LOCOMOTION AND OTHER BEHAVIOR OF THE DIPPER

By WILLIAM R. GOODGE

As a part of a study of adaptations for aquatic life in the North American Dipper (*Cinclus mexicanus*), an effort was made to learn more about the locomotor behavior of this species in order to form a basis for interpretation of structural modifications. In this paper the locomotion of the dipper, with particular regard to underwater progression, is described and analyzed by the use of information obtained through field study and by observation and motion picture photography of captive birds in the laboratory. Although a thorough field study of nesting behavior was not a part of this work, some data of this nature obtained during the study of locomotor behavior will be included. The latter material, although fragmentary, supplements previously published information. Until the work of Hann (1950) there had been no intensive study of the nesting habits of this species in spite of the fact that its unusual mode of life for a passerine bird makes it an especially interesting species.

MATERIALS AND METHODS

Dippers were observed in the field at many localities in the state of Washington, but the majority of the observations were made on a pair of birds nesting along the upper Raging River in the western foothills of the Cascade Mountains near North Bend, Washington, at an elevation of about 1000 feet. Other nesting dippers were observed along Icicle River near Leavenworth on the east slope of the Cascades at an elevation of about 2500 feet. Most of the field work was done in 1954 and 1955.

To supplement field studies, seven specimens were captured alive by means of a Japanese "mist" net placed across a stream just above the surface of the water. The dippers were kept in the laboratory in cages for varying periods of time and used in several phases of the work. Soon after their capture, three of the birds were placed in glass-fronted tanks of still water used in the University of Washington College of Fisheries for rearing fish. The tanks, which are 60 inches long, 24 inches wide, and 28 inches high, were covered with netting to prevent escape and were filled one-half full of water. A floating board provided a resting place for the bird. Either the birds were caused to dive by movements of the hand or, in one case, the bird actively pursued small trout placed in the tank. The activities of the dippers were observed and motion pictures were taken. A 16-mm. Cine-Kodak special number 2 motion picture camera was used with Kodak Super-X fine grain reversal film. Two number 2 photoflood lamps provided overhead lighting. Outside light was not excluded, but with the room lights turned off, reflection from the glass was prevented.

In order to study the locomotion of the dipper in moving water one specimen was placed in a flume in the Hydraulics Laboratory. The flume measured ten feet in length, one foot in width, and one and one-half feet in height. The bottom of the flume was covered with small stones and a waterfall was formed at the end of the flume where the water entered. Because the exit pipe was not sufficiently large to carry away the water fast enough to maintain a constant velocity and water level, a series of observations were made by alternately allowing the flume to fill up and empty. When the flume was being filled, the velocity of the water varied from about 0.75 to 1.5 feet per second. A board and several large stones provided resting places for the bird. It was observed and photographed with the same equipment used for the still water tanks. Motion pictures were made at speeds of 32 and 45 frames per second.

The films were projected by use of a Keystone projector with a speed control box capable of slowing the projector to any required speed or of stopping it for the still projection of individual consecutive frames. By means of a mirror placed at an angle of 45 degrees to the light beam the image was projected on paper. By this means enlarged tracings were made for consecutive frames in order to analyze complete locomotor cycles for both limbs.

ACKNOWLEDGMENTS

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FIELD OBSERVATIONS

Although dippers have been studied by many people, field observation of underwater locomotion has its limitations because much of the time the birds feed in turbulent water and because their movements are rapid. Only occasionally does the observer have an opportunity to see them swimming in clear, shallow water.

Grinnell and Storer (1924) state that dippers move by short hops on land, but from my own observations I agree with Hann (1950) that they ordinarily run or walk, but that they may resort to hopping on rough or steep ground.

Dippers often feed along the shore or cling to rocks while wading in the water. Frequently they stand on a submerged rock facing the current and hold the head under water, apparently obtaining food that is carried downstream by the current. On land they may stand on one leg, with the other held close to the body in the manner of wading birds.

Although there is some movement to lower elevations in winter, dippers are nonmigratory. Their flight is limited to going up and down the course of a stream, usually just above the surface of the water. The flight of the dipper is steady with rapid wing beats. The birds readily avoid obstacles along the stream such as overhanging logs or bushes. In one instance, a dipper was seen to pursue and catch flying insects by hovering over the water. On the surface of the water, they may alternately move the hind limbs in a paddling motion, but since the toes are not webbed they cannot move rapidly in this manner. To obtain more speed or to avoid being carried downstream by the current they sometimes flap their wings on the surface of the water. This method of locomotion may also be used just before flight from the surface of the water.

Dippers dive directly into the water from the air or more frequently from the surface of the water. They were never observed to wade above their own depth and they often dived under the surface by using the wings in shallow or slow-moving water. Sometimes they return to the surface after a dive and fly into the air without pausing on the surface. According to some of the sources quoted by Bent (1948) and judging from my own observations, dippers probably do not remain under for more than about ten seconds, although Cordier (1927) wrote that they may remain under for 30 seconds and Muir (1894) implies that a dive may last as long as two or three minutes.

OBSERVATIONS ON CAPTIVE BIRDS

For the most part the dippers were kept in a cage in the laboratory. They soon became adapted to confinement and took food. They were fed meal worms, earthworms, ant eggs, salmon eggs, and pieces of fish, but of these they seemed to prefer meal worms and ant eggs. The meal worms and earthworms were grasped in the bill and beaten on the cage floor before they were swallowed. When sleeping, the dippers either stood on the cage floor or perched on a horizontal rod near the top of the cage. Sometimes the birds stood or perched on one foot. The dipping which is characteristic of the species was not frequently observed in the captive birds.

When a recently captured adult dipper was placed in a tank of still water, it stood on the floating board placed in the tank or swam on the surface of the water. The birds appeared to be quite buoyant. The relative depth of the swimming bird is indicated in figure 1 by the horizontal line which represents the water level. The dipper was caused to dive by movements of the hand from above the tank. In these instances, it did not

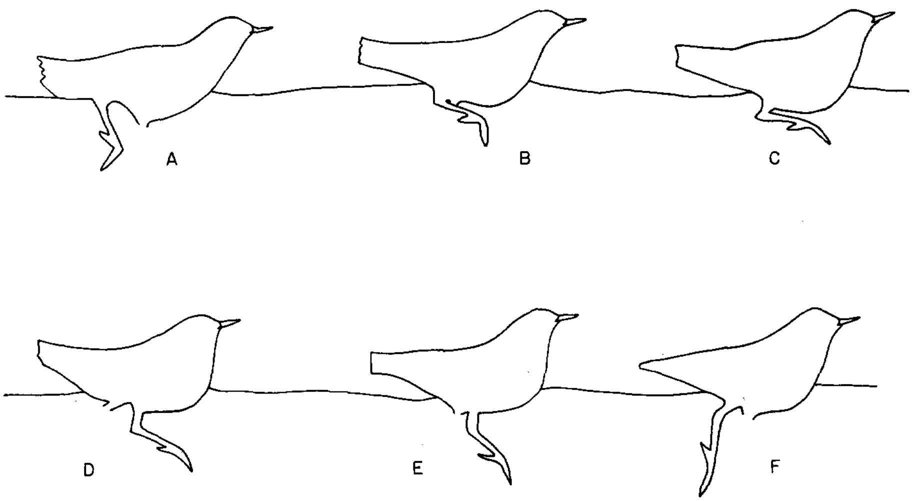

Fig. 1. Tracings from consecutive motion picture frames illustrating the hind limb cycle of *Cinclus* when swimming on the surface of the water.

dive deeply nor stay under the water long. Observations of probably more normal behavior were obtained by placing small trout in the tank. The fish were readily captured by the dipper, which in at least one case sighted the fish from the surface and dived almost vertically downward to capture it.

Vertical and horizontal progression under water was accomplished primarily by use of partly opened wings (fig. 4). The dive from the surface of the water begins with the head held under the water, the legs extended, and the posterior part of the body elevated. The wings are elevated, and one or two strokes of the wings propel the bird under the surface. The actions were somewhat obscured by splashing water, but in most instances at least the hind limbs did not appear to assist the wings. Instead, once the dive began they were flexed close to the body. Subsequent observation of the action of a bird in shallow water showed that in one instance, at least, the legs as well as the wings were employed. At the beginning of the dive, the legs were used in a paddling motion along with the first strokes of the wings and then they were brought to the flexed position and the use of the wings continued. When the dipper reached the bottom, the legs were extended in some instances and were used to assist forward progress. A sequence photographed when the bird was pursuing a fish showed this type of action particularly well. The legs were extended and used alternately in a running motion which helped to propel the bird along the bottom. When it momentarily left the bottom, the legs were either flexed or trailed behind. When it again reached the bottom, the running action was repeated. It was necessary for the bird to make continuous use of its wings in order to remain at the bottom of the tank. The tanks used in this series of observations had smooth surfaces so that there was no opportunity to test the hypothesis that dippers are able to walk along the bottom without the aid of the wings. When the bird returned to the surface, the legs were sometimes employed in a paddling motion much as they are on the surface. A more detailed description of leg and wing action follows.

A captive dipper was placed in a tank of still water about five feet long with a ramp which extended to the bottom of the tank. The ramp and bottom of the tank were covered with sand and small stones. Meal worms were put in the tank. The dipper dived for the meal worms, which were lying both on the bottom among the stones and on the ramp, but it did not walk along the bottom or on the ramp under water.

Examination of a recently captured adult bird after a series of dives in the tank showed that it remained relatively dry. Sometimes the bird shook the excess water from its plumage and vibrated its wings. It did not preen its feathers frequently during the period of observation. A fully fledged juvenal dipper placed in the tank became very wet especially on the ventral surface and it appeared to float lower in the water than an adult. The young bird was induced to dive, but it did not make much progress. Observations in the field indicate that recently fledged young usually feed along shore and do not ordinarily dive under the surface. It is probable that the water-repellent qualities of the plumage are not fully acquired until some time after fledging and possibly not until after the postjuvenal molt. Dippers in captivity apparently soon lose the water-repellent qualities of the plumage. A bird placed in a tank eight days after its capture became very wet. Crandall (1952) reports that a specimen of *Cinclus leuconotus* at the New York Zoological Park became water-soaked unless it entered the water regularly.

Behavior of the dipper in the flume was similar to that in still water. In a strong current, the bird was able to maintain its position by vigorous paddling with its feet, but it did not make any forward progress. Sometimes the wings were used in a flapping motion on the surface of the water. At the base of the waterfall there was an eddy. Frequently the dipper floated on the surface there and was thus able to maintain its position with less effort than in the current. The movements of diving and swimming under water appeared to be identical to those employed in still water. The dipper dived to the bottom to pick up salmon eggs lying among the rocks. It clung for an instant to the rocks, but wing action appeared to be necessary for it to remain on the bottom. In spite of the variation in current velocity and depth of the water, the dipper was never observed to walk along the bottom. Several times the water level was lowered so that the bird could perch on a small stone, and then the water level was gradually raised again. In these instances, the bird maintained its position until the water was about halfway up on the body and then it floated off or flew.

ANALYSIS OF LOCOMOTOR CYCLES

Impressions of locomotor behavior were confirmed by motion pictures. An analysis of the limb action was made by means of tracings of consecutive frames projected on paper. For the hind limb, the position of the skeletal elements could be determined approximately; for the wing, this was not possible since the joints are obscured by the plumage and the shoulder joint is not fixed.

Hind limb.—Figure 1 illustrates the leg action of the dipper swimming on the surface of the water. The legs are employed alternately, but for clarity only one leg is illustrated in the figure. The swimming motion consists primarily of a flexion of the tarsometatarsus during the recovery phase (A-B) and an extension of that element during the propulsive phase (C-F). It may be noted that the leg is not extended far posteriorly at the completion of the propulsive stroke. During the recovery phase, the toes are flexed; during the propulsive phase, they are extended. Examination of the leg action photographed when the bird was facing the camera clearly showed that the toes are abducted during the propulsive phase and adducted during the recovery phase. The hallux is always extended when the bird is swimming with the feet.

The relative positions of the skeletal elements during a swimming movement of the leg are shown in figure 2; A-C represent the recovery phase and D-F the propulsive phase. The position of the acetabulum was determined by measuring its distance from the tip of the tail on a fresh specimen and reducing this distance to the scale of the tracing. The lengths of the femur and tibiotarsus were also reduced to scale relative to the

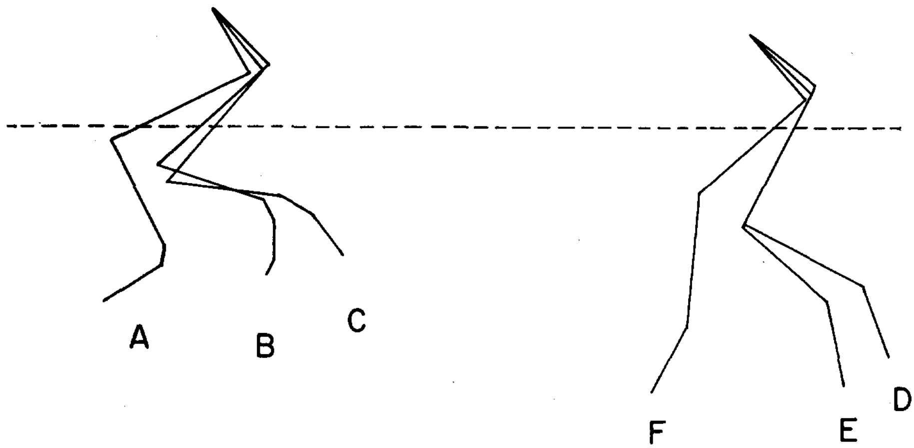

Fig. 2. Position of the hind limb elements of *Cinclus* when swimming on the surface of the water during the recovery phase (A-C) and the propulsive phase (D-F).

length of the fully exposed tarsometatarsus, and the intersection of arcs with radii of these lengths and with centers at the acetabulum and the tarsometatarsal-phalangeal joints respectively determined the position of the knee joint.

At the beginning of the recovery phase, the toes are flexed. There is also a flexion of the tarsometatarsus and tibiotarsus, which brings the foot closer to the body. Continued flexion of the tarsometatarsus and flexion of the femur follow, elevating the foot and moving it forward. Finally, some extension of the tibiotarsus and an extension of the toes occur, completing the recovery phase. During the first part of the propulsive phase, the limb is moved ventrally by an extension of the tibiotarsus and tarsometatarsus. This is followed by extension of the femur and flexion of the tibiotarsus accompanied by further extension of the tarsometatarsus carrying the limb posteriorly. During the propulsive phase, there is some flexion at the tarsometatarsal-phalangeal joint, but the toes are extended. When the bird is swimming in a straight line, the movements are anterior-posterior ones in a single plane with no apparent lateralward movement or rotation in any part of the cycle.

During the cycle, the position of the femur is changed the least. From maximum extension to maximum flexion, it moves through an arc of approximately 23 degrees about the acetabulum. At maximum flexion, the tibiotarsus forms an angle of 87 degrees with respect to the femur and at maximum extension, 108 degrees. Thus there is a change of 21 degrees with respect to the femur. The greater length of the tibiotarsus produces a greater change in the position of its distal end than that of the femur even though the degree of movement at the joint is about the same. At maximum flexion, the tarsometatarsus forms an angle of 56 degrees with respect to the tibiotarsus and at maximum extension, 137 degrees. Thus there is a change of 79 degrees with respect to the tibiotarsus, about four times as much change as for the femur or tibiotarsus. During the recovery phase, there is some flexion of the anterior toes, and the proximal phalanges form an angle of about 90 degrees with respect to the tarsometatarsus. During the propulsive phase, the phalanges are fully extended, but the toes form an angle of 160 degrees with respect to the tarsometatarsus.

For comparison, figure 3 illustrates the movements of the hind limb elements when the dipper is walking on land. Dippers sometimes move rapidly on land apparently

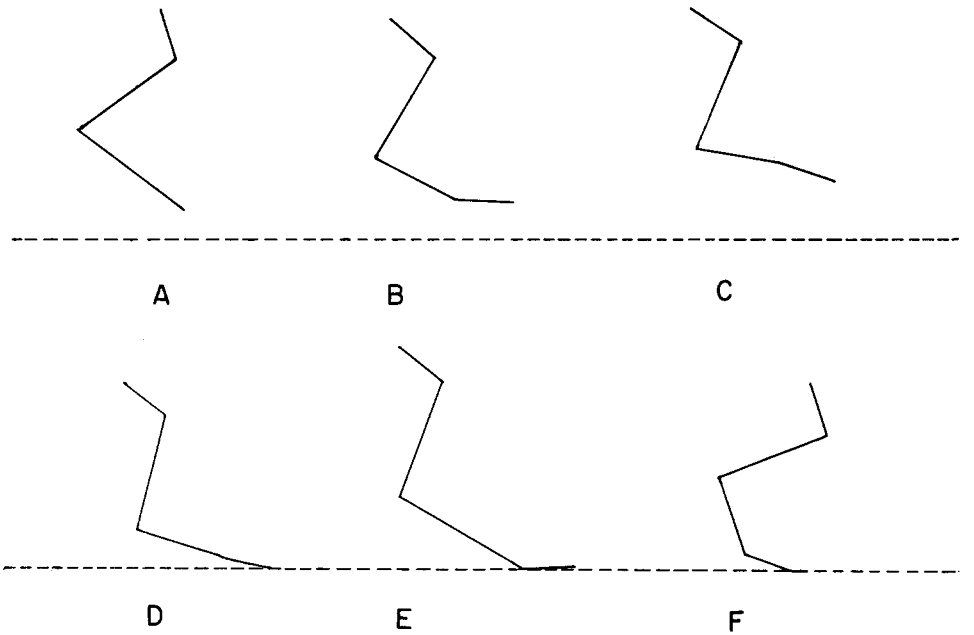

Fig. 3. Position of the hind limb elements of *Cinclus* when walking on land during the recovery phase (A-C) and the propulsive phase (D-F).

running, but actual running, that is with both feet off the ground during a portion of the locomotor cycle, was not observed in any of the motion picture sequences. Although some variation was noted, typically the body remained horizontal and close to the ground because of the shortness of the limbs as well as their position. In the recovery phase of the cycle, the foot is first raised above the substrate by a flexion of the tarsometatarsus. The toes are extended. During this part of the cycle, the body is elevated by the extension of the opposite tibiotarsus and tarsometatarsus permitting some extention of the tibiotarsus. Thus, the limb begins its forward movement. Flexion of the femur follows. Finally, there is an extension of the femur, tibiotarsus, and tarsometatarsus as the limb completes its forward movement and the foot makes contact with the substrate. The toes are slightly flexed before they strike the ground. At the beginning of the propulsive phase, there is a flexion of the tibiotarsus and tarsometatarsus. The toes become hyperextended. Next, an extension of the femur, tibiotarsus, and tarsometatarsus elevates the body. Finally, there is additional extension of the femur and a flexion of the tibiotarsus as the limb completes its posteriorward swing.

The movements of the hind limb elements during walking may be compared to those during swimming. Although in both cases the relative positions are indicated by angles of an exact number of degrees for comparison, it is recognized that the movements are not likely to be exactly the same in all instances because of differences in velocity, terrain, and other factors, and because the accuracy of the diagrams is somewhat limited

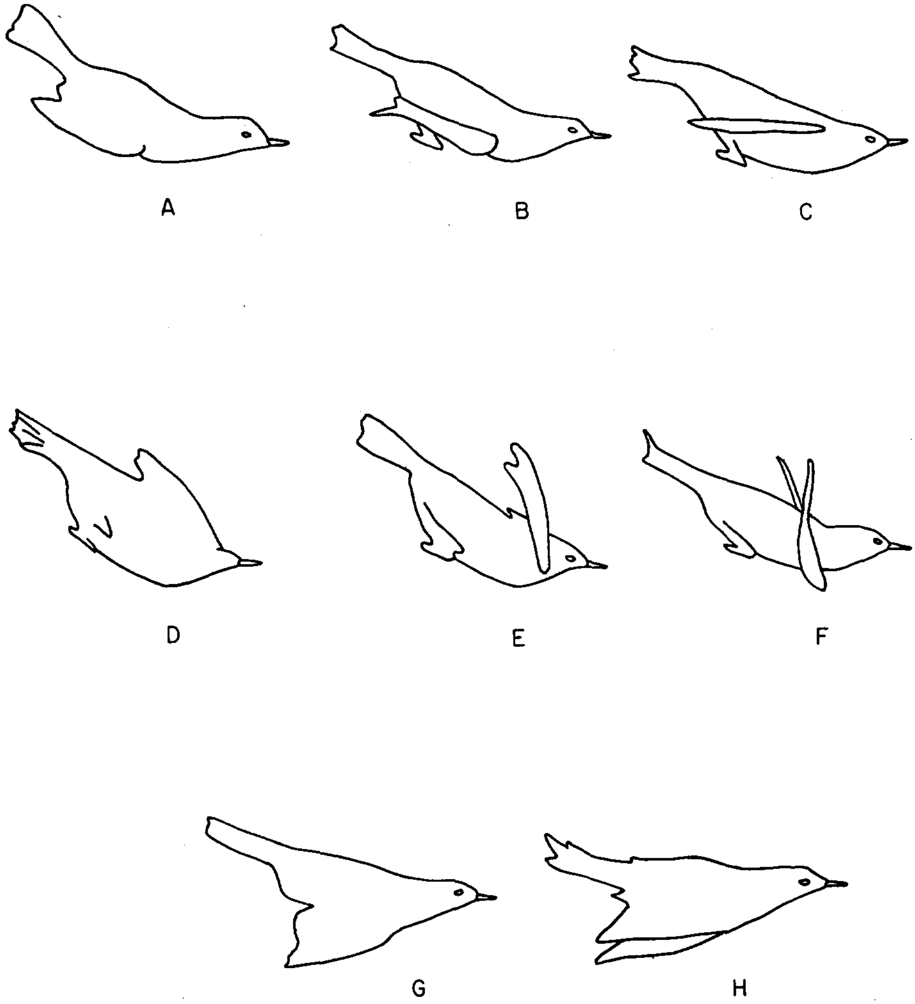

Fig. 4. Tracings from consecutive motion picture frames illustrating the wing cycle of *Cinclus* when swimming under water during the recovery phase (A-D) and the propulsive phase (E-H).

by the fact that the positions of the acetabulum and knee joint were determined indirectly. However, there are consistant differences for swimming and walking, and with due caution the limb action of the dipper could be profitably compared with that of other species. There is considerably more femoral movement in walking than in swimming. From maximum extension to maximum flexion, the femur moves through an arc of 40 to 46 degrees about the acetabulum (23 degrees during swimming). At maximum flexion, the tibiotarsus forms an angle of 76 degrees with respect to the femur and at maximum extension, 116 degrees. Thus there is a change of 40 degrees (21 degrees during swimming). At maximum flexion, the tarsometatarsus forms an angle of 75 degrees with respect to the tibiotarsus and at maximum extension, 130 degrees. Thus there is a change of only 55 degrees (79 degrees during swimming).

Wing.—The wing action of a dipper swimming under water is illustrated in figure 4. It may be noted that the wings are never fully extended throughout the cycle. The recovery phase (A-D) consists mainly of an elevation and drawing the wings anteriorly, apparently by elevation and extension of the humerus. The extreme forward position of the wings is noteworthy. During the first part of the propulsive phase (E-F), there

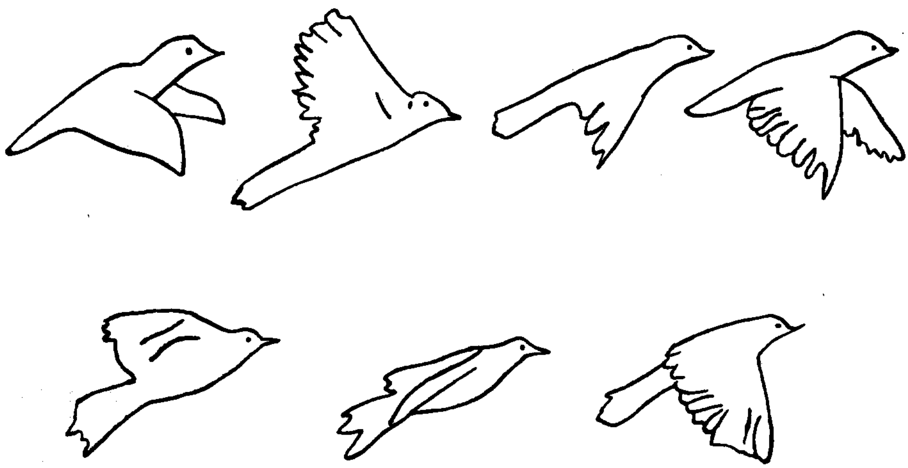

Fig. 5. Tracings from motion pictures of the wing action of the canary (from Demoll, 1930).

is a greater depression of the leading edge as the whole wing is depressed and moved posteriorly. By this means, the angle of inclination is increased. At the end of the propulsive phase (G-H), the wing is returned to a horizontal position with respect to the long axis of the body. It is by means of this tilting of the wing as it is depressed and moved posteriorly that forward motion of the bird is produced. Except when the bird is near the surface or on the bottom, the tarsometatarsus and toes are held in a flexed position close to the body.

Because the action was obscured by splashing, it was difficult to determine the exact nature of the movements of the wings used to aid the bird when swimming on the surface. It could be seen, however, that the wings are fully extended and they appear to be employed in an up and down movement.

For comparison, figure 5 shows the wing movements of the canary in air taken from a paper by Demoll (1930). Although a complete analysis of the flight of the dipper was not made because of the limitations in camera speed, it appears to be similar to that of the canary. The wings are fully extended at the end of both the recovery and propulsive phases. At maximum elevation, the wings are not drawn far anteriorly, as they are under water. In the propulsive phase, the wings are moved anteriorly, not posteriorly, as the wing is depressed. There is little noticeable tilting of the wing.

In the take-off from the ground, the dipper assumes a low crouching position as the wings are raised. Both feet are used simultaneously to assist in the take-off. In the take-off from the surface of the water, two or three wing beats directed downward and forward strike the water. Before the anterior parts of the bird leave the water, a kick, with both feet employed simultaneously, assists the take-off.

Discussion.—Much has been written about both the American and European species of dipper, but there has been no general agreement as to the exact method of underwater locomotion. Especially controversial is the claim by many authors that dippers are able to walk along the bottom under water without the aid of their wings. There are many references to their walking under water, but it is difficult to evaluate many of these accounts because much of the information is probably not based upon personal observations of the author.

It is certain that at least some of the time dippers use their wings when progressing under water, although Michael (1938) doubted that this was so. Crisp (1865), who wrote on the anatomy and habits of *Cinclus cinclus,* believed that the wings were ordinarily employed under water. He quoted Montagu, who described the under water movement as "by short jerks from the shoulder joint not with the extended wings as in other diving birds." He also quoted Macgillivray, who also thought that dippers use their wings under water, but believed that they swim with their wings extended, as in air, concluding that considerable force was necessary to keep the bird on the bottom.

Cordier (1927), writing about *Cinclus mexicanus,* reported seeing a dipper wade along the bottom of a pool, but Grinnell and Storer (1924) concluded that "the dipper dives directly into the stream, usually against the current, and then seemingly walks along the bottom, the wings assisting." This is the view accepted by Hann (1950) and others. Ingram, Salmon, and Tucker (1938) reported watching *Cinclus cinclus* "walk up the center of a rapid mountain stream without the use of its wings." They also state that breeding birds went into a pool near the nest many times and were seen to "walk on the bottom in clear water." One of the authors also observed the use of the wings under water. Dewar (1938) agreed that they do walk along the bottom and suggested a mechanism for this. He stated that the bird always faces the current with the body at an angle sufficient to use the force of the current to hold it under water and pointed out that if they are able to remain under in slight currents or in still water, the birds must have a high specific gravity. Ingram (1938) attacked Dewar's proposal, correctly pointing out (1) that there is no evidence that dippers do have a high specific gravity and (2) that in order to accept Dewar's ideas it must be assumed that the bird is in continuous motion and keeps its head down in still water. He also suggested (3) that the reason the birds swim against the current is to avoid disarray of the plumage.

Holmes (1939) observed *Cinclus cinclus* feeding in an artificial pond with no perceptible current. He saw it wade into the water to its depth, float on the surface, and dive under for never more than five seconds. The bird was not seen to walk along the bottom. Brownlow (1949), on the basis of his own observations, concluded that on the bottom the dipper uses its wings only when it cannot get a good foothold if it loses its grip, and to search for food if the bottom is unsuitable for footholds. Jones and King (1952) observed and photographed *Cinclus cinclus* swimming under water in a glass-fronted salmon tank. An up and down movement of the wings was observed and the bird was not seen to walk along the bottom.

From the evidence at hand, it may be concluded that the role of the hind limbs is secondary to that of the wings under water. As mentioned previously, the legs are sometimes used to propel the bird along the bottom, but the wings must also be used for the dipper to remain under the surface. The legs may also be employed alternately in a paddling motion on the return to the surface. The lack of webbed feet limits the effectiveness of the hind limb in water, but the resistance offered by the toes is sufficient for the dipper to swim in still water or at least maintain its position in a current. To say that it is less well adapted for this environment, however, is not correct since the presence of webbed feet would decrease its ability to cling to the rocky substrate. Unlike more highly specialized aquatic birds, the hind limb of the dipper is not carried far posteriorly at the completion of the propulsive stroke. In the former types, the distal end of the limb, which is the most effective part, exerts a thrust almost directly behind the body and not below it as in the dipper.

The locomotion of the dipper on land is not suggestive of a type well adapted for speed. The sequences that were illustrated showed that the limb swings forward close to the substrate during the recovery phase, and during the propulsive phase there is only a partial extension of the limb and consequent elevation of the body. Another sequence, photographed in the field, showed a somewhat greater extension of the limb and a more elevated body. In forms more highly adapted for speed on land, there is generally a much greater extension of the limb segments which elevates the body more and permits a longer stride. However, locomotion on land among other passerines is highly variable and the exact movements have not been thoroughly analyzed. For this reason, it is difficult to say to what degree the type of terrestrial locomotion of the dipper is to be correlated with its adaptations for aquatic activity. Whether or not dippers are able to remain under water by clinging to the bottom alone, it is apparent from observations of motion pictures that the toes (including the hallux) are used to grip the substrate when the bird is wading in still water or in a current. It is to be expected, therefore, that the dipper would have a foot adapted for clinging even though this species is more terrestrial than arboreal.

Although aerial flight of the dipper was not thoroughly analyzed, it is evident that *Cinclus* used its wings under water in a manner very different from that in air. In air, the wings provide the lift necessary to sustain flight as well as to give the bird forward motion. Under water, the problem is not one of overcoming gravity, but rather to prevent the bird, which is less dense than the water, from returning to the surface. In addition, the water offers a greater resistance to the wing during the recovery phase than does the air. In air, the downward and forward movement of the wings sustains flight and moves the bird forward, although the exact nature of the propelling forces is not completely known. Under water, the downward inclination of the anterior edge of the wings during the propulsive phase tends to move the dipper toward bottom and the posteriorward movement of the wings propels it. In the dipper, the flight feathers are not sufficiently rigid to form an effective surface of resistance under water when the wing is fully extended. In a partly extended wing, the greater part of its surface is supported by bone or the more rigid parts of the outer primaries. In addition not as great a force is necessary as for the fully extended wing since the work arm of the lever is shortened. The bending of the distal ends of the primaries is shown in figure 4F.

Several groups of birds including alcids, some ducks, diving petrels, and penguins use their wings under water, but the movements have been analyzed only for the King Penguin (*Aptenodytes patagonica*) by Neu (1931). The penguin wing is, of course, highly modified for underwater swimming. The loss of flight feathers, the flattened bones, and the rigidity of all but the shoulder joint indicate a much more efficient swimming organ than the wing of the dipper, but in spite of the structural differences, a comparison of the locomotor cycles of the two forms indicates a similarity between the two. The penguin wing cycle is shown in figure 6A; figure 6B is a similar representation of the wing movements of the dipper. Neu described the movement of the penguin wing as follows: "The up and down movement is combined with a depression of the forward edge of the wing during the downstroke—thus driving the water back with the concave surface of the wing." The entire wing forms a nearly rigid surface and is not flexed in the penguin as it is in *Cinclus*. With sufficient muscular strength to move it, the rigid distal end of the wing can produce a more rapid propulsion of the penguin body than does the wing of the dipper which must of necessity act upon water nearer to the body axis. In the recovery phase, the wings are elevated more in *Cinclus* than in the penguin. In the latter, they are raised little above the body axis. In the penguin, there is a greater anterior-posterior movement than in *Cinclus*.

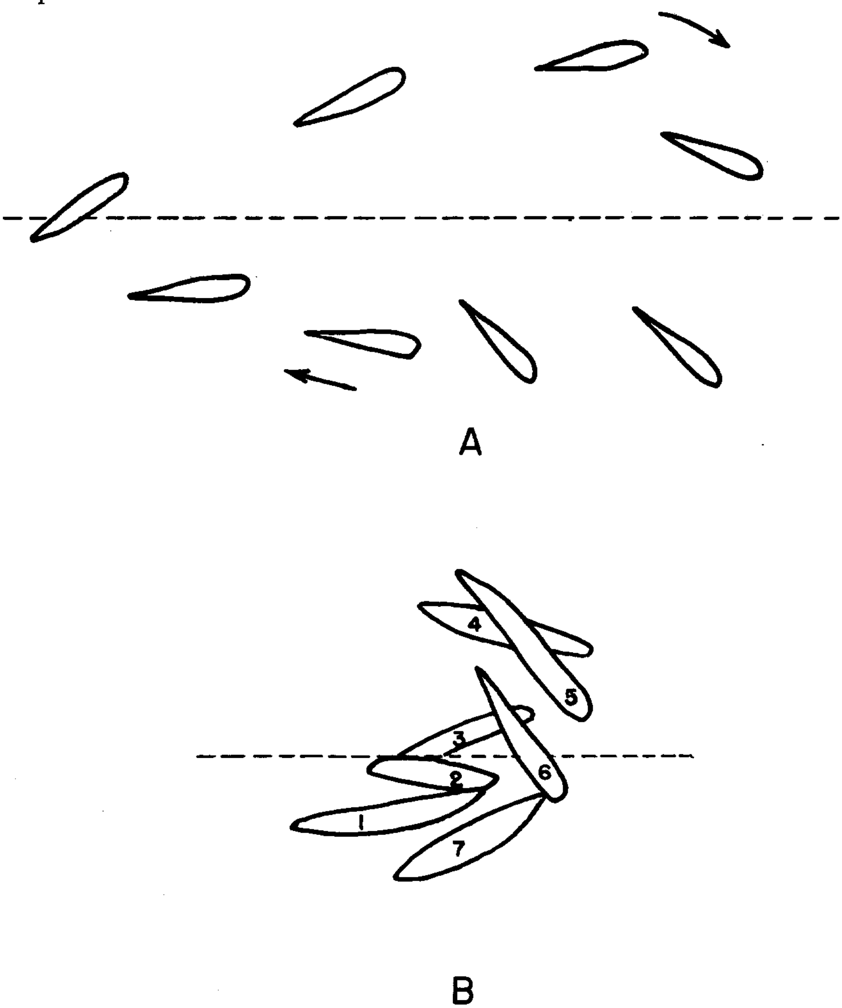

Fig. 6. Lateral view of the wing action of the King Penguin (*Aptenodytes patagonica*), from Neu, 1931, illustrated diagrammatically, (A), and of *Cinclus* (B).

It may be concluded that although *Cinclus* employs both wings and hind limbs during underwater locomotion, the most effective organs of propulsion are the wings. Although they are used in a different manner in water than in air, the wings have lost little if any of their efficiency as organs of flight. The legs are used to assist the bird's progress on the bottom as well as for swimming on the surface, but I can present no evidence that *Cinclus* is able to walk under water without the aid of its wings. It is of course difficult to deny the observations of others, but it may be suggested that with the rapid movements of the only partly extended wings and the difficulty of making observations of underwater activity in the field, previous observers have incorrectly concluded that the birds seen by them did not open their wings under water. Only motion picture photographs of *Cinclus* walking along the bottom without the use of its wings would conclusively demonstrate this ability.

OBSERVATIONS OF NESTING HABITS AND OTHER BEHAVIOR

Blinking of the white eyelid.—From observation of captive birds, it may be stated conclusively that it is the movements of the white-feathered lids (mainly the upper) which produce the white flash seen in the field. Although the birds blink at irregular intervals, in one instance in which the rate was timed it occurred at a rate of 40 blinks per minute and in another case, 50 per minute. The blinking was sometimes unilateral and sometimes bilateral. Frequent blinking of the eyelids is unusual among other passerine birds. Instead it is the nictitans that is regularly drawn across the surface of the cornea.

When the region of the lids of a captive dipper was touched, a movement of the nictitans was observed. It was seen to move only about one-half of the distance across the eye, moving in a posterior-ventral direction from the anterior-dorsal corner. It could not be determined, however, whether or not the nictitans is ordinarily moved at the same time as the lids are closed.

Courtship.—At the Raging River nest site, the birds were first observed on March 25, 1956. The nest was found on April 8, but its construction was not witnessed. One instance of courtship feeding was observed that day. One bird had what appeared to be an aquatic insect larva in its bill. The other of the pair fluttered its wings and gaped. The latter then pecked at the food several times, finally took the object, and swallowed it. Both birds dipped frequently during this activity. The male dipper sang on a rock about 100 yards from the nest on April 15. No other courtship behavior was observed throughout the nesting period.

Nesting.—Two of the nests found were built on rock ledges along a swiftly moving stream above deep water. One nest was resting on a girder of a large highway bridge, and another was built on a beam of a wooden flume. Only the last named nest was wet by spray. Examination of this nest after the young had left revealed that it was lined with ponderosa pine needles.

As might be expected, nesting begins much earlier at the lower elevations (where the present observations were made) than at the sites studied by Hann (1950) at elevations of 9000 to 10,000 feet. The most extensive observations were made of the pair nesting along the upper Raging River (elevation about 1000 feet). The female was not incubating on April 8, 1956, but had begun by April 15. The young hatched between April 26 and 28 so that if the incubation period is considered to be 16 days (Hann, 1950), incubation would have begun between April 10 and 12. The young left between May 21 and 25 or by calculation, using 24 to 25 days for the period the young remain in the nest unless disturbed, between May 21 and 23. Five other records of nests with young at Tumwater Canyon (elevation about 1700 feet) and Icicle River (elevation about 2500 feet) both near Leavenworth, Washington, indicate that the beginning of incubation was between April 5 and May 10. These birds would have left the nest by the third week in June at the latest. By contrast, the dippers studied by Hann in Colorado began incubating June 2 to 21 (all except one from June 2 to 8) and the young did not leave the nest until July 12 to August 1.

The question of second nesting is discussed by Hann. Although the early nesting of dippers at lower elevations would favor the raising of a second brood, no valid records are available. Observations were made at various times throughout the summer in the areas where dippers had nested, but no adults were observed at the nest sites during July and August at the three localities mentioned above. It is possible, but not likely, that the adults move to higher elevations to nest a second time.

Incubation was carried out by only one of the pair (presumably the female) during the periods of observation. In three instances in which times were recorded, attentive periods at the nest lasted 32, 33, and 34 minutes and periods away from the nest, 7, 8, and 10 minutes. These attentive periods are in contrast to those of one hour and twenty minutes recorded by Hann, who attributed the long periods at the nest to the fact that the female does not have to search far for food. No doubt the availability of food varies locally and there also may be other individual variation not dependent upon this factor. Observations on the feeding and brooding of the young do not vary significantly from those recorded previously. Both parents feed the young. In the instances in which times were recorded, feeding occurred every one to seven minutes (usually every two minutes) two or three days before the young left the nest at the Raging River site. Six days later, the young were observed out of the nest being fed by the parents. In one instance, a young bird was fed a small fish.

Hann reported the removal of nest-lining material by the parent birds soon after the young leave the nest, and this explains why some abandoned nests are found without lining material. The same behavior was observed in one instance during the present study.

Three juveniles were observed feeding along the Raging River on June 9, June 24, and July 7, but no adults were seen during that period. The young dippers fed mainly along the shore or waded in the water. Occasionally they swam on the surface of the water when carried away by the current. Only once, on July 7, did a young bird under observation dive under the surface. A small fish was caught.

Anting.—The behavior known as "anting" has been recorded for the European Dipper (*Cinclus cinclus*) by Creutz (1952). I observed in one instance during the present study behavior that may be described as "anting." The dipper was seen to rub the primaries with an object, possibly an aquatic insect larva (unfortunately the distance was too great for positive identification or to describe the procedure in detail). Apparently the object was finally swallowed. Other instances of "anting" should be looked for in dippers.

SUMMARY

The terrestrial, aerial, and aquatic locomotion of the North American Dipper (*Cinclus mexicanus*) is described and analyzed by the use of information obtained through field study and by observation and motion pictures of captive birds.

On the surface of the water *Cinclus* swims with its feet in a paddling motion. To obtain more speed or to maintain its position in a current the wings are sometimes used on the surface. Dippers may dive under the water from the air or more frequently, from the surface. Sometimes they return to the surface after a dive and fly into the air without pausing on the surface.

Captive dippers were observed and motion pictures were taken of the birds in tanks of still water. The birds were caused to dive by movements of the hand or they pursued small fish placed in the tank. Vertical and horizontal progression under water is accomplished primarily by the use of partly opened wings. When the birds reached the bottom the legs were sometimes extended and used to assist forward progress, but it was necessary for the birds to use their wings at all times to remain under the water.

A dipper was placed in a flume in order to study the actions of the bird in a current.

The behavior in the flume was similar to that in still water. Although the water level and current velocity varied, the dipper did not walk along the bottom under water.

From tracings of consecutive motion picture frames, analyses of the locomotor cycles of the hind limbs and wings were made. The actions of the legs when *Cinclus* is swimming on the surface and walking on land are compared. Similar comparisons are made between the action of the wings in air and under water and the differences are discussed.

No evidence is presented that *Cinclus* is able to walk along the bottom under water without the aid of the wings.

Additional notes on other behavior and nesting habits of dippers are included. Approximate nesting dates for birds breeding at low elevations in the state of Washington are given. There is no evidence for more than one nesting per season.

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