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THE BIOLOGY OF THE MOUNTAIN DUCK ON ROTTNEST ISLAND, WESTERN AUSTRALIA

by

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FRONTISPIECE. A pair of adult mountain ducks *Tadorna tadornoides* in breeding plumage. Male left and female right.

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CONTENTS

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INTRODUCTION

The taking of ducks for meat or sport in Western Australia has been recorded since the arrival of European man; however, in the past 50 years the sport of duck shooting has gained rapidly in popularity. A total of 14 species of ducks occurs in the state, one of which is protected, and of the 13 game species, only 4 make major contributions to the total bag. They are the grey teal *Anas gibberifrons*, the black duck *A. superciliosa*, the mountain duck *Tadorna tadornoides*, and the wood duck *Chenonetta jubata*. In terms of relative contribution to shooters' bags, these species have changed markedly in recent years. The first 2 have declined relative to the last 2. Part of the increase in the wood duck is attributed to increased habitat provided by stock dams. However, the change shown in mountain duck is not so easily determined, and it is the aim of the present work to investigate the problem.

Ducks of the genus *Tadorna*, known as shelducks, are distributed throughout the Southern Hemisphere. Three species are represented in Australasia: *T. variegata* the paradise shelduck of New Zealand, *T. radjah* the burdekin duck from the tropical areas of northern Australia, and *T. tadornoides* the mountain duck of southern Australia.

The burdekin and mountain duck both occur in Western Australia. The former is not common and has been listed by the Department of Fisheries and Wildlife as a totally protected species until future research and management programs can be undertaken. The mountain duck is common in the southwestern part of the state and can be taken as a game bird during the annual duck hunting season.

Gould (1848) reported that the mountain duck was nowhere plentiful but universally spread over Van Dieman's Land (Tasmania), South Australia, and Western Australia. Other early ornithologists gave a similar impression of the bird's distribution, but suggested that it was quite common (see Mathews 1915). Carter (1923) stated that thousands gathered on Lake Muir (southwestern Western Australia) when it was full. The commonness of the species has been confirmed by aerial surveys from 1965 to 1974. Concentrations of 8,000 to 10,000 mountain ducks were sighted on several lakes and estuaries in the southwestern corner of Western Australia (see Riggert 1969, unpublished doctoral dissertation, University of Western Australia, Nedlands, Western Australia, Table 24, Fig. 42 for specific location of wetland areas and numbers of birds observed, 1965–1968). The general impression from those surveys is that the species is spread evenly over the wetland areas of the Southwest and Eucla Land Divisions. However, during periods of seasonal or sporadic rainstorms, the distribution may expand inland for several hundred kilometers.

It is apparent from the aerial surveys that aggregations of the mountain duck occur along the shorelines and on sandy islands of salt lakes and estuaries. Field observations in those preferred areas indicate that the bird makes regular visits to freshwater seepages or lakes in the immediate vicinity. In the winter or breeding season, many birds shift to freshwater lakes, swamps, and stock dams. Once the young are old enough, adults and young assemble on the saltwater areas.

No doubt agricultural development, such as stock dams and sowing of grain crops, has benefited the species and resulted in increased numbers. In many farming areas, complaints have been made that mountain ducks are so numerous that they foul dams and destroy large areas of freshly sown grain.

The following are possible causes of the apparent change in status of the mountain duck: (1) actual numerical increase in mountain ducks; (2) relative increase in mountain ducks due to decrease of habitat of other game species; (3) change in shooters' tastes; and (4) increased shooting pressure, producing an overharvest of finer table birds with the consequent increase in the bag of mountain ducks relative to other species.

The destruction of duck habitat by clearing and draining wetlands on the Swan Coastal Plain has been investigated (Riggert 1966). That study showed that 30 percent of the wetlands on the study area had been drained since 1955. Other factors such as sanitary landfill, industrial pollution, mining, and recreation also utilized wetlands and caused physical changes. The final conclusion of the study by Riggert revealed that the change brought about by draining and other uses had caused degeneration of a once highly productive waterfowl area to one of low production. Similar problems of wetland drainage have been observed throughout the Southwest and Eucla Land Divisions (areas not included in Riggert's study). The full effect on the mountain duck population is not shown, but it is certain that once the activities mentioned above occur in wetland areas, waterfowl no longer frequent them.

From discussions with shooters, it seems clear that shooters' tastes have changed along with reduction in waterfowl habitat (other than saline habitat) and decline in numbers of waterfowl other than mountain duck. The foregoing suggest that a detailed study of the ecology of the mountain duck was desirable, thus allowing management procedures to be devised before an acute shortage of ducks for hunters created a serious problem.

The study area selected was Rottnest Island (19 km west of Fremantle, Western Australia), approximately 1,900 ha in area. There is a permanent field biological station with laboratory and accommodation facilities, plus a 4-wheel-drive vehicle. Daily transportation to and from the island is afforded either by boat or airplane.

Rottnest Island was gazetted an A Class Reserve in May 1917, and protection of the mountain duck on the island has been upheld since then. The first documented record of mountain ducks on the island was in 1864 (see Storr 1965), but not until Campbell (1900:1030) recorded a count of 40 in 1889 was there any information on total numbers. Many local residents living on the island more than 30 years, have given accounts of total mountain duck populations; however, on the information provided, there appears to be little difference between past populations and numbers of birds present today. All the foregoing indicates that a population of mountain ducks has occupied Rottnest Island for the past 100 years, and such a period of occupancy indicates that the island's environment is adequate for the species.

The research program on the mountain duck of Rottnest Island commenced in October 1964 and ended December 1974. During that period, 930 days were spent on the island making field observations and banding 1,690 mountain ducks. In subsequent trappings, with some birds being captured several times, there were 2,084 birds retrapped, making a total of 3,776 trapped birds.

The objectives of this study were (1) to understand the breeding biology of the mountain duck, with emphasis on behavior during the prebreeding season, reproduction, growth and development, mortality, and age at sexual maturity, and (2) to evaluate the dynamics of the Rottnest Island mountain duck population and its relationship to shooting pressure on the mainland during the annual duck hunting season.

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METHODS AND MATERIALS

Field Methods

The duck traps used on Rottnest Island were similar to those described by Addy (1956) as semiportable funnel traps. The dimensions of the traps were 6 × 6 × 1 m with a small catching pen attached to the end of the trap facing the center of the lake. Trapping conditions were optimum in approximately 25 cm of water.

The traps were baited with wheat each morning and evening after the ducks were cleared. To clear the traps, the birds were herded into the catching pen, scooped up with a hand net, bagged, and taken to the biological station for processing. As the water dropped through evaporation, it was necessary to move the trap into deeper water.

The 2 original cannon nets used for taking mountain ducks on Rottnest Island were similar to those described by Dill and Thornsberry (1950). However, in 1966, a modified type of cannon, known as the Dill, Miller, and Thornsberry cannon, designed by the U. S. Fish and Wildlife Service, was substituted for the original design. The nets used were of 2 sizes, the large net was 365 m^2 while the small net for trapping pairs of birds was 18 m^2.

When using a cannon net, it was necessary to prebait for approximately 10 days prior to firing. During the prebaiting period, the nets were covered with hessian to stop the birds from tangling the nets when walking over them. The cannons were fired electrically from a hide approximately 135 m from the trapping site. The birds caught under the net were untangled, bagged, and taken to the biological station for processing. A prebaiting period of only 4 or 5 days was required for trapping pairs with the small net.

The original bands used in the study were monel metal, size 15 (49 × 10 × 0.7 mm), which were ineffectual because the presence of sulfides in the hypersaline lakes on Rottnest Island caused them to become heavily corroded and to fragment. The average time the bands were legible was less than a year.

After consultation with I. C. I. Metals Research Division, it was advised the most suitable metal for saline waters of the concentrations on Rottnest Island was titanium. The metal was supplied by courtesy of I. C. I., stamped, and cut to size 15. No occurrence of corrosion or band wear was evident in the titanium bands used from February 1967 to December 1974.

The "A-frame" bill tags used during the study (Fig. 1) were made of "Cobex," a rigid PVC with a thickness of 0.35 mm. A silk screen printing process was used for painting the numerals and letters on 35.5 × 21.5-cm sheets of colored Cobex. The tags were given an additional 2 coats of clear

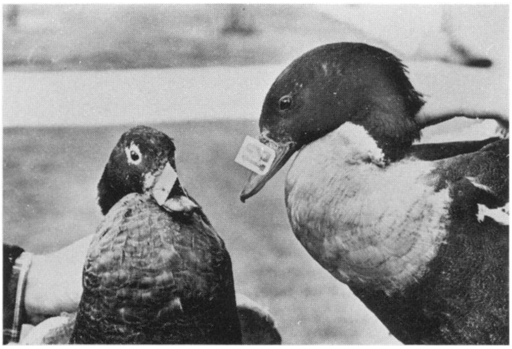


FIG. 1. Adult female (left) and adult male (right) mountain ducks wearing A-frame bill tags, Rottnest Island, Western Australia.

PVC paint to prevent sunfade of the colors and damage through abrasion.

A small hole was burnt 2 cm from each end with a small copper wire, to approximately the diameter of a 13.6-kg test monofilament line. The tags were folded in the center and placed over the bird's bill and held in position by the monofilament line, threaded through the nares, and tied on each end with a simple knot.

In the field, with good light, tags could be read at 180 m with 10 × 50 binoculars or 455 m using a zoom spotting telescope, 25-50 × 60 mm mounted on a tripod. A total of 9 different color combinations was used to denote sex and age, and during the study period, 1,012 birds were tagged.

Brood counts and population counts were made at least once a month, and usually 2 or 3 counts were taken on successive days from a 4-wheel-drive vehicle driven over a predetermined route around all salt lakes and freshwater swamps on the island. The latter half of the morning after the major feeding period of the day had finished gave the most consistent counts. The counts were averaged, and that figure was used as the population on the island for the particular month. The sightings of tagged birds and their locations were also recorded during the counts.

Aerial surveys of mountain duck populations on the mainland were conducted in 1965–1968 during October–December. The area surveyed was the lower southwestern corner of Western Australia. Estimates of the numbers of mountain ducks were made by 2 observers using a 182 Cessna or Aero Shrike Commander, both high-wing aircraft. The total time of survey each year was approximately 30 hours, commencing daily at 0830 and terminating before 1600 hours. A standard procedure of circling along the edge of the lake at an altitude of 150 m allowed all observers to see the main concentrations of waterfowl. The average of the total ducks observed by the 2 or 3 observers was taken as the population for the particular area surveyed.

Laboratory Methods

The incubation and rearing of mountain duck ducklings in the laboratory was carried out during the breeding seasons of 1965–1968. Eggs were obtained from nests in southwestern Western Australia and taken to the laboratory in a thermostatically controlled portable warming box heated with a 6-volt lamp for incubation.

A commercial incubator was used in the laboratory, thermostatically controlled at 36 C with a relative humidity level of 85 percent. The eggs were turned twice a day, and every 2 days the trays were reversed back to front. Once pipping commenced, the eggs were placed in the incubator's hatching cage and left for at least 10 hours after hatching or until the ducklings were dry and active.

Once ducklings were removed from the incubator, they were banded with colored plastic leg bands and placed in brood pens. Each brood was kept separate throughout the rearing period and fed on commercial duck starter and given tap water to drink initially.

All statistical tests of significance, unless otherwise stated, were done at the 0.05 level of significance. When the mean is given followed by ±, it signifies standard deviation, as standard error is indicated as SE. Additional methods in this study will be given in

FIG. 2. Aerial photograph of Rottnest Island, Western Australia, from the eastern side looking west. Area in immediate foreground is Thomsons Bay.

the text when deviations from standard methods have been made.

DESCRIPTION OF STUDY AREA

Geography and Geology

Rottnest Island (19 km west of Fremantle) has an area of 1,912 ha. Churchill (1959), using the data of Godwin et al. (1958) and present bathymetry, deduced that the time of isolation was 5,000 years BC; he then showed by pollen analysis that at the calculated time of isolation the flora of Rottnest Island was similar to that on the present mainland. The geology has been described by Teichert (1950), Fairbridge (1954), and mapped by the Geological Survey (Ellis 1952). The general topography of Rottnest Island is of consolidated sand dunes that rise to 50 m near the main lighthouse. On the eastern half of the island there are 8 large salt lakes that have a total area of approximately 162 ha, and in addition, there are 7 swamps, some freshwater and some brackish, each approximately 0.6 ha in size. The western end of the island consists of a plateau with several limestone ridges partially overlain by dunes. Freshwater and drainage systems are completely absent as the soil is so porous that even after heavy rains, surface water does not remain. The major geographical features are shown on the aerial photograph of Rottnest Island (Fig. 2).

Climate

Hot, dry summers and cool, wet winters are characteristic of the island. The hottest months, January and February, have an average daily maximum of 26.7 and 26.8 C, respectively. The highest temperature ever recorded by the meteorological service on Rottnest Island was 42.2 C on 29 January 1956. On numerous occasions throughout the summer, temperatures reach near 38 C. July is the coldest month with an average

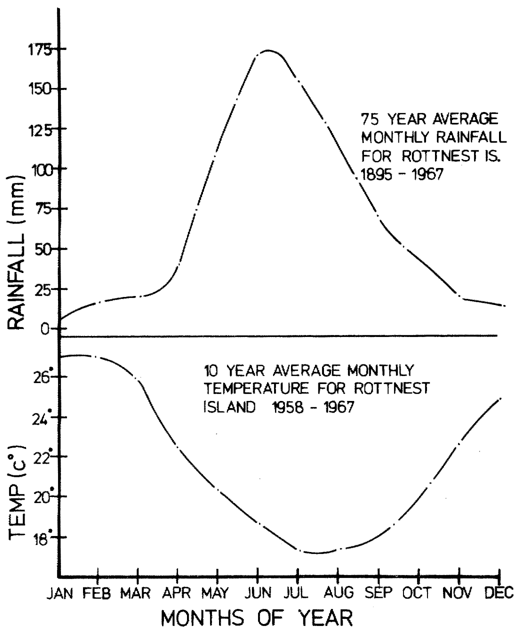


FIG. 3. Average monthly temperatures 1958–1967 and rainfall 1895–1967 on Rottnest Island, Western Australia.

daily maximum of 17.3 C and an average daily minimum of 7.7 C. The lowest temperature ever recorded was 4.7 C. Annual and monthly temperature changes for the 10-year period 1958–1967 are shown in Fig. 3.

The Government Meteorological Service on Rottnest Island has recorded the long-term annual rainfall as 73 cm. Most rain falls during June and July, and less than 10 percent of the total precipitation occurs in the summer, with some years recording as little as 5 cm between November and April. The average monthly annual rainfall for 75 years is shown in Fig. 3.

Water Impoundments on Study Area

Salt Lakes

The 8 salt lakes on Rottnest Island range in size; Baghdad, the largest, has 44.5 ha and Sirius, the smallest, has 0.4 ha (Fig. 4). Water gauges were put in 6 of the 8 salt lakes, and fortnightly records were kept of water fluctuations and changes in salinity. The mean variation from winter high water level to summer low water level on the 6 gauges was 78 cm.

The lakes, which are shallow basins, were thought at one time to be connected to the sea when the sea level was little different from the present (Hodgkin 1959). The numerous deposits of shells around the lake margins have been shown by Teichert (1950) to be of paired lamellibranch shells

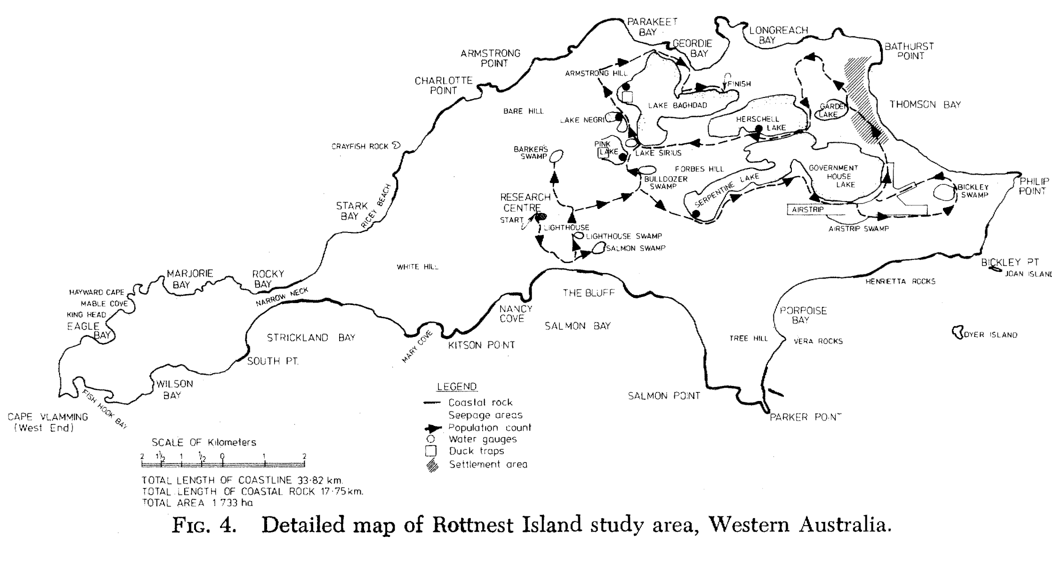


FIG. 4. Detailed map of Rottnest Island study area, Western Australia.

apparently occurring in situ. Rapid evaporation on the lakes during the summer results in high concentrations of the salts. The greatest salinity change during the years of investigation was in Pink Lake where the total soluble salts were approximately 20,000 ppm in midwinter and rose to 320,000 ppm in late summer. The greatest change in pH occurred in Negri Lake which varied from 7.8 in midwinter to 9.5 in late summer, during the normal rainfall year of 1967.

Hodgkin (1959) reported that no macroscopic plant life existed in the salt lakes. During the present study, only spheres of an algal film *Botryococcus macropogon* (Xanthophyceae) were found on the rocks or washed up on the shores. The 2 small lakes, Negri and Sirius, are considered brackish and do contain the macroscopic plants *Lamprothamnion macropogon* (Charales), *Ruppia maritima,* and *Crassula natana.*

The fauna in the salt lakes is very restricted in number of species (Hodgkin 1959). Edward and Riggert (unpublished) found that animal species and their numbers fluctuated as salinity changed throughout the year so that when salinities were low, numbers were high, and conversely.

Freshwater seepages occur along the shores of all salt lakes and appear as a film of water between high and low lake levels. Those seepages are shown as dotted areas in Fig. 4. Some seepages are large enough to form small pools that may trickle into the salt lake while others appear as spongy mats when *Sporobolus virginicus* grows on the moist area.

Freshwater and Brackish Swamps

Those swamps, as mentioned earlier, occur only in the eastern half of the island and usually are situated in interdune depressions. Their combined area is 5 ha, and only 3 of the 7 swamps have water remaining in them by the latter part of the summer. Water gauges were placed in all swamps to record water fluctuations. During the fortnightly inspections, water samples were taken and analyzed for total soluble salts, chloride, and pH (see Riggert unpublished doctoral dissertation, Table 2).

As mentioned by Edward and Watson (1959), there are 2 important factors that affect the biology of the swamps: (1) water is present only during winter (May–October), and (2) as the water starts to evaporate it becomes brackish, and marked changes in salinity occur. Collections were made and identifications listed by Edward and Watson (1959:86). Barkers Swamp, typical of the temporary swamps on Rottnest Island, is shown in Fig. 5.

Natural Vegetation around and in Lakes and Swamps

During periods of low water, samphires grow to the water's edge where the soil permits. These samphires, *Arthrocnemum arbuscula, A. halocnemoides,* and *Salicornia australis* may become completely flooded in winter, but are tolerant to waterlogging and remain healthy until the water recedes in October. As this happens, low creeping perennials such as *Hemichroa pentandia, Samolus repens, Suaeda australis,* and *Wilsonia humilis* can be found in the samphire community.

Approximately 2 m above high water level, the large tussocks of *Gahnia trifida* grow to approximately waist height. Interspersed among the tussocks are erect sedges and rushes *Scirpus nodosus, Hypilaena* sp., and *Juncus maritimus.* Also, bushes such as *Myoporum viscosum, Atriplex paludosa,* and *Arthrocnemum halocnemoides* occur infrequently. On some lakes, a perennial grass *Sporobolus virginicus* occurs between the tussocks of *Gahnia.* The grass forms a spongy mat and is highly nutritious food for waterfowl. A more detailed description of the vegetation on Rottnest Island was given by Storr et al. (1959).

DESCRIPTION OF SPECIES

In Australia, the common name given to *Tadorna tadornoides* is mountain duck. The origin of that name has been a point of conjecture for many years. In the early 1900's,

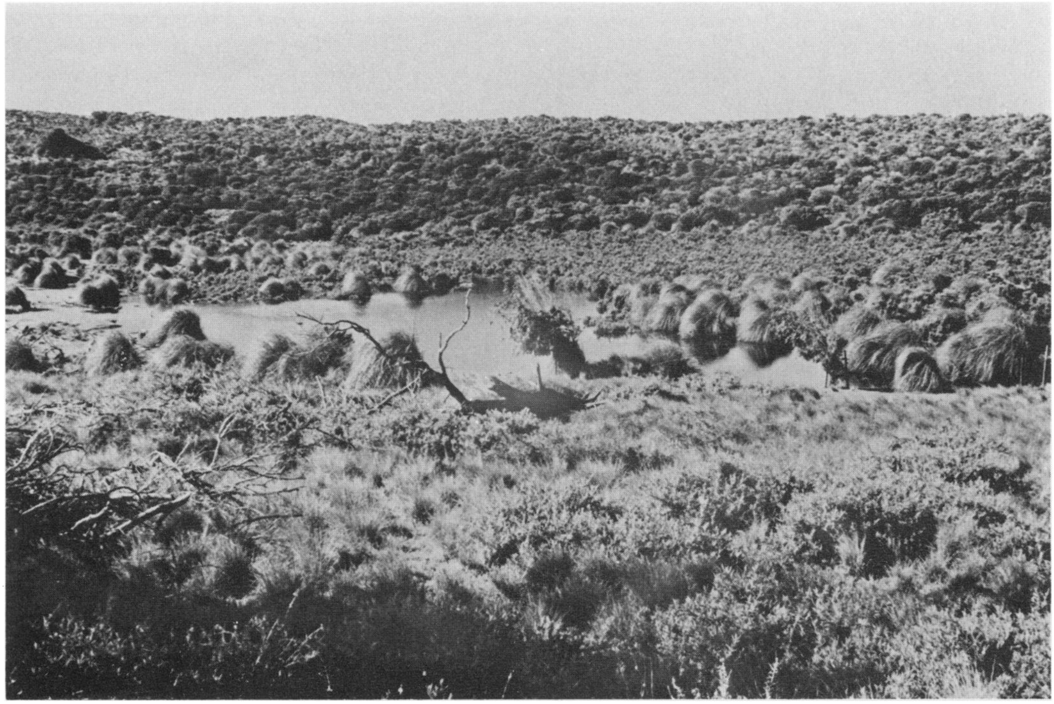


FIG. 5. Barkers Swamp, from south looking north, is typical of swamps on Rottnest Island, Western Australia. Vegetation along the shore is a samphire community. Tussocks of *Gahnia trifida* are surrounded by water when swamps are full, and it and *Acanthocarpus preissii* are primary representatives in the vegetation on the surrounding slopes and immediate foreground.

Mathews (1915), in correspondence with fellow ornithologists, sought information about the derivation of the name. At that early date, explanations were many and widely varied, making it impossible to draw any conclusions. The name "Mountain Duck" appears to be a local name made up by Australian naturalists or duck shooters, but it is definitely not descriptive of the bird's habitat.

Many recent descriptions of the species, Mathews (1915), Delacour (1954), Oliver (1955), and Frith (1967), have minor discrepancies, most of which appear due to inability to distinguish age groups. The color variation in plumage and soft parts with respect to age group will be discussed in the section on "Growth and Development." The colored frontispiece shows an adult male and an adult female mountain duck in full breeding plumage.

Subadult Plumage (Age 200–600 Days)

Male and Female

Body plumage as for adult (Front.). Wing plumage as juvenile, with incomplete iridescent green on speculum and prominent white edges on tips of ventral surface of secondaries. Legs and feet vary from charcoal gray to black.

Juvenile Plumage (Age 71–199 Days)

Male and Female

Juvenile males and females are indistinguishable by plumage. Head and neck black with many brown flecks throughout, chin generally lighter; no white collar. Lower neck, breast, and upper back light brown; scapulars, back, flank, and abdomen brown changing to dull black posteriorly; rump, upper tail coverts, and tail dull black. Under tail coverts chestnut brown. Lesser and middle wing coverts white, greater coverts light gray; primaries and their coverts dull black. Secondaries black on exposed webs except for small areas of iridescent green, white crescent on tip prominent, inner web umber gray with white crescent on tip. Tertiaries rufous chestnut on exposed web, inner web umber gray. Auxiliaries and under wing linings white with gray tips where covering primaries. Primaries black. Secondaries, inner, and outer webs umber gray except for tip which is white. Bill black. Iris brown. Legs and feet gray with some pink areas on webbing.

Duckling (Age 1–70 Days)

Downy Stage (1–35 Days)

Buff white, marked with light brown on head down to eye level and along hind neck to back, widening at back, along lower back, and widening again on rump. Wings have a continuous stripe from wing tip to wing tip. Also, a stripe on the sides of back leading toward the thighs. Legs and feet dark olive green until 17–24 days old and then turning light gray. The bill changes from olive green to light gray within 24 hours of hatching. Iris brown. Some ducklings have a cream patch under the throat that may remain for several days.

Feathered Stage (36–70 Days)

The 4 stages of feather development in ducklings are described under Growth and Development.

Voice

Adults

Frith (1967) and Johnsgard (1965) have examined the trachea and studied the calls of the mountain duck and found them similar to other "Casarcas." They both observed the ducks to be very vocal, especially in flight, and sexes could be distinguished by their calls, as the male has a strong honking call compared to the female's loud quacking call. My observations in the field and in the experimental yards of the University of Western Australia, agree with Frith and Johnsgard. In addition to the general calls, it is possible to associate specific calls with certain behavioral characteristics as alarm, defense of territories and broods, and displays of status seeking in the hierarchy.

Ducklings

The first vocalization is emitted while the duckling is still in the egg and may commence some 24 hours before pipping starts. When the duckling hatches, a frequent cheeping can be heard in the nest for the first few days. After that initial period, the cheeping is heard only at times of distress. At the age of 18–23 days, the cheeping changes to a soft-throated quack. The change from that to the adult call is gradual, and no precise age was found for that transformation. Sexing by voice is possible after the birds are 4.5 to 5 months of age.

SUMMER AGGREGATION

Postbreeding Assemblage

The total number of birds on Rottnest Island in mid-November fluctuated from 102 in 1970 to 153 birds in 1971. The composition of the group consisted of juveniles and adults. Some subadults were present, but within a few weeks their age classification changed to adult.

At that time, the majority of broods have reached the flying age (71 days) and are referred to as juveniles. Short flights are made by these birds and their parents over the salt lakes throughout the day. As the juvenile birds become stronger in flight, the family groups leave their brood territories and fly to the freshwater swamps where they forage for food and drink, and bathe. The freshwater swamps become the focal point of activity with daily gatherings of family groups and other members of the population.

To aid field observations, many birds had been tagged previously with colored A-frame bill tags, thus allowing recognition of individuals by number, year class, and sex.

Juvenile birds not tagged were easily recognized by lack of the white neck collar, drab plumage, chestnut brown under tail coverts and, when on shore, by their pinkish gray legs.

The assemblage of age groups congregating on the freshwater swamps during that period is well defined. Successful pairs with their young stay on the outside edge of the swamps, while unpaired adults, subadult females, and pairs of adult birds without young occupy the central area.

The dispersal of the groups within the congregation occurs gradually. Often, the reduction of surface water in the swamps forces the birds together on the remaining water. The family groups lose their identity as juvenile birds wander from the parent birds and mingle with the entire congregation. As the juveniles move through the congregation, they are chased by paired females protecting their mates, and this results in a complete interspersion of all age groups.

By late November, the temporary swamps start to dry out and the congregation of mountain ducks converges onto Pink and Baghdad lakes, large salt lakes containing small limestone islands. Here, all age groups are interspersed, and continuous bickering, chasing, and displaying can be observed during the early morning and late afternoon.

By mid-December, the population on Baghdad and Pink lakes commences to disperse. Many adult pairs with long-established bonds evade the constant harassment of the juvenile birds and unpaired females and leave the group. Those pairs either return to old breeding territories on the salt lakes or leave the island, presumably for the annual molt migration to the mainland. Juvenile, subadult, and adult birds that have been successful in obtaining a mate also leave the main resident population and can be seen as distinct pairs on freshwater seepages along the shores of the salt lakes. It is apparent from the band and tag returns from duck shooters on the mainland (see later) that a great exodus of birds from Rottnest Island occurs during this time each year.

The remaining resident birds on the salt lakes consisted of juvenile males and females either uninterested in pairing, unpaired, or paired with very weak bonds. Groups of adult and subadult females, that remain isolated, give the impression of not being receptive to pairing. Occasionally, adult pairs remain in this group, but the pair bonds seem so strong that no further courtship is evident at that time of year.

The sightings of changes in tagged juvenile pairs were so numerous that records of the pairings were difficult to maintain. Once the birds reached the subadult age group, the pairings became more stable, but 74 changes in partners were recorded. The adult age group had 21 changes recorded during the study period, but all took place at the end of the breeding season and not in December. A change in partners can occur in all age groups, but observations have shown that some pairs remained together throughout the study, signifying that some birds do create permanent pair bonds. The belief that mountain ducks pair for life is not supported by observations during this study.

Resident Population

Throughout January and February, the resident population takes on a fairly routine existence. The birds feed in the salt lakes and drink fresh water from the seepages and then return to the limestone islands in the salt lakes where they "loaf" during the heat of the day. Squabbling and bickering occur when lone females intrude on established pairs, but in general, the overall pattern of behavior is one of mutual acceptance and peaceful coexistence. As temperatures drop in the late afternoon, the birds drift back to the seepage areas and drink and preen for at least an hour. Feeding again takes place on the salt lakes until dark, and on moonlit nights the birds feed on into the night.

As the summer continues, the population numbers slowly dwindle with more birds leaving the island for the mainland. This pattern of movement continues until the population drops to its lowest point in late February or early March, depending on the dryness of the summer. Frith (1967) attributed movements like that to a mass molt migration similar to that of the European shelduck *Tadorna tadorna*.

This theory has merit when considering mass migration of mountain ducks in Western Australia during the spring in October and November. Aerial surveys in 1965 to 1968 found each year groups of molting mountain ducks exceeding 10,000 birds on Lakes Namming, Dumbleyung, Gore, and the Harvey Estuary. However, this does not explain why mountain ducks gradually leave Rottnest Island throughout the summer months, especially juvenile birds which will not molt for at least another 8 to 9 months.

There probably is no single reason for the birds leaving Rottnest Island for the mainland at that time of year, and contributing factors may be the following: (1) the enormous salinity changes in the lakes and swamps caused by evaporation; (2) difficulty of food getting once the swamps become dry and birds are forced to feed on the salt lakes; (3) summer monsoon rains on the mainland draw ducks for hundreds of kilometers after they pass (Frith 1959); and (4) human disturbance at that time of year as thousands of tourists use Rottnest Island as a holiday resort. Fortunately, few tourists use the salt lake areas and the disturbance to the ducks is not continuous.

Detailed examination of points (1) and (2) have shown them to be of major importance in imposing stress conditions upon the population through a shortage of fresh water and food. Water samples from Bulldozer Swamp over 4 years contained "Total Soluble Salts" that exceeded 20,000 ppm by mid-March (Riggert unpublished doctoral dissertation, Table 2). The majority of birds utilized that swamp, the largest permanent one on the island, for bathing, and it was observed that once the salinity exceeded 20,000 ppm the birds no longer used the area. Evidence of a food shortage or salt stress was found when an analysis was carried out on birds that had been retrapped numerous times throughout a summer. The weights of the birds were statistically compared to test the significance in change of weight by the Student's *t*-test. "Significant" losses of weight did occur in both adults and juveniles ($P < 0.001$ and $P < 0.05$, respectively). However, no change could be found in the subadult group ($P > 0.05$); this is thought to be due to the insufficient number of individuals tested ($n = 10$).

COURTSHIP AND PAIRING

Courting and pairing begins on the salt lakes in early December. Displaying in the initial stages of pairing takes place on the edge of salt lakes and "mock preening," "preening behind wing," and "chasing" (Lorenz 1953) take place during the latter part of the morning when feeding has ceased and the birds are drinking and preening at the freshwater seepages. As more juvenile birds join the main aggregation, the intensity of displaying increases, especially by lone females. It is interesting to note the aggressiveness of the females that are responsible for most of the friction within the group. Observations on paired females have shown them to be extremely aggressive when protecting their mates, and they often resort to physical clashes on the ground.

A second form of pairing display takes place in the water when birds move from the seepage areas and swim a short distance from shore where they begin "head dipping" and bathing (Johnsgard 1965). Lone females swim to males and begin displaying by "water thrashing" (McKinney 1965). As the tempo of the display increases, the female captivates the male's attention by duck diving beneath the water for a few seconds and then emerges to give a mocking chase after the male. This display is repeated several times until the male starts diving and chasing the female in a similar manner. The behavioral pattern is repeated on one or more males until a male responds to her "inciting"; this term, used by Lorenz (1941), described the part played by the female in pair formation. Lorenz concluded that inciting is the basic ceremony for pair formation in all Anatidae. It is certain that the mountain duck female relies on this behavioral trait to "choose" a mate. Reference is made to the female obtaining a "mate" rather than getting a "male," as often it was observed that females display to each other with great response. Usually, the females were juvenile birds, but nevertheless the displaying captivates one of the birds, and they act as though some bond has been created, sometimes remaining together until the next pairing period (mid-April to mid-May). It is possible that female pairing could come about because of the lack of male birds as will be discussed later.

Few aerial displays were observed during the December pairing period. The few seen were of paired birds trying to elude pursuing females. Some unpaired females remained in the company of paired birds for periods of up to 3 and 4 months.

Significance of Age

Pair formation occurs in all age groups; juvenile, subadult, and adult. However, brood production has been observed only in adults. Data from field observations on tagged birds during the breeding seasons of 1965, 1966, 1967, and 1968 on Rottnest Island show that 89 birds were 22 months old or older before they produced young.

The minimum age for pairing is 5–6 months. Paired birds isolate themselves from the main aggregation. Few of these pair bonds persist more than 3 months. Additionally, there is always a group of juvenile females that remain completely on their own and do not enter into the courting and pairing activities. Those birds remained in an isolated group on the study area for several months.

During the latter portion of the breeding period, unpaired subadult females migrate to the island from the mainland, but they, too, remain in small distinct groups on the study area. Few lone juvenile and subadult males were seen on the study area during the breeding season (May–September). It appears once they leave in the summer they do not return until the following year. During the summers of 1966, 1967, and 1968, there were 16 sightings on the mainland of juvenile males identified from bill tags.

Subadult birds, in many cases, have formed pairs, established brood territories, and defended them quite aggressively. However, few subadults either male or female, were observed to maintain a territory against the aggressiveness of the adult birds. Subadult females display behavioral traits similar to the breeding adults, but the lack of continuous breeding activities, i. e., nest site selection, egg laying, incubation, etc., appears to soon cause the pair bond to dissolve, with the female joining a group of unpaired subadult females. Subadult males usually remain solitary and are not seen on the island once the breeding season commences. The sex ratio in subadults observed on the island favors the female.

Prebreeding Assemblage

The first break of the summer drought on Rottnest Island usually occurs in mid-March to mid-April, but only 50 mm of rain may fall in that period (Fig. 3); however, it is sufficient to cause a change in the behavioral patterns of the resident ducks. Bickering and chasing commences, and the females guard their males from any intruders. Immigrating birds from the mainland commence to arrive, some being previously tagged on Rottnest Island as juveniles and not seen for more than a year. The new arrivals are conspicuous as they are extremely wary of humans compared to resident birds. The composition of the population has altered greatly since the early December aggregation and now consists largely of adult breeding birds. As the island's mountain duck population increases, the intensity of courting and pairing behavior increases.

The courting and pairing displays of the prebreeding season are similar to those previously described for the postbreeding period. The difference is in the increased intensity of the females inciting males and the aerial displays of paired birds eluding pursuing females.

The behavior of unpaired females when pursuing a mate is to approach and commence chasing or water thrashing with head and neck outstretched and moving from side to side making lateral pointing movements with much vocalization. As the male responds, the female maneuvers the male away from the group by continuous inciting which may last for more than half an hour. If the male is unresponsive to her displays, the female may stay close by and continue the display later, or more often, move on to another male.

In the situation where lone females are pursuing a paired male, the paired female may attack the unpaired female outright or incite the male into driving off the unpaired female. Once gone, the male returns to his female mate and displays sexually toward her by mock preening, "lateral head shaking," or "chin lifting" in the high and erect posture.

There are 2 types of aerial displays: (1) flights made by unpaired birds, and (2) paired birds eluding pursuing unpaired females. The first type of flight is the result of aggressive display or inciting by one or more unpaired females on a lone male. The lone male rises and is followed by the females. The male is maneuvered by the pursuing females forcing each other from the near position. It appears the objective of the female's behavior is to get close to the male and stay as long as possible. If the male responds to one of the females, the pair will land and immediately the female will commence inciting. The aerial display will continue until one female captivates the male and drives off all other females.

The second type of aerial display originates either on the ground or in the air when a lone female intercepts a pair and tries to separate them. It appears that the object of this pursuit is similar to the one previously described in that the female tries to fly between the members of the pair and then stay alongside the male as long as possible. In some flights, the unmated female is skilled enough at maneuvering between the paired birds that the pair will land and attack the unpaired female on the ground. Often, a female can be observed grabbing at the tail feathers of another female forcing a change in her flight direction so as to obtain a position next to the male. Five females (4 alive and 1 dead) were found with broken wings believed to have been caused from hitting obstacles while trying to maneuver in the aerial displays. That type of injury is not observed at other times of the year.

Weather conditions during the prebreeding season have a considerable influence on the behavior of displaying birds. On overcast days with rain and cool temperatures, the displaying, both on the ground and in the air, is continuous throughout the day; however, if the weather changes and becomes warm with sunny days, the birds' activities are reduced sharply. They sit for long periods on the shores of the salt lakes preening and basking in the warmth, and little courting takes place. During the winter of 1966 when Rottnest Island received less than the normal rainfall and the winter was very mild, pairing activities were greatly reduced, fewer pairs remained on the breeding grounds, and poor retention of established brood territories occurred.

Brood Territories

Paired birds leave the main congregation and establish territories for raising their broods. The basic requirement of each brood territory is that it contains a freshwater seepage. Such seepages (Fig. 6) vary in size and rate of flow but the total soluble salts present in the seepage water varies little between summer and winter (Hodgkin 1959).

The area of freshwater seepage defended by the pair depends on 2 factors, the proximity of adjacent seepage areas to the one they hold, and the irregularity of the surrounding terrain. If several seepages lie close together (Fig. 6, north side of Baghdad Lake near Parakeet Bay), the constant

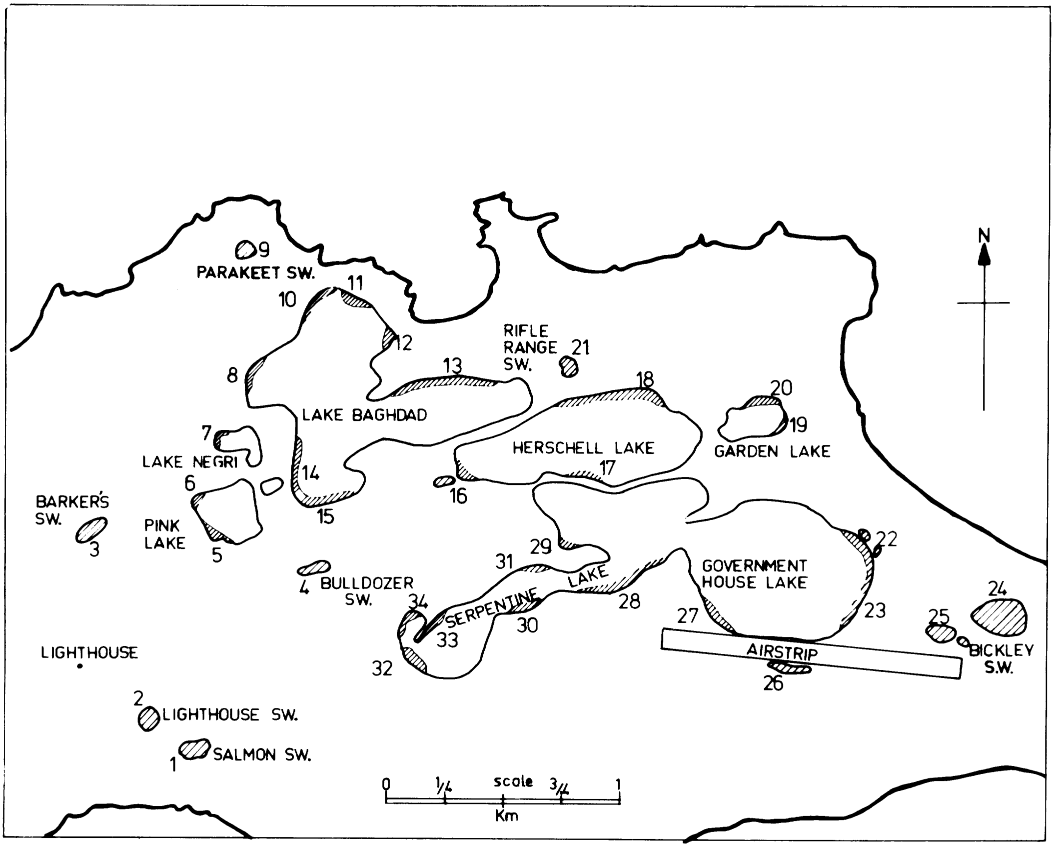


FIG. 6. Locations of brood territories (1–34) and freshwater seepages on Rottnest Island, Western Australia.

harassment of pairs seeking territories makes it impossible for birds to defend large areas. Some territories are small but their boundary lines are well defended, and the birds holding the territory are intolerant of encroachment of other pairs or single birds on their areas. In cases such as the western end of Herschell Lake where there is only one seepage area, the territorial birds seem quite unconcerned about others feeding along the shores or in the general area so long as they do not come onto the seepage.

The 34 possible brood territories on the island, the largest being No. 18 which extends along the shoreline for approximately 220 m and out over the water for 100 m, are shown in Fig. 6. The smallest territory is No. 7 on Negri Lake which has approximately 50 m of shoreline and 50 m out over the water. The usual size for a territory on the salt lakes is 100 m of shoreline by 50 m out over the water.

The retention of a territory is a continuous effort, and at first the female plays the dominant part in chasing off all intruders; however, her bickering and excitement draw the male into doing most of the fighting. This form of apparent behavioral conditioning becomes most important in the subsequent weeks as the male must defend the territory on his own while the female is away performing the incubation duties.

The primary function of the brood territory is to secure a supply of fresh water for the brood, thus imposing a determinate pattern of dispersion which allows broods to be reared without intraspecific strife resulting in deaths. The limited number of territories on the island imposes a ceiling on the breeding density and is indirectly related to food supply. Without sources of fresh water, the ducklings cannot feed in the salt lakes.

In the breeding season, the ducklings and parents feed on the brood territory. The birds are opportunistic feeders as they feed on a variety of plant and animal material in a variety of ways.

Maturity

The establishment of a brood territory is not a prerequisite to copulatory behavior, as tagged birds, whose territories were later found on salt lakes, have been observed copulating on freshwater swamps. Other tagged pairs have been observed copulating, but their territories were never found. Throughout field observations, tagged birds less than 21 months old have never been seen copulating. However, 2 of our hand-reared experimental male birds of 10 months had the same physical development of the penis as that of a field bird 21 months old. Histological examination of the testes of the hand-reared birds showed no spermatozoa. From the foregoing it appears unlikely that juvenile male birds breed in the first year.

The act of copulation and associated displays of precopulatory and postcopulatory behavior are not easily observed on the island. During the breeding seasons of 1965–1974, copulation was observed 9 times, but on only 3 occasions were all behavioral traits displayed. My field observations of copulatory behavior in mountain duck pairs agrees with the description by Johnsgard (1965). A significant part of the behavior of paired birds is the precopulatory display which demonstrates the ability of the female to captivate the male by displays involving the use of the wing speculum.

The female commences her display by preening and flashing the wing speculum, and as the male approaches her, the tempo of preening increases and is combined with water thrashing. The male soon commences water thrashing in a similar manner. As he approaches, the female swims in small circles with neck and head outstretched on the water often grabbing mockingly at his breast and lateral feathers while circling the male several times. The female repeats the performance again by swimming approximately 7–10 m away and calling the male to her. As the display continues, the number of mock attacks on the male is increased until finally the female swims around the male head down and bill half submerged in the water with body lowered and flattened causing a large bow wave. This action then transforms to a complete submergence by the female who swims underneath the male simulating the copulatory position. This display may be repeated several times before copulation takes place. It was observed that the precopulatory display did not occur with every act of copulation. The full sequence was observed in the field only 3 times during the breeding seasons.

NEST OF THE MOUNTAIN DUCK

Location

Nesting sites on Rottnest Island are confined to limestone ridges along beaches and the small offshore islands. The limestone ridges extend along 15.2 km of Rottnest Island's 29.7 km of coastline. In addition, there are 12 small offshore islands all of which contain limestone areas suitable for nesting sites. None of the offshore islands are more than 1 km from the shore of the main island.

Previously, only 2 nests of the mountain duck have been recorded for Rottnest Island, both on offshore islands. Storr (1965) was unsuccessful in his search for nests around the swamps and lakes; furthermore, local residents had never seen a mountain duck nest on the island.

By observing the daily movements of birds from their territories to the beach areas at sunrise and sundown, I located a pair nesting in the limestone ridges on the northern side of Rottnest Island. That was the first nest found on the main island, and it was apparent from the time and effort spent that finding others would be difficult because of the roughness of the terrain and wariness of the breeding pairs. During the breeding seasons of 1965–1974, 26 nests were found, and I examined 10 of them without destroying the entrance or nesting burrow. Observations on nest size, structure, contents, and previous use are based on those 10 nests.

Seeking of Nesting Sites by Paired Birds

Paired birds leave the freshwater seepage areas each day about midmorning and fly to the coastal beaches. There, displays of head throwing and lateral pointing by the male and female, respectively, were observed. An intrusion of other pairs into the area causes much fighting and bickering as the male becomes very aggressive, often attacking pairs flying past or swimming in the sea nearby. The aggressive behavior of the male at the nest site was observed only during the early stages of nest site selection.

Wind and water erosion on the limestone cliffs has created a maze of crevices and holes, each one being a potential nesting site. As the female moves from hole to hole exploring each as a possible nesting site, her tracks can be followed through the soft sand that has been blown onto the limestone. Those tracks made it possible to determine the regularity and extent of nest hunting. In following one bird's movements, I found that she had walked approximately 1 km along the ridges and entered at least 46 holes, some being previous nests of the wedge-tailed shearwater *Puffinus pacificus.* The exploratory behavior and numerous nesting possibilities in the limestone cliffs made it difficult to find nests by tracks or looking into all suitable rock formations.

The exploring of the limestone ridge areas for nesting sites by adult birds that had nested before is much quicker than for the young inexperienced breeding birds. It is certain that adult birds used good nesting sites repeatedly, as layers of egg shell membranes can be found down through the sand in nesting burrows. Observation of tagged, experienced, breeding birds show that they utilize the limestone areas close to the salt lakes and protected from the weather.

While the female is searching for the nest site, the male takes a position where he can observe the area for intruders. If the pair is disturbed, they leave the area, often not returning until the following day.

Nests

Once the female finds a suitable crevice or burrow, she begins to clean it out (Fig. 7). The nest is formed by scooping out a shallow bowl in the fine powdery sand, about 45–55 cm in diameter and 7–10 cm deep in the center. None of the nests observed had a second entrance or escape hole, a feature common in other species of *Tadorna* (Hori 1964).

The distance of nests from water, either salt lake or ocean, does not follow any pattern. Occupied nests were found as close as 5 m from ocean water and as far away as 1 km. Distances from salt lakes are even greater with nests ranging between 2 m and 9.5 km from the water. Nests have been reported on Phillip Rock and Dyer Island, a minimum of 5 km from salt lakes, but 1 km out over the open sea. The closest distance between 2 nests was approximately 10 m.

EGG LAYING AND ASSOCIATED BEHAVIOR

Egg Laying

At first light, the pair leaves their brood territory and flies to the nesting site. Seldom do they fly directly to the nest, but land nearby and observe the surrounding area. The birds may stand and observe for over an hour before the female flies directly to the nest breaking her flight only as she enters the opening of the burrow. The male remains in position, watching. If disturbed, the male sounds a high whistle and returns to the brood territory. The female remains on the nest and returns to the territory later, presumably not disclosing the location of her nest by darting out in times of danger.

The female may spend up to 40 min in the nesting burrow at the onset of laying, but as the clutch increases, the time is re-

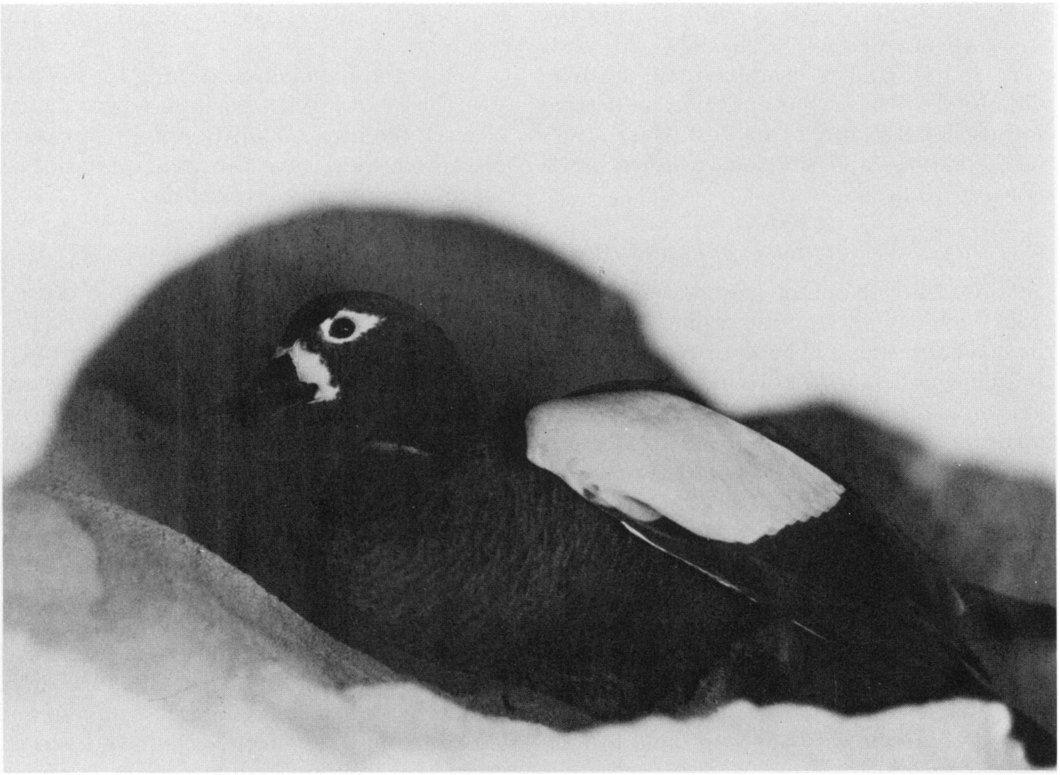


FIG. 7. Female mountain duck cleaning out nest in limestone crevice on Rottnest Island, Western Australia.

duced greatly. On 10 July 1965, a female entered and left a nesting burrow within 8 min, depositing 1 egg. The time required to complete the clutch can be prolonged greatly if the female is disturbed repeatedly at the nest site. One nest that was disturbed several times during the laying period took 21 days to complete a clutch of 11 eggs. From observations on 10 nests during breeding seasons of 1965–1968, 1 egg was laid per day. In 4 nests, the first 3 eggs laid were spaced at intervals of a day, and the female visited the nest only on the day she laid. The normal egg laying period on the island extends from the first week in June until mid-September.

At the onset of laying, care was taken to see that the disturbance did not result in abandonment of the nest by the pair. Numbers of eggs seen in nests ranged from 6 to 14, but a brood of 16 ducklings was seen on Baghdad Lake in August 1968. The large variation in clutch size could be normal for the species, but with the limited number of nests (10) available for examination on Rottnest Island it was not possible to draw conclusions on mean clutch size or standard deviation for any season, or whether the occupants of the nest were young or inexperienced breeders.

Dump Eggs

While searching for nests, numerous eggs or portions thereof were found in areas that definitely were not nest sites. This phenomenon appears to be common among Anatidae and the eggs are known as "dump eggs." Eggs were found along the edges of salt lakes, on offshore islands, and in cave areas too draughty and exposed to be nest sites. Most of those eggs probably were eaten by the silver gull *Larus novaehol-*

landiae and the Australian raven *Corvus coronoides*, but a few in covered areas were still intact and fresh.

Dump eggs could result from at least 2 causes. The adult females may choose not to enter the nesting burrow to lay if they are disturbed at the nest sites. Thus, eggs found on the lake edges could be dropped by a female unable to go to her nest. It has been possible to artificially incubate such eggs. Alternatively, groups of unpaired females are seen on the offshore islands almost daily, and the eggs found there could be left by females that are inexperienced layers, probably without nests or brood territories.

Egg Losses to Predators

There are few enemies of waterfowl on Rottnest Island. The domestic or feral cat, snakes, lizards, ravens, and sea birds are the only animals that could cause nesting losses. Feral cats are only a recent arrival on the island, being escaped pets of local residents or holiday visitors. There is no evidence to support the idea that they destroy eggs, but they do take ducklings on the journey from the nest to brood territories.

Local residents and some visiting amateur ornithologists regard the dugite *Demansia nuchalis affinis* and the bobtail skink *Trachysaurus rugosus* responsible for egg losses in ground nesting birds on the island. Examination of mountain duck nests during the breeding seasons showed that neither species was responsible for egg losses. However, both species were seen frequently on warm days in the limestone areas. Again, the limited sample of 10 nests observed does not allow definite conclusions to be drawn on nest predation by those 2 species.

Both the silver gull and the Australian raven have been observed preying on mountain duck nests on Rottnest Island. However, in both instances it is felt that those birds were drawn to the nesting burrows by our presence. After we left the nest site, the predators were searching for food scraps and inadvertently discovered the nests. The typical appearance of eggs eaten by silver gulls is shown in Fig. 8.

EGG, INCUBATION, AND EMBRYONIC DEVELOPMENT

The Egg

Eggs examined in the field usually are stained light brown by blood and dirt. If washed before incubation commences, the stains can be removed exposing the true buff cream color. The surface of the shell is smooth with a glossy finish. The color and shell surface limit light transparency, but candling is possible with a strong light source.

A total of 49 eggs from Rottnest Island and 98 from the mainland was examined, measured, and weighed. There was no statistical difference in size or weight between the 2 groups, therefore, the groups were combined to provide as large a sample as possible. The mean length and width of the 147 eggs was 68.76 ± 2.2 mm (SE=0.2) and 48.3 ± 1.0 mm (SE=0.1), respectively. The thickness of the shell was nearly uniform and measured approximately 0.33 mm (SE =0.01). The mean volume, calculated by water displacement was 79.8 ± 3.1 ml. Twenty-two eggs were weighed prior to incubation and had a mean weight of 88.3 ± 5.1 g (SE=1.1) with a specific gravity of 1.07.

Incubation

Data from 5 nests (49 eggs) on Rottnest Island and 168 artificially incubated eggs in the laboratory indicates that incubation takes a minimum of 30 and a maximum of 32 days. Incubation commences the day on which the female remains for at least 5 consecutive hours on the nest in natural conditions, or the first full day eggs are placed in a preheated incubator. Completion of incubation is defined when the ducklings escape the shell cover. Other workers such as Moody (1939) and Delacour (1939, 1954) cited approximately the same incubation period (30–33 days) for birds held in captivity.

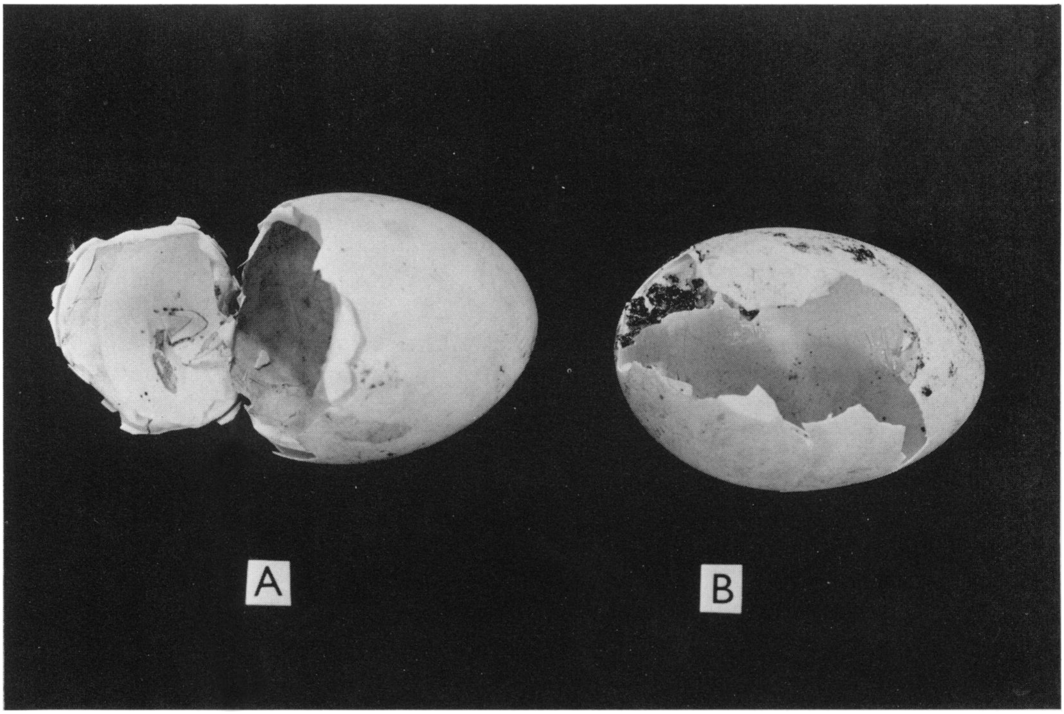


FIG. 8. A. Normal appearance of shell of mountain duck when hatching is completed. B. Mountain duck egg preyed upon by a silver gull.

As the clutch nears completion, the female plucks down from her breast and lines the nest. That behavior continues until the nest is lined completely, together with a surplus that will form a mat over the top of the eggs approximately 4 cm thick. The down cushions the eggs and presumably reduces breakages. However, another function is to insulate the incubating eggs and retard cooling when the brooding female is absent. Brooding females can be seen plucking down from their breasts on brood territories. It is not known if that behavior is incidental to normal preening activities or whether it has some significance to the male who remains on the brood territory throughout the incubation period. The appearance of loose down on the breasts of broody females can be seen throughout the incubating period.

Once incubation commences, the pair carries out their separate roles, the female incubates the eggs and the male defends the brood territory. During the early stages of incubation, the male accompanies the female from the territory to the nest site each morning. He seldom remains at the nest site, but returns to the territory where he resumes his duties of territorial defense.

There are 3 characteristic behavioral traits displayed by the male when defending a territory: "mock feeding," "standing alert," and "direct chasing." Mock feeding is performed when the male is feeding normally and an intrusion is made on the territory. He continues with the motions of feeding but no food is taken and his attention is focused on the intruder. The male does not resume normal feeding until the intruder leaves the area. Standing alert is performed by standing in an elevated position on the territory and observing the surrounding terrain. When other mountain ducks fly near, the male begins lateral head throwing and short grunting whistles. That presumably signifies the area is occupied. The most aggressive performance is the direct chase. When intruders enter the territory, the male comes into physical contact with them and often such clashes are quite violent.

If the female is disturbed while incubating, a low hissing call can be heard from within the nest burrow. That call is a threat to the intruder and becomes louder with continued disturbance. Hori (1962) referred to a similar hissing by the European shelduck and stated that he witnessed a would-be predator deterred from approaching a nesting hole by such hissing. The call was often heard when examining nests as the female would retreat to the rear of the burrow and hiss loudly. When examination of the nest was complete, the female stopped hissing and resumed incubating the eggs.

Observations of the female's movement on and off the nest during incubation were made by spreading fine sand in the entrance of the burrow. Regular checks of the burrow for tracks gave approximate times of her arrival and departure. The time a female spends on her nest during the first 2 weeks of incubation can be divided into 2 periods: (1) the daylight period, from midmorning to late afternoon, and (2) the night period from sunset to approximately half an hour before sunrise. On cold and wet days, the female may spend longer periods on the nest than on warm sunny days. Each morning and afternoon a period is spent on the territory drinking and feeding.

When the female leaves the nest to feed and drink, she seldom joins the male in defense of the territory. Both birds appear so preoccupied during that period they seem unaware of the other's presence.

At the end of the first 2 weeks of incubation, thermistors, attached to an electrothermograph by cables, were placed in a nest. The thermistors were suspended in the nesting burrow to record air temperature and placed in the down surrounding the nest to record nest temperature. A third thermistor was taped to the surface of a developing egg. During each recording of the 3 areas, it was possible to see if the female was on or off the nest, and from tracks in the sand to note whether she had been absent from the nest since the previous recording. Temperature data are given in Table 1.

TABLE 1.—MAXIMUM AND MINIMUM TEMPERATURES (C) RECORDED IN A MOUNTAIN DUCK NESTING BURROW, AND FOR NEST DOWN AND EGG DURING INCUBATION, ROTTNEST ISLAND, WESTERN AUSTRALIA

	Maximum	Minimum	Range
Nesting burrow	20.0	14.3	5.7
Nest down	22.0	17.1	4.9
Egg (first 26 days, female not always present)	38.5	24.5	14.0
Egg (last 4 days, female always present)	38.5	33.5	4.9

Temperatures inside the nesting burrow were almost constant and at all times were above the average minimal temperature for the month (July 1967) on the island. The greatest recorded temperature fluctuation inside a nesting burrow was 5.7 C. The temperature of the down surrounding the eggs also remained fairly constant regardless of the presence or absence of the female on the nest, and fluctuated over a range of 4.9 C, above the average maximum for the month (July 1967).

The temperature of the incubating egg had a range of 14.0 C. The greatest temperature fluctuation occurred during the end of the third week of incubation with a drop of 10.0 C. The female was off the nest when the recording was made. During the last 4 days of incubation, temperature recordings were made every 6 hours. The temperature varied from 33.6 to 38.5 C, a range of 4.9 C (Fig. 9). A rapid decline was noted once a hole was punched in the shell by the pipping duckling. The female was on the nest during every temperature recording during the last 4 days of incubation.

When recording whether incubating females of the European shelduck were present or absent from the nest, Hori (1965) placed a recorder under a "prepared" nest and the incubation rhythm was automatically plotted for the duration of the nesting

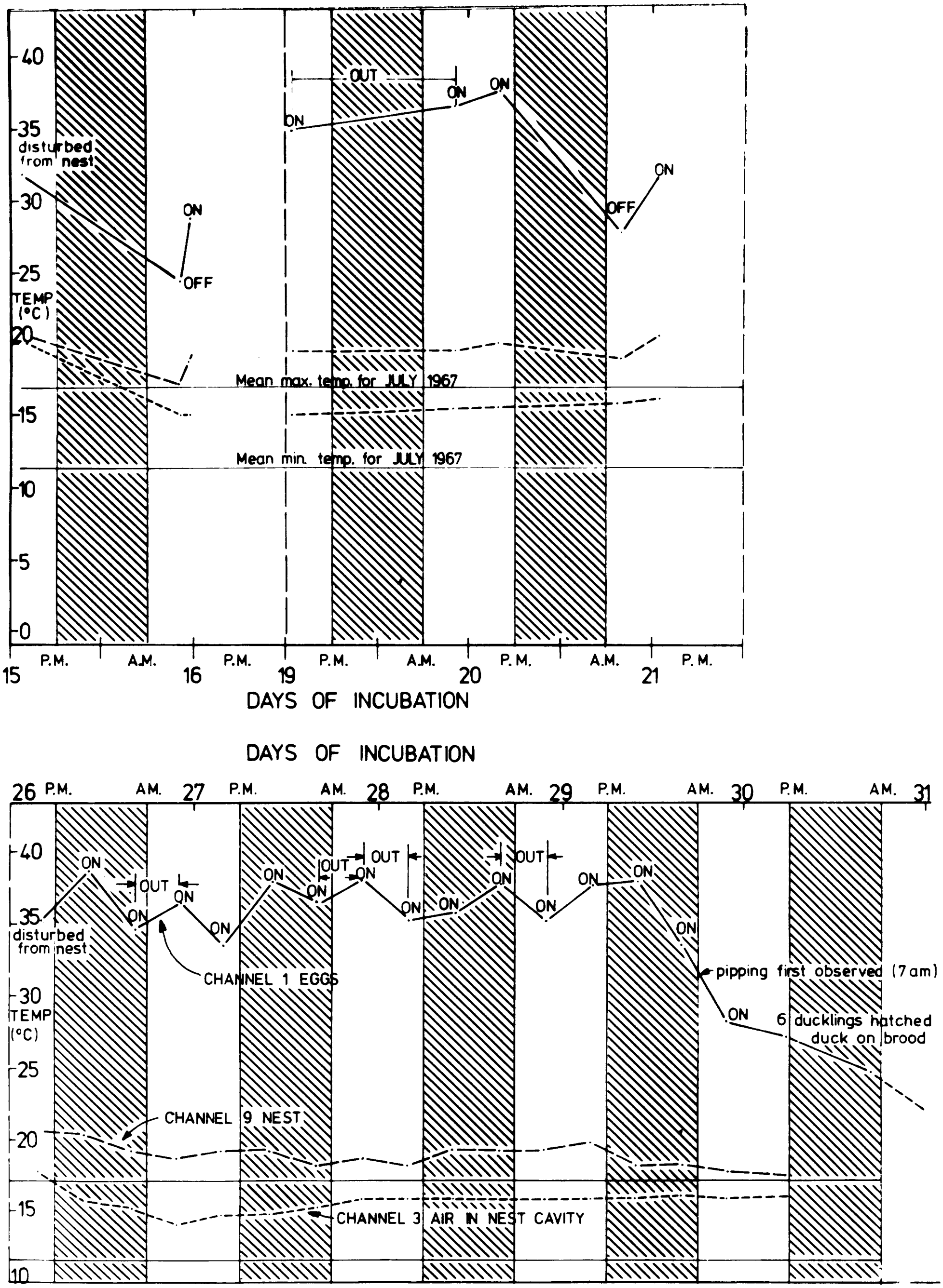


FIG. 9. Incubation temperatures of mountain duck nests, nest cavity, and eggs, Rottnest Island, Western Australia.

period. Hori (1964) found that incubating females spent 87 percent of their time incubating. That amounted to 493 of a possible 564 hours on the nest. He also found that when a clutch neared hatching, the female remained continually on the nest, and partial failure of a clutch occurred when a broody hen was kept away from her nest for 13 hours on the twenty-second day of incubation.

The significance of constant temperature for eggs in their later stage of development was confirmed when transporting mountain duck eggs to the laboratory. If the incubating eggs were less than 2 weeks old and not opaque when viewed with an egg candler, it was possible to maintain them during transportation by frequent warmings. Once the egg development reached the latter half of the incubation period (15–29 days), the eggs were sensitive to temperature fluctuation. Mortality from temperature fluctuation during the later stage was eliminated by placing the eggs in a thermostatically controlled warming box maintained at 35± 2.0 C. Eggs in the laboratory incubator were kept at 36 C and 85 percent relative humidity.

As the eggs incubated in the portable incubator in the laboratory, a gradual loss of weight was noted. Romanoff and Romanoff (1949:377–379) attributed the loss of weight in incubating eggs to water evaporation and gaseous exchange through the shell. The total weight loss, and the rate at which it was lost, was measured in the laboratory on 4 clutches of mountain duck eggs. Those clutches, totalling 48 eggs, were removed from the incubator every third day at 0900 hours and weighed on a Salter beam balance to 0.1 g until the first sign of pipping.

Clutches A and B were incubated for 30 days and had an average weight loss per egg of 6.4 and 5.2 g, respectively, during the incubation period. Weight loss per egg in Clutch C for an incubation period of 18 days was 5.0 g, and Clutch D, with an incubation period of 10 days, had a mean weight loss of 3.3 g per egg (Fig. 10). In all clutches it was

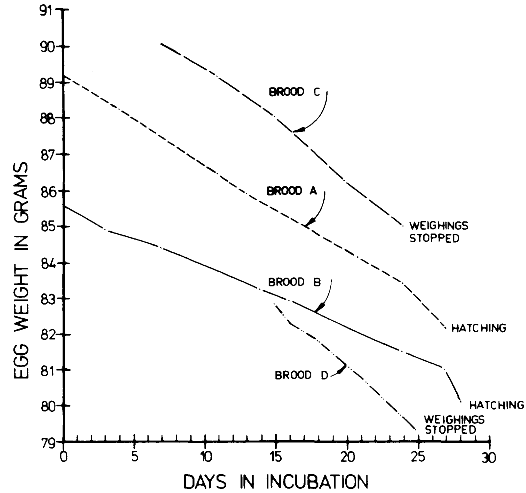


FIG. 10. Average daily weight loss in 4 clutches of incubating mountain duck eggs, Rottnest Island, Western Australia.

possible to tell when an embryo had died as it no longer lost weight in a systematic way.

Embryonic Development

The daily embryonic development of the mountain duck egg was studied in the laboratory to assist with the aging of clutches found in the field. That information made it possible to time future visits to coincide with hatching times.

The method was similar to that described by Hanson (1954); however, the use of a photographic dark room and Cannon electronic flashguns with adjustable flash times eliminated some of the apparatus described by Hanson. The film used was Ilford PAN F with a green filter. Photographs of the daily embryonic development of a mountain duck are shown in Fig. 11.

During the first 2 weeks of incubation, it is possible by direct observation with the aid of an egg candler to establish the age of an embryo. Once the development progresses to the fifteenth day and onward, age criteria must be established on egg transparency and size of the air sac only. When the bill of the duckling can be seen in the air sac at the large end of the egg, pipping has commenced.

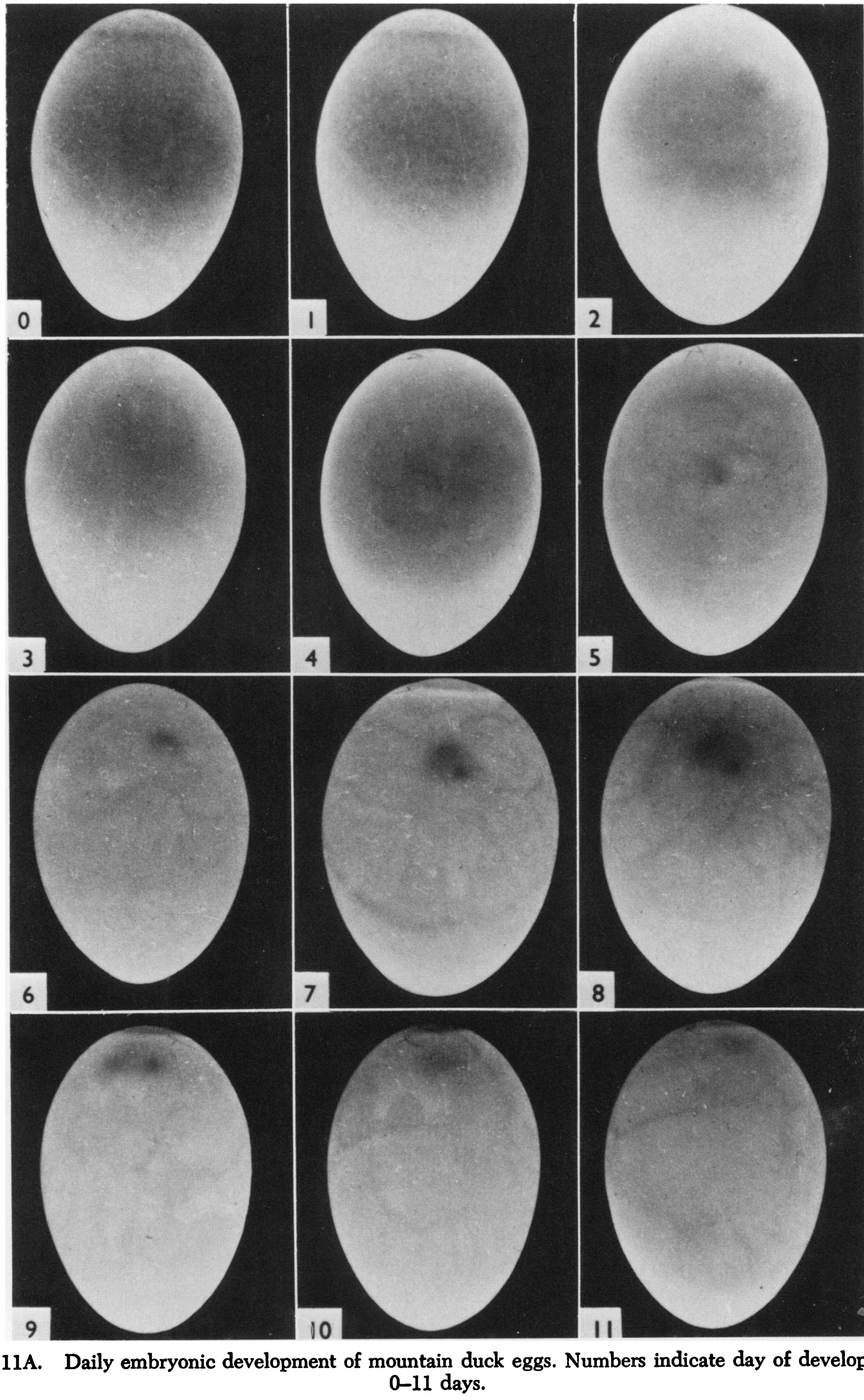


FIG. 11A. Daily embryonic development of mountain duck eggs. Numbers indicate day of development, 0–11 days.

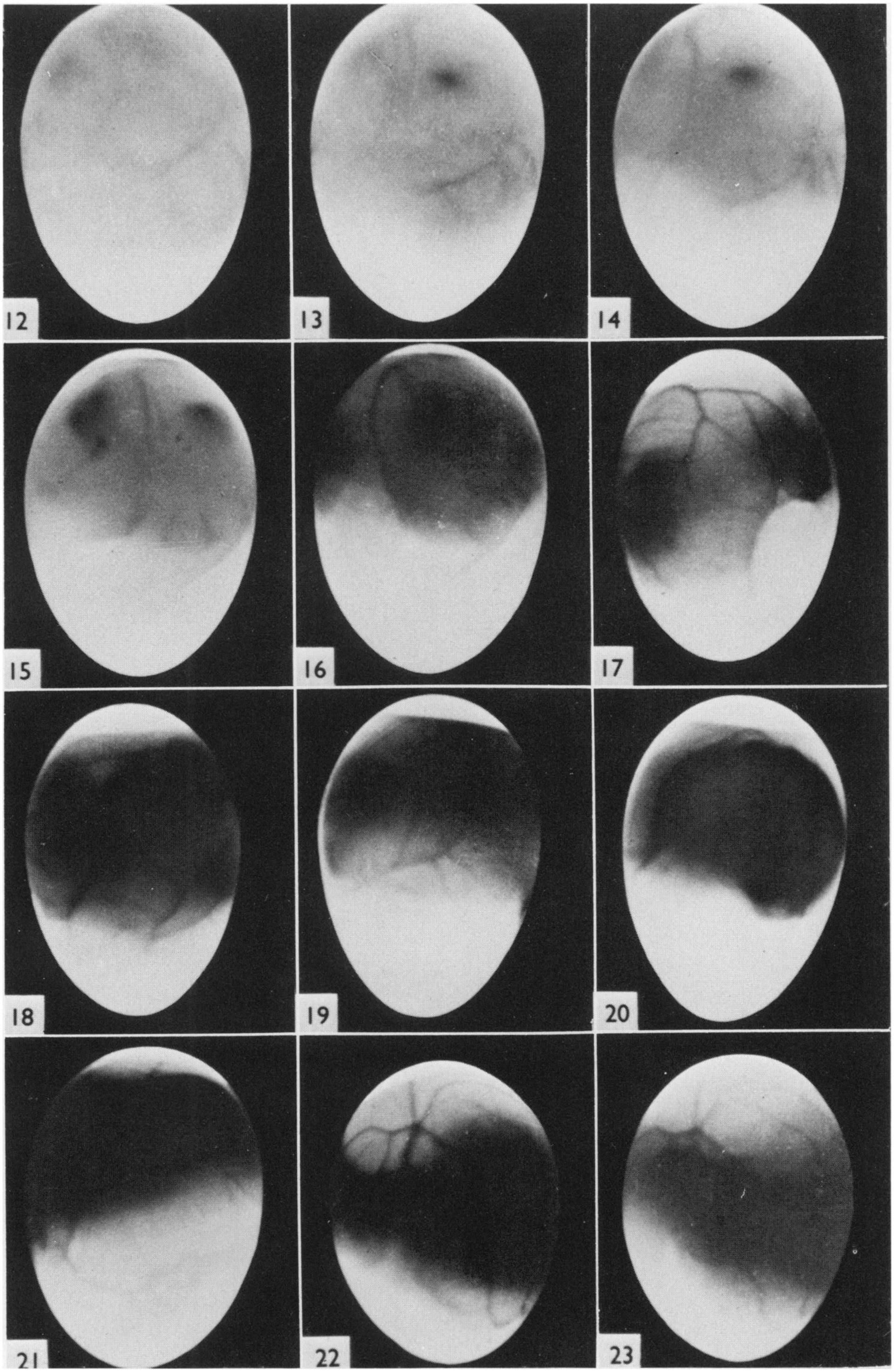


FIG. 11B. Daily embryonic development of mountain duck eggs. Numbers indicate day of development, 12–23 days.

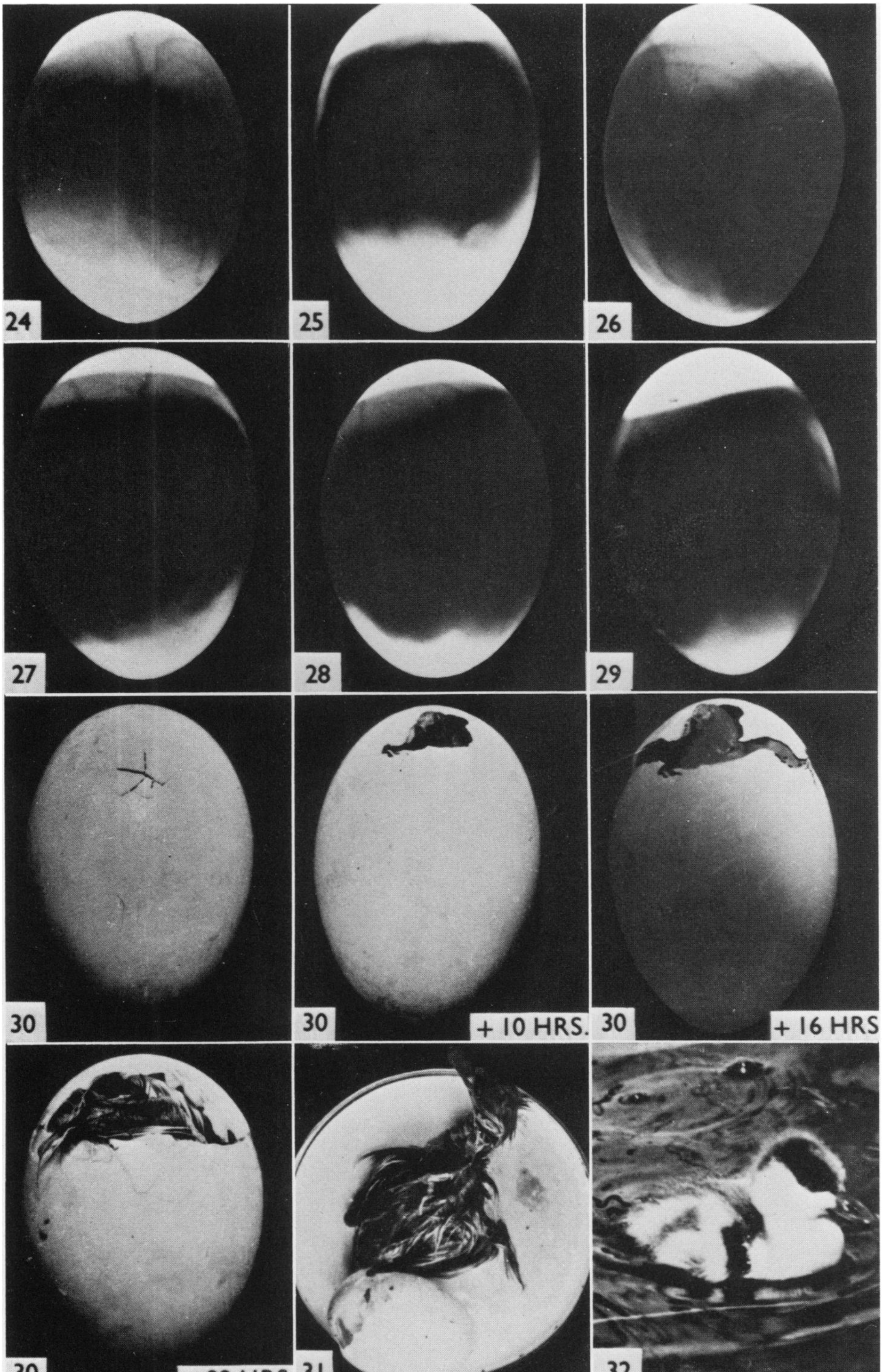


FIG. 11C. Daily embryonic development of mountain duck eggs. Numbers indicate day of development, 24–32 days.

The following descriptions of the development of a mountain duck embryo were made from eggs artificially incubated in the laboratory in 1966 and 1967. Reference was made to Romanoff (1960) for terminology of embryonic development.

Day 0 (Fresh egg)—Shell color buff, fairly translucent.
Day 1—Yolk appears darker and well defined.
Day 2—Blastodisc approximately 9 mm in diameter appears on surface of yolk.
Day 3—Area vasculosa appearing as a crown approximately 20.5 mm in diameter.
Day 4—Yolk now dark orange and well defined. Area vasculosa enlarged to approximately 29 mm in diameter and embryo visible for first time.
Day 5—Embryo and vitelline veins now prominent. Spidery shape with heartbeat visible.
Day 6—Both amnion and embryo visible when egg is rotated.
Day 7—Embryo moves regularly as muscle fibers contract in amnion. Vitelline veins have many branches.
Day 8—Eye is now very prominent and embryo and area vasculosa not easily seen.
Day 9—Embryo 16.2 mm long in flexed position. Amnion 32 mm. Embryo very active.
Day 10—Embryo becoming more obscure by growth of allantois. Air sac prominent.
Day 11—Embryo extremely active, approximately 23 mm in length.
Days 12–15—Little change during this period, but growth of embryo to approximately 34 mm or half the distance across the egg.
Day 16—Embryo now becoming slightly opaque half the distance across the egg. Movement slows.
Day 17—Embryo in relaxed condition constitutes approximately two-thirds of distance across egg. Air sac enlarges.
Day 18—Detail now obscure by opaqueness of egg.
Day 19—Embryo forms coil or ring for first time, legs and wings seen moving.
Day 20—Embryo approximately 41 mm in diameter. Little detail of egg now visible.
Day 21—Embryo occupies three-fourths of darkened portion of egg.
Days 22, 23—Thick blood vessels only detail visible.
Day 24—Embryo now extends across egg and halfway around it with large transparent portion still visible at large and small end.
Day 25—Embryo becoming black. Blood vessels not visible.
Days 26–29—Entire egg opaque except for air sac at large end of egg and a small area at opposite end. Aging of eggs during this stage depends solely on size of air sac.

Embryos that died during the first 2 weeks of development were recognized by one or all of the following characteristics: (1) rupturing of vitelline veins, (2) darkening of amnion, and (3) no movement of embryo.

Those embryos that died during the latter half of development (15–29 days) were recognized by ruptured blood vessels that appear flat, no movement of embryo when egg was rotated slowly, and entire embryo shifting to small end of egg allowing one-half of the egg to be transparent.

Once the eggs were hatched, the nests were observed continually so that the departure of family groups could be followed overland to the lakes and swamps where the brood territories were located.

HATCHING AND LEAVING THE NEST

Hatching

Progress of hatching is shown in Fig. 11C, Stage 30, +10, +16, and +22 hours. The time recorded in the laboratory for ducklings to hatch was approximately 24 hours, but ranged from 18 to 30 hours. A clutch of mountain duck eggs hatching on Rottnest Island (Fig. 12) shows the different stages of hatching within a single clutch.

FIG. 12. A clutch of mountain duck eggs from a nest at Charlotte Point, Rottnest Island, Western Australia. Note the variation in hatching progress within a single clutch.

When the duckling emerges from the shell it is wet with amniotic fluid and exhausted (Fig. 11C, Stage 31). The first movements of the duckling, even though too weak to stand, are to preen its down feathers which assists in drying. The warmth from the female assists the drying, and 12 hours after hatching the duckling is dry and capable of standing erect.

Leaving the Nest

At the age of 2 days, the ducklings are led by the male and female from the nest to the brood territory. Usually, the time of departure is before sunrise allowing the group the protection of darkness for a portion of the trip. The route to the territory is as direct as possible.

During the breeding seasons of 1965–1974, 15 family groups were observed on their way from nest sites to their territories. Because of the time of departure from the nest and the dense vegetation, it was not possible to observe the groups continually, but some insight was gained into their behavior during the journey.

As the parents lead the loosely bunched brood along, a soft throaty call is given by the male and female, presumably to aid the ducklings in following them through the dense undergrowth and to keep them together. If the parents stop calling, the ducklings remain motionless and are difficult to detect. There is little doubt that some ducklings become lost during the journey and die of exhaustion or exposure, but the only mortalities witnessed occurred from predators.

Storr (1965) reported a fisherman witnessed a pied cormorant *Phalacrocorax varius* swallowing a submerged duckling at sea. That took place during the brood's journey from an offshore island to the brood territory. During the present study, only feral cats were observed taking ducklings during the journey. On 8 August 1966, a brood of 10 ducklings was eaten by a feral cat before the parents could get them to the territory, and 2 similar instances involving partial loss of broods were recorded in 1965. Feral cats killed 70 percent of the 3 broods.

In January 1966, the Rottnest Island Board of Control commenced a project to eradicate feral cats on the island and to reduce the number of domestic cats kept as pets. During the following year, 86 feral cats were destroyed and domestic cats were reduced to 1 per household. All domestic cats remaining on the island were sterilized and it is strictly forbidden to bring cats onto the island. No losses were recorded in the 12 broods witnessed making the journey in 1967–1974.

When the group reached its territory, the parents commenced drinking from the seepage, and that behavior was copied by the ducklings. The brood spent the rest of the day drinking from the seepage and resting on shore close to the parents.

When the family group arrived at their territory, I examined the nest contents. All contained down and broken egg shells and a total of 19 eggs was found unhatched in 9 nests. There was no development in 6 eggs, and 5 others were broken during incubation. Three embryos died at 29 days of development, and 5 embryos died at 2–3 days old. No ducklings were left behind at the nest.

BROOD REARING

General Remarks

During the first week following their arrival on the brood territory, ducklings fed constantly. If the territory was on a salt lake, the ducklings spent long periods drinking and feeding at the freshwater seepage. Stomach contents removed from 5 ducklings 5 days of age contained Chlorophyta and seeds of *Salicornia australis*. Animal material consisted of ephydrid larvae and pupae and ostracods (*Cypris* spp.).

Toward the end of the first week, ducklings commenced feeding regularly on the salt lakes by diving beneath the surface. Three ducklings feeding in that manner were taken and the stomach contents contained chironomid larvae *Tanytarsus barbi-*

tarsus and large quantities of Chrysophyta. By midmorning and in the late afternoon, ducklings and parents were on the seepage drinking and preening.

Throughout the first 6 weeks, the broods usually remained in the immediate vicinity of their territory with the parents constantly present. However, instances were recorded where family groups entered neighboring occupied territories while feeding, which caused immediate fighting between the parents. Often, when 2 sets of parents fought, the ducklings became confused and became mixed together. Usually, the broods separated with their original numbers, presumably with the same individuals in each group. However, several instances were observed when the separating broods had a numerical change.

The only defense behavior displayed by parents in protecting their brood from predators, humans, and lone females was direct pursuit and broken wing display. Both parents joined in pursuing predators, but the male was the more aggressive, often leaving the female with the brood. When humans got close to the brood, the female showed a typical broken wing display. That display was seen only during times when parents were leading their brood from the nest to the territory overland, and ducklings were hiding in the ground vegetation. Ravens have been observed attacking broods on land and the parents were quick to retaliate. Silver gulls were seen swimming amongst a brood, and little notice was taken of their presence by either the ducklings or parents. However, if the gulls attacked a duckling, the parents pursued the gull and drove all other gulls from the immediate area. Lone female mountain ducks attempting to acquire ducklings were common occurrences and parent birds were quick to drive those birds away. No instances were recorded of a lone female acquiring ducklings by driving off one or both parent birds. The defense of broods by parents continued until the ducklings were able to fly.

Brood Counts

During the breeding seasons of 1965–1973, brood counts were made fortnightly on the salt lakes and swamps with the aid of a 4-wheel-drive vehicle during the latter half of the morning. A constant route was taken on each count. The total time required for a count was approximately 2 hours.

Ages of ducklings were estimated by use of a development chart compiled from hand-reared ducklings in the laboratory. The chart, plus prepared study skins, allowed broods to be classified into 8 age divisions in the field. In addition, specific identification was made by one or all of the following: (1) residence of a brood on a known territory which was mapped and numbered, (2) the presence of a numbered bill tag on one or both parents tending the brood, and (3) the age of individual broods estimated with the aid of the development chart.

During the study period, broods were present on lakes and swamps from June to December. Arrival dates of new broods varied from 19 June until 18 October. A total of 233 broods with a total of 1,737 ducklings arrived at the lakes and swamps to take up territories preestablished by the parent birds.

The largest number of ducklings observed in a single brood was 24 in 1971 on Baghdad Lake. It seems likely that that brood was the result of 2 broods that combined prior to their arrival on the territory. Several instances were recorded of parent birds arriving at the lakes with only 1 or 2 ducklings. Presumably, those family groups had been reduced in numbers by predators. The mean size of broods arriving at their territories during the study period was 7.49±0.85 with a variation from 6.52 (SE=0.67) in 1972 to 8.35 (SE=0.55) in 1968. A statistical comparison of the numbers of ducklings per brood arriving on the lakes and swamps between the years 1965–1966, 1966–1967, 1967–1968, 1968–1969, 1969–1970, 1970–1971, 1971–1972, 1972–1973, and 1973–1965 showed no significant statistical difference in numbers of ducklings per brood arriving on the territories during the study period. The mean number per brood arriving on the lakes apparently does not vary from year to year.

Observations on the broods once they were established on their territories were made at least once every 2 weeks. When a brood had developed to an "all feathered and flapper" stage (age 57–70 days), the counts on that brood were terminated and it was considered to have survived the brood period.

Survival data on broods reared in the 1968 breeding season could not be used as 24 ducklings were sacrificed from 9 of the 28 broods present for other research purposes.

The total number of ducklings to reach survival age was subtracted from the total number of ducklings arriving at the lakes and swamps. The difference was considered the mortality suffered by the broods during the developing period. There were, however, 10 broods that reached survival age with more ducklings present then than when first observed arriving at the lake or swamp. Those excess birds were termed gained as they were the result of an interchange of ducklings between broods. The total number of birds gained was subtracted from the assumed mortality to give a corrected mortality.

During the 9 years of field observations on broods, 10 broods that contained a total of 16 ducklings had definitely made a change from one brood to another. The presence of those 16 ducklings in another brood was quite obvious as the transient ducklings were either much larger or much smaller than the brood they joined. It is possible that that same phenomenon could occur in many more broods and go unnoticed if the 2 broods joined together were approximately the same age. However, brood interchange appears to occur only by accident or as a result of fighting and is not of any significant survival value.

In 1965–1967 and 1969–1973, a total of 205 broods arrived on the salt lakes with 1,503 ducklings, of which 185 broods and 1,215 ducklings (80.8%) reached the all feathered and flapper stage and were considered to have survived. Only 20 broods (0.09%) were recorded as completely missing during the study period. The mean brood size for those broods with birds that reached the surviving age (57–70 days) was 6.58 ± 0.69 with a variation of 5.46 (SE= 0.41) in 1972 to 7.24 (SE=0.47) in 1965. Broods that survived to the all feathered and flapper stage during the study period were, on the average, minus 0.91 ducklings.

The mortality among 1,503 ducklings that arrived on the lakes and swamps in the 8-year period of 1965–1967 and 1969–1973 was 288 ducklings (19.2%). The highest mortality period was during the first week on the brood territory with a mean mortality of 13.12 ± 4.26 percent that ranged from a high of 19.32 percent in 1972 to a low of 7.23 percent in 1966. No pattern of decreasing mortalities with advancement in age during the remaining weeks prior to the flapper stage could be found.

The high survival value in broods raised on the island results in a surplus of ducks being produced every year. The mean number of broods observed breeding per year during 1965–1973 was 25.8 and the mean number of ducklings surviving per year during that period excluding 1968 was 151.9 ± 30.8. A summary of the data for the 9-year period is in Table 2.

Throughout the brood counts, no ducklings were observed dying or being taken by predators on the territories. However, observations of broods before and after severe winter storms indicated that ducklings perished because of climatic conditions. Those birds were thought to have perished from exposure, exhaustion, or drowning.

Consequence of Brood Failure

Pairs of breeding birds were observed to lose their unity during the latter half of the breeding season if they were unsuccessful in bringing a brood to their territory or if they lost their brood within the first week. Observations on pair retention were made during brood counts, and it was observed

TABLE 2.—SUMMARY OF BROOD COUNTS OF MOUNTAIN DUCK DUCKLINGS FOR 1965–1973, ROTTNEST ISLAND, WESTERN AUSTRALIA. MEANS ARE PLUS OR MINUS THE STANDARD DEVIATION OF THE MEAN ANNUAL VALUE

Year	Number of Broods	Number of Ducklings Arriving	Mean Number of Ducklings per Brood Arriving	Broods Surviving to Flapper Stage (70 days old)	Ducklings Surviving to Flapper Stage (70 days old)	Mean Number of Ducklings per Brood Surviving
1965	29	241	8.31±2.9 (SE 0.54)	29	210	7.24±2.55 (SE 0.47)
1966	19	141	7.24±3.3 (SE 0.76)	18	123	6.83±3.12 (SE 0.47)
1967	26	171	6.57±3.6 (SE 0.71)	24	134	5.58±3.58 (SE 0.68)
1968	28	234	8.35±2.9 (SE 0.55)	—	—	—
1969	19	170	8.94±3.3 (SE 0.75)	18	129	7.17±3.24 (SE 0.76)
1970	27	192	7.11±3.3 (SE 0.64)	20	140	7.00±2.75 (SE 0.61)
1971	29	206	7.10±5.0 (SE 0.93)	26	178	6.85±5.4 (SE 1.05)
1972	27	176	6.52±3.4 (SE 0.67)	24	131	5.46±1.9 (SE 0.41)
1973	29	206	7.10±3.6 (SE 0.68)	26	170	6.54±2.71 (SE 0.53)
TOTALS	233	1,737		185	1,215	
Means	25.88±4.04		7.49±0.85	23.1±4.05	151.9±30.8	6.58±0.69
Minus Data of 1968	205	1,503		80.8%		

that 21 breeding pairs made changes during that period.

The breakdown of pair unity was initiated by paired or single birds entering onto an unoccupied territory and not being chased off. The new arrivals soon intermingled, the bonds of unity in the territorial pair appeared to dissolve, and soon the territory was vacated by one or both territorial birds. Often, one of the original pair was found on a new territory with a new mate. However, no ducklings were ever observed to be produced from those second matings during the same breeding season. It appears that pair unity is maintained through successful production and rearing of young.

GROWTH AND DEVELOPMENT

To establish the rate of growth and development in mountain ducks and their ducklings, observations were made on birds residing on Rottnest Island and those reared in the laboratory. Data were collected at predetermined intervals for groups of ducklings and mature birds reared in the laboratory. Mature birds from Rottnest Island were trapped and data were recorded throughout the study period. A computer was used to analyze the rate of growth in each group and to compare the growth rate between groups. The developmental sequences of plumage were established from data on observations in both groups.

The experiment was divided into 2 parts. One deals with ducklings up to 70 days of age and the second deals with flying birds in the juvenile, subadult, and adult age groups. In both sections, observations and measurements were made and recorded in a similar manner so that a continuous pattern

TABLE 2. (CONT.)

Year	Number of Ducklings Dead	Number of Ducklings Exchanged between Broods	Corrected Mortality in Ducklings	Ducklings Surviving to 70 Days Old (%)	Mortality to 70 Days Old (%)	Mortality During First Week (%)
1965	34	3	31	87.14	12.86	14.18
1966	18	0	18	87.23	12.77	7.23
1967	39	2	37	78.36	21.64	11.11
1968	—	—	—	—	—	—
1969	41	0	41	75.88	24.12	19.27
1970	53	1	52	72.92	27.08	10.59
1971	35	7	28	86.41	13.59	11.65
1972	47	2	45	74.43	25.57	19.32
1973	37	1	36	82.52	17.48	11.65
TOTALS	304	16	288			
Means Minus Data of 1968	38.0±10.3	2.0±2.3	36.0±10.5 19.2%	80.6±5.96	19.39±5.96	13.12±4.26

of growth and development could be established for all age periods of the bird's life.

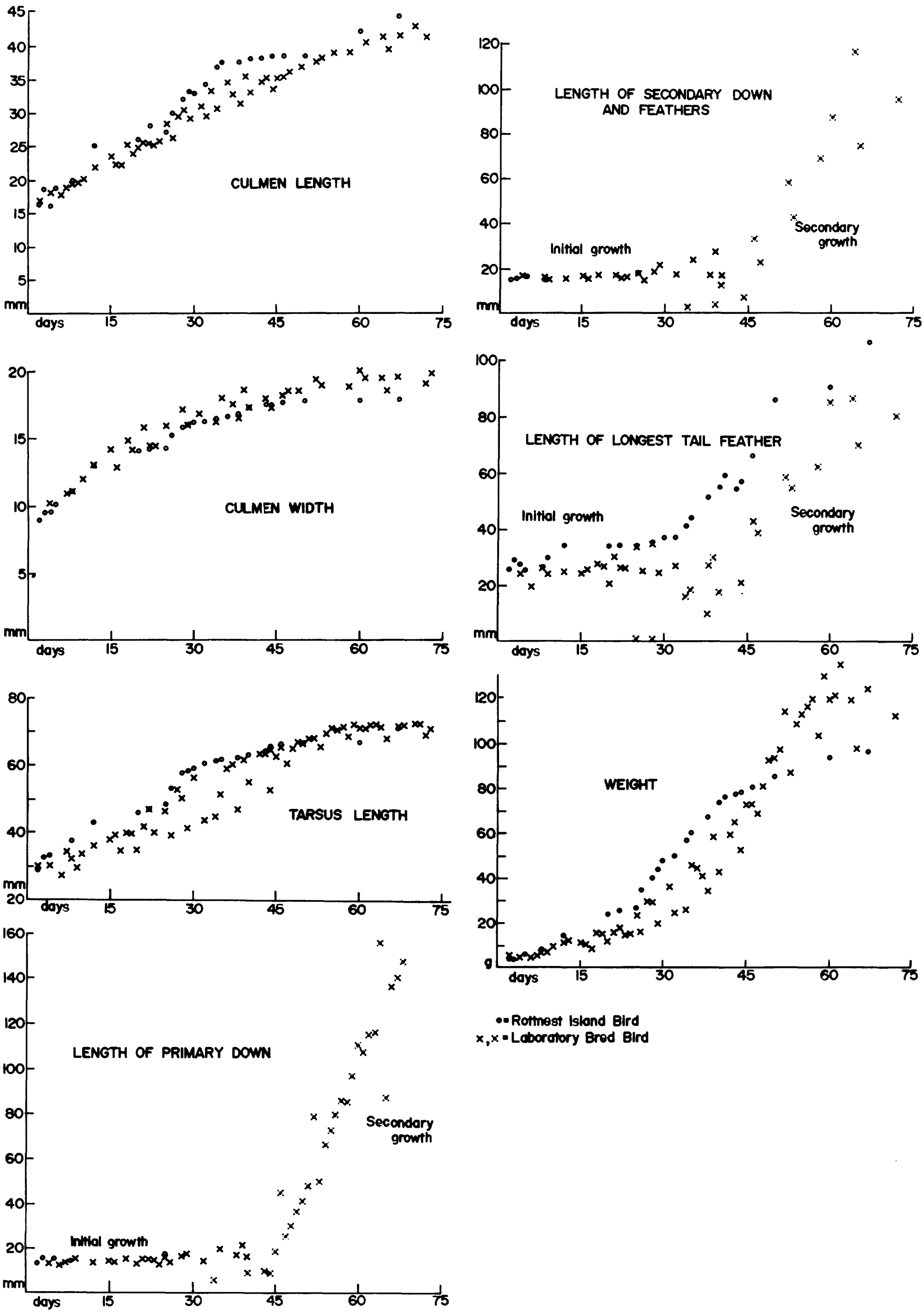
Ducklings

In the laboratory, 65 ducklings were artificially hatched and reared on commercial duck food and given tap water to drink. Measurements were taken every third day of development of plumage, soft parts (culmen, tarsus, and metatarsus), and cloacal organs as follows: culmen length, culmen width, tarsus length, metatarsus length, primary down and feathers, secondary down and feathers, tail length, and weight. Techniques for measuring the birds are given in Riggert (unpublished doctoral dissertation, Appendix II).

Wild ducklings on Rottnest Island, whose ages had been established when they first arrived on their territories, were caught and measured at predetermined times. Ducklings were caught by chasing them on a surfboard and scooping them up with a hand net. To establish the growth rate for a particular age, a minimum sample of 11 ducklings from 2 broods was required. When observations and measurements were completed, the broods were released onto their territories. When the ducklings were able to fly, or 70 days of age, recording of data for the duckling age group was terminated.

Growth

The average lengths of soft parts and feathers, and weights of ducklings reared in the laboratory and in the wild are shown in Fig. 13. In all cases except tail length, the growth rates of the 2 groups were similar. However, that similarity can only be taken as a rough approximation of the true comparison which must be analyzed statistically.


CULMEN LENGTH
mm
days
LENGTH OF SECONDARY DOWN AND FEATHERS
Initial growth
Secondary growth
CULMEN WIDTH
LENGTH OF LONGEST TAIL FEATHER
TARSUS LENGTH
WEIGHT
g
LENGTH OF PRIMARY DOWN
•=Rottnest Island Bird
x,x = Laboratory Bred Bird

The data from the ducklings were analyzed on the PDP6 University computer, and measurements of culmen length, culmen width, tarsus, and age were selected as criteria for determining growth rate. Analyses of the selected data are given in Table 3. A correlation was carried out on the 4 selected measurements of wild and laboratory birds. The correlation coefficients of the logarithm X are shown in a correlation matrix block in Table 4. The high order of the correlation .936–.976 (wild birds) and .934–.966 (laboratory birds) validates the comparison of the regression coefficients of the log–log relations.

From the shapes of the graphs in Fig. 13, the model selected to compare the growth rates of culmen length, culmen width, tarsus length, and age were of the form:

$$CL = K \times AGE^{B}$$
$$\text{Log } B2 = \text{Log } K + B \text{ Log} - AGE$$

The linear regressions of the logarithms of culmen length, culmen width, and tarsus on the logarithm of age were calculated by the computer using the above formula for the 2 experimental groups. Comparison of each of the cases showed that the slope of the regression equation for the ducklings reared in captivity was significantly larger than that for wild birds on Rottnest Island ($P<0.001$). However, the magnitude of the difference between the groups at any particular age was not great (Fig. 14).

The greatest difference between the length of the culmen in the 2 groups was 2.7 mm at 5 days of age. At 50 days of age, the culmen length for both groups was nearly the same (difference, 0.1 mm), while at 70 days of age the difference was 0.8 mm. At 15 days of age, the culmen width was nearly identical (difference, 0.1 mm) in both groups, and at 70 days of age the difference was 1.7 mm. In the tarsus, the greatest difference between the groups occurred at 5 days of age (3.6 mm). At 40 days of age, the calculated difference in tarsus length between groups was 0.2 mm, while at 70 days of age it was 2.6 mm.

TABLE 3.—STATISTICAL ANALYSIS OF THE 4 CRITERIA FOR DETERMINING GROWTH RATES IN MOUNTAIN DUCK DUCKLINGS, ROTTNEST ISLAND, WESTERN AUSTRALIA. ALL MEASUREMENTS IN MILLIMETERS

	Rottnest Island	Laboratory
Culmen length		
Geometric mean	29.50	30.50
Squariance	90.60	6,968.00
Variance	1.02	1.03
SE of mean	1.02	1.01
Standard Deviation	1.29	1.35
Maximum	44.80	78.39
Minimum	15.00	16.20
Culmen width		
Geometric mean	14.60	16.03
Squariance	15.21	537.00
Variance	1.01	1.01
SE of mean	1.01	1.01
Standard Deviation	1.22	1.22
Maximum	19.60	20.89
Minimum	8.30	9.17
Tarsus		
Geometric mean	50.67	53.58
Squariance	155.10	1.011×10^{5}
Variance	1.03	1.03
SE of mean	1.02	1.01
Standard Deviation	1.31	1.30
Maximum	72.80	75.50
Minimum	26.30	29.49
Age		
Geometric mean	22.2 days	28.40
Squariance	7.841×10^{22}	2.443×10^{37}
Variance	1.39	1.25
SE of mean	0.30	1.03
Standard Deviation	2.40	2.06
Maximum	67.00	67.00
Minimum	2.00	4.00

Development of Ducklings

The development of plumage in mountain duck ducklings has been established on 85 birds reared in captivity. The classification

←

FIG. 13. Average daily growth rate of culmen length, culmen width, tarsus length, primary down and feather, secondary down and feather, length of longest tail feather, and weight of mountain duck ducklings captured on Rottnest Island, Western Australia, or reared in the laboratory. Wild birds shown as 'o', laboratory birds shown as 'x'.

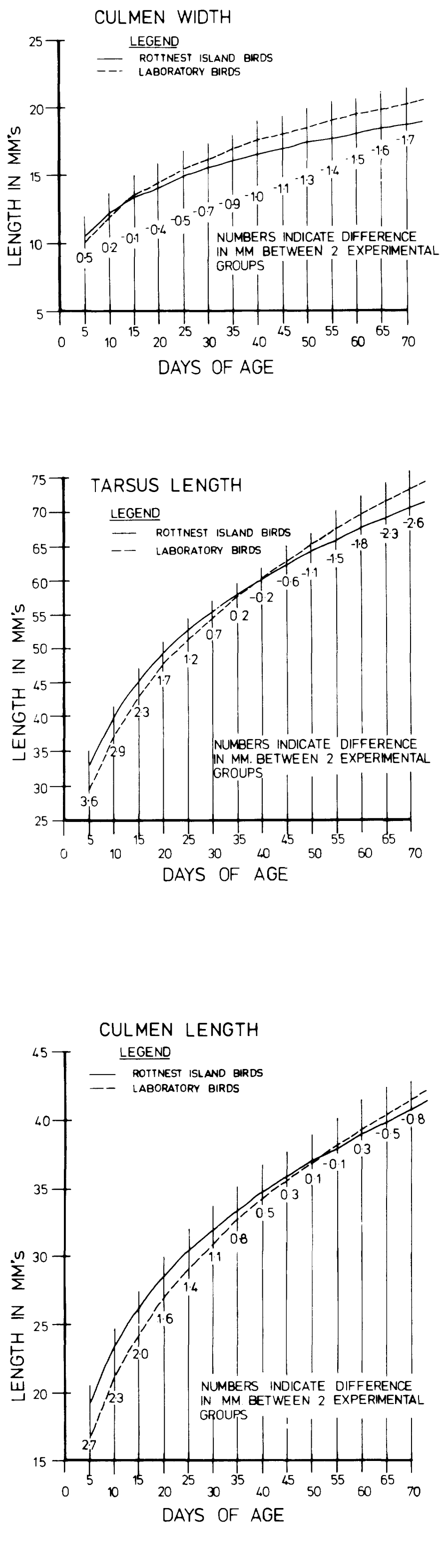


TABLE 4.—CORRELATION MATRIX BLOCKS FOR WILD MOUNTAIN DUCK DUCKLINGS AND THOSE REARED IN THE LABORATORY FOR CULMEN LENGTH, CULMEN WIDTH, TARSUS, AND AGE, ROTTNEST ISLAND, WESTERN AUSTRALIA

	Culmen Length	Culmen Width	Tarsus	Age
Wild ducklings				
Culmen length		.960	.976	.966
Culmen width	+++		.963	.954
Tarsus	+++	+++		.936
Age	+++	+++	+++	
Laboratory reared ducklings				
Culmen length		.958	.961	.957
Culmen width	+++		.934	.966
Tarsus	+++	+++		.948
Age	+++	+++	+++	

+++ Indicates significance at 0.001 level.

system has been made to conform to previously established methods and criteria for aging waterfowl broods in the field as presented by Gollop and Marshall (1954), Weller (1957), and Yocom and Harris (1966).

The classification of plumage development in mountain duck ducklings up to 70 days of age is presented in Table 5. Study skins of ducklings of each subclass of the classification system are shown in Fig. 15. The classification is intended for use in the field, and assumes the observer obtains an excellent view of the ducklings in good light. The binoculars used for field observations during formation of the development chart were 10×50 mm. Birds in the hand usually show greater feather development and lighter colors of the soft parts than indicated for the earlier classes and more down than indicated for the later classes.

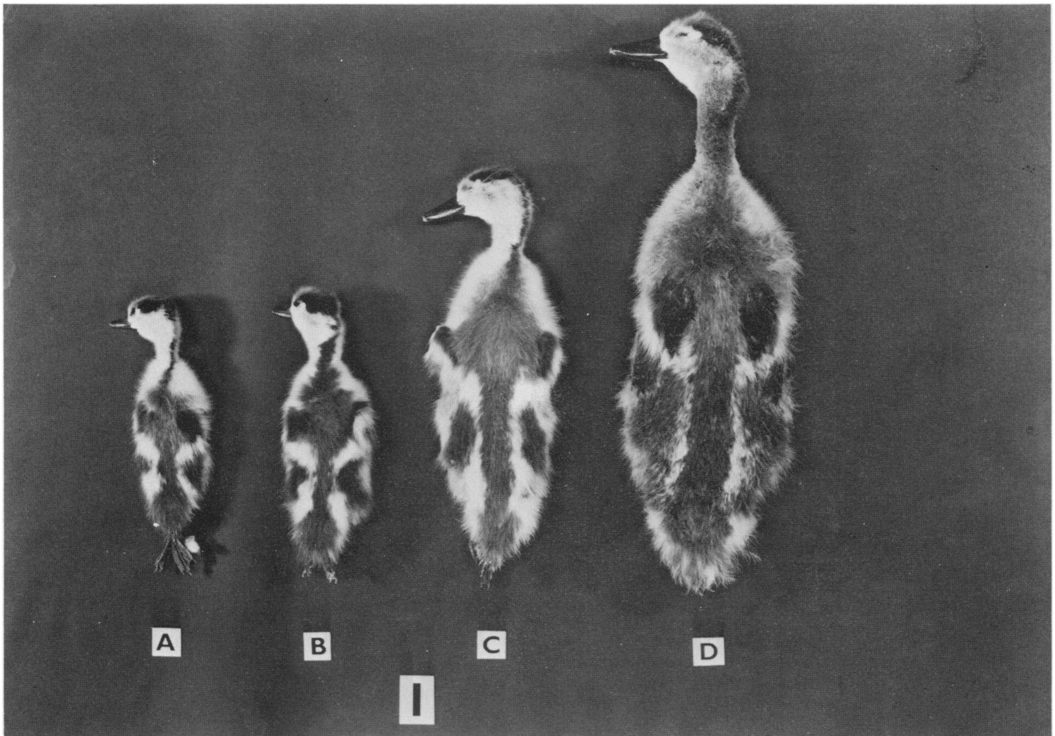
Capturing 203 ducklings on Rottnest Island which represented all subclasses allowed a comparison of plumage development between wild ducklings and those reared in the laboratory. No difference

←

FIG. 14. Growth rate of culmen width, tarsus length, and culmen length in wild and laboratory reared mountain duck ducklings established by log time (days) versus log tarsus (mm), Rottnest Island, Western Australia.

TABLE 5.—CHART OF DEVELOPMENTAL STAGES IN MOUNTAIN DUCK DUCKLINGS, ROTTNEST ISLAND, WESTERN AUSTRALIA

Plumage Class	Sub-class	Age (days)	Description
I DOWNY BIRDS	A	0–8	*Newly Hatched Young*: Patterns distinct with large dark brown stripes approximately 1.5 cm wide commencing at posterior edge of bill forming a dark brown cap which divides head just below eye and runs laterally along dorsal surface of neck and back to tail (width of stripe expands to over 2.5 cm in scapular and rump region); cheeks, throat, neck, breast, and belly all white with a creamy tinge noticeable at base of lower bill in throat area. Wing brown with transverse stripe of white at midpoint. Iris dark brown, bill olive green, with egg caruncle present and legs and feet a yellowish-green.
	B	9–16	*Bright Balls of Down*: Patterns still distinct. Head close to body, neck visible but not holding head erect as yet. Creamy tinge spreading on throat area. Bill becoming gray and more conspicuous, egg caruncle now absent. Legs and feet still olive green but turning gray. Ducklings appear approximately twice the size of newly hatched birds.
	C	17–24	*Gawky and Downy*: Patterns still distinct, head erect with neck conspicuous. Cream tinge on white throat area still persisting. Bill now obviously large, grayish-blue and nail nodule on anterior end. Legs and feet becoming sturdy and strong, color gray on legs and toes with webbing between toes darker and charcoal in color. Toenails very light in color. Tail now obvious and birds are looking about 3 times as large as newly hatched or one-fourth swim length size of adult female bird.
	D	25–34	*Dark Downy*: Patterns starting to fade, but still obvious. Head erect with small dark patch of ear down showing. Neck and breast white down being replaced by gray down. Bill gray-blue with legs and feet unchanged and toenails dark. Tail obvious, with feathers starting to replace down. Scapulars and flank feathers noticeable at close distances or when examined in hand. Birds now one-third swim length size of adult female.
II FEATHERED BIRDS	A	35–42	*First Feathers*: Patterns not present, head dark with feathers. Gray down being replaced by feathers on neck, breast, and belly with undertail feathers buffy-rust. The upper surface of tail feathers are black. The regions still containing gray down are nape of neck and lower back on occipital region. Color of bill, legs, and feet unchanged. Scapular and flank feathers completely grown by latter stage of this category. Primaries and secondaries burst quills, but greater primary coverts and greater wing coverts still sheathed. Tertiaries out of quill sheaths. Ducklings now one-third as large as adult female or two-thirds swim length of parent bird.
	B	43–48	*Feathers Well Developed*: Head feathers black with bits of gray down intermingled and more so on nape. Breast and belly feathers are a buffy-chestnut, but rust color still persisting on undertail coverts. The upper tail feathers, black, are now obvious at long distances and resemble adult parent bird. Wings now half feathers and half quill with white tips on secondaries. On dorsal surface of wing greater and middle coverts now white. Pelvic area would be only area where down occurs heavily. Juveniles approximately three-fourths swim length size of adult. The juveniles have lost duckling appearance and resemble the adults at this stage.
	C	49–56	*Mostly Feathers*: Head black and pieces of down intermingled occasionally. Breast and belly feathers well developed and color is becoming more intense. Ventral rust patch on tail still obvious and is quite noticeable when juveniles tip up to feed on submergent vegetation. Wings heavily feathered with iridescent green on speculum. The under wing lining is developing but bare patches of skin are still present. A juvenile closely resembles an adult female in size when swimming, but the juveniles neither have the white collar around neck or other white facial feathers which can be used for sex identification. Some gray down still persists on occipital region.
	D	57–70	*All Feathered and Flappers*: Head buffed black, breast light chestnut and turning darker approaching belly region. Wings fully feathered but primaries still show some sheath while secondaries are completely unsheathed. Wing lining mostly grown in by midpoint of this stage. No white ring on neck and no down present. When bird is capable of flight the brownish tertials are as fully developed as the iridescent green feathers of speculum.



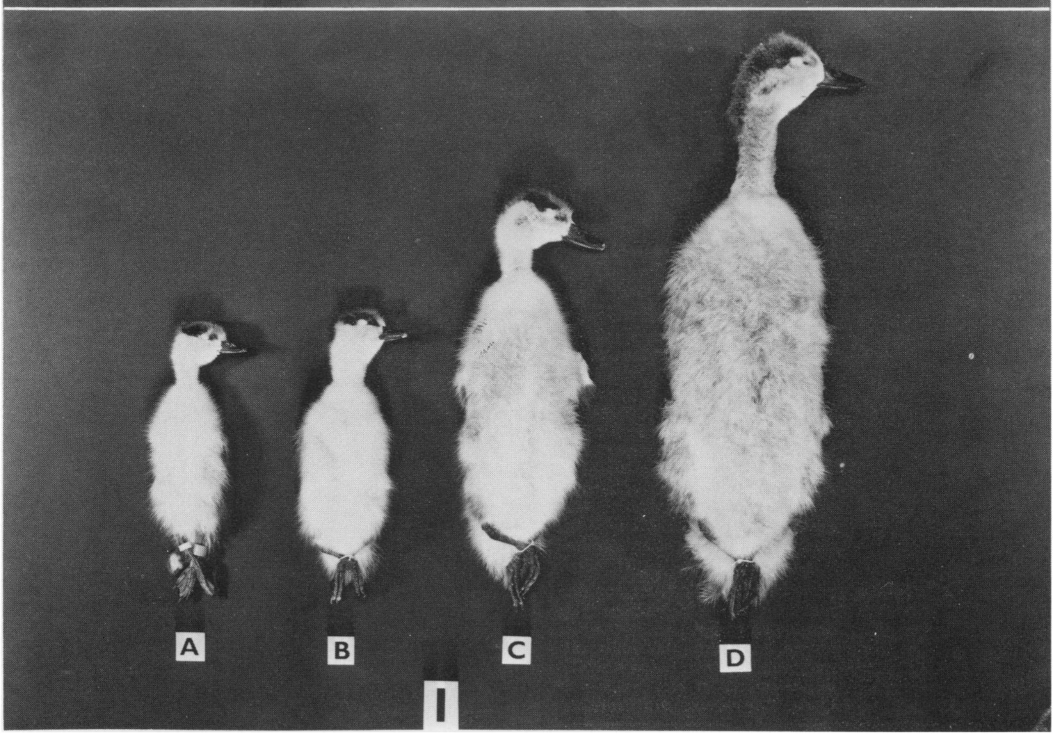


FIG. 15A. Study skins of mountain duck ducklings, downy stage, plumage class I, subclasses A–D. Upper photograph shows dorsal surface, lower photograph shows ventral surface.

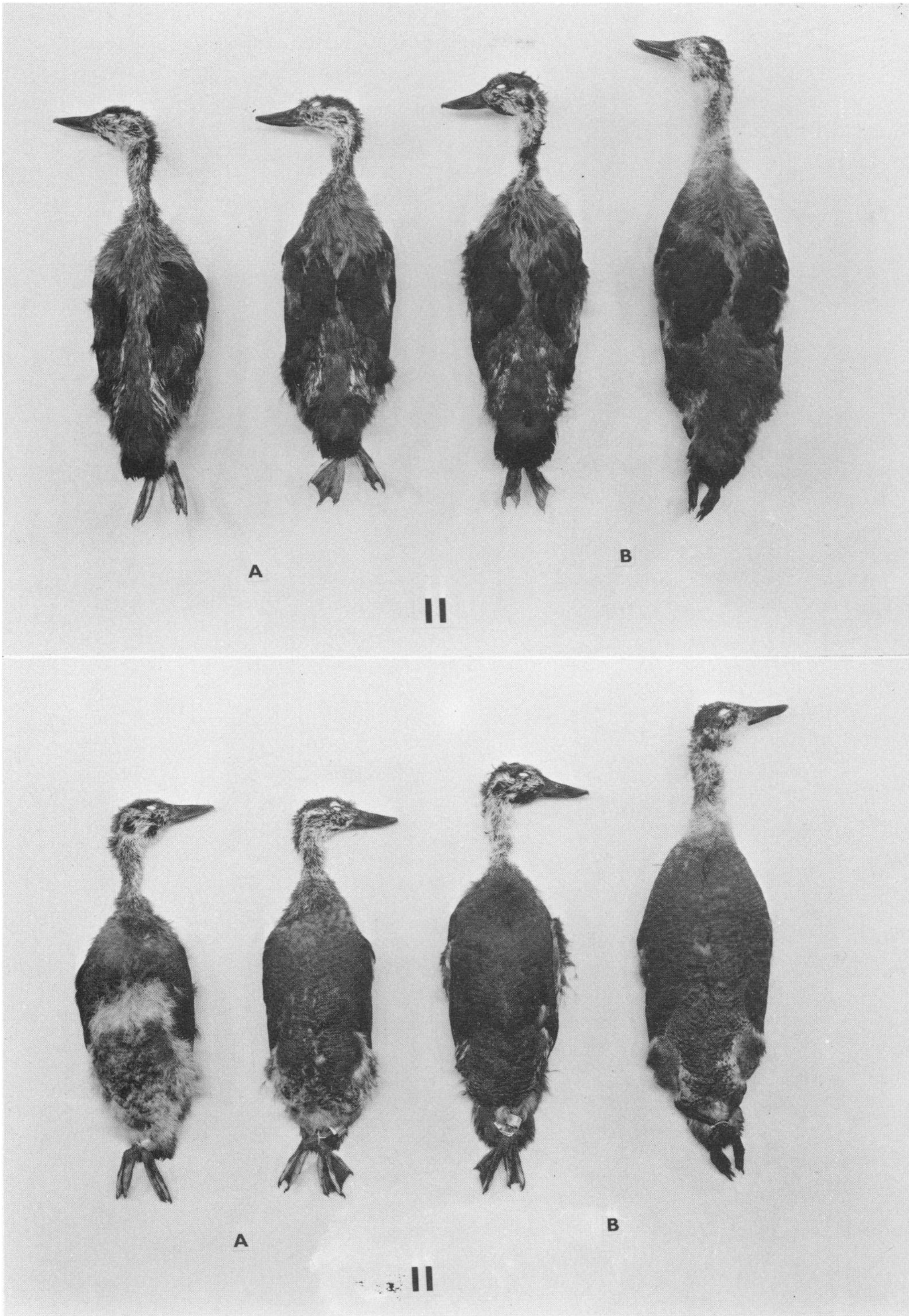


FIG. 15B. Study skins of mountain duck ducklings, feathered stage, plumage class II, subclasses A and B. Upper photograph shows dorsal surface, lower photograph shows ventral surface.

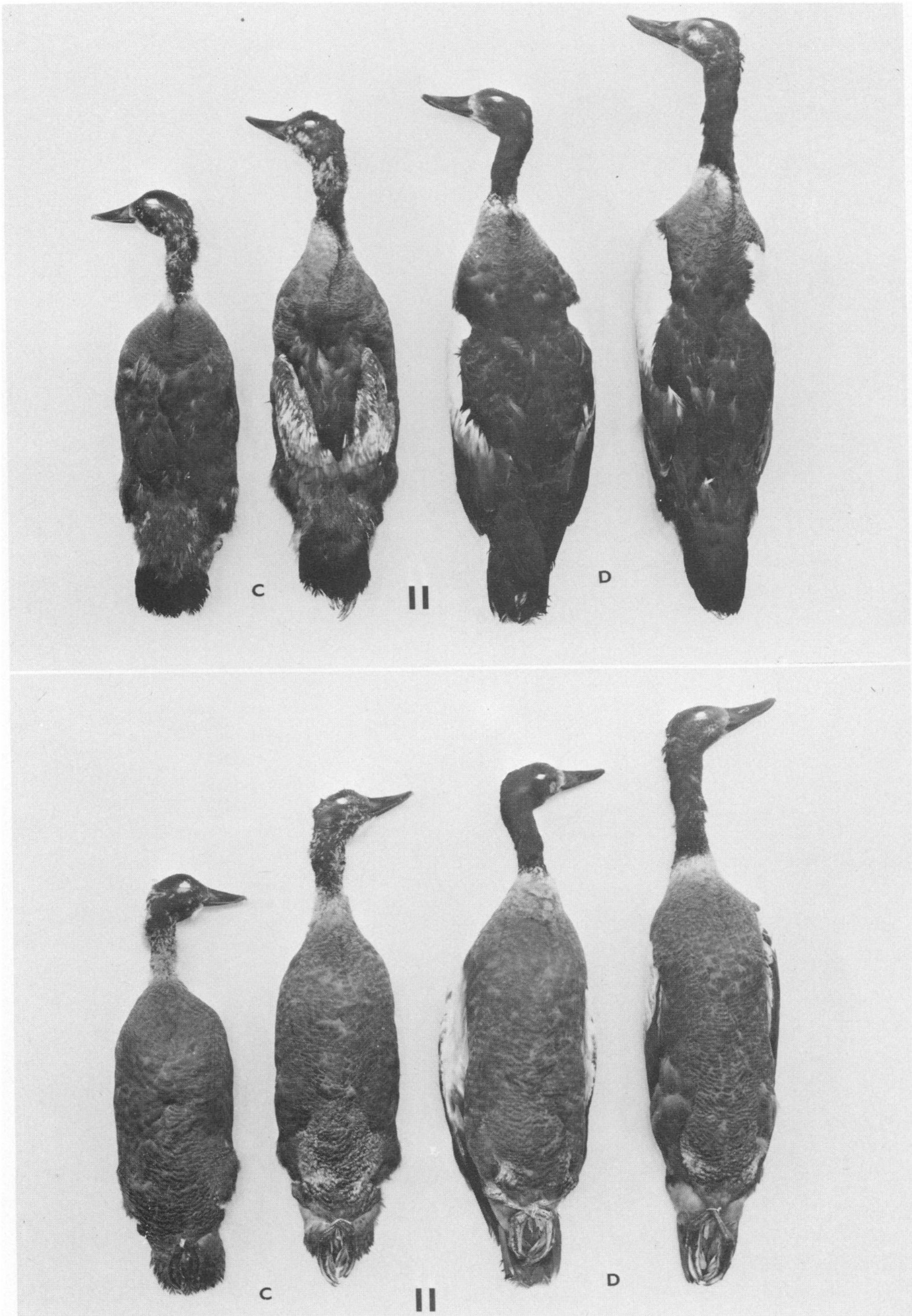


FIG. 15C. Study skins of mountain duck ducklings, feathered stage, plumage class II, subclasses C and D. Upper photograph shows dorsal surface, lower photograph shows ventral surface.

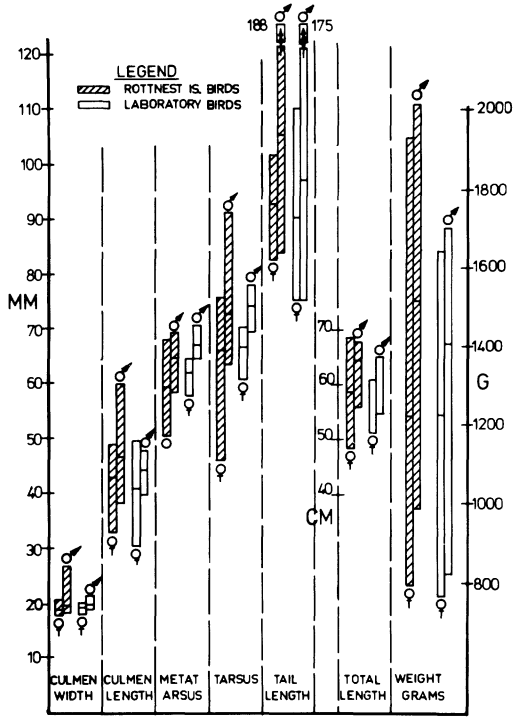


FIG. 16. Growth chart of juvenile (71–199 days old) mountain ducks captured in the wild and reared in the laboratory, Rottnest Island, Western Australia.

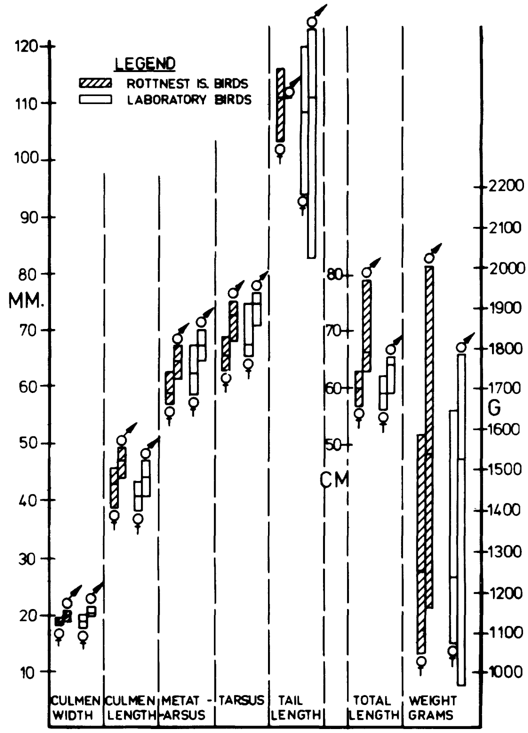


FIG. 17. Growth chart of subadult (200–600 days old) mountain ducks captured in the wild and reared in the laboratory, Rottnest Island, Western Australia.

could be detected between the groups in the sequential development of plumage or the time required to pass through the subclasses of the classification system.

Mature Birds

When the birds reared in the laboratory were able to fly (70 days of age), they were transferred to separate yards and measured once a week until they were 200 days old. Subsequent measurements were made approximately once every 3 weeks. Flying mountain ducks on Rottnest Island were captured and measured in a manner similar to the laboratory reared birds.

Data from measurements on juvenile, subadult, and adult mountain ducks reared in the laboratory or caught on Rottnest Island were analyzed on the NCR 315 computer. The measurements analyzed were: total length, wing span, culmen length, culmen width, tail length, tarsus length, metatarsus length, and weight (Figs. 16, 17, 18). Corresponding numerical data are listed by Riggert (unpublished doctoral dissertation, Appendix II).

The data were tested to see whether mature birds reared in the laboratory grew at a rate similar to that of wild birds on the island. It has already been shown that ducklings reared on Rottnest Island do not grow in a manner similar to their counterparts reared in the laboratory ($P<0.05$). Therefore, it was realized that birds in the 2 groups had little chance to be similar in the early juvenile age group, but the difference possibly would diminish with advancement toward maturity.

Data on the 2 groups are compared in Table 6. The test shows that the majority of the measurements compared are significantly different ($P<0.01$), and only the length of the tail was nonsignificantly different in all age groups for both sexes.

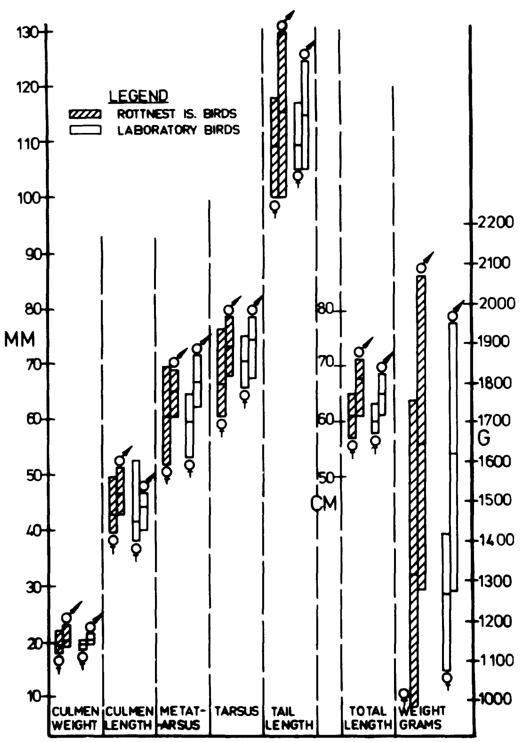


FIG. 18. Growth chart of adult (600+ days old) mountain ducks captured in the wild and reared in the laboratory, Rottnest Island, Western Australia.

In general, a similar situation exists for the growth rates of mature birds. The birds reared in captivity were larger, but though the differences between the 2 groups were quite small, they are statistically significant. Because the differences were so small, the 2 groups were considered similar for practical purposes.

Development

Once the ducklings are able to fly, the subsequent plumage development is in the form of molts. The molting sequence in mountain ducks was established by regular examination of 68 birds reared in the laboratory and 3,776 trapped on Rottnest Island. Those data show that mountain ducks of both sexes undergo 2 molts annually. No difference could be detected between the 2 experimental groups during the plumage molts.

In the first year, the mountain duck has a postjuvenile and prebreeding seasonal molt. During the second year and thereafter, the postbreeding and prebreeding seasonal molt

TABLE 6.—COMPARISON OF GROWTH RATES (mm) BETWEEN WILD AND LABORATORY REARED MOUNTAIN DUCKS BY THE STUDENT'S *t*-TEST, ROTTNEST ISLAND, WESTERN AUSTRALIA

	Juvenile		Subadult		Adult	
	Male	Female	Male	Female	Male	Female
Total length	6.6475[3]	5.5820[3]	2.7806[2]	1.9392[4]	4.4216[3]	2.8951[2]
Culmen length	7.1918[3]	4.9484[3]	5.5287[3]	4.1449[3]	6.9040[3]	3.3042[2]
Culmen width	3.1606[2]	3.8940[3]	2.3634[1]	2.6581[1]	4.4370[3]	2.0005[1]
Tail length	1.4455[4]	0.9782[4]	—	1.2500[4]	0.4454[4]	0.0899[4]
Metatarsus	9.6182[3]	6.1851[3]	5.6927[3]	6.0277[2]	5.2364[3]	0.5451[4]
Tarsus	4.1002[3]	1.9599[4]	3.3669[2]	4.5533[3]	2.5087[1]	3.2148[2]
Weight (g)	4.3650[3]	0.1428[4]	0.3711[4]	0.5103[4]	0.9668[4]	2.1928[1]
Degrees of freedom						
Total length	98	135	30	30	66	88
Wing span	120	153	22	22	59	81
Bill length	180	209	39	42	94	127
Bill width	127	165	39	41	77	100
Tail length	66	68	26	29	51	49
Metatarsus	176	209	39	42	94	126
Tarsus	180	210	39	42	94	126
Bursa	84	112	22	23	0	4
Weight (g)	258	292	60	49	142	182

[1] Significant at 0.05 level.
[2] Significant at 0.01 level.
[3] Significant at 0.001 level.
[4] Not significant.

TABLE 7.—STAGES OF POSTJUVENILE MOLT IN THE MOUNTAIN DUCK, ROTTNEST ISLAND, WESTERN AUSTRALIA

Plumage Class	Subclass	Age (days)	Time Required (days)	Description
III	A	90–115	15	1. Male head dark mottled black brown. Female head slightly mottled and no obvious white.
FIRST MOLT				2. No new feathers obvious on breast or belly but are in sheaths (pin feathers).
				3. Flank and scapulars first feathers to break sheaths.
				4. Under and upper tail coverts and rectrices not yet commenced.
	B	115–140	25	1. Male head turning darker with fewer mottled patches. Female white appearing on anterior of face.
				2. Breast coloration becoming obvious in both sexes. Belly now mottled and adult plumage appearing.
				3. Flank and scapulars now obvious.
				4. Under and upper tail coverts commenced. Rectrices obvious.
	C	140–200	60	1. Male head black with iridescent green visible. Female head black with white obvious around bill and eye.
				2. Breast almost covered with adult plumage. White collar becoming apparent.
				3. Belly almost adult appearance. Scapular and flank feathers fully developed.
				4. Under and upper tail coverts well out and have burst sheaths. Rectrices apparent.
	D	200	Complete	Feather development and patterns as described for subadult.

occurs. The postjuvenile and prebreeding are incomplete molts, while the postbreeding is a complete seasonal molt.

Incomplete Molt

Postjuvenile Molt

Prior to the commencement of the postjuvenile molt, the plumage is drab and the sexes are not distinguishable by color (Riggert unpublished doctoral dissertation). The molt commences at approximately 90 days of age and lasts for about 110 days. During the molt, the feathers from the body and tail are lost while the wing feathers remain intact. The 4 stages of the postjuvenile molt, age of the bird, time required for each stage, and a description of feather development are given in Table 7. Photographs of study skins showing the beginning of the molt (Stage A) and the completion (Stage D) are shown in Fig. 19.

Prebreeding Seasonal Molt

At approximately 10 months of age, mountain ducks undergo a second molt known as the prebreeding seasonal molt. The molt lasts for only 30 days, and under field conditions is easily overlooked. There does not appear to be any sequence to feather loss or development; the molt merely replaces some body feathers that gives the birds the contrasting plumage associated with the breeding season (Front.). No feathers are shed from the wing or tail.

Complete Molt

At approximately 15 months of age, subadult birds commence their first complete molt. Observations of 42 birds reared in captivity indicate that the first complete molt in subadult birds starts about 50 days later than in adult birds undergoing their second or consecutive molts.

Toward the end of the breeding season, mid-September to October, adult birds undergo a plumage fade. The fading, or semieclipse, occurs in both sexes and can often be observed in parents still rearing young. The term semieclipse has been used, as sexes of the birds can still be determined by plumage characteristics during that period. Subadult birds do not undergo a fade in plumage as obvious as that in adult breeding birds.

The loss of feathers during the complete molt occurs in 2 stages. The first consists of all body and tail feathers while the second consists of wing feathers only. The loss of body and tail feathers follows the identical pattern set out in Table 7; however, the time required to complete the molt is somewhat shorter, approximately 90 days. The second stage commences as the body molt nears completion and can last for 60 days.

The loss of 1 or 2 tertial feathers indicates that the wing molt has commenced. That loss is followed by the loss of the outermost primary feathers, dropped in the order of 10, 9, 8, and 7. A period of 16 days is required to advance the molt through this phase. In the following 3 to 4 days, the remaining 6 primaries are dropped simultaneously and the bird is flightless. The loss of the secondary, greater, middle, and lesser coverts follows, and all are dropped within 2 days. The wing is now void of all major feather groups, except 2–4 tertials, approximately 22 days from the beginning of the wing molt. The remaining tertials drop randomly during the regrowth period.

Regrowth of the wing feathers is rapid, and by the time the secondaries have dropped, the primaries are more than 120 mm long and half unsheathed. The secondaries have regrown fully by 44–46 days from the beginning of the wing molt; therefore, the bird is flightless for 26 days during the second stage. The number 10 primary is the last feather to finish developing, and completes the wing molt. The total time utilized in both stages of the postbreeding seasonal or complete molt was 150 days or 5 months.

Age Criteria by Wing Plumage

Examination of wing feathers in mountain ducks reared in the laboratory and those banded and recovered on Rottnest Island showed a distinct color difference between adult birds and immature birds in the secondaries. The tips of the secondaries on the ventral surface of immature birds (juvenile and subadult) had prominent white markings while adult birds had black tips.

The color change in the secondaries occurred after the first complete molt. It has been stated previously that the age of the birds at the beginning of the first complete molt is 15 months; however, the wing feathers are not dropped until the latter stage of the molt period, 18–19 months of age. Observations were made on laboratory birds that had 3 complete molts and the secondaries have been retained throughout each consecutive molt. Also, no white tips were found on the secondaries of adult birds banded and recaptured on Rottnest Island.

The application of aging birds by the coloration of secondary feathers allowed adult birds capable of breeding to be separated from subadult nonbreeding birds. This proved to be of major importance once the birds reached 1 year of age and cloacal examination for age determination was no longer accurate.

The Cloaca and Related Structures

The cloaca and its related structures are widely recognized as criteria of sex and age in waterfowl (Gower 1939, Hochbaum 1942, Elder 1946, Hanson 1949). In examining the organs of a living bird (sphincter muscle, penis, oviduct, and bursa), it is necessary to hold the bird so that struggling is reduced to a minimum and good observation of the organs can be obtained. The bird should be held belly up, tail away, with the outer finger of each hand holding the wings and legs. See Cowan (1963) for technique for inspecting the cloaca, probing the bursa, and illustrations of genital organs of male and female waterfowl.

Sphincter Muscle

The appearance of the sphincter muscle in juvenile mountain ducks is white and remains so until the birds are fully feathered. By the completion of the postjuvenile molt, the sphincter is white intermingled with charcoal gray. At the age of 10 months, the

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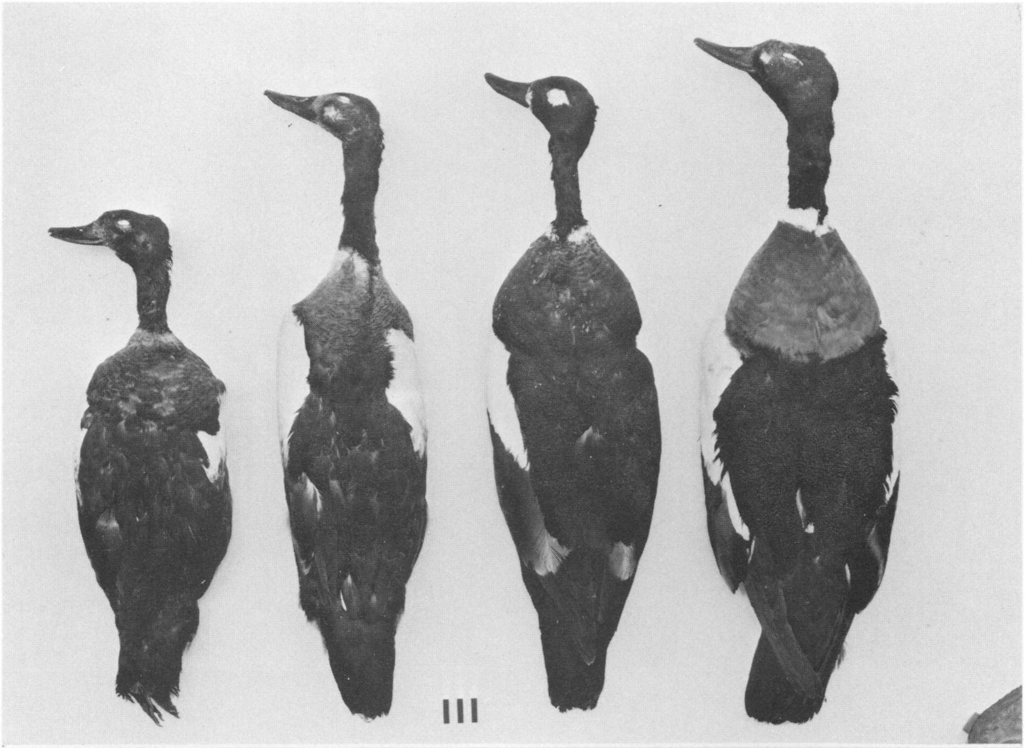
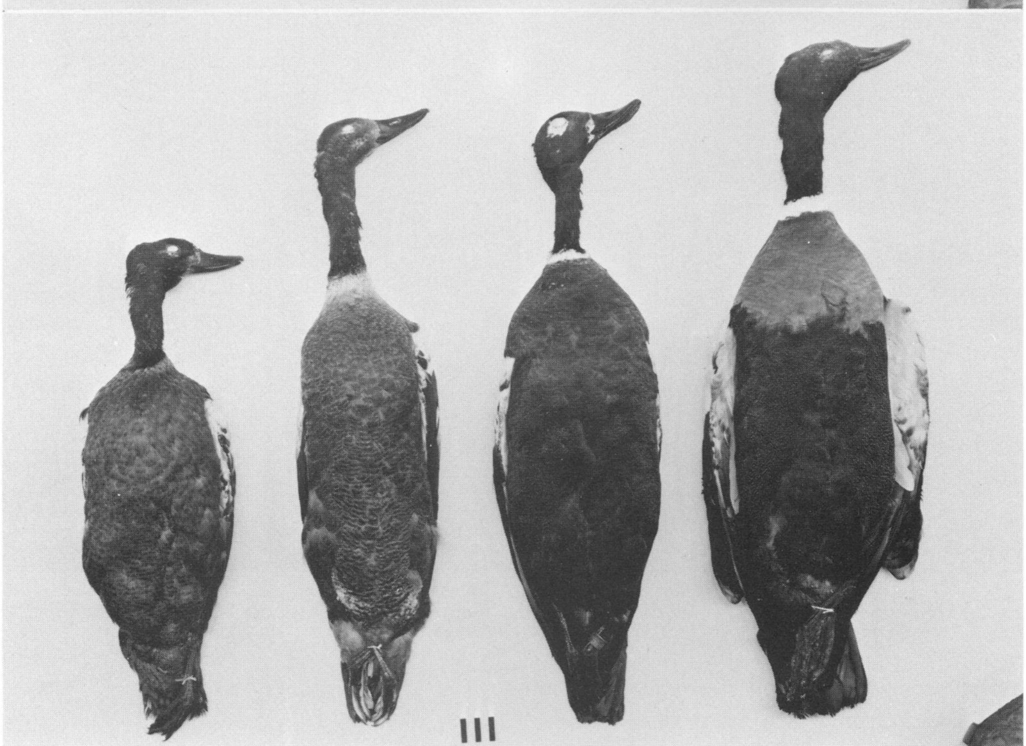
FIG. 19. Study skins of mountain duck plumage class III, subclasses A and D, left and right, respectively. Upper photograph shows dorsal surface, lower photograph shows ventral surface.





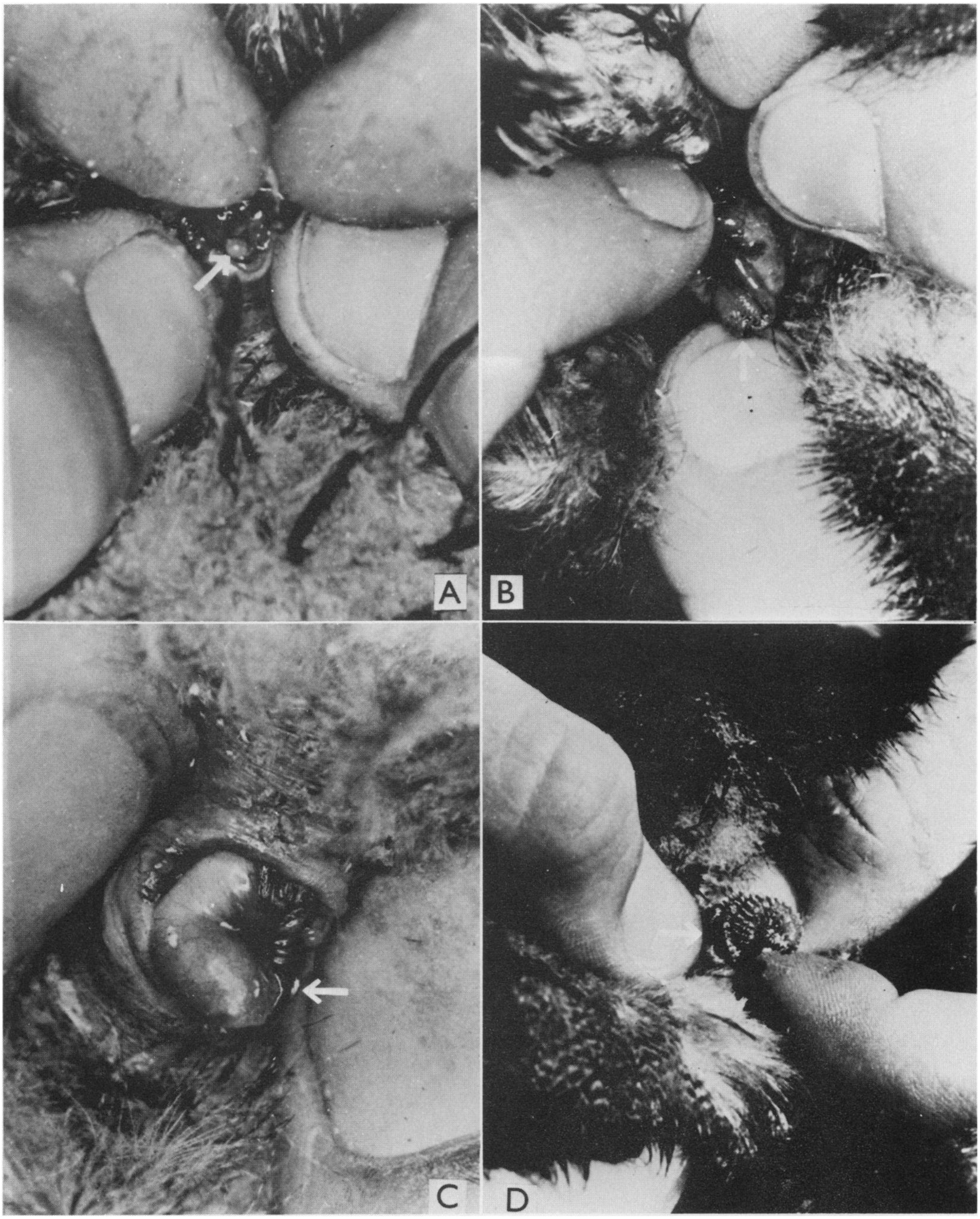


FIG. 20. Stages of development in the penis of the mountain duck, Rottnest Island, Western Australia.

sphincter becomes black, and often maroon color is apparent. The bare flesh area of the sphincter is much larger in mature males than in mature females.

The Penis

The penis of a mountain duck lies on the wall of the cloaca, on the anterior side in young birds and on the left side in adults.

As the cloaca is exposed by holding the bird in the manner just described, the penis will protrude if present. The 4 stages of development can be seen in Fig. 20. Sexing is possible at an age of 4 days by this method. However, it is important to know the exact location of the penis in ducklings as the organ is inconspicuous and can be easily overlooked. In the cloaca of a male duckling aged 35 days, the position is pointed out by the white arrow in Fig. 20A. In the cloaca of a juvenile male 90 days old, the penis indicated by the arrow is unsheathed, small, and very dark (Fig. 20B). The position of the penis is the same as in the duckling in Fig. 20A. Once the birds advance to subadult stage (200 days), a major change is noticeable; the position changes from the anterior to the left side, a conspicuous sheath covers the penis, and it is no longer straight. The color changes to white at the base turning red toward the tip (Fig. 20C).

Full development of the penis is attained when the bird becomes subadult. A fully developed mountain duck penis measures approximately 13×6 mm when extended and appears as a corkscrew-shaped organ with a conspicuous lefthand twist (Fig. 20D). The penis is white during the breeding and nonbreeding seasons from that age on.

Observations on 31 male birds reared in captivity showed that full development could be reached as early as 300 days of age. Usually, the time required was 450 days which coincided with the end of the normal breeding season on Rottnest Island. Therefore, aging by development of the penis alone is not foolproof, as a subadult with a well-developed penis could be mistaken for an adult male during the breeding season.

The Oviduct

Sex in female mountain ducks usually can be determined in both the subadult and adult age groups by the white ring of feathers at the base of the bill and around the eye. However, in juveniles 71–199 days old, the white feathers are not prominent and other sexing criteria are necessary for positive identification.

The membrane that covers the opening of the oviduct into the cloaca usually is not resorbed until the end of the first winter breeding period or at an age of 450 days. If the opening of the oviduct is present it will be seen on the left wall of the cloaca. Examination of the cloaca for the oviduct is done in the same manner as described previously. However, the use of a fine blunt probe may be necessary in searching for the opening. Therefore, the first year nonbreeding female mountain ducks can be detected that way with reliability, but a good check to verify it is the presence of the bursa of Fabricius.

The Bursa of Fabricius

The use of the bursa to distinguish immature from older waterfowl has been described by Gower (1939:427) and Hochbaum (1942:304–360) and for Canada geese by Elder (1946:106–108). However, little work has been done on the bursa as an aging device in Australia where breeding cycles are much different from those in North America.

Measurements of the depth of the bursa were made on 60 mountain duck ducklings reared in the laboratory. Measurements were commenced when the ducklings were 25 days old and were continued at regular intervals until the bursa was closed. A graduated stainless steel probe was used in the measurements.

The depth of the bursa in juvenile males varied from 38 to 20 mm with a mean of 29±6 mm, and in females from 45 to 26 mm with a mean of 32±5 mm. The bursa remained fully open at those depths until 300 days of age (subadult). Once the birds exceeded that age, the bursa closed rapidly. At 330 days of age, the mean depth was 8 mm and by 355 days it was 5 mm or less in all birds. The closure rate was the same for both sexes (Fig. 21).

On Rottnest Island, depth measurements of the bursa were made on 110 males and 139 females in the juvenile and subadult age groups. A statistical comparison of the bursa depth of wild birds and those in the laboratory by the Student's *t*-test showed no sig-

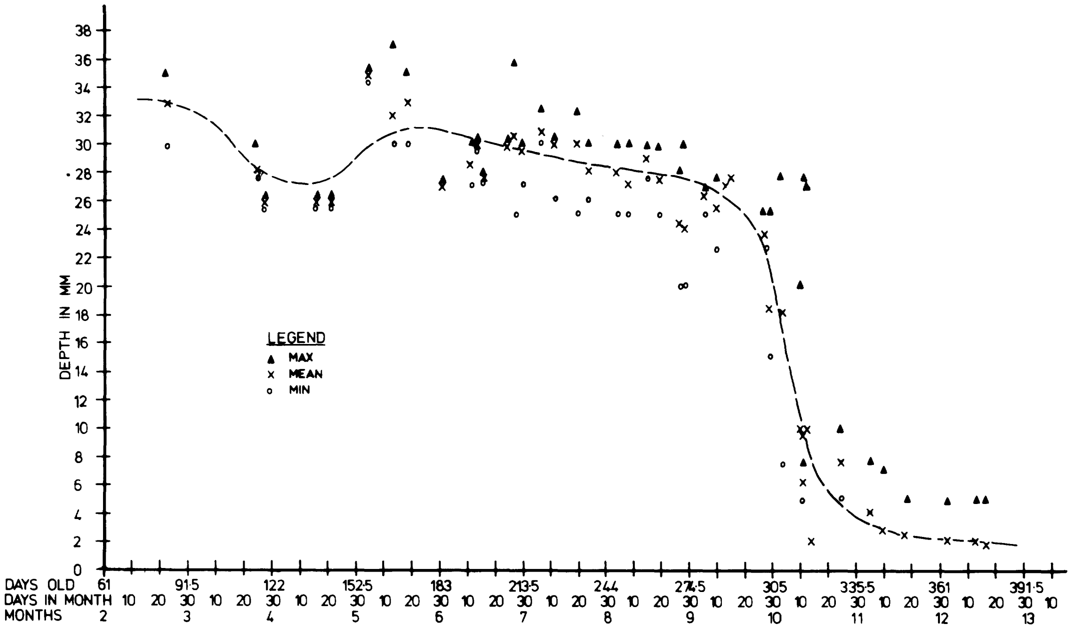


FIG. 21. Average daily depth of the bursa of Fabricius in mountain duck ducklings, Rottnest Island, Western Australia.

nificant statistical difference between the 2 groups. Observations of bursa closure in wild birds, whose approximate age was known from banding records, showed that the bursa closed at the same age as in laboratory birds.

Absence of a bursa in either sex identifies that bird as at least 1 year old. A bird with a bursa depth of 10 mm or greater and an undeveloped penis or membrane covering the oviduct can be categorized with certainty as a nonbreeding first year mountain duck. The greatest value of bursa probing is the aging of female birds, as determination of age by use of the oviduct can be misleading and unreliable. Proficiency at aging female mountain ducks by cloacal examination is important in establishing true figures for the proportion of the flock less than 1 year old.

UTILIZATION OF SALINE HABITAT

It is common knowledge among duck shooters and ornithologists that mountain ducks tend to frequent salt lakes and brackish lagoons. Aerial surveys throughout southwestern Western Australia confirm that supposition. The salt lakes of Rottnest Island are typical of the habitat frequented by mountain ducks.

Salt concentrations of the Rottnest Island salt lakes varied from approximately 2.5 to 24.5 percent sodium chloride in 1 year, and over that range, ducklings and mature birds have been observed feeding on the lakes. The avian kidney is well known for its inadequacy in eliminating high concentrations of salt, and this tends to conflict with habitat preference of the mountain duck. Investigations into the development and function of the supraorbital salt gland made it possible to understand how that gland permits utilization of saline areas (Riggert unpublished doctoral dissertation, Chapter 12). Examination of the salt glands removed from 71 mountain ducks showed them to be well developed, highly vascularized, and similar in function to the salt gland of several species of Anatidae described by other workers (Heinroth and Heinroth 1926–1928, Schildmacher 1932, Technau 1936, Scothorne 1959, and Cooch 1964).

The salt glands of ducklings from the salt lakes on Rottnest Island showed a marked change with increased age. It was evident from the appearance of the glands that they were undergoing hypertrophy in response to the osmotic stress imposed by the intake of saline water from Baghdad Lake. Salt glands of ducklings residing on the salt lakes and those on varying concentrations of salt as drinking water from the laboratory commenced secreting at approximately the same time, 6 days of age. The concentrations of sodium ions emitted in the initial and subsequent nasal secretions averaged the same for both the wild and laboratory groups.

The development of ducklings reared in the laboratory on drinking water concentrations that exceeded 2.0 percent sodium chloride showed marked decreases in body weight and growth rate; however, once fresh water was substituted for the salt solutions of more than 2.0 percent, there was an increase in weight followed by a general improvement in the ducklings' physical condition. Ducklings that resided on Rottnest Island salt lakes gained weight in a steady manner with increasing age (see Growth and Development p. 36).

The information gained from the experiments was utilized in the field to interpret behavior of paired birds in selecting brood territories that contained a supply of fresh water. Initially, ducklings require at least 6 days for the salt gland to hypertrophy and become functional, and during that time are unable to survive without fresh water. Secondly, as ducklings feed on the salt lakes where concentrations of salt exceed 2.0 percent throughout the year, the ducklings require a source of fresh water to flush out the salt gland and the renal system to maintain an electrolyte balance. If the fresh water is not available, erratic weight and growth rates occur followed by physiological deterioration and death.

Mature mountain ducks may breed on freshwater swamps on the island and need not be forced to move to saline waters until conditions of summer drought. The accompanying shrinkage of fresh water under such conditions forces ducks to deal with salt solutions for the first time.

Experimentation with wild birds and laboratory birds demonstrated that the majority in all experimental groups previously subjected to salt water excreted a greater volume of fluid than received during salt loading with a stomach tube, thus suffering a net loss of fluid as a result of saltwater loading, and yet none cleared the salt load. It seemed clear from the experiments that the birds can only excrete the full amount of the salt loading by seeking fresh water when they can drink so that fluid is available for further excretion through the salt gland. Birds not exposed to previous saltwater experiments were quite unable to handle salt loads (Riggert unpublished doctoral dissertation, Table 19).

Field observations on Rottnest Island support the evidence that some mountain ducks are not capable of handling the high concentrations of sodium chloride found in the salt lakes. Several mature mountain ducks were incapable of flight through partial paralysis of the wings and legs, and their feet were greatly swollen with fluid under the skin. Autopsies showed those birds to have physiological damage similar to laboratory birds reared on concentrations of sodium chloride exceeding 2.0 percent in their drinking water. The salt glands also had the appearance of being only semifunctional. Since none of the birds was banded, the following interpretation may be made: (1) there are birds reared on freshwater sites where hypertrophy of the salt gland did not occur; (2) following the onset of summer conditions, the birds shifted from the freshwater swamps or migrated to Rottnest Island from the mainland and fed in the salt lakes where a heavy salt load was ingested along with the diet, and (3) the salt loading was such that "salt intoxication" occurred within the 6 days necessary before the salt gland could hypertrophy and commence excreting the salt load.

That interpretation suggests that sudden onset of summer drought following very wet

TABLE 8.—NUMBERS OF MATURE MOUNTAIN DUCKS ON ROTTNEST ISLAND, WESTERN AUSTRALIA, EACH MONTH EACH YEAR, TOGETHER WITH THE ANNUAL MEANS FOR THE ENTIRE STUDY PERIOD, 1965–1974. NUMBERS WERE ESTABLISHED BY DIRECT COUNT

Year	Jan	Feb	Mar	Apr	May	Jun	Jul	Aug	Sep	Oct	Nov	Dec
1965	249	195	158	—	255	131	95	139	88	51	100	150
1966	217	92	101	84	128	37	32	102	75	122	130	136
1967	145	—	82	76	166	138	101	39	98	105	113	130
1968	235	250	150	195	—	185	100	105	99	—	150	330
1969	303	162	135	153	—	95	85	118	91	156	175	142
1970	189	123	—	131	147	101	96	110	64	78	102	194
1971	295	252	117	211	241	152	135	135	85	110	153	230
1972	307	223	112	186	185	221	86	104	74	117	107	250
1973	230	251	205	268	—	—	100	104	85	120	116	310
1974	374	306	205	275	—	182	121	61	71	75	149	363
Mean	254.4	206.0	140.6	175.4	187.0	138.0	99.1	101.7	83.0	103.8	129.5	223.5
SE	21.0	23.1	14.5	23.9	20.9	18.5	5.7	9.7	3.7	10.4	8.2	27.6

winters may lead to mortality among birds reared on freshwater sites but forced onto saline waters by the drought. Conversely, it would appear that those birds reared at sites where brackish water was available would be little inconvenienced by seasonal drought which forced them to saline situations, and under such circumstances would suffer no mortality.

The movements of mountain ducks on Rottnest Island are influenced by the location of fresh water for drinking and bathing. During the summer months, freshwater seepages are the primary source of drinking water, and birds congregate each morning at the seepages on the edges of the salt lakes. The permanent freshwater swamps adjacent to the salt lakes are used primarily for bathing, and movement to those areas occurs daily in the late afternoon or early evening. On numerous occasions, over 70 percent of the island's mountain duck population could be observed simultaneously on the larger freshwater swamp, approximately 0.5 ha in area. Once autumn rains recharge the wetlands on the island, the movement of mountain ducks is not as regimented at specific times or locations.

POPULATION DYNAMICS

Population Counts

The numbers of mountain ducks, excluding ducklings, recorded each month on Rottnest Island during the study period are given in Table 8. The maximum population found was 374 in January 1974 and the minimum was 32 in July 1966. The mean number for all years of the study was 140.6 (SE =14.5).

The peak population on Rottnest Island occurs in December and January when the ducklings reared on the island are able to fly and are counted as part of the mature population. As the summer continues, the population declines slowly until the first rains of March or April break the summer drought. The first rains bring migrant birds to the island, and the peak population for the breeding season is reached by mid-May. From that influx, the island obtains the majority of its breeding pairs.

As the breeding season progresses, the population slowly declines and falls to its minimum in September. It is noteworthy that during the breeding seasons of 1965, 1966, 1967, 1969, 1970, and 1972, the population had a sudden increase, and the majority of the new arrivals were unpaired females that moved about in small distinct groups of up to 14 birds. The numerous bill tags on birds in those groups identified them as subadults or nonbreeders. The groups of nonbreeding females stayed on the island approximately a month.

In October and November, the population slowly increased with a few birds arriving on the island with the addition to the popu-

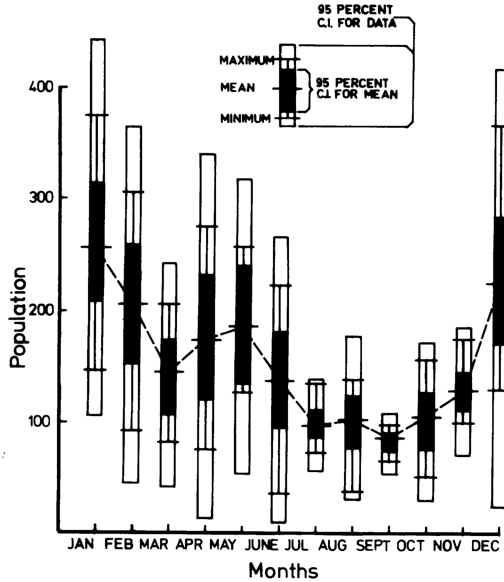


FIG. 22. Numbers of mature mountain ducks counted each month 1965–1974 on Rottnest Island, Western Australia.

lation of early hatched birds able to fly. The great range between maximum and minimum population counts each year, taking into consideration the number of birds produced, reflects the fact that the mountain duck population of Rottnest Island is not an entirely separate community from the population on the mainland. The fluctuation in numbers by month is shown in Fig. 22.

Age Ratio

Records of tag sightings during population counts in November, December, and January throughout the study period show the age ratio of mountain ducks on Rottnest Island as 4 juveniles:1 subadult:2 adults. The proportion of the population tagged ranged from 49 percent in January 1967 to 84 percent in March 1969.

In March or April prior to the breeding season, a rapid increase occurred in the island's population, and by May the age ratio shifted to approximately 3 subadults:7 adults. As the population decreased to the minimum for the year in September, the age ratio was 1 subadult:6 adults.

A computer was used to analyze the data on the ages of 870 new birds and 579 retrapped birds taken during 1965–1969, inclusive, and in November, December, and January of the same year. The age groups were juvenile, subadult, adult, and unaged birds. The numbers in each group and for all groups are given in Tables 9 and 10 and analyzed for each year and for all years combined.

To test the hypothesis that all age groups (sexes combined) of mountain ducks were being taken by the traps each year in similar proportions, a Chi-square analysis was significant ($P<0.001$) on both tables; therefore, age composition varied significantly between years. A possible explanation of the bias shown in the age–year sampling could be the high numbers of juveniles taken in 1966 and 1968 while other age groups remained nearly constant.

A second Chi-square analysis was carried out on the data to test the hypothesis that age ratios of the birds taken by traps in November and December were the same as those observed from tag sightings (4:1:2) during population counts over the same months. For both new and retrapped birds, the ratios for trapped birds differed significantly from the tag sighting ratio of 4:1:2, $\chi^2=33.63$ on 2 df, $P<0.001$, and $\chi^2=23.56$ on 2 df, $P<0.001$, respectively. During the trapping period, many juvenile birds became "trap happy" and were trapped several times, while some adults were observed never to be in the vicinity of the traps; that could explain the differences shown in the ratios.

Sex Ratio

Sex ratios of the mountain duck population on Rottnest Island were determined from field observations and trapping. During regular population counts, sexes of subadult and adult birds were established by plumage characteristics. Juvenile birds could not be sexed by observation with certainty unless they had been tagged. All trapped birds were sexed by cloacal examination.

TABLE 9.—CHI-SQUARE ANALYSIS OF NEW BIRDS AND RETRAPPED BIRDS TAKEN ALL YEAR, 1965–1969, ROTTNEST ISLAND, WESTERN AUSTRALIA

			1965	1966	1967	1968	1969	TOTAL	χ^{2*} (sex)	df
NEW BIRDS	Juvenile	♂	30	50	25	90	8	203	4.56	4
		♀	49	56	43	106	17	271	NS†	
	Subadult	♂	2	61	9	9	10	36	0.97	2
		♀	5	4	6	11	1	27	NS	
	Adult	♂	24	24	17	32	7	104	3.71	3
		♀	20	35	31	46	2	134	NS	
	Unaged	♂	39	1	0	0	0	40		
		♀	53	1	1	0	0	55		
	Total Aged and Unaged	♂	95	81	51	131	25	383	4.37	4
		♀	127	96	81	163	20	487	NS	
RETRAPPED BIRDS	Juvenile	♂	13	45	17	41	6	122	5.69	3
		♀	20	36	8	50	1	115	NS	
	Subadult	♂	3	3	9	1	4	20	8.01	2
		♀	4	3	2	12	1	22	NS	
	Adult	♂	9	33	14	19	7	82	1.96	4
		♀	10	67	30	37	10	154	NS	
	Unaged	♂	12	4	3	0	0	19	0.005	1
		♀	28	13	3	1	0	45	NS	
	Total Aged and Unaged	♂	37	85	43	61	17	243	7.55	4
		♀	62	119	43	100	12	336	NS	

* χ^2 .05(1)=3.84, χ^2 .05(2)=5.99, χ^2 .05(3)=7.81, χ^2 .05(4)=9.49.
† NS, Not significant ($P > 0.05$).

TABLE 10.—CHI-SQUARE ANALYSIS OF NEW BIRDS AND RETRAPPED BIRDS TAKEN DURING NOVEMBER, DECEMBER, AND JANUARY 1965–1969, ROTTNEST ISLAND, WESTERN AUSTRALIA

			1965	1966	1967	1968	1969	TOTAL	χ^{2*} (sex)	df
NEW BIRDS	Juvenile	♂	29	47	22	65	6	169	5.22	4
		♀	39	49	41	70	13	212	NS†	
	Subadult	♂	2	6	8	5	8	29	1.07	2
		♀	2	4	6	4	1	17	NS	
	Adult	♂	18	15	5	16	3	57	6.65	3
		♀	11	23	14	19	2	69	NS	
	Unaged	♂	23	1	0	0	0	24		
		♀	22	1	1	0	0	24		
	Total Aged and Unaged	♂	72	69	35	86	17	279	5.24	4
		♀	74	77	62	93	16	322	NS	
RETRAPPED BIRDS	Juvenile	♂	9	38	7	19	1	74	0.92	3
		♀	9	29	4	12	0	54	NS	
	Subadult	♂	3	1	4	1	0	9		
		♀	0	3	1	3	0	7		
	Adult	♂	8	16	7	1	3	35	4.8	3
		♀	5	37	12	8	2	64	NS	
	Unaged	♂	11	2	1	0	0	14	2.0	1
		♀	11	8	1	0	0	20	NS	
	Total Aged and Unaged	♂	31	57	19	21	4	132	3.05	3
		♀	25	77	18	23	2	145	NS	

* χ^2 .05(1)=3.84, χ^2 .05(2)=5.99, χ^2 .05(3)=7.81, χ^2 .05(4)=9.49.
† NS, Not significant ($P > 0.05$).

Throughout each year and the entire study period, assessment of sex ratios during population counts indicated that females were more abundant than males. The observed sex ratio was 66.7 males to 100 females; however, during the breeding seasons of 1965 and 1966 some assessments rose to a male to female ratio of 25:100. As much as 50 percent of that weighted sex ratio toward females during the breeding season can be attributed to the groups of nonbreeding females.

Sexes of 870 new birds and 579 retrapped birds analyzed are given in Tables 9 and 10. In addition, an analysis was made of sex ratios of birds captured in November, December, and January, 1965–1969. That period of the year is known to have a high proportion of juvenile birds reared on the island.

A Chi-square analysis of the data on sex ratios showed that there were significantly more females than males, $\chi^2=12.43$ on 1 df, $P<0.001$.

To determine if the trapping on Rottnest Island through the years was biased toward one sex or the other, the data tested by Chi-square showed that the sex ratios of birds taken by traps through the years were not significantly different ($P>0.05$). Even though juvenile birds were observed to become trap happy, it could not be shown that retrapped individuals of one sex were taken more frequently than the other. Therefore, the sex ratio of trapped birds was representative of the population, and, on the average, the male:female ratio of mountain ducks on Rottnest Island was 81.8:100.

Band Recoveries

During the study period, 147 bands were recovered from mountain ducks banded on Rottnest Island, 8.69 percent of the 1,690 birds banded. Shooting afforded the largest portion of band returns with 108 birds (73.5% of the bands recovered; 6.39% of of all bands) (Table 11). The remaining 39 bands recovered (26.5% of bands recovered; 2.30% of all bands) were divided into 3 groups: (1) 35 birds found dead, (2) 2 taken for experimental purposes, and (3) 2 accidentally killed during cannon net trapping.

TABLE 11.—NUMBERS AND PERCENTAGES OF BANDS RECOVERED FROM MOUNTAIN DUCKS TAKEN BY HUNTERS, 1965–1974, ROTTNEST ISLAND, WESTERN AUSTRALIA

Year	Number	Percentage of Total Bands Recovered
1965	17	15.74
1966	26	24.07
1967	14	12.96
1968	16	14.81
1969	14	12.96
1970[2]	5	4.63
1971[1]	4	3.71
1972[2]	4	3.71
1973[1]	5	4.63
1974[1]	3	2.78
Total	108	100.00
Mean=10.8±7.33.	SE=5.64.	

[1] Drought conditions reduced duck shooting activities.
[2] Drought conditions precluded duck shooting season.

Bands recovered from the mainland were separated into 2 groups, those taken above latitude 32° and those taken below. Latitude 32° passes through Rottnest Island forming a north–south boundary. That separation shows that bands recovered north and south of Rottnest Island are at a ratio of 1:4, respectively.

The majority of band recoveries (Fig. 23) were from the Mandurah Estuary or associated lakes area. That water mass is the largest on the Swan Coastal Plain (Riggert 1966) and very similar to the salt lake habitat of Rottnest Island. No doubt the protection afforded by the Rottnest Island sanctuary causes many birds to be shot unaware in the Mandurah area.

The farthest recovery from Rottnest Island was 603 km southeast at Lake Gore near Esperance. The farthest north a band has been recovered is at Snag Island salt lakes, a distance of 233 km, and the farthest south was at Lake Muir, a distance of 297 km.

The ages of the 108 birds taken by shooters were: juvenile, 54 (50.00%); subadult, 1 (0.92%); adult, 35 (32.41%); and un-

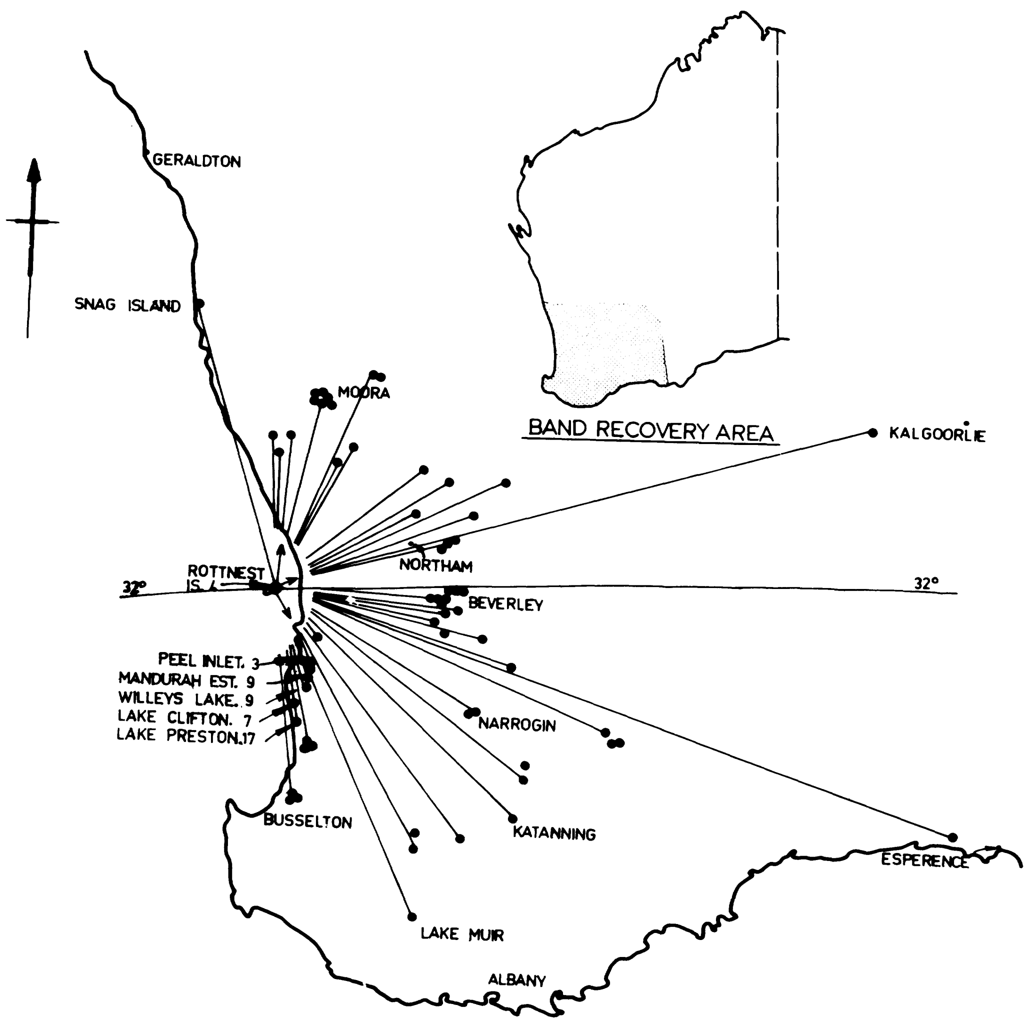


FIG. 23. Locations of band recoveries from mountain ducks banded on Rottnest Island and recovered on the mainland of Western Australia.

aged, 18 (16.67%). To determine whether the ratio of age groups taken by shooters was similar to that on Rottnest Island, viz., 4 juveniles:1 subadult:2 adults, a Chi-square analysis showed that birds were not shot in the same ratios ($\chi^2=12.1$ on 2 df, $P<0.01$). Juvenile birds were taken more frequently than other age groups.

The 108 birds taken by shooters consisted of 58 males (53.7%) and 50 females (46.3%). To test the hypothesis that birds were shot in the same sex ratio as they exist in the population (male:female, 81.8:100), a Chi-square analysis on the adult and juvenile age groups showed no significant difference in the sex ratio between the 2 groups ($\chi^2=3.64$ on 1 df, $P>0.05$) and ($\chi^2=2.0$ on 1 df, $P>0.05$), respectively.

Aerial Surveys

Aerial surveys of mountain duck populations on the mainland were conducted in 1965–1968 during October–December. The area surveyed was the Southwest and Eucla Land Divisions in the lower southwestern corner of Western Australia. The numbers

TABLE 12.—NUMBERS OF LAKES SURVEYED ON THE MAINLAND, WESTERN AUSTRALIA, AND NUMBERS OF MOUNTAIN DUCKS ON THOSE LAKES ESTIMATED BY AERIAL SURVEYS, 1965–1968

	Numbers of Birds on Each Lake										
	<100	<300	<500	<1,000	<1,500	<3,000	<7,000	<10,000	>10,000	Total Birds Observed	Lakes Surveyed[1]
	Numbers of Lakes Surveyed										
1965	41	22	7	5	2	8	8	4	2	131,216	99
1966	47	12	10	6	2	11	9	2	5	166,450	104
1967	43	15	13	6	4	9	14	5	2	185,059	111
1968	47	9	11	6	2	10	11	2	3	133,434	101

[1] Survey included only lakes that contained water. That number varies greatly from year to year.

of mountain ducks seen on each lake surveyed and the total observed each year was given in detail by Riggert (unpublished doctoral dissertation). A summary of the surveys giving the numbers of lakes containing mountain ducks in 9 categories ranging from fewer than 100 to more than 10,000 birds is shown in Table 12. In the 4 years the surveys were conducted, the mean number of mountain ducks observed was 154,039 with a maximum of 185,059 in 1967 and a minimum of 131,216 in 1965. The driest of the 4 years surveyed was 1966, which could account for the large number of mountain ducks seen congregated on the remaining waters.

From the aerial surveys, it is evident that mountain ducks prefer brackish or salt lake habitat during the nonbreeding period similar to that on Rottnest Island. Also, the birds tend to choose those lakes that contain islands or sandbars where they can retreat and rest during the day.

The distribution of the mountain duck in Western Australia is broadly established along the coast from Geraldton to Esperance, and in normal rainfall years may extend 480 km inland; however, even though the birds are capable of moving long distances inland when cyclones pass, they are essentially coastal birds seeking the coastal salt lake waters as their habitat.

DISCUSSION

Population Fluctuations

For nearly 100 years a population of mountain ducks has been known to live on Rottnest Island, Western Australia. The work of Storr (1965) showed that mountain ducks were regular breeders on the island and produced a surplus of young which he suggested migrated to the mainland. The present study found, through banding and tagging birds on the island that not only do they emigrate to the mainland but also return to the island and breed there when they come of age. As the study progressed, it became evident from the predictable increases or decreases in numbers of birds on the island at certain times of the year, that a complex system of population regulation existed between the birds and the island's natural resources.

The annual periods of population increase and decrease are presented in Fig. 24. The basis of the diagram was extracted from Fig. 22 utilizing the mean monthly population counts as an index of population fluctuations throughout the study. Each year on the island, 2 distinct population groups formed; one was the summer aggregation and the other the breeding congregation. Separating the 2 groups are transitional periods in which the birds assemble before and after the breeding season for social reassessment.

The population undergoes 2 major reductions in numbers each year. The first decline occurs in the summer from late December through March and the second in the winter from June through September. In each period, the population has a different status, sex, and age composition. The summer aggregation is gregarious and composed of juveniles, subadults, and adults in a ratio of 4:1:2, respectively, with a male: female ratio of 81.8:100. The winter breed-

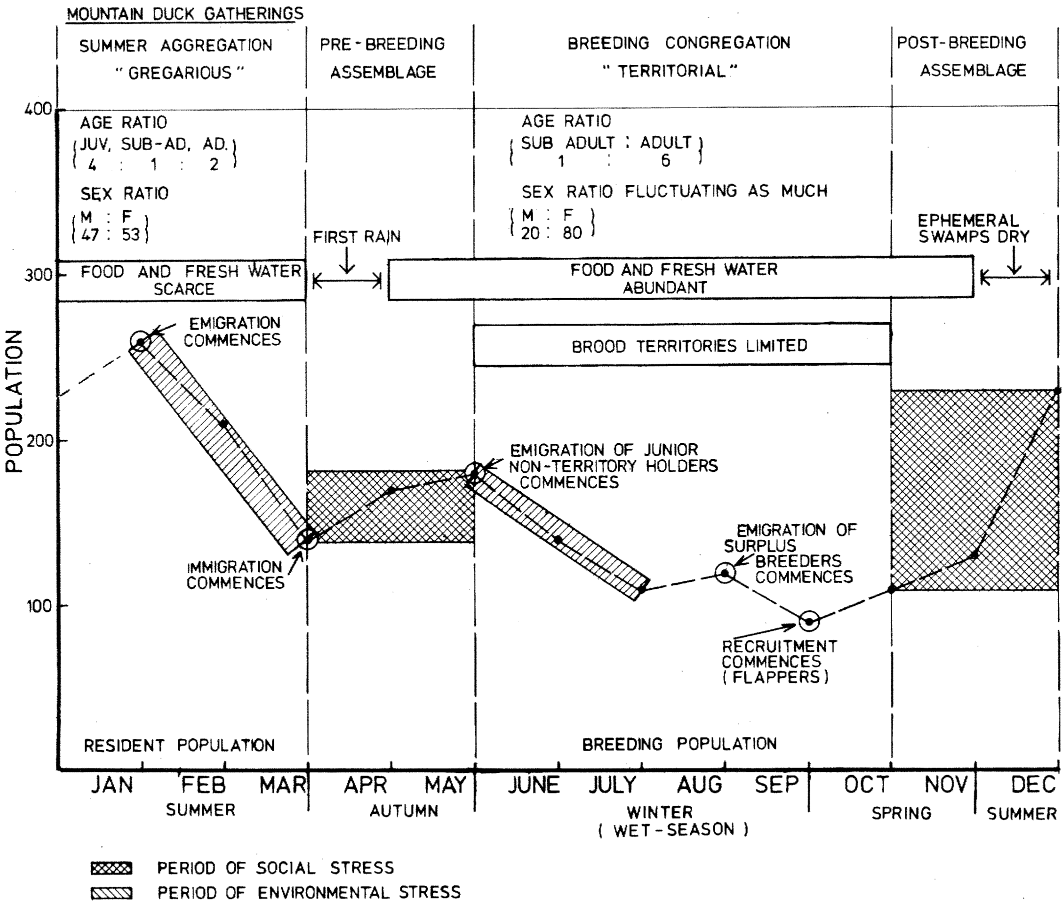


FIG. 24. Annual fluctuation in numbers of mountain ducks on Rottnest Island, Western Australia, showing the periods of social and environmental stress.

ing congregation is territorial and composed of subadults and adults in a ratio of 1:6, respectively, and a sex ratio which favors females, fluctuating as high as 25:100, males:females.

Birds in the summer aggregation commence leaving the island in late December, and the population slowly declines as drought continues to reduce the area of surface water, the number of freshwater seepages, and increase the salinity in the permanent waters. Band recoveries from the mainland support the observation that birds emigrate from the island at that time. Field observations on tagged birds have shown that 81–95 percent of the juveniles has left the island by late March.

Observations on food supplies and fresh water available during the summer months indicate that they are in short supply. That hypothesis was tested statistically and found to be correct in that juvenile and adult birds caught numerous times throughout the summer showed significant loss in weight ($P<0.05$ and $P<0.001$, respectively). The decline in weight, as it does in all birds, argues for food shortage. If fresh water had been responsible, it would be expected that only those birds unable to compete for access to it would have suffered the decline. In addition to the statistical testing, the following observations support the hypothesis that food was in short supply:

(1) No single food item was a principal source of food. Birds utilized different feeding techniques and changed feeding sites regularly indicating that food sources were limited in quantity.

(2) Birds became increasingly aggressive at the remaining freshwater seepages as summer progressed, indicating that fresh water was becoming scarce and the remaining resources had become objects of competition. No age group or individual birds were observed to be able to continually dominate a freshwater source.

(3) Once trapping operations terminated and wheat was no longer used as bait, the number of birds on the island decreased immediately.

The second major decline in population numbers is associated with the limited number of brood territories available to the breeding population in winter. The mean number of territories taken up each year throughout the study period was 25.9±4.0. Population counts during the study in June, July, and August, when brood territories are established, showed that numbers of breeding pairs on the island was 48.3±15 pairs which exceeds the number of brood territories by nearly 50 percent. The following observations support the theory that territories are limited in number and are competed for by breeding pairs:

(1) Removal experiments by cannon netting showed that on 11 occupied territories once the territorial pair was removed, the vacant territory was taken up almost immediately by a new pair.

(2) Twenty-one marked breeding pairs, successful in rearing a brood, retained their territory for 3 breeding seasons or longer.

(3) Field observations showed that both male and female territorial holders were frequently observed defending their territory and would resort to violent physical clashes to maintain their area.

Periods of Social Stress

When the population is increasing in number each spring and autumn by recruitment and immigration, respectively, it undergoes a period of social stress. The first period of such stress is in April and May and known as the prebreeding assemblage. At that time, birds are actively seeking mates and thus a position in the dominance hierarchy. The sex ratio always favors females by approximately 65 percent, and those birds are the initiators of the social stress imposed on the population.

The following observations made on tagged or banded birds supports the hypothesis that social stress does exist:

(1) Observations on tagged adult breeding pairs associated with assemblages showed that they took positions outside the main gathering and maintained a relatively uniform distance from other birds. This indicated that those adult pairs have well-formed pair bonds and are capable of defending themselves and their chosen area against challengers.

(2) Of the known 21 pairs that held territories for 3 years or more, 15 were permanent residents on the island. Observations on those resident birds showed them to be on a high level of the dominance hierarchy and rarely are subjected to competition for their brood territories or nest sites, nor have they been observed taking part in the prebreeding assemblage gatherings.

(3) In the 11 removal experiments, when members of the original territorial pair were released, they won back their territory from the new arrivals without exception.

(4) Tag observations on inexperienced breeders showed them often to be unable to exclude pursuing females, and those females remained with the pair for 3 to 4 months; the consequence was that those groups of 3 or more birds have never been observed with ducklings.

The second period of population increase occurs in November and December and is from recruitment of young now able to fly that have survived the brood period. The postbreeding assemblages gather initially on the ephemeral waters but shift to the salt lakes as the temporary swamps become dry. The first matings of juvenile birds are early in December along with rematings of territory holders that were not successful in rearing a brood the past breeding season. Evidence that social stress occurs at that time has been observed as follows:

(1) The gathering of birds in the postbreeding season assemblage motivates courtship displays and females to incite males. Juvenile birds stimulated by the displaying of mature birds display to each other resulting in 2 juvenile females forming a pair bond. Such a situation suggests that pair bond formation during the assemblage is motivated by displaying of unpaired birds even though most are sexually immature.

(2) Parent birds with well-established pair bonds usually are not seen in the assemblages. Those that have been observed did not take part nor were they challenged by juvenile females seeking a mate.

(3) Field observations on mate selection and pair retention behavior have shown that all age groups do make changes. Juvenile birds made so many changes that records could not be maintained; subadults made 74 changes and adults made 21. That indicated that some males are more sought after than others, and females select for the more desirable males.

(4) Observations of tagged birds in the island have shown that the most subordinate group is the unmated juvenile. Once juveniles are paired, they are elevated in rank, but still subordinate to adult pairs with well-established pair bonds. All age groups, whether single or paired, are subordinate to adult resident pairs that have reared broods successfully.

Population Regulation Mechanisms

The foregoing statement on the forces of social and environmental stress imposed upon the Rottnest Island mountain duck population demonstrates the action and reaction that occurs twice a year that adjusts the numbers of birds on the island to the level of the prevailing requisites, food and fresh water. The availability of food and fresh water in summer is noticeably less than in winter when seasonal rains produce ephemeral waters on the island rich in plant and animal life. As resource levels change, so do the objects of competition; thus, birds competing for food and fresh water in the summer for self-preservation are observed in the winter to compete for brood territories that contain fresh water. Those freshwater sources are critical if the brood is to make use of the food resources of the saltwater lakes without suffering disturbance of electrolyte balance that at best reduces growth rate and at worst results in death of the young. The freshwater source is imperative up to 6 days of age, after which the supraorbital salt gland is functional and the young have greater salt tolerance. Even though the environmental influence of the population changes markedly in the 2 periods, the mechanisms of population regulation, intraspecific competition, do not.

Population densities increase in the spring through recruitment of juveniles that survive the brood period and enter summer aggregation. The consequence of the first period of social stress in late December showed that birds either removed themselves from the postbreeding assemblage or left the island. Those that remained, even though fewer in number and not actively competing for mates, were nevertheless still subjected to continuing social stress imposed by the shortage of food and fresh water by the drought conditions.

In the resident population, direct physical competition for food was rarely seen except at the trap sites where birds congregated to feed on wheat, and again in late summer when supplies of fresh water are limited and the birds were forced together at the remaining freshwater seepages to drink. In those 2 periods characterized by physical competition for food and fresh water, some birds are dominant while others are submissive, the latter giving way to feed or drink in other areas or at other times. That reaction is in effect density dependent and is the proximate stimulus to emigration invoked by the birds themselves as predicted by Wynne-Edwards (1962:480) "those members of the society standing higher in the hierarchy will continue to exert stress on those lower in the scale, until the population is thinned down to a threshold recognized to be conventionally consistent with the remaining food resources." A similar concept was given by Lack (1954:242), and both authors agreed that the individuals evicted were the junior hierarchy or juveniles, respectively, which has proved to be the case in the present study.

As the breeding season approaches and the prebreeding assemblage increases in number of birds immigrating onto the island, the intensity of epideictic displays increases (Wynne-Edwards 1962:16). That behavior was particularly noticeable on days with overcast skies and rain, and no doubt the climatic condition stimulated the excitation and tension among the birds. The social reassessment that takes place during this period is one of status seeking to gain a position in the dominance hierarchy which in turn allows the pair to secure a brood territory. The preassessment by rivals in the assemblage means that once a territory is acquired, rarely has its tenure been lost to another pair.

The primary function of the brood territory is to secure a supply of fresh water for the brood, thus imposing a determinate pattern of dispersion which allows broods to be reared without intraspecific strife that results in social mortalities. The limited number of brood territories on the island imposes a ceiling on the breeding density and is directly related to food supply, as without sources of fresh water the ducklings cannot feed in the salt lakes. This conclusion supports the prediction of Wynne-Edwards (1962:164) that the ceiling imposed on breeding densities is related to "local carrying-capacity (or food-productivity)."

The breeding surplus which varies from 19.5 to 67 percent with a mean of 43.8 percent during June, July, and August, consists of those birds that have been unable to obtain a territory. On 4 occasions (12 June 1967, 9 July 1967, 5 June 1971, and 22 June 1972), tagged pairs whose brood territories were never found, were observed copulating. That could account for dump eggs found in areas that were not nest sites.

Field observations suggest that obtaining a brood territory is a precursor to nest selection, but evidently not to copulation. Also, the meticulous behavior of females when searching for a nest site by entering numerous crevices and burrows before making her selection, and the excitation of the male standing in observation suggest that the behavior has some psychosomatic role in the reproductive cycle.

By late September, the end of the nesting period, the population falls to its lowest numbers of the year. The reasons for the departure of the last surplus breeders at that time could be:

(1) Nearly all brood territories are occupied by family groups and the possibility of obtaining a vacancy is remote.

(2) The time required to rear a brood is at least 3 months; therefore, young hatched in late October would not fly until late December or January. Such late hatching has never been witnessed on the island.

(3) Annual molt migrations to specific lakes on the mainland begin in October.

The rate of recruitment in this population appears to be regulated by restricting the number of females breeding. The maximum number is determined by the 34 territories available. The mean percentage of birds to survive the brood period over the study period was 80.6±5.96, ranging from 72.92 in 1972 to 87.23 in 1966. This infers that on the average 25.8±4.0 pairs were capable of rearing 151.9±30.8 birds annually. Thus, the replacement rate of breeding participants was threefold or 300 percent.

The average annual mortality in broods over the study period was 19.39±5.96 percent, ranging from 12.77 in 1966 to 27.08 in 1970. The annual mortality of flying birds (70 days and older) was 8.69 percent, and, assuming that no loss of bands occurred, shooters were responsible for 6.39 percent of the deaths. The information on mortality suggests that the numbers of birds that died as ducklings or flying birds is not great, and seems unlikely as a mechanism to control the rate of recruitment. However, since emigration does occur, there could be additional mortalities unaccounted for as follows:

(1) Banded birds die on the mainland and are not found.

(2) Banded birds remain on the mainland and are not taken by shooters.

(3) A combination of points (1) and (2).

The remaining 2 ways to control the recruitment rate as suggested by Wynne-Edwards (1962:527) are to restrict the frequency of successive broods and to hold down the number of ova fertilized per female. Neither of those appears applicable to this population since a regular annual breeding season occurs in which the majority of adult pairs that hold a territory produce a brood. The large range in numbers of ducklings that arrive on their brood territories (1–16), and numbers of undeveloped eggs (6) in the 9 clutches observed, suggest that control of recruitment by holding down fertilization of ova seems most unlikely.

The basis of this system of population regulation is one of population balance that culminates in a condition of equilibrium, thus, as Nicholson (1954:50) wrote, "The densities (N) of populations and those (G) of their governing requisites are counterposed, and any change in these quantities (whether produced by the environment or by the action of the population itself) sets up reactions which tend to cause approach to a condition of equilibrium." The forces found to be counterposed were those of social stress governing densities (N) and environmental stress governing the population's requisites (G). Those forces became counterposed twice yearly, once during the summer with the resident population and again during the winter in the breeding population.

To determine if the population had the stability in numbers predicted by Nicholson (1954:50) or Wynne-Edwards (1962:484), the data of the average monthly population counts were tested statistically. The slope of the regression line fitted to the data differed significantly from zero ($t=2.72$, df=8, $P<0.05$), and hence it seems reasonable to assume that the population was increasing by an average of 7 birds per year over the study period. One of the following deductions may present an acceptable conclusion on the stability of numbers in the Rottnest Island mountain duck population:

(1) The slight increase, by an average of 7 birds per year, in the population over the study period seems likely to fall within the limits set by both Nicholson and Wynne-Edwards.

(2) The period of observation on the population may be too short to observe the full cycle of fluctuations in numbers in the island's population.

(3) The resident population has been supplied with an unnatural food resource through using wheat for bait in trapping operations. That could allow more birds to remain on the island or even survive, thus giving a slight increase in the population over the study period.

(4) The system of population balance or stability may not be totally understood until the mortalities that occur on the mainland become known in detail.

Of the 4 deductions, I favor (1), and believe (2) would, in fact, reduce the slight numerical increase in the population over the study period if the period of observation were extended another 10 years.

Success of the Species

The mountain duck is a successful species in Western Australia and maintains a large population. It is able to exploit varied wetland habitats both saline and freshwater, and has readily adapted to utilizing man-made waters, such as stock dams, for rearing young or as a source of fresh water. The birds exhibit facultative feeding habits, grazing, surface dabbling, upending in shallow water, padding and sifting biotic ooze, and combing the shorelines, and are opportunistic feeders. Also, they are able to make use of varied nesting sites from rock crevices to high treeholes.

Its success also derives from its effective pair forming and pair bond maintaining mechanisms, thus resulting in a high reproductive success rate. Other patterns that promote successful reproduction include:

(1) Population aggregation and mixing on breeding grounds after the breeding season which results in rematings of single birds to establish pair bonds well in advance of the next breeding season.

(2) Establishment of a brood territory by the parents which is maintained for the exclusive use of the young.

(3) Large clutch size, and close parental care of the broods, which result in a high rate of survival of young.

(4) The establishment of permanent pair bonds, if the pair is capable of successful reproduction (i. e., nest site selection, egg laying, and producing young).

The unusual environmental conditions within the breeding environment of the mountain duck have selected in favor of prolonged pair bonding. In that way, both parents establish strong 'rights' to the fresh-water seepages essential to successful rearing of the brood. This is characteristic of the primitive anatids.

The mountain duck also has the capacity to remate quickly if the pair is broken, thus assuring the maximum proportion of the adult population the opportunity to contribute to the maintenance of the population. That trait is more typical of the advanced anatids.

SUMMARY AND CONCLUSIONS

This study on the biology of the mountain duck is an attempt to elucidate the reasons for its apparent increase in abundance throughout southern Western Australia.

Life history data from Rottnest Island indicate that sexual maturity is not reached until an age of 22 months, and, while pairing occurs in younger birds, no young are reared and the bonds are not permanent. Furthermore, most pairs, irrespective of age, that failed to breed successfully tended to dissolve pair bonds.

Nest site selection, an important aspect of successful rearing of a brood, is a lengthy process, and selection of favored sites correlates with age. The incubation period varies from 30 to 32 days, and predators such as silver gulls and ravens have been found to prey upon unattended nests. Feral cats prey upon ducklings moving overland from nest sites to brood territories.

The limited number of brood territories imposes a ceiling on the number of pairs breeding during the annual breeding season. Fresh water in the brood territories is essential for ducklings which appear unable to excrete salt the first 6 days of life. Once safely in territories, there is little mortality among ducklings except for inclement weather. Ducklings reach the flying stage at an age of 57–70 days, when family groups break up.

Investigation of the bursa of Fabricius as an age criterion showed the bursa closed by 1 year of age. Study of marked birds showed that there are 2 molts (complete and incomplete), but in only the complete molt are the birds flightless and hence susceptible to predators. Additionally, the study of marked birds showed that the Rottnest Island population is part of the mainland population and there is a migration to and from the island. The analysis of trapping data showed an excess of female birds in the population ($P<0.001$). Bands recovered from the mainland as a result of shooting confirm the widespread movement of birds reared on Rottnest Island.

Studies on the ability of laboratory reared and wild birds to excrete salt loads administered by stomach tube suggested that birds reared on fresh water are at a disadvantage when forced to saline habitats during summer drought. The capture of salt intoxicated birds on Rottnest Island suggests that mortality induced in that way is not uncommon.

The loss of monel metal bands early in the study negated any attempt at census except by direct count of birds on salt lakes and swamps on Rottnest Island. However, those counts showed considerable changes in population size throughout the year and from year to year, and those changes formed a cyclic pattern. The present banding work using titanium bands allows for future censuses of the population by methods other than direct counts.

Assuming no loss of bands, the shooters' returns indicated that 6.39 percent of birds banded on Rottnest Island were shot. Further analysis of hunters' returns showed a significantly higher proportion of juveniles were shot than older birds.

From the foregoing, it is possible to conclude that:

(1) The mountain duck is able to live in highly saline situations provided it has access to fresh water. Fresh water within brood territories appears essential for successful rearing of broods.

(2) Birds reared on fresh water are at a disadvantage compared with those reared on brackish water during severe summer droughts. Indications are that sudden dependence on saline water leads to salt intoxication and death.

(3) Assuming that shooting pressure on Rottnest Island birds reflects the pressure on the total population, it seems clear that mortality induced by shooting is low.

(4) Since the mountain duck is capable of handling saline water (provided it has access to freshwater seepages), it seems likely that the species has been able to maintain its numbers because brackish and saline marshes and lakes have remained little affected by the agricultural development which has drained so many freshwater situations (Riggert 1966). Nevertheless, the saline habitats now persisting probably cannot in themselves sustain a larger breeding population than at present because the number of freshwater seepages which form the nucleus of brood territories is limiting. The creation of sources of fresh water through farmers' building stock dams has meant that birds are substituting them for freshwater seepages, and hence population increases are occurring in areas where birds have been sparse or absent previously. Breeding on ephemeral fresh water in very wet seasons can lead to significant increases in population size. However, since the birds cannot handle salt readily, they are likely to suffer considerable mortality should there be a summer drought which forces the birds onto brackish or saline localities. Under such circumstances, the hunting pressure, high susceptibility of juveniles to hunters, and the mortality induced by salt intoxication, are likely to combine to severely deplete the year class.

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