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Diving Birds of North America: 5 Comparative Pair-Forming and Copulatory Behaviors

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5. Comparative Pair-Forming and Copulatory Behaviors

All species of loons, grebes, and auks are monogamous, with adults forming strong pair bonds that are established or reestablished each year, probably during the spring prenesting period. The extent of remating by birds mated the previous year in these groups is still largely undocumented, though at least in alcids it is fairly high, given the relatively long life-spans and the tendencies of the birds to return year after year to essentially the same territory and sometimes to the same nest site. Such conditions would promote reestablishment of contracts between previously paired birds, since it is not believed that in these birds pair or family units normally remain intact through the winter. Although in some grebes such as the horned grebe breeding site tenacity and mate fidelity may be very strong (Fjeldså 1973c), in others such as the colonial-nesting eared grebe there is no evidence of this and mate fidelity is poorly developed (Fjeldså 1982a).

Pairing behavior in the loons is certainly understood the least well of all these three groups, and as such is very difficult to summarize. It is apparent (table 22) that all loons are highly vocal and that vocalizations are extremely important social signals, especially in territorial advertisement. It is also evident that much of the described "courtship" behavior of loons is little more than variably ritualized hostile behavior, since it is often extremely difficult to distinguish between hostile territorial encounters and actual pair-forming displays between potential mates. Indeed the most complex and spectacular displays of loons, like those of some grebes, seem little more than highly ritualized aggressive behavior that probably serves to avoid serious fighting and promote social bonding between these sexually monomorphic species. It is thus not surprising that, as in some grebes, "racing" ceremonies are often present, as are erect "penguin" postures that involve treading water while maintaining an essentially threatening posture. The variable visibility of the species-specific throat and neck markings of loons is associated with differential amounts of bill tilting, neck stretching, and sometimes also head turning; in general the degree of exposure of these throat and neck patches seems to be directly related to the degree of hostility or sexual intensity of the display. The conspicuous back patterning of loons is not obviously utilized during display, and it seems likely that their white underparts are related to countershading requirements rather than being important as social display features.

Copulatory behavior has been described for all four species of loons, and the general pattern seems to be highly stereotyped and very similar in all (fig. 24). Thus, unless visual aspects of species-specific plumages are significant, copulatory behavior in loons is unlikely to serve as an effective reproductive isolating mechanism. McIntyre's (1975) observations on the common loon are probably representative of loons in general and involve a large sample of twelve observed copulations. She found that either sex might initiate copulation, which always occurred on land but not on a specific "copulation platform" as has at times been alleged. If the male precedes the female to land he typically utters a "soft" call while waiting for her to approach the copulation site, which often later becomes the nest site. The female's receptive posture is one of lowered head and bill (fig. 24A,D), and when the male mounts he stands on the female's back or scapular area with his head directly over hers (fig. 24B,E). After treading the male walks over whichever one of the female's shoulders is nearer to water (fig. 24C). No specific postcopulatory displays occur in loons, though preening and bathing behavior often are performed by both sexes. Some nest-building behavior may also follow copulation.

Pair-forming behavior in grebes, by contrast with that of loons, is extremely conspicuous and highly ster-

Table 22: Social Behavior Patterns and Calls of Loons

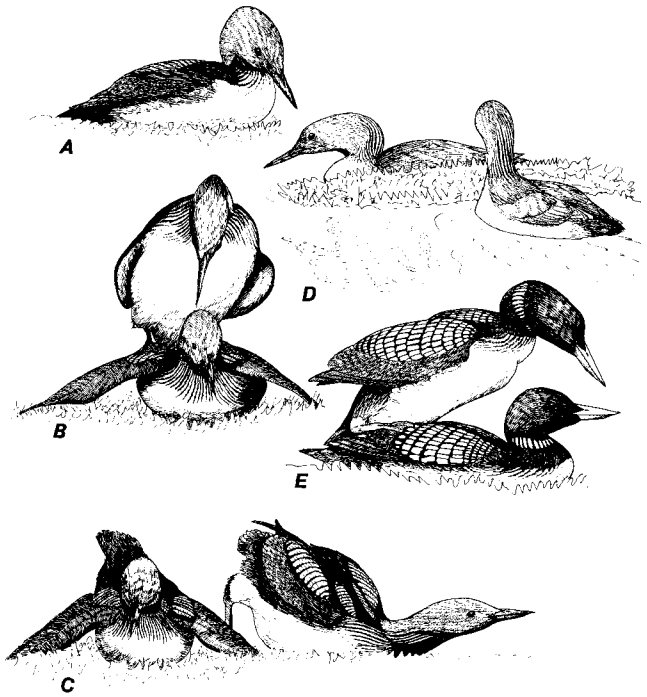
Behavior	Red-throated	Arctic	Common	Yellow-billed
Calls				
Croaking	X	X		
Wailing	X	X	X	X
Moaning	X	X	X	X
Long call/yodeling			X	X
Tremolo calling			X	X
Short call		X		
Posturing				
Antagonistic (appeasement/alarm)				
Neck stretching/alert	X	X	X	X
Alarm/prone	X	X	X	X
Antagonistic (threat/attack)				
Hunched/forward	X	X	X	X
Bill dipping	X	X	X	X
Splash diving	X	X	X	X
Fencing/penguin/bow jump	X	X	X	X
Surface rushing	X	X	X	X
Mutual or group displays				
Plesiosaur race/surfing	X			
Snake ceremony	X			
Circle dance/pivoting		X	X	X

NOTE: See species accounts for descriptions and possible functions.

eotyped and exhibits a high degree of species specificity (table 23). Why such differences exist between loons and grebes is not at all clear, since in general there seem to be no differences in relative need for reproductive isolation among sympatric and congeneric forms in the two groups. As with the loons, most of the species-specific nuptial plumage characteristics of grebes are concentrated in the head and neck region, and furthermore in both groups the displays and calls are performed mutually and apparently identically between the sexes. Indeed, one might wonder how sexual recognition is attained in these groups; possibly it is achieved by relative dominance and submissive behavior.

Most of the classic observations on grebe pair-forming and pair-maintaining behavior have been performed on the great crested grebe, beginning with the studies of Huxley (1914) and continuing through to much more recent work by Simmons (1955, 1975). A variety of papers by Fjeldså (1973c, 1975, 1982a) and Storer (1962, 1967, 1969, 1971, 1982) have contributed greatly to our understanding of grebes and their displays. Simmons has divided crested grebe courtship into two categories, water courtship and platform behavior. The first of these is not confined to pair formation but occurs both during and after pairing, though it is largely limited to the pre-egg stage of the reproductive cycle. Platform behavior includes soliciting, copulation, and sometimes ceremonial nest building. Such platform behavior may precede nesting by several months. It probably serves both in establishing pair bonds and later also as a mechanism for fertilization of the female, and as such it may appropriately be called "platform courtship."

Solitary grebes of at least nearly all *Podiceps* species as well as the western grebe and the white-tufted grebe exhibit advertising behavior. This calling, performed by solitary birds of either sex, occurs in unpaired birds seeking a mate, in paired birds visually separated from their mates, and in parents that have lost contact with their chicks. The advertising calls are typically species specific but may also have sufficient individual variability to permit individual recognition. Mutual calling, or "duetting," has also been recorded in all six of the



24. Comparative sexual behaviors of loons: A, soliciting, B, copulation; and C, postcopulatory behavior of arctic loon (after photos in Höhn 1982); D, soliciting and precopulatory approach of red-throated loon (after Cramp and Simmons 1977); E, copulation in yellow-billed loon (after Cramp and Simmons 1977).

Table 23: Interspecific Distribution of Some Sexual Behavior Patterns in North American Grebes

Behavior	Least	Pied-billed	Eared	Red-necked	Horned	Western
Courtship behavior						
Duetting	X	X	X	X	X	X
Crest erection	—	—	X	X	X	X
Head turning/shaking/waggling	—	X	X	X	X	X
Discovery ceremony (cat—ghostly penguin)	—	—	X	X	X	—
Penguin dance	—	—	X	X	X	—
Weed ceremonies	—?	X?	X	X	X	X
Triumph ceremonies	X	X	X	X	X	—
Barging or parallel swimming	X	X	X	X	X	X
Rushing ("racing")	—	—	—	—	—	X
Habit preening	—	—	X	—?	X	X
Threat pointing	—	—	—	—	—	X
Platform behavior						
Female behavior						
Inviting	X	X	X	X	X	X
Rearing	—	X?	X	X	X	—
Breast stroking	X	X	—	—	—	—
Male behavior						
Copulation call	X	X	X	X	X	X
Water treading	—	X?	X	X	X	?

NOTE: X indicates presence of behavior; X? indicates uncertain ritualization; — indicates apparent absence.

North American grebe species (table 23). In some species this behavior is called a "triumph ceremony," and at least in the horned grebe it is the only mutual display that is frequently produced by well-established pairs (Fjeldså 1973c). In that species it often occurs after territorial combat or when a pair meets after a temporary separation. A triumph ceremony without calling occurs in the red-necked grebe.

Crest erection, often in conjunction with various kinds of head turning or head shaking, is common in many grebes and occurs in at least five of the North American species. Frequently it is incorporated into more elaborate ceremonies such as the "discovery ceremony" or "penguin dance" or, as in the crested grebe, may form a conspicuous part of an elaborate head-shaking ceremony.

A major ceremony of grebes during the period of initial pairing, and also later among paired birds on territory, especially as a greeting ceremony after brief separations, is the "discovery ceremony." In this ceremony one of the birds (the searcher or "ghost diver") takes the active searching role while the other waits to be "discovered." In the crested grebe the approach by the "searching" bird resembles the threatening approach made during antagonistic encounters, while in other species such as the red-necked grebe, horned grebe, and eared grebe the searching bird periodically exposes itself in a "bouncy" posture, with the plumage depressed and the breast well puffed out. When within about a meter of the waiting bird, the searching bird suddenly rises vertically out of the water in a "ghostly penguin" posture. The waiting bird, which in some species such as the horned grebe and great crested grebe has assumed a raised wing and expanded tippet "cat posture," now rises in the water in synchrony with the other, and the two perform a mutual "penguin dance." A penguin dance has been described for nearly all of the typical *Podiceps* species, although in the great crested grebe it is replaced by the head shaking ceremony. Most probably the discovery ceremony is ritualized or symbolic at-

tack and the cat display is similarly a ritualized defensive posture.

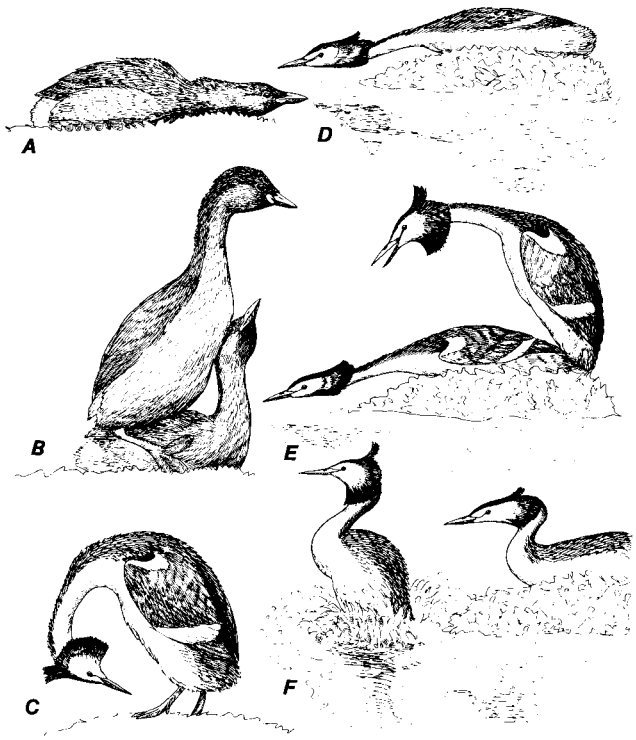
In some species the penguin posture is also assumed while both birds are holding aquatic vegetation in the bill, a variation Simmons (1975) called the "weed dance" to distinguish it from those species that do not use weeds and thus perform typical "penguin dance" ceremonies. Simmons has pointed out that, unlike the discovery ceremony, in the weed ceremony of the crested grebe the roles of male and female are identical throughout, and during this posture both birds rise breast-to-breast in penguin postures and perform a weed dance. This kind of ceremony has been observed in both red-necked and western grebes and has also been reported in some populations of horned grebe but not others.

A somewhat similar ceremony of some grebes is the "weed rush." In the horned grebe this occurs when, after the discovery ceremony, the two birds appear at the water surface with plant material in their bills. They thus emerge from the water in straight-necked attitudes and swim toward one another. As they collide they rise in the water into penguin attitudes and swim parallel for a distance in a weed rush ceremony. Although red-necked and western grebes have essentially stationary weed dance ceremonies, only the horned grebe among the North American grebes performs the weed rush. However, the rushing display of the western grebe is distinctly similar, and the slower "barging" of the eared grebe may also be related. Likewise, the least grebe performs parallel swimming displays, accompanied by loud calling. In other species of grebes, parallel swimming or barging often terminates with unison diving, as is also the case with the western grebe's rushing ceremony (Fjeldså 1973c). Fjeldså suggested that in the more primitive grebes such as *Tachybaptus* and *Podilymbus* there is much weed-presenting behavior but that such weed ceremonies are not incorporated into breast-to-breast or parallel swimming displays. He thus suggested that the weed rush ceremony, like the penguin dance ceremony, originated from attack behavior. He further suggested that the discovery ceremony allows potential mates to attain close contact, which might be necessary for sex recognition in grebes. More recently (1982a) he has reaffirmed his position that the discovery ceremony probably plays a central initiating role in pair formation of several *Podiceps* species and that this and other complex rituals have most probably evolved from antagonistic responses. Furthermore, he believes that no pair bonding develops (at least in *Podiceps*) unless the birds perform another ceremony, usually with weeds, after the discovery ceremony. In gregarious, colony-nesting grebes incipient partnerships apparently change often, and promiscuous platform behavior may be an important aspect of attaining mutual recognition.

Beyond these major ceremonies, several less complex displays occur in various species of North American grebes, such as "habit preening" and "threat pointing," which are both highly developed aspects of courtship behavior in western grebes but seem to have no counterpart in other North American grebes, except possibly for the less conspicuously ritualized preening that occurs in the eared grebe.

Copulation in grebes invariably occurs on floating vegetation or land. Usually it is done on platforms that initially are built for this specific purpose and later are often modified to serve as nests. However, at times these preliminary platforms are too exposed or otherwise prove unsuitable for nesting, and thus a new and better site may be selected for the nest. In apparently all grebes, not only do both sexes solicit copulation, but either one can take the active role during treading. Such "reversed mounting" was initially reported for the crested grebe (Simmons 1975) but has been observed in several other species. However, during the period immediately before and during egg laying nearly all copulations are of the normal type. Simmons used the term "mating ceremony" for the solicitation, copulation, and postcopulatory sequence and "platform behavior" for all the calls and behavior associated with copulation as well as with collecting materials and building mating structures. Although an "inviting on the water" behavior has been seen in crested grebes, soliciting typically occurs on the mating platform, when the inviting bird assumes an immobile, nearly prone posture (fig. 25A,D). At times, especially when the other bird approaches, it may also assume a "rearing" posture with the body raised and neck arched downward, at times performing wing quivering. Treading involves a rather erect posture by the active bird (fig. 25E). Its bill may be open or closed, and it typically utters a trilling or rattling call. It does not hold the nape of the passive partner, which in *Podiceps* and *Aechmophorus* holds its head as low as or even lower than during inviting, though its bill may be tilted upward. However, in *Podilymbus* and *Tachybaptus* the passive bird raises its head and rubs it against the other's breast (fig. 25E). Apparently intermediate behavior occurs in *Rollandia* (Fjeldså 1982a). Dismounting in grebes is often accompanied by water treading by the active partner (fig. 25F), while the passive bird simply raises its head. In some species such as the silver grebe and red-necked grebe a rather stereotyped postcopulatory posturing is also present.

Copulatory behavior in the grebes thus appears to be extremely conservative and similar throughout the en-



25. Comparative sexual behaviors of grebes: A, soliciting and B, copulation in least grebe (after Cramp and Simmons 1977); C, rearing, D, solicitation, E, copulation, and F, postcopulatory display of great crested grebe (primarily after Simmons 1955).

tire group, and as such it is less likely to offer opportunities for reproductive isolation than is aquatic courtship, which is far more species specific. Testing of behavioral reproductive isolating mechanisms has scarcely begun for grebes, although Nuechterlein (1981a) concluded that they are attained in the two morphs of the western grebe by differences in the advertising call rather than by any postural differences, which appear to be lacking altogether. Fjeldså (1982a) was unable to find any evidence of ethological character displacement among sympatric versus allopatric populations of species in the genus *Podiceps*.

The alcids, like the loons, are often extremely long-lived, and not only do most species return to the same breeding colony year after year, but the birds typically return to the same burrow, cliff ledge, or other specific nesting site. Such nest site tenacity occurs in at least eleven species of alcids (Leschner 1976), and successive-year mate retention has been reported for the dovekie (Norderhaug 1967), razorbill (Lloyd 1979), thick-billed and common murres (Tuck 1960), pigeon guillemot (Drent 1965), black guillemot (Preston 1968), ancient murrelet (Sealy 1975a), Cassin auklet (Manuwal 1974a), crested and least auklets (Sealy 1975a), rhinoceros auklet (Leschner 1976), and Atlantic puffin (Ashcroft 1976, 1979). These monogamy-promoting behaviors may ease the need for highly species-specific signals in alcids, which nonetheless do have specific bill shapes or colors and sometimes distinctive head plumages and which also tend to have distinctive vocal signals associated with pair interactions. Yet by comparison with the grebes, the posturing tends to be relatively simple and frequently is very similar between closely related species (table 24).

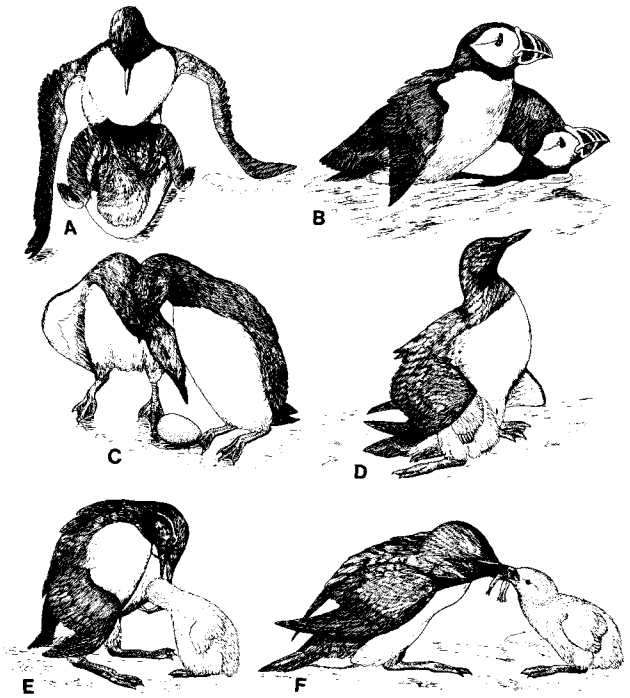
Even in the most fully studied alcids, the murres, there is still a good deal of uncertainty about the timing and mechanisms of pair bonding. Tuck (1960) noted that there is no conclusive evidence that murres are mated before they return to their nesting sites, though some authors have claimed this is so. He mentioned "joy flights" and "water dances" as important social flock activities associated with the birds' return to their nesting colonies and judged that such communal displays may help stimulate and maintain their reproductive condition. He reported a high level of individuals' remating with previous mates and judged that perhaps pairing normally occurs among birds that choose potential nesting sites close to one another. Thus if males (which are normally the first to arrive) gradually come to tolerate females that attach themselves to the particular site already occupied by the male, pair bonding may easily develop or redevelop. In any event, at least among murres and razorbills, mutual billing and preening behavior is apparently a major pair-maintaining mechanism that occurs throughout the entire breeding season, even after the young are hatched. Mutual billing and preening or its solicitation, and mutual billing in the absence of preening as occurs in the puffins, certainly place maximum visual and tactile significance on the bill and facial region and thus might help explain the bright colors and head plumages typical of so many alcids. Among species where mutual billing or preening does not seem to be present, as in the murrelets, the facial plumage and the bill shape and coloration seem undeveloped compared with that of other alcids.

In contrast to the loons and grebes, copulation in the alcids may occur either in water or on land, depending upon the species (fig. 26 and table 24). In the murres, razorbill, guillemots, and dovekie copulation occurs on a solid substrate, often but not necessarily the nesting site itself. In the murres at least it may also rarely occur in water, and thus there may be no hard and fast taxonomic distinctions among the alcids as to the distribution of this kind of behavior. During copulation solicitation the female leans forward and raises her

Table 24: Distribution of Various Structural and Behavioral Traits Associated with Reproduction in Auks

Trait	Dovekie	Razorbill	Murres	Guillemots	Murrelets	Small Auklets	Rhinoceros Auklet	Puffins
General nuptial traits								
Mutual billing	X?	X	X	X	?	X	X	X
Mutual preening	—?	X	X	—	?	—?	—?	—
Bill enlarged and colorful	—	—	—	—	—	X	x	X
Head plumes or crests	—	—	—	—	—	X	x	x (1 sp.)
Colorful feet	—	—	—	X	—	—	—	X
Primarily nocturnal	—	—	—	—	X	x (1 sp.)	X	—
Food presentation display	—	—	X	?	?	?	?	—
Duetting	—	—	—	—	X	X	?	—
Copulatory behavior								
Land copulation typical	X	X	X	X	?	X?	?	—
Water copulation typical	—	—	—	—	?	X?	?	X
Precopulatory circling	—	—	—	X	?	?	?	—

NOTE: X indicates trait well developed; x indicates variable or limited development; X? indicates probable presence; — indicates apparent absence.



26. Comparative sexual behaviors of auks: A, copulation in common murre; B, copulation in Atlantic puffin; C, nest relief behavior of common murre; D, brooding, and E, parental feeding by common murre; and F, parental feeding by razorbill. After Glutz and Bauer 1982.

rump. The male mounts from the side, either drooping his wings over her or at times flapping his wings to maintain balance. The female then opens her bill and utters a hoarse call. As treading is completed the female usually rises, causing the male to slide off her back.

On the other hand, copulation in some alcids, including at least all three typical puffins, normally occurs on water. The situation in the rhinoceros auklet is still unknown, but copulations or at least attempted copulations have been observed among swimming crested and least auklets, although nest site copulations have also been observed in these two species (Sealy 1968; Thoreson, in press). Atlantic puffins sometimes attempt to copulate on land, but these attempts are usually not successful. In the puffins, copulation is typically preceded by a male's following a female and performing head jerking and probably also uttering vocalizations. If the female is receptive she will allow the male to approach from behind, alight on her back, and cause her to become completely submerged except for her head. During copulation the male flaps his wings to maintain his balance, and copulation is usually terminated by the female's diving and resurfacing some distance away (Wehle 1980). Unlike copulation, billing in puffins may occur either in the water or on land and is usually initiated when one bird nuzzles the other's throat and breast feathers. Billing occurs in all four

puffins and often serves as a greeting, in a "triumph ceremony" after an aggressive encounter by one member of the pair with another bird, during courtship, or in other situations. In guillemots billing typically initiates a copulatory sequence; in the pigeon guillemot billing is a certain sign that the birds are a mated pair (Drent 1965), and billing with associated vocalizations is apparently of great importance in establishing and maintaining the pair bond. Like the murre's mutual preening behavior, billing in guillemots is performed by pairs whenever they meet throughout the breeding season. According to Drent (1965), "twitter billing" in the pigeon guillemot is functionally comparable to silent mutual billing in the Atlantic puffin and to the combination of billing and allopreening behavior typical of common murres and razorbills. Mutual billing also occurs in at least some of the auklets, but it does not seem to have been described yet for the murrelets. However, food presentation behavior, which is a frequent part of precopulatory ceremonies in the murres, is apparently absent in razorbills and puffins and is of questionable occurrence in guillemots. It has not yet been observed, but might occur, in the auklets, given the adults' ability to carry substantial amounts of food back to the nesting burrow in special throat pouches. Thus billing seems to be the most universal form of pair-maintaining behavior in the alcids and billing invitation behavior apparently plays an important role in the earlier stages of pair formation, while mutual billing is a regular part of alcid pair-maintaining behavior. In murres and razorbills, preening has supplemented and to some degree replaced billing in fulfilling these roles, but the two behaviors are closely related in occurrence and function. Like the discovery ceremony of the grebes, billing is probably derived from hostile behavior, and it too may well have evolved as a mechanism for allowing two potential antagonists to approach one another and establish individual contact. Vocalizations may play a larger role in individual recognition in the alcids than in the grebes, and this is likely to be especially true in the nocturnal forms such as the murrelets and nocturnal auklets.