canvas-back nest three dozen fleas were found, and probably an equal number escaped observation. No fleas were found on any of the adult canvas-backs examined, but fleas could be seen crawling through the natal down of the newly hatched ducklings. A brief review of the literature on Siphonatera indicated this may be the first record of fleas being found in a duck nest, and may also be the first record of the occurrence of fleas on ducks. No fleas were noted in nests other than floating ones. From the standpoint of mortality of the host, these fleas probably had little if any importance. However, infested ducklings may have been more restless in the presence of this source of possible irritation, and thereby influenced the female to leave the nest with the brood before hatching was completed.

In possible association with the occurrence of bird fleas in canvas-back nests, Peale's meadow mice occasionally built nests and reared young in the canvas-back nest structures. The mouse nests were found only in canvas-back and
redhead nests over water—never in terrestrial nests of any duck species, and were made by shredding the duck nest material. The mouse nests were usually located to one side of the nest bowl and the entrance led to the outside of the duck nest. Birth of the mouse litter more frequently occurred after the female duck had left the nest, although when the female mouse became a tenant early in the duck nest history, the litter was born while the duck was yet incubating.

The presence of mice and their nests was not known to interfere directly with the normal nesting of the canvasback, but all observed duck nests having field mice nests also contained bird fleas. Other fleas of the genus Ceratophyllus, normally occupying birds as hosts, have been found on various rodents and other mammals (Hubbard, 1947), and it does not seem beyond reason that the meadow mouse might be an alternative host on which the flea spends the winter. Consequently, the fleas may occur with canvasbacks only at the duck nest, and remain with the mice either in the mice nest or on the mouse itself throughout the winter. Infestation the following year could then be accomplished upon a visit to the duck nest by the mouse.

The conditions which foster mouse occupancy of over-water duck nests are not well understood. Some seasonal ponds of the Blitzen Valley are dry during the late fall, winter and early spring. As these ponds are flooded during
the spring and the mice are displaced, they may remain in
the dense bulrush clumps. They were not marooned, however,
for the mice were seen to go readily into the water and to
swim rapidly, the aquatic habitat apparently providing no
special hardship for them.

The only other ectoparasite found directly on a full-
grown, juvenile canvas-back was a bird louse (*Austromenopon
leucoxanthum*).

In the intestine of a juvenile, full-grown, female
canvas-back found dead on Goose Lake near Jewell, Hamilton
County, Iowa in November, 1947 by Dr. Paul L. Errington of
Iowa State College and kindly presented to the writer, were
collected the following endoparasites as determined by
Mr. Allen McIntosh of the Bureau of Animal Industry, U.S.
Department of Agriculture: nine tapeworms (*Hymenolepis
megalops*) and one fluke (*Echinostomum revolutum*) from the
large intestine, and another fluke (*Zycotyle lunatum*) from
the caecum. O'Roek (1928) reported finding tapeworms
(*Hymenolepis sp.?*) in two of three canvas-backs collected
in California.

No mortality of canvas-backs could be traced to the ac-
tivities of ectoparasites, but the severe emaciation and
ultimate death of one adult, male canvas-back was believed
a result of intense endoparasitic infestation. This bird
was easily captured during July, 1947 in a small pond of
Unit 8, for it seemed too weak to fly. All flight feathers
were present and their frayed appearance indicated that the drake had not yet passed through the flightless period. Desiring to follow the molt of this bird, it was shipped to Iowa late in the fall. By the end of December, the bird was thinner and appeared to be weaker, dying January 23, 1948.

The dead bird was taken to the Diagnostic Laboratory of the School of Veterinary Medicine at Iowa State College for examination and its death was attributed to severe helminthic infestation. The lumen of the small intestine was found to have been completely occluded by tapeworms (Hymenolepis sp. and Diorchis wigginsi?) in some parts. In the upper part of the trachea were found four flukes (Typhlocoelum cymbium) believed to have been responsible for an earlier "sneezing" or "coughing" of the bird; an unusually heavy infestation of the fluke (Tetrameres cram) in the glands of the proventriculus included more than 50 females and 20 males; and some small nematodes (Amidostomum sp.) were inhabiting the submucosa of the gizzard. Both Amidostomum anatis and A. acutum have previously been reported to infest the canvas-back (Cram 1927).

Coincidentally with the other symptoms of sickness, the drake had made a slow progress into eclipse, but had neither molted the flight feathers nor proceeded to the nuptial plumage by the time of its death in January. Perhaps the severe parasite infestation affected the bird's
physiological processes to the extent of retarding the molting. Were this condition very prevalent it could constitute a lethal handicap for waterfowl by preventing migration of the infested individuals during the fall. It might also explain the summering of some waterfowl far south of their breeding range.

Nest Parasitism

The term parasitism, as used in the following pages, refers to ovipositing by some female birds in the nests of other birds, either of their own species or of other species. The biological definition presented by Webster's Collegiate Dictionary (1945, p. 720) of a parasite is "A plant or animal living in, on or with, some other living organism (its host) at whose expense it obtains food, shelter, etc."

Because ducklings from foreign eggs in canvas-back nests were complementary as well as supplementary to canvas-back broods (Table XXV), the eggs and progeny of the intruder obtained care (nest maintenance, incubation, brooding and feeding of juveniles) at the expense of the host species. The word parasitism has been widely used in social nesting studies of birds (Herrick 1901, 1910a, 1910b, 1935; Chance 1922, 1940; Friedmann 1928, 1929, 1932; Davis 1940, 1942, 1945; Miller 1946, and many others).
Although representatives of many living orders of birds have been known to have promiscuous egg-laying habits, these tendencies have become firmly established in certain species of only five families of birds. Previously, the Old World cuckoos (Cuculidae) were the only known social parasites among birds, but early in the nineteenth century, Alexander Wilson established the strictly parasitic habits of the American cowbird (Icteridae). In addition to the preceding families may be added certain of the African weaver-birds (Ploceidae) and honey-guides (Indicatoridae), and the black-headed duck (Heteronetta atricapilla) of south-central South America (Herrick 1935).

Friedmann (1929) has given a good summary of existing hypotheses on the origin and evolution of the parasitic egg-laying of birds. In a subsequent paper (Friedmann 1932), the important contributions toward an understanding of the parasitic habits of some ducks are summarized. Swynnerton (1918) made an extensive study of the rejection of intruder eggs in bird nests in which the parasitic offender was the European cuckoo. Chance's (1940) detailed observations of cuckoos, together with a comparison of the parasitic habits of the European cuckoo and cowbird by Chance and Hann (1942), also are worthy of consideration.

The occurrence of this parasitic habit in representatives of diverse groups of birds, including such highly specialized nest-builders as weaver-birds, indicates that this phenomenon
is a relatively recent, independent development rather than a vestige of a more extensive, primitive, ancestral habit. If this is true, the trait must have evolved independently in each of the five groups of habitually parasitic birds (Allen 1925). Thus, an explanation of the habit which might apply with the European cuckoo need not necessarily be relevant among the remaining groups. Much more experimentation and observation have been devoted to the European cuckoos and cowbirds than to other intruding groups. Some of the suggestions for the origin of the habit resulting from these studies may find analogous applications in the Anatidae or may point toward conditions which foster the habit among some ducks.

The principal contributions of Herrick (1935, pp. 106-7), who did most of his work with the American cuckoos, arose from his

... study of the cyclical instincts which characterize the reproductive cycle in birds. Normally these instincts are so well harmonized or attuned that the entire cycle is unfolded without a break: pairing accomplished, the nest is built, the eggs are laid and hatched, and the rearing of the young is brought to a successful conclusion. There is commonly no loose or defective part in the whole mechanism. Nevertheless, the cycle can be interrupted in divers slight ways, or even thrown hopelessly out of gear, through but little understood causes that lead to a lack of harmony in its various elements. Of all the perturbations that are liable to arise at any point in the sequence, perhaps the most common is related to the nest and the need for it, or to nest-building and egg-laying. Too often ... the eggs are ready before there is a nest to receive them; and at this point it seems probable that parasitism in the cuckoo may have taken its
start. Whenever acceleration in ovulation and egg-laying or retardation of nest-building became common and the gap was extended, the door would be opened wide to the development of the nest-stealing and eventually of the full parasitic habit.

It must be noticed, however, that a mere upset in the reproductive rhythms, or lack of attunement between the nest-building and other instincts, or whatever else might lead to stealing of nests or waste of eggs could have no vital significance with reference to such a habit unless a long train of contingencies were met in rather definite ways—such as finding proper nests and complacent owners, or gradual lapses of old instincts as well as the equally gradual development of substitutes.

Philosophizing on duck parasitism in the literature, Herrick (1935, pp. 105-6) observed that

... instances of nest-stealing might have occurred on the North American continent from time immemorial without undermining the domestic polity of a single species. On the other hand, it is not unlikely that the black-headed duck of South America, who has traversed the whole road leading to social parasitism, may have begun with lapses similar to those which are now taking place in the North American redhead. At any rate, it seems to me probable that this lack of harmony between nest-making and egg-laying may be the "loosened screw" that makes the acquisition of such a habit possible.

The term "nest-stealing" applied by Herrick to the use of other nests by redheads is misleading, for in nest-parasitism among ducks, the nest is occupied by the intruder only during laying of the eggs. Complete appropriation rarely, if ever, takes place. The eggs are left unattended in the case of "dump nests" or may be ejected from the nest or incubated by the host female. They are not shown additional care by the intruding female.
The findings of Friedmann (1929, pp. 349-350) with the cowbirds parallel those of Herrick.

One of the possibilities is that parasitism may have arisen from the occasional laying of eggs in strange nests by birds that are very sensitive to the ovarian stimulus provided by the sight of a nest with eggs resembling their own . . . Chance's field observations on the European Cuckoo are more or less in accord with this idea as he believes that the sight of her victims building their nests acts as a stimulus to ovulation so that the female parasite has an egg ready to be laid five or six days later. This is also true of some of the Cowbirds.

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 of its own nest. Even if the sight of eggs in strange nests stimulated egg production in a bird that was not parasitic its own natural instincts would associate the resulting eggs with its own nest and the bird would probably lay them in its own nest, unless . . . its attachment to its nest were greatly diminished. Then too, after it has laid the proper number of eggs, "whose contact stimulus would satisfy," its brooding instinct, it would normally begin to incubate and stop laying. If its nest-attachment were sub-normal in strength, the bird might then wander about to some extent and, on receiving more visual stimuli might revert to egg-laying.

Concerning the origin of the parasitic habit in the cowbirds, Friedmann (1929, p. 353) continues

... it may be said that the immediate cause of the origin of the parasitic habit in the Cowbirds was the loss of the protecting instinct of the male. The fact that the female, still earlier in the history of the group, lost most of her protecting instincts cannot be called a causative factor because as long as the male retained his instincts of defense . . . the birds were not parasitic. What caused the almost complete loss of these instincts in the male we cannot definitely say, but the factor which started the weakening, and finally brought their destruction was the reversal of the territorial and nesting habits.
The same writer (1929, pp. 354-355) then shows his agreement with Herrick's ideas.

In this lack of attunement between the territorial instincts of the male and the egg-laying instincts of the female the parasitic habit probably had its origin. This lack of attunement seems to have been caused by the diminution of the protecting territorial instincts of the male and this diminution seems in turn to have been started by the reversal of the territorial and nest-building instincts . . . .

In a theoretical consideration of the parasitic habit in the ducks Friedmann (1932, p. 4) linked the development of this trait among ruddy ducks with " . . . the high frequency of carelessness with regard to the nest . . . " in which they lay their eggs, the increasing or latent form of maleness in females and possible heat-retaining or heat-generating properties of the large ruddy duck eggs. Regarding the compound nests of other diving ducks Friedmann (1932, pp. 5-6) advanced the following hypothesis.

With the growth of this tendency is correlated an independent factor, namely, the heat-retaining, or perhaps heat-generating, properties of the eggs. Thus it may be that the so-called "dumping nests" of the redhead and canvasback, mentioned by Bent, are extra nests of birds that have lost some of the single-nest limitations and contain eggs that have been partially incubated and that are left to their own heat resources. Whether the eggs of the redhead and canvasback are able to meet such a situation is immaterial; the fact that such a habit is practiced indicates that it may well be expected in the ruddy ducks as well, and probably was a stage in the development of the present parasitic habit of the black-headed duck of Argentina. In the ruddy ducks the eggs seem to be able to meet such a thermal situation. The large size of these eggs is possibly correlated with their heat-adapting abilities, and may therefore be an indirect correlative of the parasitic habit. It
has not yet been demonstrated whether the eggs of *Heteronetta* also possess these thermal abilities; there are two alternatives to be here considered. If the eggs of this duck are heat adaptive, their survival in strange nests is easily accounted for, as the victims undoubtedly do take care of them to some extent. If they are not heat adaptive, then the parasitic habit is the sole cause for the survival of the species, for if eggs unable to cope with thermal difficulties are laid in nests where they are uncared for, as in the "dumping" nests, the chances are all against their survival. If, however, they are laid in nests where they are given incubation by some other bird, they will have a good chance to hatch out. Therefore, if the eggs of *Heteronetta* are not thermally adaptive, the fact that they are laid in cared-for nests is the secret of their survival.

Friedmann (1932, p. 7) terminated his discussion of this topic with the following two sentences:

Furthermore ... it appears that the origin of the parasitic habit in the Anatidae is bound up with the heat adaptability of the eggs of the ruddy and black-headed ducks. If their eggs did not have this peculiarity, any lessening of incubation would have resulted in the extermination of the species; the fact (?) that they have, has allowed for the development of parasitism in this group of birds.

Rodriguez (1918) reported finding the eggs of the rosy-billed duck (*Metopiana pelecanoides*) in nests of the Coscoroba swan (*Coscoroba*), crested screamer (*Chauna*), South American limpkin (*Aramus*), gulls (*Larus*), coots (*Fulica*), white-faced glossy ibises (*Plegadis*), black rails (*Pardirallus*), and chimango or southern caracara hawk (*Milvago chimango*). Two years later, Daguerre (1920) indicated that much of the nest parasitism of Argentinian waterfowl attributed to the rosy-billed duck was actually done by the black-headed duck which was identical with the supposed "rosy-billed
duck eggs" which Rodríguez had been finding. The belief of Daguerre has been recently upheld by Delacour and Mayr (1946) who reported obtaining a black-headed duck egg from a nest of the red-gartered coot (Fulica armillata).

The black-headed duck is rare, being found mainly in the basin of the La Plata River and central Chile in south-central South America according to Phillips (1923). Combining characteristics of both surface-feeding and diving ducks, its affinities are not yet well established. It dives actively like diving ducks but lacks the hallux lobe of the diving group. According to some notes received by Phillips (1923, p. 96) from Dr. A. Wetmore, the black-headed ducks

"... frequented pools surrounded by rushes, where the water was from two to three feet deep, and were shy and retiring, so that it was difficult to observe them. On my first encounter I found two pairs on a small pond with Coots, and other ducks. To my astonishment the Black-headed Ducks dove when startled and disappeared like so many grebes, evidently seeking the shelter of the rushes... When in the water the birds suggest Ruddy Ducks (Oxyura jamaicensis), though the tails are not held at an angle as in the ducks of that genus.

"Black-headed Ducks were evidently breeding during the first week in November. The females noted swam about with their heads erect, behaving like other ducks. Males followed them or faced them with necks drawn in and throats puffed out, at intervals raising the point of their bills and giving a low note, quah-quah, barely audible at forty-five yards...."

No nest of this species has ever been described and it is believed to be the only duck entirely parasitic in its egg-laying habits.
A brief review of the more important literature on erratic egg-laying habits, excepting the voluminous data on cuckoos and cowbirds, may provide perspective for a better understanding and evaluation of the findings at Malheur. In a study of a California gull nesting colony in Utah, Sugden (1947) found eggs of the pheasant, coot, shoveller, and cinnamon teal in gull nests. He believed that the gulls had raided other nests and brought the eggs back for food, but the nesting impulse then overpowered the feeding impulse, so that the exotic eggs were incubated along with the gull eggs. All nests involved in this interesting habit contained single, foreign eggs. The raven nest containing one road-runner egg and three raven eggs reported as parasitism by Pemberton (1925), as well as the incidence of royal tern eggs in laughing gulls' (Larua atricilla) nests reported by Robert P. Allen (1937), may involve Sugden's explanation. None of the above are considered as promiscuous egg-laying.

Co-occupation of bird nests has been reported for females of the same species and for females of very diverse species. Two wood ducks occupied the same nest-box simultaneously, incubating a total of 34 eggs, and hatching 29 ducklings (Bellrose 1943). Phillips (1923) stated that Barrow's golden-eye females frequently laid eggs together. Fannin (1894) found two osprey eggs and three Canada goose eggs in an arboreal osprey (Pandion haliaetus carolinensis) nest with both potential parents

(Continued on the next page)
in attendance of the nest. Leaving only one goose egg in
the nest, he found the osprey covering it on a later return.

Miscellaneous egg-laying habits are frequent among the
Galliformes. In Iowa Bennett (1938) reported hen pheasants
victimizing nests of the mallard, blue-winged teal, shoveler,
Virginia rail, king rail (Rallus elegans elegans), and
European partridge (Perdix perdix perdix), with a maximum
of 11 pheasant eggs deposited with a clutch of 14 blue-
winged teal eggs. He observed that, with the exception of
the large, blue-winged teal compound clutch, all of the
duck clutches had less than the average number of eggs
found in unparasitized nests. Bennett (1938) also reported
that pheasants parasitized nearly five per cent of the blue-
winged teal nests under observation. Compound clutches
among other Galliformes have been noted by Stoddard (1931),
McAtee, et al (1945), Baskett (1947) and many others.

Although many of the puddle or river ducks (Anatinae)
are known to lapse occasionally in their laying habits, the
number of eggs that they drop in the nests of other birds
is small. The habit is much more frequent with some species
of diving ducks in North America, especially among redheads,
ruddy ducks and various tree ducks (Dendrocygninae).

Phillips (1923) has included a tremendous number of
records, from many sources, of compound nests among many
species of ducks most of them of the diving duck group.
Of special interest was a mallard found on a nest containing
In early June, before (1906) (found a nest with seven eggs and four redhead eggs and four redhead

The common of one of the last three nests

found the head of a red head and one red head egg, and one
two red head duck and one canvas-back ducks and an
east with the head of a red head duck and one
to the head of a red head and one canvas-back ducks and seven

a canvas-back nest with seven host eggs and four red-
east with the head of a red head duck and four red-

compound estuaries with the found a nest of

of the Western Goose

also reported finding an egg of the red head

is the same author

at canvas-back nests found confused from one to four eggs

at the North Deacon Study, Bent (1902) (found one canvas-

or from the common estuaries the uncommon instances

The common of one of the uncommon instances

mattered and found six red head eggs in different stages of

five red head, two fresh canvas-back, live well-inundated

was given.

Redhead Goose. The common of one of the last three nests

found the head of a red head and one red head egg, and one

found the head of a red head and one canvas-back eggs and an

east with the head of a red head duck and one canvas-back ducks and seven

a canvas-back nest with seven host eggs and four red-

east with the head of a red head duck and four red-

compound estuaries with the found a nest of

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at the North Deacon Study, Bent (1902) (found one canvas-

or from the common estuaries the uncommon instances

The common of one of the uncommon instances

mattered and found six red head eggs in different stages of
Of two, canvas-back nesting records in northwest Iowa, each contained redhead eggs. A nest reported by Bennett (1937) held four canvas-back, three redhead and one undetermined egg. This clutch terminated unsuccessfully just prior to the time it should have hatched. The other nest was found by Provost (1947) who indicated in conversation that it contained seven canvas-back and four redhead eggs and was abandoned following flooding.

Rockwell (1911) found a redhead nest containing five fresh and nine incubated eggs, apparently a compound clutch, on a muskrat lodge. Another of his reported nests contained five redhead and five ruddy duck eggs.

Low and Nelson (1945) reported finding a canvas-back nest with eight host eggs and two of the redhead at Gray's Lake in Idaho during May, 1944. In his Iowa study, Low (1945) recorded parasitic intrusion in 24 of 160 redhead nests during the three years, 1938-1940. Low (1941a) also found ruddy duck nests victimized by redheads and other ruddy ducks, and ruddy duck eggs occurred in both redhead and coot nests. Some of the embryos of ruddy duck eggs left in ruddy duck nests were still alive four or five days after the female had left the nest. None of the intruder redhead eggs hatched.

Job (1902) found two redhead nests with 22 and 15 redhead eggs, apparently compound clutches, in North Dakota, and three canvas-back nests with eight, seven and eight host eggs, and three redhead, four redhead and one ruddy duck egg, respectively.
In central Saskatchewan, Furniss (1938), during 1935 and 1937, found that 15 per cent of 108 nests of 12 species of ducks contained eggs of intruding female ducks, being most noticeable with redheads and canvas-backs. He believed that a large number of nest desertions may have been partly instrumented by nest parasitism.

From the foregoing, the promiscuous egg-laying habits of the redhead and the ruddy duck can be seen to be well established on some of the more important breeding grounds. By inference these habits might be expected to exist throughout the ranges of these species although the degree or extent of intrusion from year to year could vary. Additional, more intensive studies are expected to establish this as a fact.

The preceding discussion has dealt largely with a definition of parasitism and hypotheses on the origin and development of the parasitic habit in birds, together with noteworthy records of the incidence of nest parasitism among the waterfowl. The remainder of this section will largely concern a presentation of the findings with consideration of the conditions which may have encouraged the parasitic habit among diving ducks on the Malheur Refuge during the three seasons.

Along with observations on the nesting of canvas-backs, records of 77 redhead nests, four ruddy duck nests and one nest of a lesser scaup were examined for comparable data
on parasitism. Of these 82 nests, 66 histories were followed to their completion. No special effort was made to find these nests by careful search of the nesting cover. Consequently the comparatively few ruddy duck nests found do not constitute a true measure of their abundance, for the population of this species equalled that of the redhead. Since nesting ruddy duck females were more secretive in their nesting habits, they were rarely seen leaving the nest. The nesting habits of the redhead, on the other hand, paralleled those of the canvas-back, and methods used in nest-searching for canvas-back nests found similar application with the redhead.

Only four species of waterfowl victimized observed nests of the canvas-back at Malheur. Redheads were the most frequent intruders, laying 497 eggs, ruddy ducks were next with nine eggs, and the American pintail (?) and American coot each laid one egg in canvas-back nests. Of the above intruder eggs, only 131 of the redhead and the single pintail (?) egg were successful (Table XVI). Since data on redhead parasitism are much more extensive than information on the other three intruders, the nesting of the redhead will receive first consideration in the following discussion. Of 77 redhead nests observed coincidentally with canvas-back nests during the three years, 74 nest histories were complete enough to permit analysis of egg data. These data are found in Table XXVIII. In addition
Table XXVIII. Nest and Egg Success of the Redhead on the Malheur Refuge, Oregon

<table>
<thead>
<tr>
<th>Year</th>
<th>Total</th>
<th>Total eggs</th>
<th>Average clutch size</th>
<th>Clutches with known fate</th>
</tr>
</thead>
<tbody>
<tr>
<td>1942</td>
<td>34</td>
<td>371</td>
<td>10.9</td>
<td>19</td>
</tr>
<tr>
<td>1946</td>
<td>20</td>
<td>237</td>
<td>11.8</td>
<td>19</td>
</tr>
<tr>
<td>1947</td>
<td>16</td>
<td>194</td>
<td>11.4</td>
<td>16</td>
</tr>
<tr>
<td>3-year totals</td>
<td>70</td>
<td>802</td>
<td></td>
<td>54</td>
</tr>
<tr>
<td>and</td>
<td></td>
<td></td>
<td></td>
<td>11.4</td>
</tr>
</tbody>
</table>

<table>
<thead>
<tr>
<th>Year</th>
<th>Nest success</th>
<th>Total eggs</th>
<th>Hatched eggs</th>
<th>Clutches</th>
<th>Egg success in all clutches</th>
<th>Avg. clutch size</th>
</tr>
</thead>
<tbody>
<tr>
<td>1942</td>
<td>5</td>
<td>26.3</td>
<td>41</td>
<td>30</td>
<td>73.2</td>
<td>8.1</td>
</tr>
<tr>
<td>1946</td>
<td>13</td>
<td>68.4</td>
<td>147</td>
<td>105</td>
<td>71.4</td>
<td>44.3</td>
</tr>
<tr>
<td>1947</td>
<td>10</td>
<td>62.5</td>
<td>106</td>
<td>81</td>
<td>73.5</td>
<td>41.8</td>
</tr>
<tr>
<td>3-yr totals</td>
<td>28</td>
<td>294</td>
<td>216</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>avgs.</td>
<td>52.4</td>
<td></td>
<td>72.7</td>
<td>31.4</td>
<td>10.0</td>
<td></td>
</tr>
</tbody>
</table>
to the intruded eggs of other redheads, nests of this species contained four mallard eggs, 12 ruddy duck eggs and the canvas-back egg previously reported.

Several criteria for identifying an egg as that of an intruder or host redhead could have been employed in some instances. Eggs added to clutches which had been completed and were being incubated evidenced parasitism, and many nests having more than a dozen eggs probably represented compound clutches. The study of embryos in unhatched eggs at the termination of the nest history gave further evidence on the number of intruded eggs together with the approximate dates of intrusion. The number of eggs laid in redhead nests by intruding redheads prior to incubation was difficult to ascertain, except when the clutch was expanded quickly through the contributions of several parasitic females. Even then, the total number of eggs laid by the host female was difficult to determine. In view of these obstacles to a correct count of host and intruder redhead eggs in redhead nests, no attempt has been made to distinguish between them in the following discussion.

The average size of redhead clutches for the three seasons was 11.4 eggs. It will be noted that the smallest, average number of eggs in clutches (10.9) occurred in 1942 during the year of heaviest parasitism of canvas-back nests. The largest average clutch of 11.8 eggs in 1946 accompanied the lowest parasitism and highest success in canvas-back nests.
For direct comparison, nest, nesting and egg success of canvas-back and redhead nests for the three years have been given in Table XXIX. Here it is seen that success percentages for nests, nesting and eggs were generally quite similar, although the 1942 figures for the redhead nests were somewhat higher. In the column of average number of eggs in nests, however, differences are apparent. The size of canvas-back clutches during each of the three years (previously shown to have been influenced by the degree of nest parasitism) shows inverse relationships with the size

Table XXIX. Comparative Nest, Nesting, and Egg Success of the Canvas-back and Redhead on Malheur Refuge, Oregon

| Year | Nests of Nests success percentage Nesting success percentage Avg. no. eggs in the nests Per cent of eggs hatched |
|------|-----------------------------------|---------------------------------|-----------------|----------------|-----------------|
| 1942 | Canvas-back | 15.6 | 27.3 | 18.2 | 6.7 |
|      | Redhead | 26.3 | 38.5 | 10.9 | 8.1 |
| 1946 | Canvas-back | 68.4 | 76.5 | 9.4 | 59.8 |
|      | Redhead | 68.4 | 76.5 | 11.8 | 44.3 |
| 1947 | Canvas-back | 60.9 | 70.0 | 10.0 | 42.2 |
|      | Redhead | 62.5 | 66.7 | 11.4 | 41.8 |
| 3-year averages | Canvas-back | 48.3 | 58.1 | 12.5 | 36.2 |
|      | Redhead | 52.4 | 60.6 | 11.4 | 31.4 |
of clutches in redhead nests. While the success of canvas-back nests, nesting, and clutches was inversely proportional to the size of canvas-back clutches, the opposite was true with redhead nests, indicating that during years of most intense parasitism, the nesting success of this species is reduced. It also appears to suggest that sustained parasitism by redheads was largely limited to promiscuous ovipositing in canvas-back nests.

It is believed that an explanation of the origin and development of the parasitic habit in some ducks is closely associated with the progression of instincts (or responses to external and internal stimuli) during each annual breeding cycle. Herrick (1935, p. 105) has used the phrase "... lack of harmony between nest-making and egg-laying ..." instincts, but Howard (1929) avoids the use of the term instinct and prefers to believe that actions of birds are simply reactions or responses of varying intensity to both external and internal stimuli. The latter author further believes that susceptibility of individual birds to various seasonal stimuli varies not only in seasonal intensity of response but also in daily intensity of response in a serial and cyclical procession of reactions. Both writers agree in that the breeding cycle is believed to be characterized by a serial parade of responses governed directly by the physiology of the bird.
Herrick (1910a, p. 536) stated that, for convenience, the breeding cycle may be described as made up of a series of terms as follows:

1. Migration to Breeding Area;
2. Courtship and Mating;
3. Nest Building;
4. Laying Eggs in Nest;
5. Incubation and Care of Eggs;
6. Care of Young in Nest;
7. Care of Young out of Nest;
8. Migration to Feeding Area.

Beginning at 2, 3 or 4, according to circumstances, the cycle may be repeated one or more times within the breeding season, or a new cycle may be begun, and stayed at any step from nest-building to laying of the eggs. Again, an entire cycle may be brought near the close, then scamped, the young being left to die.

The reproductive cycle may be graphically represented by a number of tangent circles, each of which stands for a distinct sphere of influence or for a subordinate series of related impulses. It is evident that these serial instincts must be in relatively perfect harmony, or if regular perturbations occur, new and permanent adjustments must be forthcoming to meet them, if the species is to continue to exist. One act or series of related sets must be performed in preparation for that which follows. The nest must "anticipate" the eggs, and not the egg the nest. Upon the whole the serial instincts of birds are well attuned, yet disturbances more frequently occur than is commonly supposed, and by conditions of this kind much that is anomalous or eccentric in the behavior of birds can be explained . . . . The number of terms, of which eight are given above, is unimportant, so long as it is recognized that they occur in serial form, and that many activities such as brooding, and feeding the young, are recurrent.

The following discussion of influences which may have affected the more "normal" egg-laying habits of the redhead and given rise to varying intensity of parasitism during the three years of the study is largely based on the above explanation of bird behavior.
The earliest canvas-back nests, as previously stated, seemed to be less frequently victimized by redheads, presumably because the redhead nested later. However, during the remainder of the nesting season, there was no observed variation in the intensity of parasitism during any year. Because no other species of duck (excepting ruddy ducks for which few data were collected, and a small number of mallards) regularly nested in canvas-back and redhead nesting habitat, that redhead parasitism was largely restricted to the nests of the last two species is not surprising. Of these, nests of the canvas-back were more heavily parasitized during 1942, as shown in Table XXIX, while redhead nests in that year showed a smaller clutch size.

In considering various factors which might lead to differential intensity of parasitism in the nests of canvas-backs and redheads, one conclusion always stood out: nests of a given species were more vulnerable to inter- than intra-specific parasitic intrusion. Two possible reasons for this condition were apparent: (1) either the habits of nest attendance in the canvas-back were more favorable for intrusion by redheads than the habits of redhead females, or more likely, (2) host female redheads were more successful in defending their nest from intrusion by another redhead female, while canvas-back females were more tolerant in permitting redhead females to occupy their nests during ovipositing. The second explanation is favored, for although examples of sus-
tained parasitism in redhead nests were found each year (Fig. 39), most of the nests did not receive the bulk of the parasitic eggs until after the nest had been deserted following initial, light parasitism. Therefore, the female redhead is believed to be much less tolerant of parasitic intrusion by other redheads than is the female canvas-back, especially during incubation.

Fig. 39. This unsuccessful redhead nest contained nine eggs with embryos and 15 eggs that showed no development, apparently abandoned by the female following intrusion of the first few parasitic eggs.

While incubating the host female spends more time close to or on the nest, and would be more likely either to observe acts of intrusion, or would be more apt to
recognize additions to her incubated clutch than when eggs were added concomitantly with her own. In agreement with this belief Low (1945, p. 46) observed that "Parasitic eggs laid in nests late in incubation increased the chances of nest failure, while in some of the nests eggs deposited simultaneously with the rightful owners' eggs were hatched successfully." With the canvas-back, however, the average duration of unsuccessful nests in 1942 was 14.5 days or somewhat less than half of the average duration of successful nests. This indicates that the female canvas-back exhibited about the same tendency to abandon at any period of the nest history up to the last two or three days of incubation when audible pipping of the embryos may have increased the female's persistence.

The nesting habitats of the redhead and canvas-back were almost identical, and ranged from land situations near water to nests over several feet of water. The average depth of water at the nest site for both species was 21.3 inches, but showed variations each year. Average depths at redhead nests were 17.6 inches in 1942, 22.3 inches in 1946 and 23.4 inches in 1947, while at canvas-back nests the depths, respectively, were 24.2 inches, 17.9 inches and 21.7 inches (Table XXX). The greatest average number of foreign eggs was found in canvas-back nests occurring in intermediate depths of water, but these data hold only for 1942 and 1946 and are not conclusive.
Table XXX. Extent of Nest Parasitism in Relation to Water Depths at Canvas-back Nests on the Malheur Refuge, Oregon

<table>
<thead>
<tr>
<th>Year</th>
<th>Avg. water depths at nest sites (inches)</th>
<th>Avg. no. of foreign eggs in parasitized nests over given water depths</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>Canvas-back nests</td>
<td>Redhead nests</td>
</tr>
<tr>
<td>1942</td>
<td>24.2</td>
<td>17.6</td>
</tr>
<tr>
<td>1946</td>
<td>17.9</td>
<td>22.3</td>
</tr>
<tr>
<td>1947</td>
<td>21.7</td>
<td>23.4</td>
</tr>
<tr>
<td>Avg. water depths</td>
<td>21.3</td>
<td>21.3</td>
</tr>
</tbody>
</table>

In his Iowa study of the redhead, Low (1945, p. 68) found that "The amount of promiscuous laying was inversely proportional to the nesting success and directly proportional to the fluctuation of the water level." On the Ogden Bay Refuge in Utah, Nelson (1943, p. 203-204) also found fluctuating water conditions to result in aberrant nesting.

Nesting on the undeveloped marsh was seriously affected by unstable water levels. This area alternately flooded and drained during the months of the spring runoff. Flooding destroyed 35.4 percent of all eggs tabulated in this area. The loss was especially high for redheads, being 65.5 percent. A total of 87 eggs had been spilled from one redhead nest during the bird's efforts to progressively raise the nest. The bird was incubating 9 eggs when the nest was checked.

Parasitism by redheads was pronounced in this lower area where the birds' nesting efforts were so disturbed by flooding. Parasitism was especially severe on cinnamon teal and common mallards.
Judging from Nelson's tabulated figures the following average numbers of eggs in each nest were found for species nesting in the undeveloped marsh: redhead, 11.4; cinnamon teal, 9.2; mallard, 15.9; gadwall, 13.5; American pintail, 12; and ruddy duck, 12. His table showed that all puddle duck nests and the single ruddy duck nest contained eggs of the redhead, but did not indicate exactly how many eggs. The large sizes of the parasitized clutches given above were mainly a result of redhead parasitism. It will be noticed that mallards were especially subjected to heavy parasitism, while the redhead probably contained a smaller proportion of foreign eggs, further supporting the contention that redhead nests are less subject to parasitism by other redheads, possibly a result of intraspecific intolerance.

The possibility of the nesting habits of the redhead being altered in 1942 by adverse weather conditions, especially during the first half of the nesting season was considered. However, the weather was quite similar during the last half of the nesting season in each of the three years, while the degree of parasitic intrusion showed no corresponding changes.

As with Low's (1945) study of the redhead in Iowa and Nelson's (1943) findings in Utah, the incidence of promiscuous ovipositing by the redhead appeared to show closest correlation with water level conditions. In 1942 the level of Malheur Lake showed a gradual rise until June 7, followed
by a gradual decline. From the standpoint of nest-flooding, this slow change in levels may not have been important, for nesting ducks should easily have been able to keep the clutch above water which raised at the rate of slightly more than one foot in three months. However, this change in depth was accompanied by such a radical change in surface acreage (Fig. 7) that the extensive margins of the lake grown with bur-reed, cat-tail, Baltic rush and various grasses and sedges were affected much more by the high water condition. In the Blitzen Valley ponds and marshes with an early surplus of water in 1942, even sagebrush upland was flooded in some situations. The surplus water in the valley was largely released into Malheur Lake by the time that most canvas-backs were nesting, and the ponds had more static levels, though they were still deeper throughout most of the season than during the other two years.

Promiscuous egg-laying by the redhead could not be correlated directly with high water conditions or variable levels throughout the nesting season on both Malheur Lake and in the Blitzen Valley, for in the latter area water levels were stable through most of the later part of the nesting season. It is believed, however, that the early condition of unusually high water was principally responsible for most of the early promiscuity. A reason for the continuation of promiscuous egg-laying later in the season in spite of stabilized water levels is difficult to establish.
It is not supported by variations in comparative population densities of the redhead and canvas-back, for, except on Malheur Lake, ratios for the two species remained similar throughout the study.

Most redheads arrived at Malheur from two to three weeks after the majority of canvas-backs. The differences in nesting periods showed a similar lag. With the onset of redhead nesting, the first redhead eggs were found in canvas-back nests. Many of the resident redheads were not believed to have persisted in the parasitic habit in 1942 for successful redhead nests were found throughout the season. Very nearly the same proportion of canvas-back nests found each year were subjected to intrusive egg-laying. In 1942, though, parasitism was much more sustained. It would appear that in 1942 the same proportion of redhead females were promiscuous, but most of them continued this habit throughout the season. In 1946 and 1947, parasitism was discontinued after the laying of only a small part of their eggs and the female redheads then went on to complete a clutch in a nest of their own. The period of nest inceptions for redheads embraced all but the first two or three weeks of the canvas-back nesting period, extended for nearly a month after the last canvas-back nest history had terminated, and did not show any single period of heaviest nest inceptions. This may explain the reason for a lack of concentrated or more intense parasitism during any part of the canvas-back nesting season.
From the above, two lines of reasoning concerning the parasitic tendencies of redhead females may be advanced. The parasitic eggs laid in canvas-back nests may have represented the first laying of the redhead before a nest had been prepared, or else the eggs had been laid following abandonment of an earlier attempt. Perhaps both conditions held true. At any rate, the habits of females laying parasitically in canvas-back nests were similar in at least six respects. The intruding redhead female did not (1) assist in the construction or maintenance of the nest through addition of vegetation to the structure; (2) remove down feathers from its body for lining of the bowl; (3) turn the eggs; (4) form the clutch into a concave, body-fitting layer; (5) cover the eggs prior to leaving the nest; or (6) incubate. Thus, although the inclination to lay eggs in a nest was evident, none of the usual responses in diving ducks to nesting stimuli were apparent. In fact, the only accomplishment of the redhead at the canvas-back nest was the laying of eggs.

Female intruding redheads almost invariably were accompanied by a drake which remained at some distance from the nest. The fertility of intruded eggs showed no variation with the fertility of eggs of the host. Furthermore, males remained with the females throughout the time that the latter were engaged in laying eggs, in two instances, for more than two months. As parasitic females did not
incubate while on canvas-back nests they retained the attention of the male. Females seen with mates near abandoned nests for more than a month following cessation of ovipositing, were believed to have exhausted their potential for egg production. Eventually the pair abandoned the area together. The intruding female redhead was never seen to remain unattended by a male.

Returning to Herrick's (1910a, p. 536) ideas on chronology of the breeding cycle, his first four terms ("1. Migration to Breeding Area; 2. Courtship and Mating; 3. Nest Building; 4. Laying Eggs in Nest ... ") may now be considered. Evidence of a manifestation of number 1 and 2 with the redhead is given by the appearance on the area of parasitic females with mates. The instinct in redheads to maintain the victimized canvas-back nest (comparable with number 3) does not appear, however, and the redhead instead lays eggs (number 4). Apparently, the instinct to build a nest either never manifests itself in the redhead intruder, or else this instinct becomes ineffectual after abandonment of an earlier nest.

The instinct to lay may have been a response to visual stimulation provided by the sight of the canvas-back nesting female or nest and eggs. Completion of a clutch did not evoke the incubation response, as indicated by the fact that the female redhead did not form the eggs in a single layer after desertion by the canvas-back female, nor incubate
the eggs, but left the eggs heaped in the nest until it sank in the water or, presumably, her egg-laying capacity had been exhausted. With the redheads which assumed the role of intruder throughout the nesting season, the only parts of the cyclic breeding instincts which their actions manifested were the migration, courting and mating and the egg-laying instincts.

For some undetermined reason, or combination of reasons, egg-laying was not accompanied by the nest-building and incubation responses among the persistent intruders of 1942. On the other hand, those individuals which laid only a few eggs in canvas-back nests during the three years, may have experienced a rise in the nest-building instinct while laying eggs in other nests, and departed to construct another nest, lay eggs and incubate. In the first case, the egg-laying instinct was neither directly preceded by nest-building nor followed by incubation. In the latter instance, egg-laying preceded nest-building, the premature laying was supplanted by the nest-building urge, then again followed by egg-laying, incubation, and the other responses in orderly fashion. Under both conditions, parasitism seems to have been a result of the "lack of attunement of instincts" in the breeding cycle of the female redhead, and this lack of synchrony seems to have been influenced to a varying degree by the habitat conditions during the three years.
Parasitism in canvas-back nests has been shown to be a depressant of canvas-back production both by causing the female to desert and by reducing the number of canvas-backs hatching through the substitution or complementary influence of the intruded redhead eggs. Promiscuous egg-laying may be detrimental to the intruding species in at least three ways: (1) the intruder may not abandon the parasitic habits to build its own nest during the season, reducing the number of resident females which could produce broods; (2) if the intruding female builds a nest after earlier promiscuous laying, the clutch size may be reduced; and (3) even during years of high nesting success of the host species intruded eggs meet with much lower success.

Consequently, parasitic habits of the redhead, generally, represent a drain on rather than an aid to perpetuation of this species. The South American black-headed duck, which appears to be completely parasitic, is one of the rarest of the Anatidae, and cannot be considered a successful species from the numerical standpoint. Secretive habits (Phillips 1923) seem mainly responsible for the survival of the black-headed duck. Since the redhead decoys readily and is comparatively easy to shoot, its perpetuation may largely be influenced by the tendency to lay large clutches of eggs. The parasitic habit will not be to the advantage of redhead propagation unless this duck successfully deposits eggs in other nests early in the history of
the host nest without subsequent desertion by the host.

Thermal adaptation of eggs supplies another possible substitute for parental or host incubation, but in the light of the findings of this investigation and of Low (1945), together with the lack of concrete evidence in favor of this idea in other literature, heat-retaining qualities of intruded eggs of the ruddy duck and redhead cannot be considered an important factor in the survival of these species. Of the promiscuous habits of the redhead and ruddy duck, only those of the redhead have been found to result in hatched young, while none of the ruddy ducks hatched (also found by Low 1945). Consequently, of these two species, intrusion by the redhead seems to have been more successful.

Postnesting Dispersal and Fall Migration

The first postbreeding movements of adult canvas-backs locally, as well as into and out of the research area, may have begun in June when the drakes began to collect on open ponds near nesting habitat, but extensive movements did not become apparent until during July and August. The north side of Malheur Lake and Boca Lake became heavily populated locally, where, during 1946, as many as 75 drakes in both breeding and eclipse plumage, some flightless, were seen on a half-section of water surface. The earliest record
for a drake in eclipse was May 25, 1946.

At least three characteristics were shared by all areas occupied by postnesting drakes: (1) the water was completely open or had a few, scattered stands of hardstem bulrush; (2) the water averaged two feet or more in depth and was at least 30 acres in size; and (3) an abundant growth of sago pondweed was present. As the habitat changed during the three years, elimination of any one or more of the three characteristics could be correlated with the termination of use of the water area. In 1947, with low water conditions prevalent on most areas, only Baca Lake and a northward extension of Malheur Lake retained all three of the desirable features of a postnesting area for drake canvas-backs. These areas held approximately the same numbers of drakes as were present in 1946, though altered situations showed very few or no canvas-backs.

As the marshes to the north of the refuge near the city of Burns were drained in July and August to permit haying, the canvas-back residents of that nesting area were believed to have moved to the refuge lakes to undergo their flightless periods. Judging from fluctuating numbers of male canvas-backs among postnesting individuals on the refuge, a certain proportion of those seen during August and later were from areas outside of the Harney Basin. Some Malheur resident canvas-backs, especially during 1947, were believed to have left the refuge to spend their flightless period on distant waters.
Full-grown, juvenile canvas-backs soon left the valley ponds, usually during the first half of August, and joined the adult males on open water of the lakes. A few adult females usually were present in these groups. The feeding and loafing activities of such aggregations were often interrupted by much washing and preening. In these noisy actions, the head, neck and front part of the body were pushed under the surface of the water, then raised almost vertically in a head-and-back-washing motion, immediately followed by vigorous wing-thrashing which shed much of the water. The bathing was then continued, the birds rolling nearly over on their backs in preening breast and belly feathers. Preening was more commonly witnessed among ducks approaching the eclipse period or already in eclipse than at any other part of their life history at Malheur.

Canvas-backs did not always remain in the water but continued dressing their plumage and loafing out of water. Parts of Cole Island Dike were heavily occupied by most species of resident ducks, including canvas-backs, and Canada geese late in summer. These situations often were depadded of vegetation (Fig. 40) by the loafing activities of hundreds of waterfowl, many of them flightless.

Both male and female canvas-backs entered the post-nuptial eclipse dress, but their habits during the eclipse period were dissimilar. While the male was nearly always seen on or near relatively open water, females which had
been relieved of nesting and/or brood-rearing remained in vegetated areas similar to the nesting habitat of ponds and lakes. The female kept out of sight if warned of the observer's approach, while the males merely swam away and would dive only if chased or if confronted unexpectedly at close range. During the study only three observed females were believed to have been non-breeders. The females, believed to be the same individuals seen on each encounter, were observed throughout the season on the same areas until the middle of September when they disappeared, presumably to undergo the postnuptial molt.
The postnesticg dispersal is considered by some as being part of the fall migration of a duck species, but the writer considers this movement merely as a postnesting, multidirectional diffusion of ducks into or out of an area, while the fall migration is interpreted as the more or less direct travel of a species from the molting area to the wintering grounds. Because the writer did not remain on the refuge after the middle of September during any year, the few fall migration data available for study were found in refuge records or were provided by members of the Malheur Refuge staff.

Gabrielson and Jewett (1940, p. 157) have recorded a hypothesis on the route followed by canvas-backs entering western United States from Canada.

It seems evident that most of the Canvas-backs come down the Columbia River from the great midcontinent nesting grounds rather than down the coast. All observers report the species as decidedly uncommon Puget Sound, which would not be the case if there were a coastal flight line. On the contrary, it is regularly and commonly found on the Columbia River and on the Oregon coast.

On the basis of limited banding records from the Malheur Refuge files presented in Table XXXI, the majority of canvas-backs passing through the refuge appeared to winter coastally along the northern half of California and interiorly in the San Francisco vicinity and in the Nampa and Sacramento Valleys.
Table XXXI. Nine Returns from 95 Full-grown Canvas-backs Banded at Malheur Refuge, Oregon

<table>
<thead>
<tr>
<th>Sex</th>
<th>Date banded</th>
<th>Date recovered</th>
<th>Recovery locality</th>
</tr>
</thead>
<tbody>
<tr>
<td>Male</td>
<td>10-13-37</td>
<td>12-10-40</td>
<td>Fruitland, Idaho</td>
</tr>
<tr>
<td>Male</td>
<td>10-29-40</td>
<td>12-13-40</td>
<td>Lower Klamath Lake, Oregon</td>
</tr>
<tr>
<td>Male</td>
<td>11-6-35</td>
<td>1-1-36</td>
<td>Canyonville, Oregon</td>
</tr>
<tr>
<td>Male</td>
<td>11-25-40</td>
<td>12-13-40</td>
<td>Monterey County, California</td>
</tr>
<tr>
<td>Male</td>
<td>11-17-40</td>
<td>12-30-40</td>
<td>Malheur Refuge, Oregon</td>
</tr>
<tr>
<td>Male</td>
<td>3-25-42</td>
<td>11-12-44</td>
<td>Solano County, California</td>
</tr>
<tr>
<td>Female</td>
<td>3-25-42</td>
<td>12-25-44</td>
<td>Courtland, California</td>
</tr>
<tr>
<td>Female</td>
<td>4-8-41</td>
<td>11-22-41</td>
<td>Petaluma Creek, California</td>
</tr>
<tr>
<td>Female</td>
<td>10-26-40</td>
<td>11-30-40</td>
<td>Richmond, California</td>
</tr>
</tbody>
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The main flyway between the refuge and wintering area apparently passes through the Klamath Lakes where one banded bird was recovered. Among the lakes of this part of Oregon and northern California the flyway may divide, one route proceeding down the Sacramento Valley of California and the other proceeding down the Sacramento Valley of California and the other extending westward to the creeks, marshes and coast of southwestern Oregon where another Malheur bird was recovered from a mink trap near Canyonville in Douglas County.
body were accepted by ducks for use as a resting station
between Henry Lake on October 28, 1945. Indications that this
phenomenon, the presence of approximately 6,000 ducks on an abundance of food seemed to be most heavily populat ed
of the leks and lekker ponds. Although the areas hav ing
wading-thinkers canence-brokers frequented open or semi-open water
in a spring-red pond near the refuge headquarters. The
or a few that remained throughout the winter of 1941-1942
nearby all canence-brokers had departed, with the exception
water begun to freeze on October 28. By mid-November,
middle of October and the first week in November when the
most fall wading-thinkers canence-brokers were seen between the
Texes, New Mexico, Arizona and Mexico.

northern and on the way to uninterrupted grounds in Nevada,
in Utah and then across to the bear river refuge in
direction, forming a segment of the bear river southeasterly
march, another one may possibly exist, in a southeasterly
in addition to the flyway passing southeasterly from
in the general region of san francisco.

canence-brokers were of interest in that all were recovered
california coast. The bandsite remains of three females
of the flyway would appear to extend southeasterly along the
cost of the north half of california, the other part
indicating from the numerous canence-brokers seen in waters of

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Hunting was prohibited within the refuge boundaries, but a varying amount of shooting was done just outside its limits, especially along refuge fences and in the passes between portions of the refuge. Since most of this hunting was accomplished away from the open-water areas, the toll of canvas-backs taken was not great. A total of 60 hunters, contacted by Refuge Manager L. R. Ramelli between October 26 and November 7, 1946, had 23 geese and 177 ducks only six of which were canvas-backs. Of all species of ducks taken 55 were mallards, followed by 50 gadwalls and 40 baldpates. The remaining 32 ducks were distributed among eight species. Eight pintails were taken and six (3.4 per cent) each of redheads and canvas-backs. Four species of geese were taken consisting of 16 Canada geese, one cackling goose, three white-fronted geese and three lesser snow geese.

According to reports from the refuge, hunters during the 1947 season met with little success. The fact that several favorite areas adjacent to the refuge were closed to hunting, coupled with a greatly reduced migrant flight during the hunting season, seemed mainly responsible for this decline. Perhaps the extremely low waters of Malheur Lake and Harney Lake, together with a reduced production on more northerly breeding grounds was instrumental in producing the lighter fall migration.
Food Habits

Findings herein reported on the food habits of the canvas-back in southeastern Oregon were based principally on field observations supplemented by the examination of the contents of six canvas-back stomachs obtained from duck hunters during the hunting season in October, 1946, on or near Malheur Refuge, and analysis of the contents of 13 canvas-back stomachs secured from hunters during the October-November 1940 hunting season at Tule Lake in northern California.

The spring migrant canvas-backs at Malheur were usually found in open water areas or water with sparsely scattered bulrush. The six, lead-poisoned canvas-backs found in 1942 had few food items in their stomachs, hardstem bulrush achenes dominating, followed by seeds of sago pondweed. Broad-fruited bur-reed and coontail were also represented by occasional seed occurrences. All six stomachs contained gravel.

Examination of the areas in which canvas-backs were seen feeding, together with close observations of feeding birds, indicated that the spring food consisted largely of all parts of musk-grasses, seeds or achenes of sago pondweed, coontail, hardstem bulrush, bur-reed, marestail, and small molluscs and crustaceans obtained from a variety of submerged plants, mainly from water milfoil. Very limited quantities of various smartweeds (Polygonum), other bulrushes
(Scirpus), arrowhead (Sagittaria), water plantain (Alisma) and spikerushes were believed taken because they either were not common in migration habitat or were otherwise unavailable in that season. In dredged bottom samples of the better canvas-back migrating areas, sago pondweed and hard-stem bulrush achenes exceeded in number and volume all other potential "seed-food" present. During receding water levels or following strong winds, windrows of seeds of bulrush, bur-reed and marestail frequently lined the shores. Fewer pondweed and smartweed seeds were drifted in this manner for they seemed to have a higher specific gravity and sank more quickly.

Although the adult canvas-backs and broods avoided milfoil-vegetated water after this submersent began to flower and greatly impeded swimming during low lake or pond levels, canvas-backs seemed attracted to milfoil growth on Malheur Lake in the spring. As evidence of utilization of this plant or the animal life found thereon by ducks, coots and muskrats, much milfoil was found uprooted and torn apart, lying as a drift on the windward sides of bulrush stands.

While diving for food in about four feet of water, the canvas-back arched its back, pointed the bill straight downward, brought both feet forward under the breast and propelled itself into the dive, the entire body, excepting the feet, leaving the water to begin the descent in a loon- or grebe-like manner. The tail was spread as the bird
descended when about half of the body was submerged.

In water of 15 to 20 inches depth, canvas-backs stirred up the surface water with visible foot movements or water eddies in their efforts to remain submerged. In this attitude they could be seen head-downward with tail and feet occasionally breaking the water-surface, the legs pointed down and slightly spread, being used to propel the duck slowly forward in feeding.

Canvas-backs showed little intolerance towards other species of migrating waterfowl on the feeding grounds. Baldpates frequently were seen feeding on material brought to the surface by coots, and one pair of baldpates and two coots were seen following a canvas-back drake. Little food was obtained from the canvas-back, however, for the diving duck consumed most food under water. When a canvas-back returned to the surface with pondweeds clinging to its body, one of the coots quickly snatched them.

In April, May and June when an abundance of mayflies (Ephemeroptera) and midges (Chironomidae) was present throughout the refuge, canvas-backs, along with other ducks and coots, could be seen snapping at these insects on the water surface. Since no canvas-backs were killed for food habits study purposes, actual verification of these observations was not practicable. Midges were most abundant during April. On some days adult midges formed towering, columnar clouds over the rank, ballast vegetation on the
sides of Cole Island Dike, until the road appeared as an aisle between these dense clouds. Mayflies first became abundant during the last days of April. In skimming insects from the water, canvas-backs swam low with neck looped and head thrust forward at the water surface.

When water was turned into the temporary pond basins in the spring, the submergent plants were dormant. Usually within a week, the pondweeds began to send up shoots and these apparently were acceptable to the canvas-back and redhead for the utilization of such ponds increased during the second week after flooding.

Preservation, identification, volumetric measurement, enumeration and tabulation methods in handling the two series of stomach material followed standard food habits procedure (Cottam, 1936, U.S.D.I. 1942). In both collections plant materials comprised nearly 100 per cent of the total food contents. Animal matter was represented by remains of insects which could be listed only as "traces." Snail shell fragments occurred in both groups.

In the Malheur series of six stomachs, the item, number of stomachs containing the item and volumetric percentage of food contents in stomachs containing the given items were as follows: sago pondweed achenes, six, 35 per cent; sago pondweed tubers, two, 46 per cent; undetermined pondweed achenes, two, 11 per cent; bur-reed achenes, three, 16 per cent; hardstem bulrush achenes, five, 19 per cent;
Cyperaceae achenes, one, trace; marestail achenes, three, nine per cent; miscellaneous plant leaves, two, 54 per cent; undetermined Coleoptera, two, trace; and non-food items, principally grit, were found in all six stomachs, comprising 58 per cent of the total volume of stomach contents.

Comparable data for the 13 gizzards from Tule Lake were as follows: sago pondweed achenes, 11, 38 per cent; sago pondweed tubers, two, ten per cent; undetermined pondweed achenes, one, trace; hardstem bulrush achenes, two, 50 per cent; river bulrush (<em>Scirpus fluviatilis</em>) achenes, nine, 19 per cent; undetermined bulrush achenes, one, trace; cultivated barley (<em>Hordeum vulgare</em>) fruit, one, trace; miscellaneous plant leaf material, three, 14 per cent; one insect, one trace; and non-food items, principally grit, were found in each of the 13 stomachs, comprising 45 per cent of the total volume of stomach contents.

From the above information, sago pondweed appeared to be the single most important species for food, occurring in 17 of the 19 stomachs, while bulrushes ranked second. Bur-reed seeds were taken by a few ducks and marestail seeds were also taken sparingly. The low percentage of green plant material may be typical of late fall and winter feeding, but it is believed that green material forms a much larger part of the food during the spring and summer. Food and food habits of the canvas-back in various parts of the United
States have received detailed treatment by Kubichek (1933), Martin and Uhler (1939), Cottam (1939), and McAtee (1939).

Management

The following discussion of management is based on observations of conditions in southeastern Oregon which appeared most propitious to the production and perpetuation of the canvas-back. The refuge serves many of the waterfowl passing through or resident in this part of the State, and management practices must endeavor to provide optimum conditions for the majority of important local species in a form of multiple usage of refuge facilities. Any plan of this type produces some conditions which are not always to the best advantage of certain species, but management on many waterfowl refuges realizes its goal when providing maximum benefits for a maximum number of the important or endangered species.

Management plans at Malheur also involve certain agricultural practices which can be included under the headings of cropping, haying and grazing. These are subordinated to the needs of waterfowl and are considered advantageous to the migrating and resident birds. The monetary return from refuge agriculture, together with returns from muskrat share-trapping on Malheur Lake, is another inducement for carrying on these activities.
In parts of Units 6 and 9 in the Blitzen Valley, grain fields provide excellent feeding grounds. During August and September, over 200 sandhill cranes frequently are found in a single field. Many flights of Canada geese and puddle ducks pass up and down the valley early in the morning and at sunset to feed on grain. In addition to field utilization by various birds some grain is harvested and stored for emergency feeding of waterfowl during severe winters. Some grain is also used in feeding the captive trumpeter swans.

Small grain farming is accomplished by two methods. Refuge personnel tend a substantial proportion of the grain fields each year and an equally large, and often larger, acreage is farmed by private individuals (permittees) on a "50-50" share basis. At harvest time the Government's share may be harvested and stored or left in the field for waterfowl use. By thus providing supplementary feeding facilities on the refuge, the birds are given additional protection during the hunting season, and depredations on the grain of adjacent farms or ranches may be decreased. Grain farming does not directly affect the canvas-back to any great extent, for it is accomplished on land which is irrigated only briefly during the spring. Some grain fields planted around the receding shorelines of Malheur Lake and Mud Lake during 1947, however, could serve as feeding grounds for the canvas-backs and other ducks, geese and swans, if this land becomes flooded during the spring of 1948. Small grain
cropping around Malheur Lake is undertaken in an opportunistic manner and only during low water conditions when the land used is of little if any value to waterfowl. Totals of 790 acres in 1942, 1,018 acres in 1946 and 1,600 acres of land in 1947 were planted with small grain. As long as dormant emergent cover is avoided in cultivation during low water years, these cropping practices are believed compatible with good waterfowl management at the Malheur Refuge.

Haying and grazing may be discussed together. Most refuge hay is cut by permittees on the 50 per cent share basis and after being cut and "bunched" or stacked, may be fed to cattle or horses in the hay fields on an "animal unit month" basis, i.e., the payment by the lessee of $0.50 for each animal over six months old for each month of use. Hay cutting is usually begun some time after July 15 when few ducks are still nesting, and is completed within two or two and one half months. During "late" seasons, haying is postponed until brood observations indicate that there is little danger of destroying nests of terrestrial nesting ducks.

In marshes having only a limited amount of usable hay growth which cannot profitably be cut, cattle and horses are turned in to graze, usually after the end of July, and in hayed fields, the stock is turned in after haying operations are completed. When cutting hay, dense emergent plant cover (bulrush, cat-tail, bur-reed) is avoided (Fig. 41).
Fig. 41. Heavy, emergent plant cover is avoided during mowing in order to leave adequate nesting cover for diving ducks during the following year.

thereby insuring adequate cover for diving ducks the following spring and summer when the land again is flooded. Hay cutting also stimulates the growth of grass and sedges in the fall and spring, providing better grazing areas for geese and sandhill cranes. Most of the grass and weeds used by puddle ducks for nesting cover is either among shrubby growth in higher situations and therefore avoided in mowing, or in the case of late-nesting gadwalls and cinnamon teal, the current year's growth provides adequate cover by the time these species are ready to nest. This mowing practice is also favorable to canvas-backs and redheads in providing vegetation-free water for flushing and
much additional "abrupt edge" where most of their nests are located. By mowing close to the heavier stands of coarse vegetation, the "insular" pattern or clumping of vegetation may be maintained, for pioneering sparse growth around the clumps is cut back each year, thus preventing the development of vast, unbroken, heavy cover avoided by most nesting ducks.

The effect of grazing on waterfowl habitat is much more difficult to evaluate. Canada geese nesting in heavy bulrush cover in a swamp of Unit 3 (Fig. 42) either nested on

![Image: Dense hardstem bulrush of pond in Unit 3 was opened by muskrats (center of picture), dynamiting (lower right) and later in the season, by stock trails (not yet visible).]
musk rat lodges near open water or along trails trampled by stock and deer through the dense vegetation. When some of this vegetation is completely flattened by a surplus of stock it is avoided by most waterfowl during the following year. Excessive trampling is avoided largely by careful determinations of the capacity for utilization of each grazed area.

The grazing problem in Unit 12 is somewhat different. With high water, livestock remained well back in the meadows surrounding Malheur Lake, but in 1946 and 1947, the animals trampled and grazed marginal vegetation while coming to the lake shore for water (Fig. 43). Little nesting by
either puddle ducks or diving ducks might be expected in
the temporarily destroyed cover during the following year
should the shoreline continue to recede, but with higher
water during the succeeding year, marginal vegetation would
be in poor condition for nesting. Furthermore, in obtain-
ing water livestock usually trampled excellent nesting cover
provided by ballast vegetation both on Cole Island Dike
and on dikes in other parts of the refuge. Much of this
trampling could be avoided in Unit 12 by pumping water for
livestock from shallow wells equipped with windmills to be
located east and north of Malheur Lake, and by erecting
permanent fences where needed. Fencing of some other dikes
may be advisable, though continued studies are required to
establish this practice as necessary.

The best water-cover management for canvas-backs and
redheads is also consistent with good water-cover management
for Canada geese, sandhill cranes, diving and puddle ducks,
coots, rails, grebes, and other waterfowl. On the Malheur
Refuge various administrative units gradually are being
developed toward providing good migration, nesting, and
brood-rearing habitat for the waterfowl which visit or
remain to breed there. Cover-water interdispersion, water
depths, and aquatic plant food utilization by canvas-backs
and to some extent by other waterfowl has already been dis-
cussed. The same ponds in the Blitzen Valley which are
utilized by canvas-backs in nesting and rearing broods are
Fig. 44. This Canada goose nest was located about 50 feet from a later canvas-back nest in the Buena Vista pond, one of the two greatest goose nesting concentration areas on the refuge.

Fig. 45. Nesting pair of sandhill cranes flushing from bulrush-spikerush plant community occupied by canvas-backs nesting in shallower Blitzen Valley marshes.
also occupied by nesting Canada geese (Fig. 44) and sandhill cranes (Fig. 45), while all species of locally nesting ducks (excepting American mergansers) rear their broods in this habitat. Some of the larger and more open ponds (Fig. 46) provide fine puddle duck migration, resting and feeding areas, while both larger and smaller ponds (Fig. 47) are used in nesting and brood-rearing. In all of these ponds, whether permanent or temporary, an attempt should be made to fill them as quickly as possible with available water in order to induce a maximum number of waterfowl to remain as residents, and to provide stationary water levels throughout the nesting season.

Water conservation is especially important on the Malheur Refuge because of the limited water supply and rapid rate of evaporation and transpiration. In order to determine the comparative rates of water loss from free-water surfaces and certain marsh vegetation, a phytometer was set up. Using five 50-gallon steel drums, two blocks each of dormant vegetation from broad-fruitied bur-reed and from hardstem bulrush were placed in the drums. One remaining drum was kept free of vegetation. The battery of five drums was submerged to within six inches of the open ends and the drums were filled with water to within two inches of the tops.

When the green growth had attained nearly full size (except with bulrush which remained smaller than usual)
Fig. 46. The nesting vegetation was limited but most local species of ducks and geese, as well as other waterfowl, occupied this permanent pond during migration and brood-rearing.

Fig. 47. This temporary or seasonal pond was used by ducks and geese until August when they sought larger ponds for the brood-rearing and flightless period.
the experiment was begun and continued for one month in late July and most of August. Throughout the month water was added on alternate days or oftener during hot windy weather. In 30 days the two drums with bur-reed had lost 51.0 and 43.8 gallons of water, respectively, bulrush drums each had lost 46.4 and 38.6 gallons, and the drum without vegetation had lost only 7.2 gallons of water, giving a bur-reed:free-water surface ratio of water lost of 6.58:1, and a bulrush:free-water surface ratio of water lost of 5.9:1. Bur-reed growing in the drums attained average size but bulrush remained smaller than other bulrush growing nearby. Perhaps the water loss from larger bulrush from larger bulrush growing in the natural state may equal or exceed that of bur-reed.

The experiment indicated that cover of this type tends to lose water about six times faster than water surfaces without emergent vegetation. In this way, opening up of ponds in the Blitzen Valley through the activity of muskrats or increase of water depths not only increases the valuable "edge effect" and the amount of area in which submerged plant foods may be produced and in which broods may be reared, but also demonstrates good water economy by reducing effective evaporating surfaces.

Proper management of Malheur Lake in the best interests of waterfowl is not possible at present since a part of the lake basin still is privately owned with attendant "water
rights," and the levels can not be manipulated as desired. When all of this land is brought under Governmental ownership, installation of a dam at the outlet of Malheur Lake will provide much greater stability of desirable water levels. Excess water which now passes through Malheur Lake during spring can be prevented from continuing into Mud Lake and Harney Lake, except during good water years. A higher, stabilized water level will furnish a maximum amount of water surface and plant cover for migrating and resident waterfowl and will help to prevent drastic reduction of the water surface acreage (Fig. 48) and concentration of ducks and geese during their flightlessness, brood-rearing and the time of most botulism outbreaks. The canvas-back may also be benefited indirectly by a possible reduction in promiscuous egg-laying by the redhead and ruddy duck with controlled water levels.

Closely associated with control of water entering and leaving Malheur Lake is management of the extensive muskrat population of this large bulrush-grown body of water. Each year from 15,000 to 20,000 muskrats are trapped on Malheur Lake. Judging from the large number of muskrats seen each spring after the end of the trapping season, the annual surplus which could be trapped is much greater than the number that is now included in the annual fur harvest. Each year following the trapping season, thousands of dead and dying muskrats are found in Malheur Lake and on Cole
Island Dike. During the spring of 1942 this mortality was especially evident, for dead muskrats were found at the rate of one for each linear 50 yards on the seven-mile Cole Island Dike, while more than half of the muskrat lodges in the south half of Malheur Lake contained carcasses of dead muskrats. The causative agent of this muskrat epizootic has not yet been satisfactorily determined. In spite of the depressing effect of this sickness, the muskrat populations responded well and an abundance of muskrats was seen by September each year.

By heavier trapping, populations of muskrats could be
reduced prior to the usual "outbreak" period and many of
the skins which otherwise would be wasted could be saved.
In addition, by increased trapping on certain areas of
heavy muskrat concentrations, present damage to bulrush
stands might be reduced. In order to bring about a favor-
able cover-water interspersion through controlled or semi-
controlled water levels and muskrat management (Fig. 49),
utilization of the bulrush by muskrats must be closely
watched during the building of lodges in the fall to deter-
mine the abundance and distribution of muskrats. Then
trapping can be directed at the more heavily populated
places where damage to the vegetation and possible localized

Fig. 49. Proper cover-water interspersion on
Malheur Lake is primarily dependent
upon wise management of muskrats
and maintenance of suitable water
depths.
epizootics would be expected to occur.

Predator control on the Malheur Refuge has been limited for the most part to suppressing the numbers of coyotes and ravens. A local Government trapper has been taking coyotes through trapping (Fig. 50), den-hunting, and the use of "coyote-getters" or cyanide-gun baits, the last being especially effective. "Coyote-getters" consist of a cartridge equipped with primer, powder charge, and a quantity of cyanide, the cartridge being inserted into a detonating device. When the scented trigger mechanism is grasped by the coyote, the cyanide is discharged into its mouth, kill-
ing it quickly. Coyotes are also hunted, the greatest success being obtained by the use of a plane. By this method, most successfully accomplished during winter, the pilot flies the plane over the coyote at very low altitude and a passenger kills it with a shotgun.

During the winter of 1946-7, the Division of Predator Control of the Fish and Wildlife Service undertook a coyote-poisoning campaign on the refuge and surrounding area, dropping baits poisoned with a "1080" preparation from an airplane. The success of this procedure was reflected in a very noticeable decrease in the coyote population on the refuge. By August in 1947, however, coyotes were again quite common on the refuge. Many of them probably were pups reared by surviving females, but some were believed to have drifted into the refuge from the surrounding land. For coyote control measures to be successful, the poisoned area should include the entire refuge and general vicinity. Southeastern Oregon being essentially grazing country for cattle and sheep, rigid control of the coyote is especially beneficial to these ranching practices.

The raven population also fell perceptibly following the broadcasting of poisoned baits for coyotes. Although as many ravens and raven nests as possible are destroyed by refuge personnel each year, this method is much less successful, for many nests are located in inaccessible places in the rimrock. Like the coyote, ravens also flocked into the
refuge when the surrounding country became very dry in the late summer. By that time, most ducks and geese had hatched so these ravens arriving late in the season were of little importance as waterfowl predators.

A limited amount of nest predation by minks was evident. Since a number of these mustellids is caught during winter trapping each year they have not increased beyond a rather low population. The use of upland sections of the refuge by badgers is not detrimental to waterfowl. A few badgers located in areas of concentrated terrestrial nesting such as on Cole Island Dike were very methodical and complete in destroying most nests within their habitat. These individuals should be eliminated by poisoning or trapping, or should be trapped and released elsewhere. A number of raccoons are also trapped each year but do not seem to prey importantly on adult or juvenile waterfowl or their eggs.
SUMMARY

1. The object of this study was to obtain information on the life history and ecology of the canvas-back in south-eastern Oregon, with special attention to interspecific nesting relationships.

2. Field work was carried out on the Malheur National Wildlife Refuge and adjacent marshland, Harney County, Oregon during the spring and summer months of 1942, 1946 and 1947.

3. A review of the literature on the description, distribution, migration and status of the canvas-back was presented.

4. Water levels on the refuge were high in 1942 and low during 1946 and 1947. The spring of 1942 had lower, average, daily temperatures than for the same season in 1946 and 1947.

5. Thirty-one species of Anseriformes have been recorded on the Malheur Refuge, 14 of which nest there.

6. Canvas-backs usually appeared on the research area early in March and were most abundant between March 15 and April 20. The last spring migrants passed through by May 10.

7. The average flight speed of canvas-backs was about 46 miles per hour.

8. Migrating canvas-backs remained in open or semi-open water except while a strong wind was blowing when they sought more protected situations.

9. Approximately 18,000, 16,000 and 15,500 canvas-backs
passed through the Malheur Refuge during 1942, 1946 and 1947 respectively.

10. Warm weather in the spring was correlated with an accelerated migration of canvas-backs from the refuge. Departures were delayed during cold weather.

11. Distribution of migrant canvas-backs on the larger lakes appeared to be governed by water depths, cover-water interspersion and species and availability of submerged plants.

12. Most of the earliest migrants were males and about 68 per cent of the canvas-backs were paired during the height of migration. Average male: female ratios for the three years were 1.47:1, 1.52:1 and 1.63:1 based on counts of 7,162 migrants.

13. Courting of canvas-backs was seen most frequently during calm, warm days. Inclement weather checked courting.

14. Although canvas-backs were monogamous, occasional promiscuity was evident.

15. Mated drake canvas-backs followed the female in flushing.

16. Periods of egg-laying were from April 10 to July 15, 1942, March 22 to June 28, 1946 and April 20 to June 11, 1947. Periods of hatching were from June 5 to August 5, 1942, April 26 to July 31, 1946 and May 24 to July 14, 1947. Total nesting seasons for each year were from April 10 to August 5, 1942, or 118 days; March 22 to July 31, 1946, or 132 days; and April 20 to July 14, 1947, or 86 days.
17. About 564 resident canvas-backs (3.1 per cent of the total canvas-back spring migrants) in 1942, 308 residents (1.9 per cent) in 1946, and 236 residents (1.5 per cent) in 1947 remained on the refuge.

18. The habitat occupied by nesting canvas-backs contained a larger proportion of vegetation to open water than migration habitat.

19. While the female attended the nest the male remained on a waiting site in the vicinity.

20. Canvas-back drakes defended the mate, not a "territory," against intrusion.

21. The length of time required to complete the clutch largely determined the length of time that the male remained with the mate after construction of the nest.

22. Incubation usually was commenced during laying of the last two or three eggs in a clutch.

23. Females abandoned by males after the onset of incubation were not known to have renested.

24. The male took no part in selection of the nest site, nest construction, incubation or brood-rearing.

25. The most important condition determining the use of habitat in nesting was cover-water interspersion.

26. Most canvas-back nests (83.8 per cent) were located in vegetation containing hardstem bulrush.

27. Utilization of vegetation in nest construction was largely determined by the pliability of the plant materials.
28. The distance from nests to flushing areas varied from 0 to 75 feet and averaged 11.7 feet.

29. Canvas-back nests were found in two general types of plant cover: (1) clumps in semi-open ponds or lake, and (2) edges of moderately dense stands of bulrush or other vegetation margined by spikerush in shallower ponds or sloughs.

30. The canvas-back female covered the eggs with nest materials prior to her departure from the nest to feed or rest.

31. Nest bowls were lined with down prior to and during incubation. The rate of loss of visible down was directly proportional to the rate at which new plant materials were added to the nest.

32. The average number of eggs laid in canvas-back nests was 18.2 in 1942, 9.9 in 1946 and 10.0 in 1947. Eggs were laid during most hours of the day.

33. The average number of eggs laid by canvas-back females in interpreted initial nesting attempts was 9.9.

34. Fifty-nine (79 per cent) of the observed canvas-back nests contained intruded eggs. Indirectly, nest parasitism caused an increase in the average number of host eggs laid.

35. The proportion of intruded eggs in canvas-back clutches was 65.4 per cent in 1942, 24.6 per cent in 1946, and 36.5 per cent in 1947.

36. In the 74 canvas-back nests were deposited 482 canvas-back eggs, 497 redhead eggs, nine ruddy duck eggs, one American
pintail (?) egg and one American coot egg.

37. The average incubation period of canvas-back eggs was 25 days. Female canvas-backs flushed least readily late in incubation.

38. The percentage of nest success was inversely proportional to the per cent of females renesting and promiscuous egg-laying of other species in canvas-back nests.

39. The average duration of canvas-back nest histories was 15.7 days for unsuccessful attempts and 33.5 days with successful nests.

40. Forty-two (57 per cent) of 74 canvas-back nests for the three years were unsuccessful, 27 of these failures occurring during 1942.

41. Thirty-three (80 per cent) of the unsuccessful nests were abandoned and nine (20 per cent) were destroyed. Of the abandoned nests, 27 (82 per cent) were believed deserted because of nest parasitism.

42. Renests could not be distinguished from initial attempts on the basis of physical features of the nest or clutch size.

43. American ravens were the most important predator, destroying eight canvas-back nests. One nest was destroyed by a weasel or mink.

44. Nesting success, taking renests into consideration, was estimated to have been 27.8 per cent in 1942, 76.5 per cent in 1946 and 70.0 per cent in 1947.

45. Female canvas-backs rarely parasitized other nests on the research area.
46. Of all eggs deposited in canvas-back nests the per cent hatching was 6.7 in 1942, 59.8 in 1946 and 42.2 in 1947.

47. The proportion of canvas-back nests with foreign eggs each year remained about the same, but the average number of intruded eggs in nests each year varied widely.

48. Eggs lost over the side of the nest constituted the most important factor reducing the number of canvas-back eggs which hatched in parasitized nests.

49. An average of 7.3 canvas-back ducklings was hatched in unparasitized nests. Of an average of eight ducklings hatched in parasitized nests, six were canvas-backs and two were of the intruding species.

50. The ratio of canvas-back:redhead ducklings hatched in canvas-back nests was 1.44:1 in 1942, 4.35:1 in 1946 and 6.46:1 in 1947.

51. The greatest motility of broods occurred during the first week after hatching. Older broods usually remained on an area until influenced to leave by habitat changes or until the ducklings reached flight age.

52. Various hypotheses on the origin of the parasitic habit among birds, and with ducks particularly, were discussed.

53. The promiscuous egg-laying habits of the redhead and ruddy duck seemed to result from a "lack of attunement" of nest-building and egg-laying instincts, which in turn, appeared to be responsive to external stimuli of weather and habitat.
54. Variations in breeding densities of the canvas-back and redhead, depth of water at the host's nest site, advancement of the season, species of nesting cover and period in the nest history did not seem to be factors which governed incidence or extent of parasitic egg-laying.

55. The female showed about the same inclination toward desertion throughout its nest history until about the last three days of incubation.

56. Nesting habitat and nesting success percentages of the canvas-back and the redhead were quite similar. Nesting of the canvas-back was about three weeks earlier than nesting of the redhead.

57. Canvas-back nests were more heavily parasitized than redhead nests in 1942.

58. In canvas-back nests the fertility of both host and intruder eggs was similar.

59. The intruding female did not (1) assist in the construction or maintenance of the host's nest, (2) remove down feathers from its body for lining the nest bowl, (3) turn the eggs, (4) form the clutch into a concave, body-fitting layer, (5) cover the eggs prior to leaving the nest, or (6) incubate.

60. Drakes remained in attendance of the female intruders while the latter were attending the hosts' nests.

61. Nest parasitism was a depressant on canvas-back production by causing the female host to desert and by reduc-
ing the number of canvas-backs eggs hatching through the complementary influence of the intruded redhead eggs.

62. Nest parasitism was detrimental to the intruding species for (1) the intruder may not have abandoned its promiscuous habits to build a nest during the season, reducing the number of resident females producing broods; (2) nests built later by the intruders appeared to contain smaller clutches; and (3) intruded eggs met with much lower success than eggs laid in the intruder's own nest.

63. The attention shown juveniles by parent canvas-backs decreased with the advance of the season.

64. Ducklings from other nests were not readily adopted by canvas-back females.

65. By August 15 most juvenile canvas-backs had broken away from the parental brood to join local concentrations of juvenile canvas-backs in more open water than had been occupied by the brood.

66. The canvas-back juveniles began to make short flights shortly after the tenth week.

67. The annual reproductive increment of canvas-backs each year was 196 in 1942, 494 in 1946 and 347 in 1947. Along with the canvas-back ducklings, 123 redheads in 1942, 114 in 1946 and 54 in 1947 were hatched in canvas-back nests and reared.

68. The adult: surviving juvenile ratio on the Malheur Refuge was 1:0.56 in 1942, 1:1.97 in 1946 and 1:1.70 in 1947.
69. The incidence of observed canvas-back duckling mortality was low.

70. The only known sicknesses of canvas-backs at the Malheur Refuge were botulism and lead-poisoning, accounting for one and six dead ducks, respectively.

71. Bird fleas (Ceratophyllum) infested the over-water nests and ducklings in the nest's of canvas-backs on the Malheur Refuge. No bird fleas were found on adult ducks.

72. Peale's meadow mouse frequently nested and reared young in the nests of canvas-backs and redheads.

73. The only ectoparasite found on full-grown canvas-backs was a louse (Austromenopon leucoxanthum).

74. Endoparasites collected from the alimentary tract and trachea of canvas-backs were Hymenolepis megalops, Hymenolepis sp., Diorchis wigginsi (?), Echinostomum revolutum, Typhlocoelum cymbium, Zygocephylus lunatum, Amidostomum sp. (prob. A. anseris) and Tetrameres sp. (near T. fissaipina).

75. The first postbreeding movements of adult male canvas-backs began in May and early in June.

76. Postnuptial molting areas for canvas-back drakes were the larger, deeper, and more open waters of the refuge.

77. Although some canvas-backs loafed on land during part of the molting period, most of them remained in water far from shore.

78. Most full grown canvas-back juveniles left the valley ponds during the first half of August.
79. Many of the canvas-backs breeding on Malheur Refuge appeared to winter in the San Francisco region and in the Sampa and Sacramento Valleys of California.

80. Nearly all canvas-backs left the refuge before November 15 each year.

81. Management of the canvas-back was consistent with overall wildlife management on the refuge.

82. Cropping, haying and grazing, together with muskrat management, when properly undertaken may be useful tools in improving habitat for waterfowl utilization.

83. Stabilized water levels during the nesting season are vital to improved nesting habitat and increased nesting success of the canvas-back and certain other waterfowl.

84. Predator control on the Malheur Refuge was concerned mainly with suppression of the numbers of ravens and coyotes. Minks and raccoons were trapped in limited numbers. Badgers should be excluded from waterfowl nesting habitat on the Malheur Refuge.
LITERATURE CITED


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


Bond, James. 1940. Check-list of the birds of the West Indies. Acad. of Nat. Sci. of Philadelphia. 1940.


Chance, Edgar P. 1922. The cuckoo's secret. London. Sidgwick and Jackson, Ltd.

1940. The truth about the cuckoo. London. Country Life Ltd.


Daguerre, J. B. 1920. Observaciones sobre los patos "Neteo-
plana pepeosaca" y "Heteronetta atricapilla." El Hornero 
2: 61-62. (Original not seen; cited in Phillips 1923, 
vol. 3, p. 96)

Davis, David Edward. 1940. Social nesting habits of the 

-------- 1942. The number of eggs laid by cowbirds. Con-
dor 44: 10-12.

-------- 1945. The development of social nesting habits 

Dawson, William Leon and John Hooper Bowles. 1909. The 

Delacour, Jean and Ernst Mayr. 1946. Supplementary notes 

DeMay, Lda S. 1941. An avifauna from sub-Recent deposits 

No. 3, Fish and Wildlife Serv. U.S.D.I.

Elliot, Daniel Giraud. 1898. The wild fowl of the United 
States and British Possessions; or, the swan, geese, 
F. P. Harper.

Elliot, Samuel A. Jr. 1936. Florida records of interest. 
Auk 43: 346-347.

Erickson, Arnold B. 1943. Sex ratios of ducks in Minnesota, 
1938-1940. Auk 60: 20-34.

Erickson, Ray Charles. 1942. Breeding habits of the canvas-
back, Nyroca valisineria (Wilson), on the Malheur Na-
Iowa State College Library.

Errington, Paul L. 1942. On the analysis of productivity in 
6: 165-181.

Fannin, John. 1894. The Canada goose and opeyrey laying in 
the same nest. Auk 11: 322.


McIlhenny, E. A. 1934. Twenty-two years of banding migratory wild fowl at Avery Island, Louisiana. Auk 41: 328-337.


------- 1942. Laboratory procedure in wildlife food studies. Wildlife Leaflet No. 222.


Yamashima, Y. 1931. Six additions to the list of Japanese birds. Tori 7. (Original not seen; cited in Auk 48: 642)
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