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Diving Birds of North America: 3 Comparative Egocentric and Locomotory Behaviors

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3. Comparative Egocentric and Locomotory Behaviors

As used here, "egocentric behavior" means those categories of individual survival and maintenance behaviors that are exclusive of such social interactions as aggressive, sexual, and parental behaviors, which will be considered in detail in the individual species accounts and also will be separately summarized in chapter 5. A discussion of the ecological aspects of foraging behavior will also be deferred until chapter 4, though behavioral aspects of underwater locomotion and prey catching will be considered here.

Comfort and Maintenance Behaviors

Self-directed maintenance behaviors relate to basic individual survival needs such as thermal regulation, drinking, food ingestion, and waste elimination. Other more periodic and generally leisurely types of egocentric behavior concern apparent comfort and body care, such as preening, oiling, bathing, sunbathing, stretching, shaking, and the like. These behaviors are fundamental to all birds and do not tend to differ greatly among rather distantly related groups, at least beyond the constraints set by anatomy and proportions.

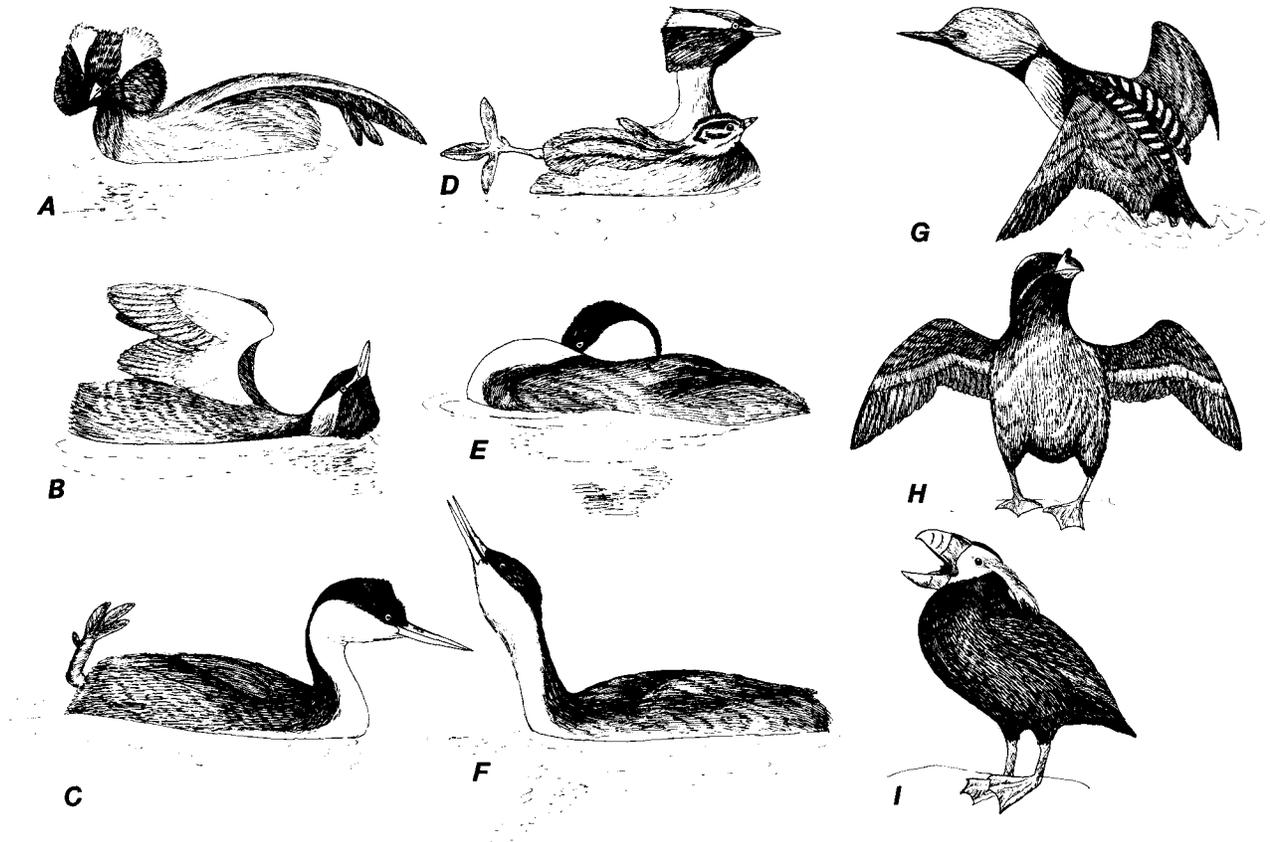
The loons, auks, and grebes all spend considerable time preening and oiling their plumage. In all these groups the birds usually perform these behaviors while on the water, frequently rolling over on their sides to varying degrees while preening their breast and underpart feathers. Loons may remain in this partially inverted position for several minutes, waving the upper foot slowly in the air (Olson and Marshall 1952). Grebes sometimes also slowly wave one foot in the air well above the water surface while maintaining a normal swimming position (fig. 10C); the purpose of such behavior is uncertain but may relate to drying or warming. McIntyre (1975) described a probably comparable "foot wagging" in common loons, during which the

foot is extended and shaken and then placed under a wing. This behavior sometimes occurs when the bird is maintaining its position with the aid of only one foot. Preening in grebes often also occurs in a social situation during display, during which a ritualized version of preening, called "habit preening," often occurs. Similarly, preening of another individual, or "allopreening," is an extremely important social and sexual activity in various auks, especially the murre and the razorbill.

Stretching behavior in these birds takes two common forms. One is the wing and leg stretch, during which one wing and the corresponding leg are stretched laterally and posteriorly to the maximum degree (fig. 10A,D). The other common type of stretching motion is a simultaneous stretching of both wings above the back, while the neck is stretched forward to varying degrees (fig. 10B). Probably all three groups perform these behaviors in much the same manner, usually while on the water, though close comparisons remain to be made.

Wing flapping is similarly performed in much the same manner among all three groups. Among loons it is usually performed while the bird is swimming on the surface (fig. 10G), with the body often only partially raised from the water and the primaries sometimes striking the water at the bottom of the downstroke. A similar but much more erect wing flapping occurs during threat display in loons, providing an example of a ritualized form of behavior that coexists with its non-display precursor. Wing flapping in grebes also usually occurs on water, but among auks it can often be observed among birds resting on land or perched on rocky sites (fig. 10H). Wing flapping has not been obviously ritualized into a display function in either grebes or auks.

General rotary shaking movements, involving only the head and neck (fig. 10F) or at other times the entire body, are frequent in all species and perhaps serve to



10. Some general behavioral traits of loons, grebes, and auks: A, wing and leg stretching, horned grebe; B, wing and neck stretching, horned grebe; C, foot shaking, western grebe; D, wing and leg stretching, horned grebe chick; E, resting in "pork

pie" posture, western grebe; F, drinking, western grebe; G, wing flapping, arctic loon; H, wing flapping, rhinoceros auklet; I, yawning, tufted puffin. After various sources.

free the bird of loose feathers or possibly foreign materials attached to the feathers. The same also applies to various head shaking or bill flicking movements that occur in diverse forms.

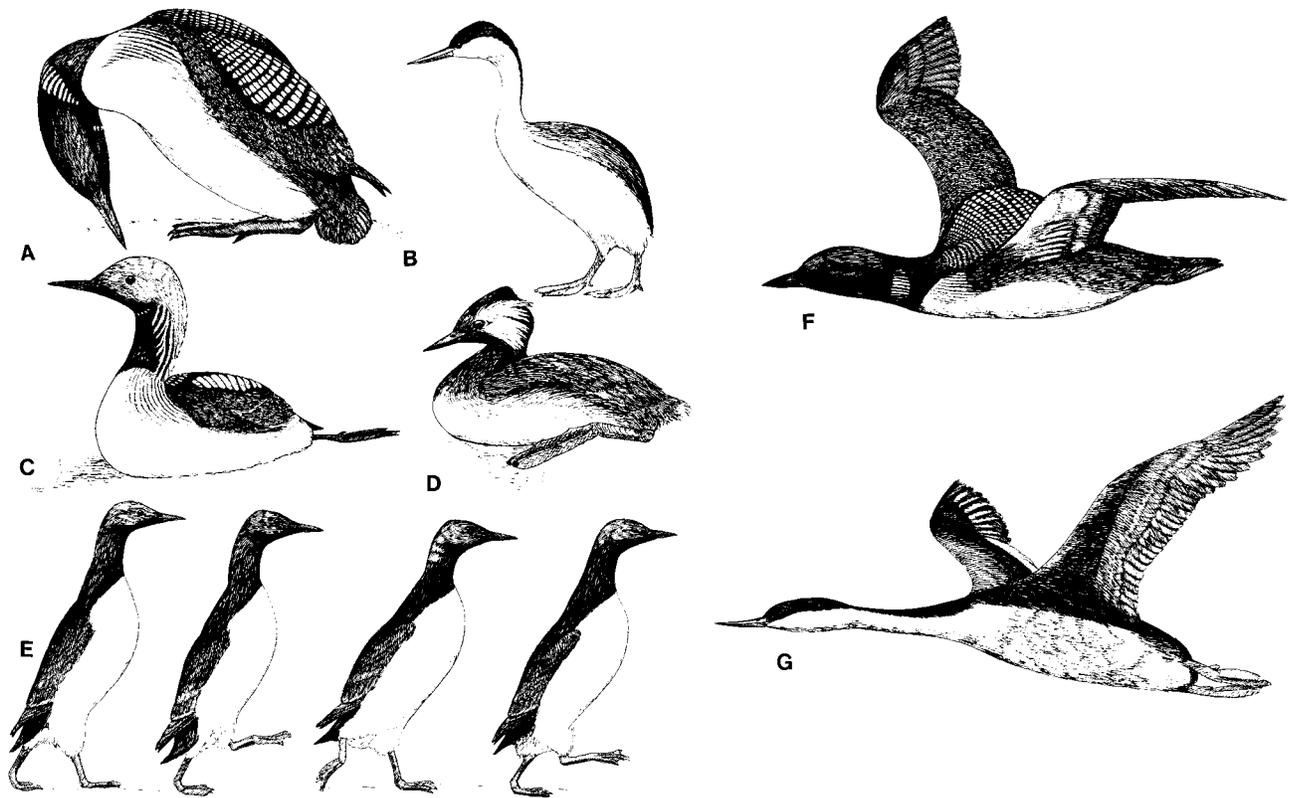
Last, there are a few minor kinds of behavior such as the bill stretching or "yawning" movement (fig. 10I). These movements seem to be more prevalent in puffins than in other species of diving birds, and their function is rather obscure. Grebes are said to perform both jaw stretching and true yawning behavior, and they also perform direct head scratching, throat touching to drain water from the bill, and feather eating (Cramp and Simmons 1977), the last of which will be discussed under foraging behavior.

Sunbathing behavior is well developed in some grebes. The birds orient themselves away from the sun and both lift their folded wings and tilt them somewhat forward so that the fluffy rump feathers are exposed to the sun. While resting or sleeping, grebes typically keep

the head directed forward and lay the neck and nape back on the scapular feathers, assuming a flattened posture that has been called the "pork pie" position (fig. 10E). On the other hand, loons twist the head around and tuck the beak into the scapulars while resting or sleeping, as do the auks.

Terrestrial and Aerial Locomotion

The ability to stand on dry land is very differently developed among these groups of birds, as a reflection of their very different pelvic and leg structures. For loons standing appears to be extremely difficult, and I believe the birds rarely if ever are able to attain a digitigrade posture by lifting their tarsi above the ground. Instead they adopt a partially raised body posture (fig. 11A), and even this is assumed only when absolutely necessary, as when an incubating bird rises in the nest to turn or inspect its eggs. A very similar posture is assumed by



11. Some postural traits of loons, grebes, and auks: A, standing, common loon; B, standing, western grebe; C, resting on ground, arctic loon; D, resting on ground, eared grebe; E, walk-

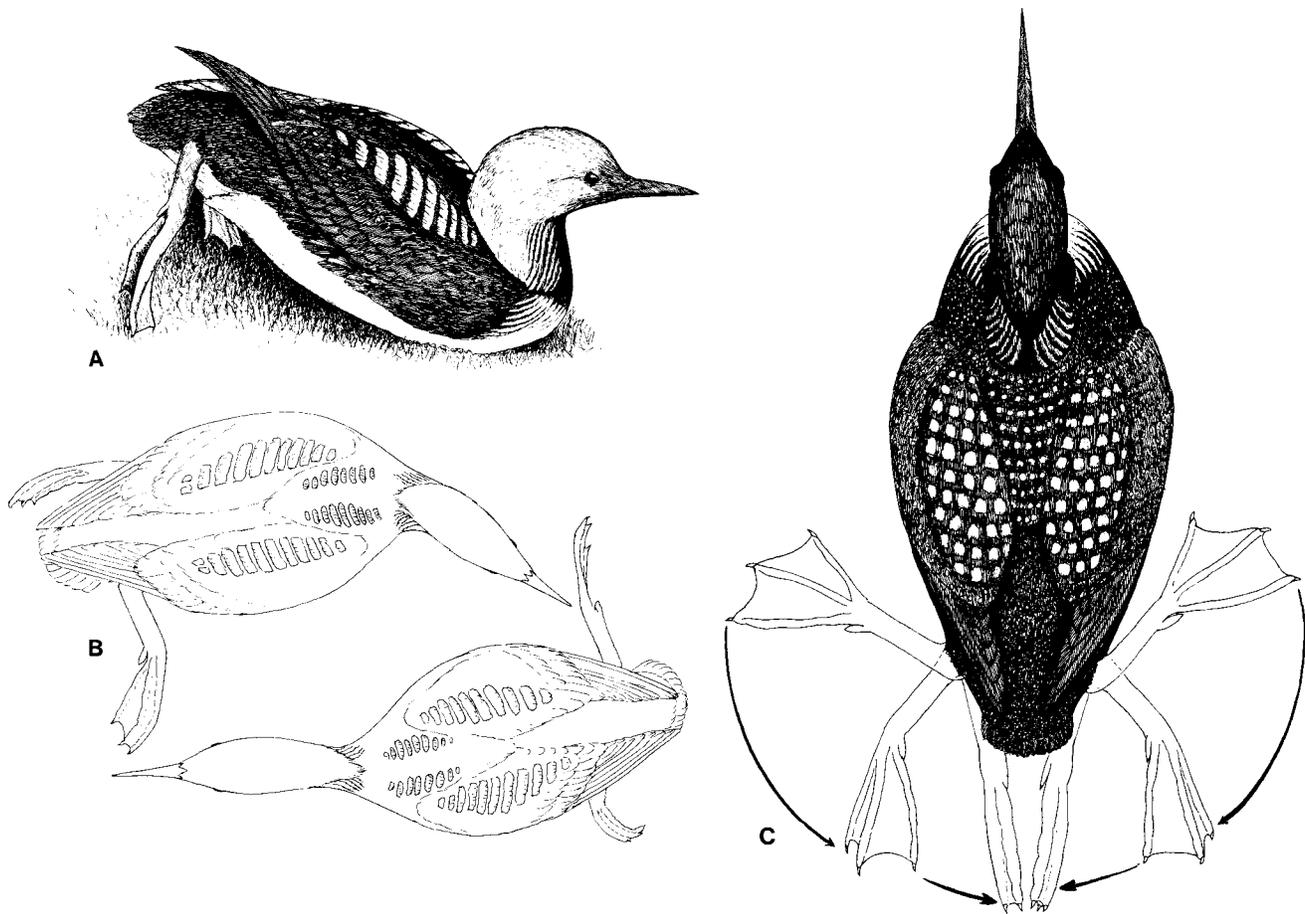
ing, common murre; F, flying, common loon; G, flying, western grebe. After various sources.

grebes in the same circumstances (fig. 11B), though it is clear from observations of nesting western grebes that the birds can assume a digitigrade posture and can even run if necessary (Nero, Lahrman, and Bard 1958). When resting on dry land, loons and grebes typically let their long legs and feet splay out to the front or back (fig. 11C,D) while resting all their body weight on the substrate. Auks stand relatively erect much of the time, although when resting for extended periods many of them rest on their breasts. Auklets and murrelets typically stand in a plantigrade manner, as do the larger alcids with the exception of the puffins, which are more inclined to stand erect in a digitigrade manner. Puffins have the relatively longest legs of any of the alcids and are adapted not only for efficient walking and running but also for burrow-digging (Kozlova 1961). However, digitigrade walking is possible even for the relatively large murrelets, especially the common murre (fig. 11E), when an erect, penguinlike posture is assumed. I have seen no evidence that walking is regular in loons, though it has been noted that for short distances the red-throated loon can assume a semierect posture and

walk forward with its neck bent forward and its bill near the ground (van Oordt and Huxley 1922). However, in my experience loons move about on flat ground by pushing themselves forward with both feet simultaneously (fig. 12A), lifting the breast from the substrate only temporarily at the start of each propulsive effort.

Flight in loons is swift and powerful (see table 9), with the head, neck, and body all held in essentially the same plane (fig. 11F) or the head and neck slightly lower, resulting in a slightly humpbacked body outline. During landing the wings are stiffly outstretched or may be raised in a sharp dihedral as the bird loses altitude, drops its feet, and skids into the water. At times a gliding flight, with the wings held in a V above the back, has also been observed in loons, and these flights may represent a kind of aerial display (Olson and Marshall 1952).

Flight in grebes is infrequent and very poorly studied. The flight posture assumed by the western grebe (fig. 11G, after a photo by Gary Nuechterlein) is much like that of loons, but most observers have noted that the birds rarely attain any great altitude during flight, and



12. Walking and swimming behavior of loons: A, "walking," arctic loon; B, underwater swimming, arctic loon; C, swim-

ming, common loon. After photos by author except for C, which is in part after Heilmann 1927.

Nuechterlein (1982) suspected that during its nesting season the western grebe may become incapable of flight because the breast muscles atrophy. I have seen flight in pied-billed, western, eared, and red-necked grebes but have been unable to estimate flight speed in any. Storer (1971) noted that a flying New Zealand dabchick was soon outdistanced by a group of New Zealand scaup (*Aythya novaeseelandiae*) and that it remained within a yard or so of the water most of the time it was airborne.

Takeoff in grebes and loons is preceded by a long running takeoff along the surface of the water. Olson and Marshall (1952) estimated that for the common loon the distance of this takeoff varies from 20 yards to as much as a quarter of a mile, and such long takeoff requirements are no doubt a severe handicap for loons and grebes when they are forced down on small water areas or, worse yet, on land. The red-throated loon is the only loon that has so far been reported as being able to take off from land (Harle 1952), and it also typically takes

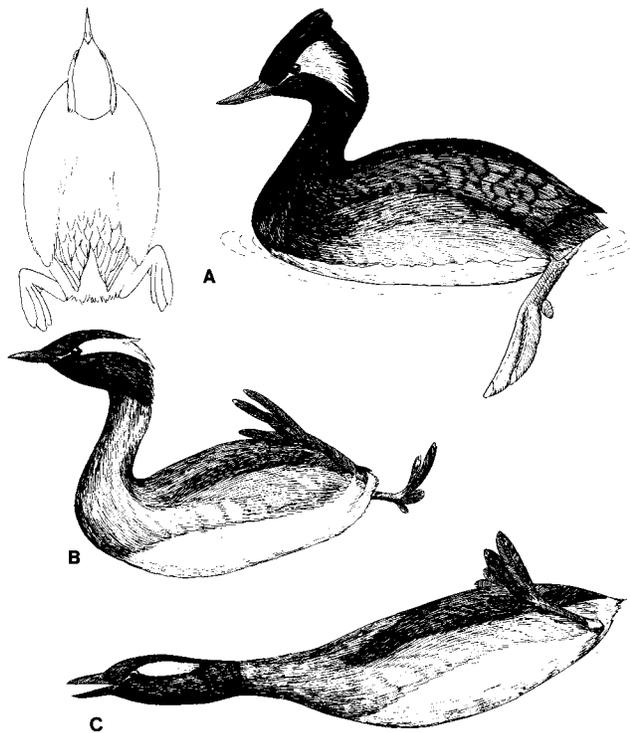
flight from water after skittering 15 to 40 meters (Norberg and Norberg 1971).

Many of the auks regularly nest on cliff sites, and thus landing and takeoff require different capabilities from those of loons or grebes. In particular an effective braking ability, often facilitated by an upward stall just before landing, is needed for cliff landings. Takeoff from such sites is much easier and simply involves falling forward as the wings are spread. For water takeoffs or land takeoffs by the burrow nesters and surface nesters these tactics clearly are inappropriate, and as with the loons and grebes, rapid running over the substrate is required until flight speed is reached. When murres are taking off from water they may run along the water for as little as 6 feet or as much as 50 feet or more, depending on wind conditions; takeoffs are against the wind whenever possible. Airspeeds in murres probably range from 60 to 100 kilometers per hour, and the wingbeat rate may approach 500 per minute (Stettenheim 1959). Similar rates seem to be typical of other alcids (table 9).

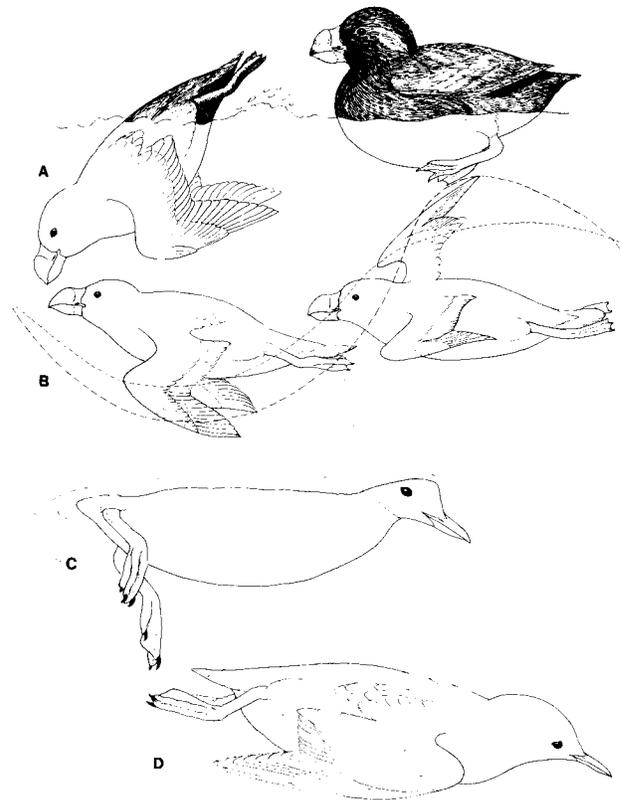
Swimming and Diving

Swimming behavior in auks, loons, and grebes is surprisingly poorly documented, and except under special conditions of captivity it is rather difficult to observe. When grebes are resting on the water, their feet are oriented almost directly below them (fig. 13A). Slow paddling is done with alternating foot movements and varying degrees of lateral spreading of the legs. However, when underwater grebes exhibit an extreme degree of lateral foot orientation, with the legs being lifted to the midplane of the body or even above it, and locomotion is attained by simultaneous or alternate foot thrusts (fig. 13B,C), the former being associated with more rapid swimming (Fjelds  1973a).

In loons the legs are more or less permanently splayed to the side, and during surface swimming they are moved in laterally, typically more or less simultaneously (fig. 12C). Such lateral orientation probably allows the feet to serve better as a rudder (H hn 1982), and perhaps a maximum separation of the two feet also is more efficient in reducing drag and turbulence. Similarly, when underwater the feet also move in a lateral orientation, and in this case they may be moved either



13. Swimming behavior of grebes: A, top and side views of surface swimming, eared grebe; B, slow and C, rapid swimming under water, horned grebe. After Fjelds  1973c and photos by author.



14. Underwater swimming behavior of auks: A, diving by tufted puffin; B, underwater swimming by tufted puffin, with paths of wingtips and wrist indicated by dotted lines; C, peering by pigeon guillemot; D, underwater "gliding" by pigeon guillemot. After photos by author and David Rimlinger.

simultaneously or alternately. A lateral extension of one foot also seems to be employed as a turning mechanism (fig. 12B).

In the auks, paddling while surface swimming is ducklike (fig. 14) with the legs oriented directly downward and moved alternately, simultaneously, or sometimes singly when the bird is slightly adjusting its orientation in the water. Additionally, paddling may occur while alcids are underwater. However, in the cases I have observed such paddling is used (by guillemots) not for propulsion but simply to hold the bird more or less motionless just above the substrate as it probes the bottom for food. Stettenheim (1959) observed similar "hovering" behavior in the common murre, with the two wings used independently, supplementing the propulsive effects of foot paddling. At the end of such a feeding session the paddling stops and the bird quickly returns almost vertically to the surface, its wings partly spread and its feet trailing behind. Likewise in grebes

the return to the surface is done passively, in a posture similar to that shown in figure 13B (Fjelds  1973a).

Often during such surface swimming the bill and head are partially immersed, the eyes slightly below the waterline (figs. 14C, 15D). This "peering" behavior is particularly prevalent in the alcids, but a comparable behavior occurs in loons (Olson and Marshall 1952). Peering also is common in grebes, and Fjelds  (1973a) illustrates a similar posture in a horned grebe capturing submergent prey while surface swimming.

These birds dive in a variety of ways. A typical manner of diving in grebes is shown in figure 15A, in which first the head and then the rest of the body slips under the water, with little apparent effort expended. Nuechterlein (1981a) calls such dives "level dives," compared with the more energetic "springing dives" in

which the body is almost lifted out of the water as the bird dives in a more nearly vertical fashion. Similar springing dives are typical of loons (fig. 15C), and I have not seen the wings used during the dives of either loons or grebes. However, Olson and Marshall (1952) stated that during rapid escape dives (as when shot at) the wings are used to strike the water and propel the loon down out of sight. A similar kind of emergency dive, or "crash dive," also occurs in grebes, especially among the species of *Podilymbus* and *Poliiocephalus* (Fjelds  1983b). In this behavior the bird suddenly sinks directly downward by rapid vertical propulsion with the feet (fig. 15E). Apparently least and pied-billed grebes do not typically swim great lateral distances during escape dives, but in the closely related giant pied-billed grebe a lateral movement of up to 90 meters has been reported, and



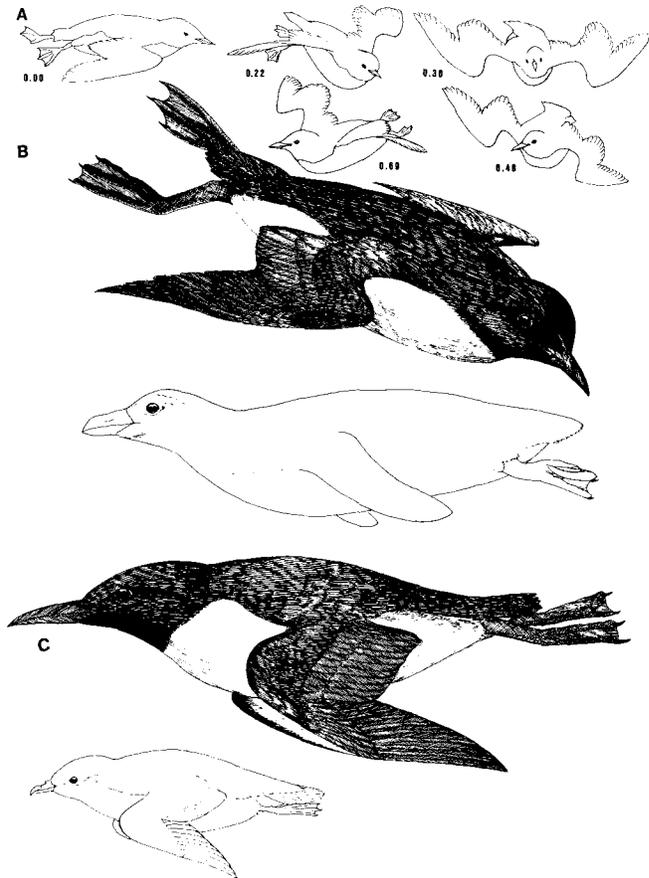
15. Diving behavior of loons, grebes, and auks: A, low and B, high dives of western grebe (after Nuechterlein 1981a); C, diving by common loon (after photo by author); D, diving by

horned puffin (after photos by author); E, diving by common murre (after photo by David Rimlinger); F, crash dive by hoary-headed grebe (after Fjelds  1983b).

red-necked grebes have moved underwater as far as 60 meters (Bleich 1975). Underwater speeds of up to 2.2 meters per second have been estimated for grebes (Bowes 1965). In the arctic loon lateral movements of from 400 to 600 meters have been reported, and underwater swimming rates of 2.5 to 5 meters per second appear to be common (Lehtonen 1970). Underwater movements by several species of alcids observed in captivity at Sea World had average speeds of from 0.96 to 1.13 meters per second, with little interspecies variation among puffins, rhinoceros auklet, and murres (Kenneth Fink, pers. comm.; see table 9).

When diving, the alcids hardly spring upward at all; instead, the wings are quickly opened and swept downward on the first power stroke as the bird submerges. The feet likewise go backward but sometimes seem to contribute little if any propulsive force (figs. 14 and 15). The angle of the dive is steep, which places the wings under the water surface immediately, and the partially folded wings are then quickly swept downward and backward, which together with a simultaneous backward kick of both feet pulls the bird completely underwater (Stettenheim 1959).

Underwater propulsion of the alcids is extremely interesting and warrants special consideration. When swimming underwater, alcids move their partially folded wings in a vertical action quite different from the wing action used during flight (fig. 14B). The wings are scarcely raised above the level of the back, and during the downstroke they are distinctly down-tilted, producing a hydrofoil effect that propels the bird forward. During this phase the wing is rotated as a single unit, with the wrist turning nearly 180° by the action of the humerus, while the rest of the wing components maintain a constant relation to one another (fig. 16A; 0.22 to 0.30 seconds). Then the humerus is swung posteriorly in a horizontal plane, pushing the forearm and hand posteromedially (fig. 16A; 0.30 to 0.48 seconds) and providing the second propulsion phase. Finally, the forearm and hand swing back medially, and the wing is raised for another power stroke (Spring 1971). Veering can be achieved by asynchronous wing movements, and turning is performed with the aid of the feet, by extending the foot on the side of the body toward which the bird is going to turn and using its extended webs as a brake. Turning may also be assisted by paddling with the opposite foot. Spring (1971) described three types of underwater turning in murres and noted that the thick-billed murre exhibited only two of the three types, suggesting greater dexterity in the common murre than in the thick-billed. However, he judged on the basis of anatomical differences that in the air the thick-billed murre should be an energetically more efficient flier

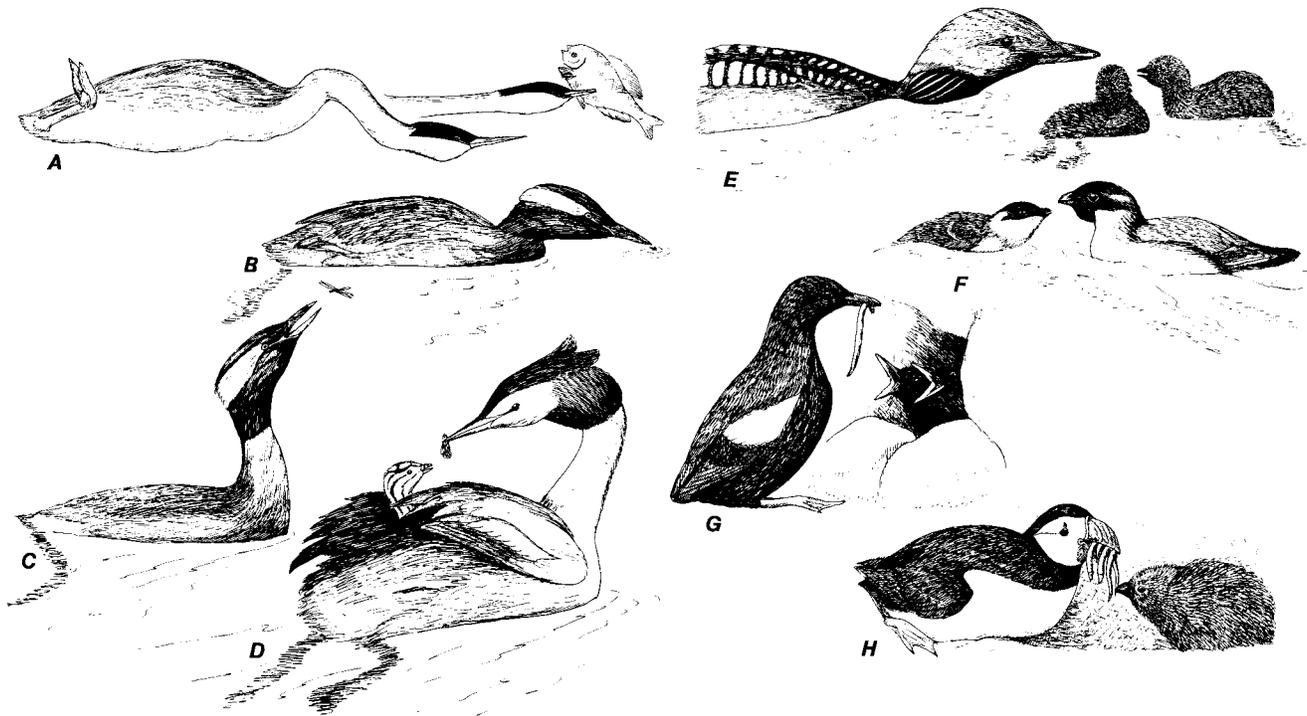


16. Swimming behavior of auks: A, turning sequence, common murre (after Spring 1971, with intervals in seconds); B, turning in common murre (after photo by author); C, comparison of underwater profile of common murre with that of a penguin and diving petrel (after photos by author except for diving petrel, which is based on a museum specimen).

and should also be capable of moving over greater underwater distances than the common murre.

When swimming underwater, alcids assume a fusiform body shape that is strongly similar to that of a penguin underwater (fig. 16D). Comparable photographs of the underwater posture and wing movements of diving petrels are not available, but judging from their anatomy it seems likely that these birds are virtually identical in shape and behavior to such alcid species as the ancient murrelet (Kuroda 1967).

When "flying" underwater, alcids do not move their wings continuously, but often "glide" for a time with their wings held close to their bodies (fig. 16D). This tends to reduce the average wingbeat rate while submerged, which in general tends to be only about 25 or 30 percent of the rate attained in aerial flight. Perhaps because of the varied rate of wing flapping underwater,



17. Foraging and parental feeding behaviors of loons, grebes, and auks: A, spearing by western grebe; B, surface and C, aerial catching of insects, horned grebe; and parental feeding of

young in D, crested grebe; E, arctic loon; F, ancient murrelet; G, black guillemot; H, Atlantic puffin. Mostly after drawings by Fjeldså 1973c, 1975.

there is no clear relation between body size and wing-beat rate while underwater (see table 9).

Although wing movement and overcoming relative environmental resistance during flying and underwater swimming must be very difficult in alcids, I have seen murres plunge directly underwater from flight and emerge from dives directly into the air. Kenneth Fink (pers. comm.) once saw a horned puffin perform "porpoising" behavior, alternating dives of 3 to 6 feet horizontal distance with short flights 18 to 24 inches above the water and repeating the sequence several times in a few minutes, apparently out of sheer exhilaration. Direct diving into the water from flight has also been observed in Atlantic puffins, razorbills, and guillemots (Stettenheim 1959).

Foraging Behavior

Loons, grebes, and auks capture prey in varying ways, depending on its speed, abundance, and elusiveness. There do not appear to be any good descriptions of prey catching in loons, but there can be little doubt that it is chased down visually and caught in open-field chases, judging from the kinds of fish that usually make up their diet. Fjeldså (1973a, 1975) has described and illus-

trated the underwater behavior of various grebes, especially the horned grebe. The horned grebe feeds mainly by diving and underwater pursuit, though this may be supplemented by such techniques as picking up individual floating items from the water surface (fig. 17B), skimming the surface for masses of floating invertebrates, or even snatching insects from the air (fig. 17C). In the western grebe the prey may initially be speared with the needlelike bill (fig. 17A), but probably most grebes capture their prey by grasping it between the upper and lower mandibles.

There are few observations on prey catching in auks, but at least in captivity it is clear that such species as murres regularly obtain their prey by visual pursuit. In puffins it is quite regular for the birds to capture additional prey while still holding crosswise in their beaks with the aid of their fleshy tongues fish that they have captured earlier. At times a half-dozen or more fish may accumulate in the beak of a puffin (fig. 17H), often neatly organized in an efficient alternating left- and right-handed manner. Apparently this rather remarkable arrangement is made possible by the bird's swimming in a school of fish and alternately making prey-grasping movements to the right and left, automatically "stacking" prey in its bill. Razorbills likewise often

carry two or more fish crosswise in their beaks, but with no special orientation. Fish carrying is done differently by the murrelets, however, with a single fish typically carried head-inward in the beak, with only the tail dangling out near the end of the bill. Similarly, guillemots carry single prey items back to their young by holding them crosswise in the bill, grasped at the head end. Curiously, at least in the black guillemot, individual birds show a preference for carrying their prey with the head held to either the left or the right side of the beak, though there is no obvious advantage to this kind of preference (Slater 1974). The dovekie and all five species of auklets have special gular pouches that facilitate the capture and carrying of large loads especially of plankton-sized prey, and at least in some species prey size varies with the reproductive state of the bird (Speich and Manuwal 1974). Neck pouches are not

known to occur in any of the murrelets, but the young have unusually well developed feet, probably allowing them to begin diving and feeding on their own well before their wings are sufficiently developed to aid much in diving. However, one or both parents tend to remain with their still-flightless chicks for some time after they go to sea and continue to feed them there (fig. 17F). In grebes and loons there are no neck pouches, and the adults directly feed their young individual bits of food by offering it bill to bill (fig. 17D,E).

Depths and Durations of Dives

As predatory birds, loons, grebes, and auks spend a good deal of time and energy capturing their prey while underwater, and it is of some interest to compare their relative diving efficiencies, at least indirectly. This

Table 10: Relative Depths (as Percentages) of Foraging Dives in Loons, Grebes, and Auks

Water Depth (ft)	Common Loon (N = 226)	Red-throated Loon (N = 207)	Great Crested Grebe (N = 282)	Horned Grebe (N = 156)	Little Grebe (N = 102)	Razorbill (N = 453)	Common Murre (N = 208)	Dovekie (N = 58)
1-6	0%	16%	29%	71%	100%	36%	24%	95%
6-12	8	54	48	29	0	52	25	5
12-18	46	24	20	0	0	11	37	0
18-24	36	4	20	0	0	1	12	0
24-30	9	2	3	0	0	0	2	0
30-36	1	0	0	0	0	0	0	0
Maximum depth (ft)	33.5	29	21	12	6	24	28	8

SOURCE: Data of Dewar 1924. NOTE: Depths are of waters in which diving occurred rather than known diving depths.

Table 11: Average Durations (in Seconds) of Observed Foraging Dives in Loons, Grebes, and Auks

Water Depth (ft)	Common Loon	Red-throated Loon	Great Crested Grebe	Horned Grebe	Razorbill	Common Murre
1-6	—	18.2	22.1	14.9	18.9	15.0
6-12	28.2	27.6	26.6	25.2	24.8	24.9
12-18	35.5	27.6	33.3	—	34.2	36.8
18-24	49.3	35.2	45.6	—	48.7	49.1
24-30	60.2	47.8	—	—	—	61.0
30-36	68.0	—	—	—	—	—
Maximum depth (ft)	69	67	50	41	52	68

SOURCE: Data of Dewar 1924. NOTE: Sample size as in table 10.

question was first addressed seriously by Dewar (1924), who spent several years gathering data on the behavior of not only these three groups of birds but other divers such as cormorants and diving ducks. He accumulated a great deal of interesting comparative data, some of which are summarized in tables 10 and 11 for the species of loons, grebes, and auks that he was able to ob-

serve. In general he found that loons tend to dive deeper than auks or grebes and that the durations of dives of representative species of all three groups are very similar in water of comparable depth, but that the maximum duration of observed loon dives tends to average somewhat greater than for auks or grebes.

Using a variety of criteria, including the longest dive

Table 12: Reported Maximum Diving Records for Loons, Grebes, and Auks

Species	Record	Reference
<i>Duration of Dive</i>		
Loons		
Common loon	180 seconds ^a	Palmer 1962
Arctic loon	302 seconds	Lehtonen 1970
Red-throated loon	90 seconds	Höhn 1982
Grebes		
Horned grebe	180 seconds	Eaton 1910
Red-necked grebe	60 seconds	Cramp and Simmons 1977
Great crested grebe	56 seconds	Cramp and Simmons 1977
Eared grebe	50 seconds	Cramp and Simmons 1977
Auks		
Cassin auklet	120 seconds	Dewar 1924
Thick-billed murre	98 seconds	Glutz and Bauer 1982
Black guillemot	78 seconds	Glutz and Bauer 1982
Common murre	74 seconds	Glutz and Bauer 1982
Razorbill	74 seconds	Glutz and Bauer 1982
Dovekie	71 seconds	Glutz and Bauer 1982
Tufted puffin	61 seconds	Personal observations
<i>Depth of Dive</i>		
Loons		
Common loon	60–70 meters	Höhn 1982
Arctic loon	46 meters	Höhn 1982
Grebes		
Great crested grebe	30 meters	Cramp and Simmons 1977
Horned grebe	25 meters	Palmer 1962
Auks		
Common murre	180 meters	Piatt and Nettleship 1985
Razorbill	120 meters	Piatt and Nettleship 1985
Black guillemot	50 meters	Piatt and Nettleship 1985
Rhinoceros auklet	31 meters	Stettenheim 1959
Atlantic puffin	60 meters	Piatt and Nettleship 1985

^aSubmersion to 15 minutes has been reported in a wounded bird (Schorger 1947).

duration, the "dive/pause ratio" (the average duration of dive per unit of resting between dives), and the rate of increase in pause time per fathom of diving depth, Dewar concluded that the auks are the most efficient of the divers, followed sequentially by loons, cormorants, grebes, and diving ducks.

Since Dewar's studies, many additional observations on diving depths and durations have been made by various observers. In general they prove difficult to compare directly, since such variables as water depth, food abundance, speed of swimming, and perhaps other factors enter into the question of diving efficiency. Thus, table 12 presents various observations on maximum observed dive durations and depths of dives, suggesting that maximum dive durations are sometimes much greater than those Dewar reported for the same species and frequently exceed a minute in species of all three groups. Diving depths also have been reported to exceed those Dewar observed, and almost incredible depths of more than 500 feet have been reported for the common murre. Olson and Marshall (1952) have mentioned that for a diving bird to reach a depth of 200 feet it must be able to withstand a water pressure of 86.7 pounds per square inch as well as deal with the problems of oxygen availability. It is well known that most of the needed oxygen comes from stored oxyhemoglobin in the blood and muscles (Schorger 1947), and additionally the metabolic rate during diving is probably sharply decreased by a drastic reduction in heart rate and the temperature of peripheral organs, especially the feet, judging from stud-

ies of diving ducks. Höhn (1982) has reviewed the major physiological aspects of diving in loons, and I will not repeat them here.

Storer (1945, 1952) has suggested that alcids such as murres and razorbills are considerably better adapted for diving than such genera as *Cepphus*, for example, which is anatomically more generalized. The limited data in table 12 suggest that maximum depths and durations of dive in murres average somewhat greater than those of guillemots, though the differences are not marked. Similarly, in a common display tank at Sea World where both species were maintained in captivity, the average foraging dive duration of common murres was only slightly longer (mean 27 seconds, range 17–39 seconds, sample of 10 dives) than those of pigeon guillemots (mean 21.7 seconds, range 4–36 seconds, sample of 36 dives). However, the dive/pause ratio of the common murre was 5.46:1, while that of the guillemot was 2.07:1, suggestive indeed of a considerably greater degree of diving efficiency in the murre than in the guillemot. Typical dive/pause ratios in grebes appear to be in the range of 1.5 to 2.7:1, at least for foraging dives (Bleich 1975; Storer 1971). Dewar's (1924) data on dive/pause ratios in loons indicated a ratio range of from 1.6 to 3.9:1, with the higher ratios generally associated with deeper rather than shallower dives, as might have been imagined. This might lead one to question the value of dive/pause ratios as a direct measure of diving stress.