

April 1987

## *Diving Birds of North America: 6 Comparative Life Histories and Reproductive Success Rates*

Paul A. Johnsgard

University of Nebraska-Lincoln, pajohnsgard@gmail.com

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## 6. Comparative Life Histories and Reproductive Success Rates

### Life Histories

It is now well recognized that, like behavior, a species' life history characteristics, such as age at sexual maturity, clutch sizes, and incubation, brooding, and fledging patterns, are evolved traits that may be strongly influenced by a variety of ecological factors (Lack 1968). Within the auks, loons, and grebes one can find variations in the age at sexual maturity and time of first breeding ranging from as little as 1 to as many as 5 or 6 years, average clutch sizes that range from 1 to 4 eggs, and substantial variations in adult survival rates and maximum longevity (table 25). However, compared with such similar-sized aquatic birds as ducks and geese, all three groups tend toward relatively small clutches, a greater tendency to defer sexual maturity and breeding, and substantially higher adult survivorship rates and thus potentially greater maximum longevity. In general such characteristics are associated with groups of birds that breed under relatively difficult conditions, where age and experience probably are significant factors influencing breeding success and for which, therefore, it is advantageous to the species to limit reproductive efforts to older individuals, who are most likely to be successful. In these three groups all the species are exclusively monogamous, with both sexes participating in incubation, brooding, and to varying degrees in feeding the young, which though generally precocial cannot capture prey on their own until they are relatively well developed (see figs. 17, 26, and 27).

Clutch sizes in loons are highly uniform, with two-egg clutches typical. However, single-egg clutches are not uncommon, usually because one of the eggs is lost from the platformlike nest. Olson and Marshall (1952) reported an average clutch of 1.55 for 47 common loon nests, and McIntyre (1975) found a mean of 1.67 eggs in

51 nests of this species. Bergman and Derksen (1977) reported average clutch sizes of 2.0 eggs for arctic loon nests and 1.86 eggs for 21 red-throated loon nests. Peterson (1979) found an average clutch of 1.93 for 43 arctic loon nests, and Lehtonen (1970) found that 78 first clutches of arctic loons had an average of 1.88 eggs. A collective total of 39 first clutches of red-throated loons averaged 1.79 eggs (Cramp and Simmons 1977). The available records of yellow-billed loons clutches are nearly all of 2 eggs; Bailey (1948) reported 22 such clutches.

There are apparently as yet no definitely established records on the age of initial breeding in loons, though the definitive adult plumage is not attained until the third year of life, by which time some believe breeding occurs (Palmer 1960). However, Lehtonen (1970) has postulated that in the arctic loon initial breeding may not occur until the birds are 6–7 years old, which would require a very high adult survival rate. Indirect evidence supporting the probability of such high adult survival rates are records of individual banded arctic and red-throated loons that lived over 20 years, though no similar records have yet accrued for common loons. In North America there are still regrettably few loon banding results. As of 1979, only 5 recoveries had been obtained for red-throated loons and 2 for arctic loons (Jonkel 1979). As of 1981, 624 common loons had been banded, with 82 recoveries (Clapp et al. 1982). This 13 percent recovery rate is appreciably higher than might have been expected for a protected species that has little contact with humans.

For grebes the information is little better. Fjelds a's (1973b) rather indirect calculation of an approximate 50 percent adult mortality (and recruitment) rate in the horned grebe seems to be the only available estimate of adult survivorship for grebes. Horned grebes and eared grebes account for the largest numbers of grebes banded

Table 25: Life History Data for Representative Loons, Grebes, and Auks

Species	Annual Adult Survival (%)	Maximum Known Longevity (yr)	Age at First Breeding (yr)	Modal Clutch	References
Loons					
Common	? > 80 <sup>a</sup>	7	2–3 (?)	2	Clapp et al. 1982
Arctic	89	28	2–3 (?)	2	Nilsson 1977
Red-throated	? > 85 <sup>a</sup>	23	2–3 (?)	2	Bauer and Glutz 1966
Grebes					
Eared	?	5	1	3	Clapp et al. 1982
Horned	ca. 50	6	1	4	Fjelds� 1973b
Great crested	? 45–50 <sup>a</sup>	9	2 (?)	4	Cramp and Simmons 1977
Auks					
Cassin auklet	83	5	2–3	1	Speich and Manuwal 1974
Black guillemot	80–85	17	2–3	2	Glutz and Bauer 1982
Common murre	87.0–93.7	32	4–5	1	Glutz and Bauer 1982
Razorbill	89–92	25	4–6	1	Glutz and Bauer 1982
Atlantic puffin	95.0–95.2	18	4–6	1	Glutz and Bauer 1982

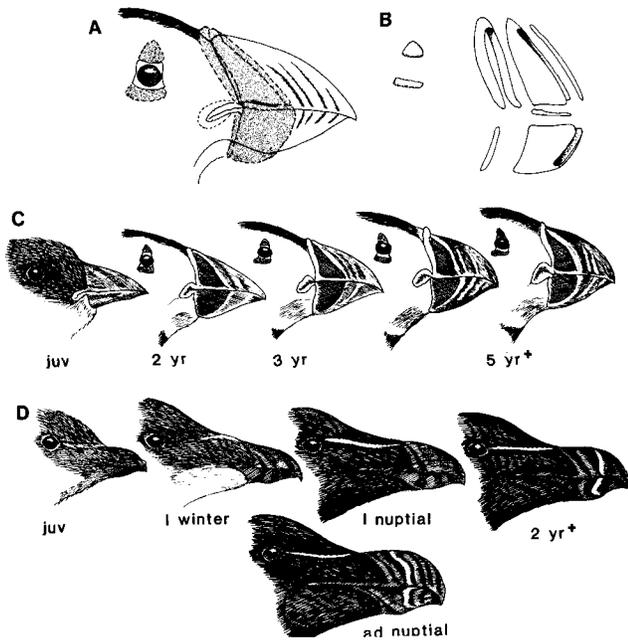
<sup>a</sup>See figure 29.

in North America; as of November 1, 1984, there had been 69 recoveries of banded horned grebes and 57 recoveries of eared grebes. Maximum survival after banding was about 5 years for the horned grebe and 6 years, 1 month for the eared grebe. Additionally, there had been 55 recoveries of western grebes, with a maximum survival after banding of almost 8 years. There have been 8 recoveries of red-necked grebes, with a maximum survival of 4 years after banding (Bird Banding Laboratory records, Patuxent, Maryland). Compared with the loons, where the recovery rates have averaged more than 10 percent, grebe recovery rates in North America of about 2.5 percent are relatively low. Although inadequate to construct life tables, these data do not suggest high survival rates for the grebes, and the maximum record of survival in grebes seems to be one of 9 years, 8 months for a great crested grebe (Rydzewski, cited in Cramp and Simmons 1977).

As with loons, there is still some uncertainty about the age of initial reproduction in grebes. In the case of the great crested grebe, which is certainly the best-studied grebe species, it is known that young birds acquire their nuptial plumage in their first year. They may also pair and seem to be capable of breeding by then, at least in years when the population has been depressed following a severe winter (Simmons 1955, 1974). However,

first-year birds may be unsuccessful at breeding because of competition with older and more experienced birds. Fjelds  (1973c) thus observed that some presumed "first-year" horned grebes gave up sustained attempts to establish territories and finally moved elsewhere. On the other hand, those "first-year" birds that were members of a flock before the breakup of ice at the nesting sites exhibited a productivity level almost as high as in "old" birds.

Clutch sizes in grebes tend to vary considerably around a mean rather than being somewhat rigidly fixed as in loons and alcids. In the great crested grebe the usual clutch is of 3 or 4 eggs in Britain, although clutches of 2 or 5 are not infrequent (Simmons 1974). A similar finding seems typical of Europe and southern Africa, though there may be significant local differences in average clutch size from site to site or year to year in the same general area (Cramp and Simmons 1977; Dean 1977). Fjelds  (1973c) found that clutch sizes of horned grebes in favorable (fertile) habitats were larger than those in food-poor and infertile lakes and ponds, and he also reported that "old" pairs of horned grebes nesting on traditional sites had an average clutch size of 4.89 eggs, while the mean clutch of "first-year" birds was only 3.62 eggs. There may also be a gradual reduction in average clutch size through the breeding season, which



27. Bill characteristics of Atlantic puffin and razorbill: A, B, deciduous portions of the rhamphotheca; changes in bill with age in C, the Atlantic puffin and D, razorbill. After Glutz and Bauer 1982.

may well reflect smaller clutches in second breeding cycles. Second broods constitute about 1–5 percent of the total broods in Great Britain and Lower Saxony, and such second broods average considerably smaller than first broods (Zang 1977).

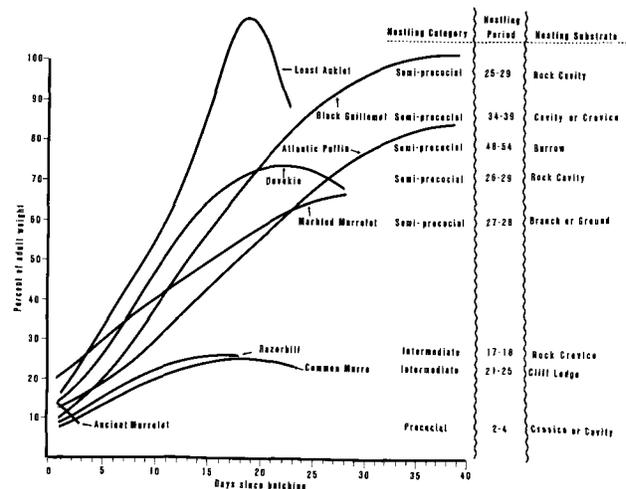
Grebes vary greatly in their relative coloniality, with eared and western grebes being examples of highly colonial species and the pied-billed grebe an example of a highly territorial species. Fjelds  (1973c) reported that in Iceland the horned grebe's relative territoriality was inversely correlated with abundance of food; thus congregations of grebes in infertile and food-poor lakes resulted in such adverse effects of high territorial conflict as highly asynchronous egg laying and correspondingly reduced fecundity.

These two major variations, of clutch size and of relative territoriality, may be important devices for grebes in terms of their reproductive adaptations. Other important mechanisms that might also be important in Simmons's (1974) view include a limited degree of asynchronous hatching of the young so that the first- and second-hatched chicks have improved chances of survival, brood division of the young by the two adults, with consequent reduced food competition within the family, and a capacity for re-nesting and sometimes also for double brooding. There may also be a favoring of

specific chicks by each parent for receiving limited food, while others may receive little or none, and asynchronous hatching may give adults the option of taking a reduced brood away from the nest and abandoning some viable eggs if food is limited. Some additional reproductive adaptations, such as the prolonged dependence of young grebes on their parents, no doubt help to increase chances of survival while the young are learning to forage for themselves.

Life history data are generally far better for the alcids than for the loons and grebes, largely because they are much easier to capture on their nesting sites. As a result, a considerable amount of survival and longevity information is available (table 25), which strongly suggests that alcids are among the longest-lived of any North American birds, sometimes attaining adult mortality rates of less than 10 percent per year. Lloyd (1974) noted that British razorbills had an adult annual mortality rate of only 11 percent, and the sample of 626 birds included an individual with a maximum longevity of 20 years following banding as an adult. A very similar annual adult mortality rate of 12 percent was calculated by Birkhead (1974) for British common murre. Even lower adult mortality rates of about 5 percent were estimated by Ashcroft (1979) for British puffins, although she also estimated a very high overall mortality rate of about 85–90 percent between fledging and probable initial breeding at 4 years of age.

The relatively long 4 to 6-year period to reproductive maturity in such species as puffins, razorbills, and



28. Comparative chick-growth characteristics of various auks. Mainly after Glutz and Bauer 1982, with addition of least auklet (Byrd and Knudtson 1978), ancient murrelet (Sealy 1976), and marbled murrelet (Simons 1980).

murre is of special interest, and at least in the case of puffins and razorbills it is accompanied by fairly conspicuous age-related differences in the size and appearance of the bill. These differences might be important bases for age estimation and individual recognition between mates or potential mates, and they also have relevance in human estimates of age in these species. Bill features in puffins are fairly indicative of age up to the fifth or sixth year of life (Peterson 1976), and similar progressive changes are evident in the razorbill for the first several years (fig. 27).

In all the alcids the newly hatched young are very similar in appearance and slightly resemble downy

loons (see fig. 49). In contrast, grebe chicks usually are patterned with stripes and spots, especially on the head region. They typically also have bare spots on the head that are variably colorful and quite possibly serve as important signals between parents and offspring (see plate 11). One of the major ways the alcids differ among themselves is in the length of the nesting period, which ranges from a minimum of 2 or 3 days in some murrelets to 50 days or more in the puffins. On this basis the alcids can be classified as precocial (the nidifugous species whose young leave the nest almost immediately) to semiprecocial (the species whose young remain in the nest until they are nearly ready to fly). Intermediate sit-

Table 26: Biological Traits of the North American Auks

Species	Relative Hatching Weight (% of adults)	Age of Initial Thermoregulation (days)	"Fledging" Weight <sup>a</sup> (g)	Age of Sexual Maturity (yr)	Maximum Known Longevity <sup>b</sup>
Dovekie	13.4	?	114.3 (71.4%)	2	9 yr
Common murre	9.6	9–10	200 (19%)	4–5	32 yr
Thick-billed murre	11.0	9–10	260 (26%)	4–5 (?)	22 yr, 8 mo
Razorbill	9	3–4	140 (20.4%)	4–6	25 yr
Black guillemot	9.4	3–4	384 (89%)	2–3	17 yr
		(brooded 5–6)			
Pigeon guillemot	9.2	3–5	411 (91%)	2–3 (?)	9 yr, 3 mo
Marbled murrelet	11.7	1–2	157 (70%)	?	—
Kittlitz murrelet	11	?	?	?	—
Xantus murrelet	17.3	2	?	?	—
Craveri murrelet	?	2	?	?	—
Ancient murrelet	15	2	26 (12.6%)	?	5 yr
Cassin auklet	10.6	5–6	150 (90%)	2–3	5 yr, 8 mo
Parakeet auklet	9.8	ca. 3	223 (78%)	3	—
		(brooded to 6)			
Least auklet	ca. 9	ca. 5	81 (88%)	2–3	—
Whiskered auklet	16.5	?	?	?	—
Crested auklet	10.2	ca. 3	228 (80%)	2–3	—
Rhinoceros auklet	11.5	ca. 4	357 (69%)	?	6 yr, 2 mo.
		(range 0–9)			
Tufted puffin	7.8	5–6	561 (70.4%)	4–5	—
Atlantic puffin	9.4	6–7	283 (59%)	4–6	20 yr, 2 mo
Horned puffin	7.9	6	407 (68%)	4–5	—

NOTE: Adapted primarily from Thoresen, in press, and Sealy 1972, 1973b.

<sup>a</sup>Percentages of average adult weight in parentheses. "Fledging" refers to nest departure rather than flight attainment.

<sup>b</sup>Noncaptive. After Glutz and Bauer 1982 and Clapp et al. 1982.

uations also exist, as in the murre and razorbill. In the ancient murrelet, and probably also in the Xantus and Craveri murrelets, the newly hatched young are not fed at all by the adults, and the chicks lose weight until they leave the nest and make their way to sea (fig. 28). Young murre and razorbills are fed by both parents until they reach approximately one-fourth of the adult weight, at which time they too flutter down from their nesting ledges and take to the ocean, approximately 3 weeks after hatching. In the largest number of species, including the puffins, guillemots, auklets, dovekie, and marbled and Kittlitz murrelets, the nestling period is typically at least 4 weeks, and the young attain a weight ranging in various species from about half of adult weight to full adult weight before leaving the nest site. Such a prolonged nestling period obviously is advantageous to the young in keeping them safe from preda-

tors, chilling, and other hazards associated with early sea life, but it places considerable strain on the parents to carry enough food to maintain them. Thus among the small murrelets only the species that have precocial young regularly have clutches of two eggs; among the alcids with semiprecocial young only the guillemot species normally have two eggs, with one-egg clutches the norm for all the rest. The evolution of special throat pouches for carrying food has apparently promoted the evolution of a prolonged nestling period in the small auklets, whereas the precocial murrelet species tend to attain thermal regulation remarkably soon after hatching (table 26), in conjunction with their extremely short nestling periods.

The relative length of the nestling period in alcids is highly variable (tables 27 and 28) and is probably influenced by a wide variety of ecological factors, including

Table 27: Nest, Egg, and Nestling Traits of the North American Auks

Species	Nesting Site	Usual Clutch Size	Relative Egg Weight (%) <sup>a</sup>	Incubation Period (days)	Nestling Type	Nestling Period (days)
Dovekie	Cavity, crevice	1	15.0	29	Semiprecocial	26–29
Common murre	Ledge	1	10.8	33	Intermediate	25
Thick-billed murre	Ledge	1	11.3	32	Intermediate	23
Razorbill	Ledge, crevice, cavity	1	12.5	37	Intermediate	18
Black guillemot	Cavity, burrow, surface	2	12.5	30	Semiprecocial	34–39
Pigeon guillemot	Cavity, burrow, surface	2	12.5	30	Semiprecocial	35
Marbled murrelet	Tree crotch, ground	1	16.2	ca. 30	Semiprecocial	28
Kittlitz murrelet	Rocky tundra	1	15.2	?	Semiprecocial	ca. 21?
Xantus murrelet	Crevice, cavity, ground	2	23.7	31–33	Precocial	3–4
Craveri murrelet	Crevice, cavity	2	23.7	ca. 32	Precocial	2–4
Ancient murrelet	Burrow, crevice	2	22.0	34	Precocial	2–3
Cassin auklet	Burrow	1	16.8	38	Semiprecocial	41
Parakeet auklet	Cavity, crevice	1	13.0	35	Semiprecocial	35
Least auklet	Cavity, crevice	1	19.0	31–36	Semiprecocial	29
Whiskered auklet	Cavity, crevice	1	21.4	35–36	Semiprecocial	30+
Crested auklet	Cavity, crevice	1	14.2	36–41	Semiprecocial	34
Rhinoceros auklet	Burrow	1	14.8	45	Semiprecocial	42–60
Tufted puffin	Burrow, crevice	1	11.4	45	Semiprecocial	42–50
Atlantic puffin	Burrow, crevice	1	11.8	46	Semiprecocial	48–52
Horned puffin	Usually crevice	1	9.5	42	Semiprecocial	36–42

NOTE: Adapted in part from Sealy 1972, 1973b and Thoresen, in press.

<sup>a</sup>Expressed in percentages of adult weight as estimated by Thoresen, in press.

Table 28: Reproductive Traits of Alcids That May Influence the Length of the Fledging Period

Coloniality	Clutch Size	Adult Foraging Ecology	Foods and Feeding of Chicks	Diurnality; Nest Visibility	Chick Feeding Rates	Ratio of Fledging to Incubation	Species
Coastal, colonial	One-egg clutches	Larger offshore fish eaters	<i>Long foraging flights, one fish/load</i>	Diurnal; <i>exposed</i>	3-8 <i>food flights/day</i>	ca. 70	Murres
			Mostly shorter foraging flights; Several fish/load	Diurnal; <i>exposed</i>	2-5 <i>food flights/day</i>	ca. 50	Razorbill
				Diurnal; <i>hidden</i>	5-6 <i>food flights/day</i>	ca. 100	Puffins
	Two-egg clutches	Smaller offshore plankton eaters	Plankton carried to young in throat pouches	Nocturnal; <i>hidden</i>	1-2 <i>food flights/night</i>	120-50	Rhinoceros auklet
				Variable; <i>hidden</i>	Feeding rates Variable	ca. 100	Dovekie, small auklets
	Inland, solitary	One-egg clutches	Inshore foragers; mostly small shoal fish eaten	Short foraging flights; one fish/load	Diurnal; <i>hidden</i>	Up to 16 <i>food flights/day</i>	115-70
Chick diet unknown				Nocturnal; <i>hidden</i>	<i>Chicks not fed at nest</i>	ca. 10	Ancient, Craveri, Xantus murrelets

NOTE: Traits in italics are those that are likely to favor increased precocity (reduced fledging/incubation period ratio) in species.

the number and length of food-carrying trips adults can make each day (or night) to feed their young, the amount of food they can carry on each trip, the relative vulnerability of the chicks at the nest to predators, the total length of the season suitable for rearing young at the nest, and the competition between chicks (in cases where two are hatched) for being fed. Some species such as the rhinoceros auklet have seemingly extended the nestling period far longer than might be expected, in conjunction with relatively slow growth rates in the chicks, while others such as several murrelets have evolved an absolute minimum nestling period in favor of taking the young to water and to begin feeding them at offshore foraging areas.

Sealy (1972) summarized data supporting the view that nest site tenacity, which is typical of alcids, is probably adaptive inasmuch as it allows experienced birds to occupy known nest sites as early as possible in the breeding season. He listed known cases of nest site

retention for seven species of alcids, including instances when the same site was used for as many as four successive seasons. He also pointed out that available sex-ratio data suggest that adult sex ratios in alcids approach equality, thus reducing competition for mates. He further noted that diurnality and nocturnality differences in alcid attendance at the colonies are marked, but that their biological significance is unknown though certainly complex. For some species, such as plankton feeders, it may be related to the diel cycles of prey availability rather than being solely a means of diurnal predator avoidance, which has often been offered as an explanation. However, predation certainly plays a role in the diel cycles of some species, and it is likely that the nocturnal egress of alcid chicks to sea is adaptively related to avoidance of such diurnal predators as gulls.

Sealy also pointed out that in alcids there is a correlation between breeding dispersion and food supplies,

in that those species (such as guillemots and the two *Brachyramphus* species) that nest solitarily, or nearly so, tend to be inshore feeders, whereas colonial nesters typically forage far from shore. However, the presence of safe nesting sites is probably the major factor affecting relative coloniality, and limitation of acceptable nesting spaces (narrow cliff ledges, talus slopes, soil suitable for burrowing) is also likely to have profound effects on local nesting distribution. Obviously, broad controls on distribution and abundance of alcids are determined by general availability of food resources; this is evident from the apparent relation between oceanic productivity levels and the locations of extremely large alcid colonies, as shown in chapter 1.

Average durations of incubation between nest reliefs by the mate, and of intervals between successive visits to the nest with food for the young, are related to the distance the adults must fly for food and the ease with which it can be gathered. Sealy has pointed out that these intervals are shortest in the diurnal, inshore-foraging guillemots and longest in the nocturnal, offshore-foraging ancient murrelet. In most other species the incubation shifts usually occur at 24-hour intervals, although during brooding of the young this pattern is markedly altered and feeding is much more frequent.

The egg characteristics of the alcids also exhibit a number of interesting attributes (table 29). As might be expected, cliff-nesting and highly colonial species of alcids lay heavily spotted eggs that are probably less visible than unspotted eggs and may also aid individual egg recognition by adults (Tschanz 1959). However, spotted eggs also rather inexplicably (perhaps atavistically) are laid by such crevice nesters as Xantus, Craveri, and ancient murrelets as well as by the more diversely nesting guillemots. These three murrelets also lay the relatively heaviest eggs of all the alcids, and their newly hatched young are likewise among the heaviest relative to adult weight (tables 26 and 27). This is of course related to the precocity of their young, and the fact that they are apparently not fed by their parents before leaving the nest site. The stress of laying such large eggs is magnified because in these species the usual clutch size is two eggs laid, at least in the case of the ancient murrelet, about 7 days apart (Sealy 1976). In *Cepphus* the rather typical occurrence of two-egg clutches is probably related to the inshore foraging behavior of guillemots and their corresponding ability to make numerous foraging trips each day for their young. Single-egg clutches apparently are typical of younger birds, probably those breeding for the first time, and it is probably adaptive that such inexperienced birds have only one offspring per pair to brood and feed efficiently. Egg

Table 29: Typical Nesting Sites and Egg Patterns of Alcids in North America

Nesting Habitat	Breeding Species		Egg Pattern or Color
	Pacific Coast	Atlantic Coast	
Mature forests	Marbled murrelet (N) <sup>a</sup>		Spotted
Rocky tundra	Kittlitz murrelet		Spotted
Cliff ledges	Common murre	Common murre	Spotted
	Thick-billed murre	Thick-billed murre	Spotted
Ledges or crevices		Razorbill	Spotted
Soil burrows	Tufted puffin	Atlantic puffin	White
	Rhinoceros auklet (N)		White
Rock crevices	Horned puffin		White
	Xantus murrelet (N)		Spotted
	Craveri murrelet (N)		Spotted
Talus cavities	Parakeet auklet	Dovekie	Bluish white
	Cassin auklet (N)		White
	Whiskered auklet (N)		White
	Crested auklet		White
	Least auklet		White
Cavities or burrows	Ancient murrelet (N)		Spotted
	Pigeon guillemot	Black guillemot	Spotted

<sup>a</sup>(N) indicates a nocturnally active species.

shape in alcids also varies considerably and is obviously related to the danger of rolling.

### Reproductive Success

Information on relative breeding success under varying ecological conditions and at different times provides important clues to optimum breeding conditions and maximum tolerance limits of various species, and it may also allow for determination of recruitment rates for a species, which can be compared against survival rates and thus used to project population trends.

Reproductive success in at least three loon species seems to be positively correlated with lake size (table 30). It appears that the red-throated loon is highly adapted for breeding on small water areas of generally

Table 30: Loon Breeding Densities and Breeding Success Rates Reported for Various-Sized Lakes

Species and Lake Area (ha)	Total Pairs	Hectares per Pair	Fledged Young	Nesting Success <sup>a</sup>	Young per Pair	Fledging Success
Red-throated loon <sup>b</sup>						
1	193	2.1	79	—	0.41	—
1–5	59	7.7	23	—	0.39	—
5	35	—	4	—	0.11	—
Total or average	278	—	106	47.8%	0.37	63.4%
Arctic loon <sup>c</sup>						
200	385	96 <sup>e</sup>	106	—	0.28	—
200–1,000	105	—	53	—	0.50	—
1,000	213	160 <sup>f</sup>	60	—	0.28	—
Total or average	703	—	219	—	0.31	—
Common loon <sup>d</sup>						
500	9	35	2	—	0.22	—
500–4,000	88	53	43	—	0.49	—
4,000	187	111	71	—	0.76	—
Total or average	284	—	116 <sup>g</sup>	57.7%	0.41	94.4%

<sup>a</sup>Percentage of all nesting pairs having young, including possible renesting efforts.

<sup>b</sup>Adapted from Bundy 1976, 1978 for Shetland Islands, 1973, 1974, and 1976.

<sup>c</sup>Adapted from Andersson et al. 1980 for Sweden, 1971–73.

<sup>d</sup>Adapted from McIntyre 1975 for various areas in Minnesota (tables 15 and 23).

<sup>e</sup>Based on reported usage of available waters of that size range; midpoint of range assumed as average water area.

<sup>f</sup>Based on a sample of eight lakes for varying numbers of years.

<sup>g</sup>Data did not distinguish young according to age; number thus includes unfledged young.

less than 5 hectares, and these birds also seem to attain their highest average number of fledged young per pair on such small waters. Bundy (1978) estimated that the average territory size of red-throated loons on larger waters is only about 0.5 hectare, while on smaller waters of up to 1.0 hectare the entire area is defended. On the other hand, the highest nesting success in the arctic loon, based on Swedish data, seems to be on lakes ranging in size from 200 to 1,000 hectares. Territories in this species tend to be considerably larger than in red-throated loons. They were estimated by Lehtonen (1970) to range from 100 to 150 hectares in Finland, and they ranged from 43 to 96 hectares in Norway according to Dunker (1974). In the common loon territories are extremely large and may range from areas less than 10 hectares in the bays of some lakes to entire lakes of 40 hectares or more (Olson and Marshall 1952). Reproductive success as well as overall usage by this species ap-

parently increases with increasing lake size (tables 30 and 31). Sawyer (1979) found that in Maine only 8 percent of the loon usage was on lakes up to 40 hectares, while 56 percent of the total loon usage was on lakes larger than 200 hectares (500 acres). Similarly, lakes up to 10 hectares had only 18.8 percent utilization, those of 40 to 100 hectares had over 80 percent utilization, and those over 100 hectares had over 90 percent utilization (Cross 1979). Likewise, McIntyre found that about half of all Minnesota lakes surveyed that were larger than 4 hectares had resident pairs, but almost 80 percent of those larger than 20 hectares had resident pairs. She judged that from 40 to 80 hectares are typically needed per resident pair, with birds on smaller lakes using adjacent water areas for supplemental feeding.

The average number of young fledged per breeding pair of loons generally ranges from as little as 0.3 in some years and areas to as high as 0.8 in others, but in

Table 31: Reported Loon Densities in Various Regions

Species	Density (ha/pair)	Reference
Red-throated loon		
Shetland Islands (3 areas)	118–28 (avg. 124) <sup>a</sup>	Merrie 1978
Northern Alaska (5 years)	125–67 (avg. 146) <sup>a</sup>	Bergman and Derksen 1977
Arctic loon		
Western Alaska (2 years)	20–65 <sup>a</sup> (avg. 42.5) <sup>a</sup>	Petersen 1979
Finland	100 <sup>a</sup>	Lehtonen 1970
Northern Alaska (2 years)	125 <sup>a</sup>	Bergman and Derksen 1977
Sweden (8 lakes >10 km <sup>2</sup> )	100–500 (avg. 160) <sup>b</sup>	Andersson et al. 1980
Arctic and red-throated		
Scotland and Hebrides (5 areas)	275–3,033 (avg. 1,268) <sup>a</sup>	Merrie 1978
Common loon		
North America (5 areas)	39–502 (avg. 196) <sup>b</sup>	Table 37
Yellow-billed loon		
Northern Alaska	2,000 <sup>a</sup>	Derksen, Roth, and Eldridge 1981

<sup>a</sup>Includes both water and associated land areas.

<sup>b</sup>Includes water areas only.

general seems to average about 0.4–0.5 per nesting pair (table 30). This means an average egg or chick mortality between laying and fledging of 75–80 percent, much of which seems to occur before hatching (table 32). Loon eggs are often lost because of water fluctuation or wave action, and predation by mammalian and avian predators is frequently significant. Losses during the egg stage are partially compensated for by replacement clutches in loons, at least in more southerly populations. In Minnesota up to two replacement clutches have been reported for common loons (Olson and Marshall 1952; McIntyre 1975). Bundy (1976) estimated that 14 of 22 pairs of red-throated loons he studied in the Shetland Islands laid replacement clutches, and Lehtonen (1970) stated that 7 of 85 Finnish clutches he observed were replacement clutches. However, the incidence of renesting in these species in high-arctic areas appears to be very low or nil (Bergman and Derksen

1977), and very probably the same is true of the yellow-billed loon, which is exclusively a high-arctic breeder.

Compared with loons, there is relatively little information on reproductive success rates in grebes. Some of the best data are on the great crested grebe, as summarized by Cramp and Simmons (1977). One national sample of 431 pairs raised an average of 1.3 young per pair, while another British sample of 169 pairs produced an average of 1.5 reared young per pair. This compares with a general European average of 2.1 young raised per pair. A breeding success of 1.3 young per pair would mean a recruitment rate of 39 percent (assuming all pairs attempted to breed), while an average fledged brood size of 2.1 per pair would represent a recruitment rate of 68 percent. An average of these two extremes would be a 53 percent recruitment rate, which perhaps provides a very rough approximation of productivity (and mortality) rates in this species. Simmons (1974) judged that great crested grebes normally attempt to raise only a single brood, but that something less than 5 percent of the pairs raised second broods, which would tend to increase overall recruitment rates slightly. Similar rates of double brooding have been found in Germany (Zang 1977). Reproductive success data for other species of grebes, including the North American species, are equally scanty and difficult to interpret. Probably the best available data are those of Fjelds  (1973b) for the horned grebe, summarized in part in table 33. He studied the success of 721 nests, established the exact fate of some 1,332 eggs in 339 nests, and estimated an overall hatching success of 63.2 percent of all eggs laid, plus a 75.5 percent nesting-success rate. Nesting success was higher for “old” females than for “first-year” birds and was also greatly affected by nest placement, with nests around sedge-fringed islets much more successful than nests close to shore. Nest desertion in dense colonies was also an important aspect of nesting success. Survival of young to 60 days after hatching (or to fledging) averaged 1.93 young per successful pair, or an approximate 49 percent recruitment rate, assuming a nest failure rate of 25 percent. This approximates Fjelds ’s estimate of an approximate 50 percent annual mortality rate, which he based on an estimated 4.1 percent monthly disappearance rate of adults during his period of observation. Fjelds  judged that second broods were too rare to affect overall productivity, since the few cases he observed (9 clutches) were probably all too late to produce any fledged young. Apparently most of the chick mortality in Fjelds ’s study area occurred during the first 20 days following hatching, after which there were no more significant losses before fledging.

An approximate 50 percent hatching-to-fledging survival rate seems to be fairly typical of other grebes as

Table 32: Sources of Nest or Egg Failure in Loons

	Common Loon			Arctic Loon
	Maine <sup>a</sup>	New Hampshire <sup>b</sup>	Saskatchewan <sup>c</sup>	Finland <sup>d</sup>
Total nests (or eggs)	51 (nests)	130 (nests)	424 (eggs)	159 (eggs)
Total losses	18 (35.3%)	83 (63.8%)	261 (61.7%)	72 (45.3%)
Predation losses				
Mammals (raccoons)	1	35	—	—
Birds (gulls, crows, ravens)	1	4	27	31
Unknown or other sources	—	—	119	6
Eggs lost or abandoned				
Water levels or waves	8	12	59	1
Other weather effects	2	—	—	—
Eggs lost from nest	—	—	15	—
Human or dog harassment	5	6	—	26
Unknown or other causes	1	17	18	—
Eggs inviable or infertile	—	9	23	10
Cause of loss unreported	—	—	—	14

<sup>a</sup>Sawyer 1979.   <sup>b</sup>Sutcliffe 1979b.   <sup>c</sup>Fox, Young, and Sealy 1980.   <sup>d</sup>Lehtonen 1970.

well, judging from information summarized by Fjelds  for the little grebe, red-necked grebe, and eared grebe over various parts of their ranges. This seems appreciably lower than the brood-rearing efficiency of loons. However, because of their larger average clutch sizes, the number of grebe chicks fledged per successful pair usually approximates two, while in loons the average brood size of fledged young is about half that.

There also seems to be a fairly high incidence of nest failure in grebes (table 33), though the data supporting this view are still rather limited. There may be a somewhat higher incidence of re-nesting following nest failure in grebes than in loons; Fjelds  (1973c) reported that some pairs of horned grebes he studied laid as many as four clutches, and the same may also be true of red-necked grebes (Palmer 1960). Replacement clutches have also been reported for eared, pied-billed, and western grebes, and multiple broods are a regular feature of least grebes (Palmer 1960).

Reproductive success rates in the alcids (tables 34–36) do not seem to differ much between the cliff-nesting forms and those that nest in burrows or rock cavities. For the cliff-nesting murre and razorbill, all of which

have one-egg clutches, there appear to be rather substantial variations in hatching success rates but relatively high fledging success for those chicks that do hatch successfully. Egg replacement is certainly regular in these ledge-nesting forms; Tuck (1960) estimated that in a population sample of about 400 pairs of thick-billed murre at Cape Hay egg loss was continuous during the entire egg-laying period, with some 44 percent of the sample losing at least one egg during a 32 day period. Thirty percent of the pairs laid one replacement egg, 11 percent laid two replacements, and the remaining 3 percent deserted or did not lay again. Approximately 1.6 eggs were produced per nesting pair. Gaston and Nettleship (1981) reported a much lower rate of re-laying and a considerably higher nesting success at Prince Leopold Island. However, studies of the cliff-nesting murre and razorbill generally support the view that about 0.5–0.7 young per pair are typically fledged by these species. Fledging in these species occurs only about 3 weeks after hatching, however, and undoubtedly much additional juvenile mortality occurs in the first summer of life. Thus estimated breeding success rates are certainly several times higher than actual fall recruitment rates,

Table 33: Nesting Losses in Various North American Grebes

	Pied-billed Grebe <sup>a</sup>	Western Grebe <sup>b</sup>	Western Grebe <sup>c</sup>	Horned Grebe <sup>d</sup>	Horned Grebe <sup>e</sup>
Total nests	138	516	—	—	721
Total eggs	—	—	224	637	1,332
Hatched					
Nests	97 (70.4%)	353 (68.4%)	47 (10.9%)	—	75.5%
Eggs	—	—	—	30.3%	850 (63.2%)
Mortality sources					
Eggs inviable	—	—	—	—	—
Deserted	—	17 (3%)	10 (4.5%)	2%	27 (2.0%)
Depredation					
Humans	—	—	—	—	181 (13.6%)
Predators	ca. 7.5%	31 (6%)	89 (39.7%)	38%	93 (7.7%)
Other Losses					
Fell into water	—	—	—	—	17 (1.3%)
Disappeared	—	—	—	18%	20 (1.5%)
Wave action or water levels	ca.15%	111 (22%)	67 (29.9%)	12%	95 (7.1%)
Miscellaneous	—	4 (1%)	11 (4.9%)	—	9 (0.6%)

<sup>a</sup>Glover 1953.  
<sup>c</sup>Fjeldså 1973b.

<sup>b</sup>Nuechterlein 1975.

<sup>c</sup>Lindvall and Low 1982 (known-fate nests only).

<sup>d</sup>Ferguson and Sealy 1983.

judging from known adult mortality rates in murrelets and razorbills.

For the cavity- and burrow-nesting puffins, rather similar results seem to be typical. Single-egg clutches are likewise the rule, and probably a low rate of egg replacement is required in these species because of their protected nest sites. Hatching success rates seem in general to exceed 50 percent, but fledging success rates seem to average somewhat lower than in the cliff nesters. Perhaps this is a reflection of their generally longer fledging periods, which are approximately twice as long as in the ledge nesters. The productivity of successful adults is remarkably similar in all four species and approximates 0.3 fledged young per nesting pair.

The data for the guillemots are of special interest, since they typically have two-egg clutches rather than single-egg clutches as do most alcids (table 36). Studies of three species in North America suggest a rather con-

sistently high hatching success of about 50 percent (lower in one area of high disturbance in Quebec) and a fledging success rate of from about 50 to 90 percent, resulting in a typical overall reproductive success of about 0.4–0.8 fledged young per nesting pair. Preston (1968) estimated the adult survival rate of banded birds in the population he studied at about 80 percent, which would obviously require an annual recruitment rate of 20 percent to maintain. Even with a substantial postfledging mortality this should be quite feasible, assuming (as Preston estimated) that the actual breeding population represents about half of the total summering population. Indeed, with an average annual production of 0.73 fledged young per nesting pair and a nonbreeding component of 50 percent, the recruitment rate would be approximately 18 percent, very close to Preston's estimated annual mortality rate for this population.

There is still relatively little information on the re-

Table 34: Average Breeding Success Rates of Dovekie, Razorbill, and Murres

	Dovekie <sup>a</sup>	Razorbill <sup>b</sup>	Thick-billed Murre <sup>c</sup>	Common Murre <sup>d</sup>
Total number of pairs	—	—	—	486
Total number of eggs	98	170	2,015	—
Eggs produced per pair	—	—	1.05	—
Number of eggs hatched	64	143	1,587	392
Hatching success	65.3%	84%	78.8%	80.7%
Number of chicks fledged	50–62	138	1,420	349
Percentage fledging success	80–95%	96.5%	89.5%	89.0%
Estimated breeding success <sup>e</sup>	32–62%	81.1%	70.5%	71.8%
Fledged young per nesting pair	est 0.3–0.6	est. 0.8	0.75	0.72

<sup>a</sup>Data from Spitsbergen, 1974–75 (Stempniewicz 1981a).

<sup>b</sup>Data from Kandalaksha Bay, 1957–59 (Bianki 1977).

<sup>c</sup>Data from Prince Leopold Island, 1975–77 (Gaston and Nettleship 1981).

<sup>d</sup>Data from Skomer Island, 1973–75 (Glutz and Bauer 1982).

<sup>e</sup>Hatching success x fledging success.

productive success rates of the small auklets, but what is available indicates rather marked locational or yearly variations in both hatching and fledging success rates (table 36). It is obviously dangerous to generalize much from these limited data, but they suggest a rather low rate of overall reproductive success that perhaps ranges about from 0.3 to 0.5 fledged young per nesting pair. Except for the Cassin auklet, there are probably no opportunities for renesting in these primarily high-arctic forms. Further, at least in the Cassin auklet there is also a substantial “floater” population that is unable to

breed because of territorial defense of limited suitable nesting sites (Manuwal 1974b). In this species such “floaters” compose about half the total nonbreeding population, representing a productivity loss roughly comparable to 15 percent of that of the total breeding population. The estimated annual adult mortality rate of this population is 17 percent. Replacing these losses would require an annual productivity of 0.5 fledged young per pair, assuming a total nonbreeding (floater and immature) component of about 30 percent of the total population and postfledging mortality rates approx-

Table 35: Average Breeding Success Rates of Puffins and Rhinoceros Auklet

	Rhinoceros Auklet N (# studies)	Tufted Puffin N (# studies)	Atlantic Puffin N (# studies)	Horned Puffin N (# studies)
Number of burrows with eggs	—	723 (13)	552 (4)	222 (9)
Percentage of burrows with eggs	63.6%	57.3%	—	—
Number of eggs hatched	132 (4)	367 (12)	347 (4)	168 (12)
Percentage hatching success	71–91% (5)	55.9%	62.8%	75.7%
Number of chicks fledged	82 (4)	181 (12)	180 (4)	60–61 (6)
Percentage fledging success	62.1%	48.4%	51.9%	46%
Fledged young per pair	0.38 (2)	0.29 (11)	0.33 (4)	0.31 (5)
Estimated breeding success <sup>a</sup>	44–56%	27.1%	32.6%	34.8%

NOTE: Adapted from tables 49–52 in Wehle 1980, using comparable numerical data from various studies.

<sup>a</sup>Hatching success x fledging success (should approximate percentage of nesting pairs fledging young).

Table 36: Average Breeding Success Rates for Guillemots and Small Auklets

Species and Location	Hatching Success	Fledging Success	Overall Success	References
<b>Black guillemot</b>				
Kent Island, Maine	52.4% (44/84) (1.83 eggs/nest)	50% (22/44)	26.2% (22/84) <sup>a</sup> (0.47 young/pair)	Winn 1950
Kent Island, Maine	55.8% (353/633) (1.56 eggs/nest)	88.7% (142/160)	42.1% (142/337) <sup>a</sup> (0.73 young/pair)	Preston 1968
Quebec (3 areas)	32–66% (1.88 eggs/nest)	59–71%	19.5–46.9% <sup>b</sup> (0.38–0.97 young/pair)	Cairns 1980
<b>Pigeon guillemot</b>				
Washington	53.8% (42/78)	86% (50/58)	46.3% <sup>b</sup>	Thoresen and Booth 1958
<b>Cassin auklet</b>				
Farallon Islands	—	—	69% (0.69 young/pair)	Manuwal 1972
Farallon Islands	33% (25/75)	64.5%	26.6% (20/75) <sup>a</sup> (0.27 young/pair)	Thoresen 1964
<b>Parakeet auklet</b>				
Saint Lawrence Island	67.7% (21/31)	76.2% (16/21)	51.6% <sup>b</sup> (0.52 young/pair)	Sealy and Bedard 1973
<b>Least auklet</b>				
Buldir Island	67.8% (19/28)	75% (9/12)	43% (9/21) (0.43 young/pair)	Byrd and Knudtson 1978
Saint Lawrence Island	60%	34%	20.4% <sup>b</sup> (0.2 young/pair)	Searing 1977
<b>Whiskered auklet</b>				
Buldir Island	86% (6/7)	100% (3/3)	75% (3/4) <sup>a</sup>	Byrd and Knudtson 1978
<b>Crested auklet</b>				
Buldir Island	76% (45/59)	66.7% (14/21)	40% (14/35) <sup>a</sup>	Byrd and Knudtson 1978
Saint Lawrence Island	30%	—	—	Searing 1977

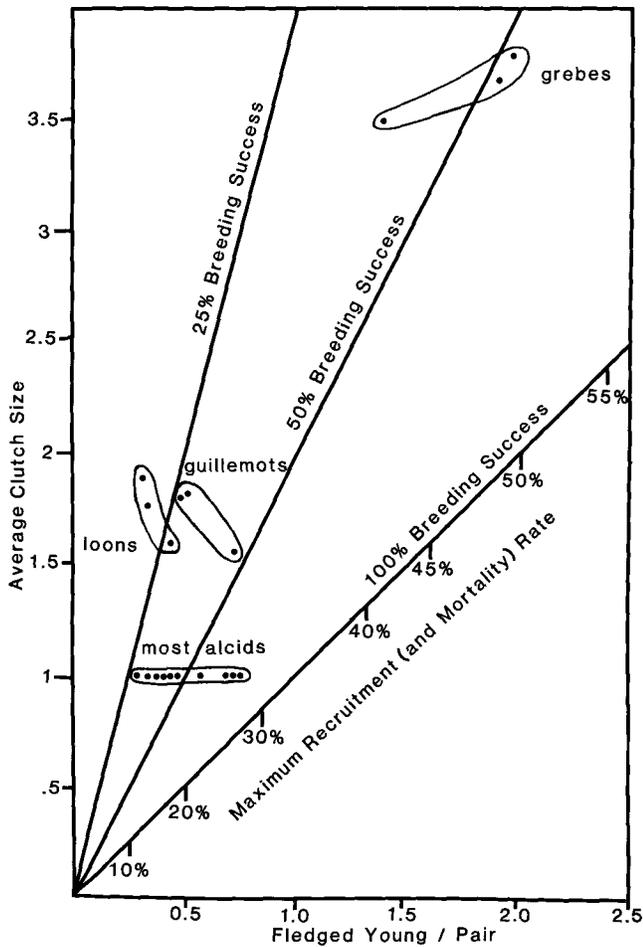
<sup>a</sup>Percentage of known-fate eggs producing fledged chicks.

<sup>b</sup>Estimated breeding success (hatching success x fledging success), assuming no re-nesting efforts.

imating those of adults. Thus, estimates of 0.3 to 0.5 fledged young per pair may not be too far from the mark for the small cavity-nesting auklets, depending on actual adult mortality rates and the incidence of non-breeders in the population.

In summary, it seems that rather different reproductive strategies have evolved among the loons, grebes,

and auks (fig. 29). Most alcids have evolved a one-egg clutch, a highly variable nestling period depending largely upon the ease with which food can be brought to the nestling for feeding, and a relatively high overall breeding success rate that reflects intense biparental care of a single egg or nestling. Guillemots (and a few murrelets) have evolved two-egg clutches. In the murre-



29. Comparative breeding success rates of loons, grebes, and auks, based on various literature sources as cited in the text.

lets this is related to the fact that the young are highly precocial and leave the nest before any parental feeding is required. In the guillemots the larger clutch size seems to occur because adult foraging is exclusively in-shore, usually within a few kilometers of the nest, and the young are fed on fairly easily captured bottom-dwelling prey. These conditions allow the guillemots to "gamble" on a slightly larger clutch and the possibility of at least occasionally raising two young per season rather than a single chick. Loons similarly have two-egg clutches, but their breeding success averages about half that of guillemots, with most losses occurring during the egg stage, since the eggs are greatly exposed to environmental dangers. Only with high adult survival rates in excess of 80 percent can the loons "afford" such a breeding strategy. Finally, the grebes have the relative advantages of fairly large clutch sizes, repeated re-nesting efforts, and occasional double or multiple brooding, the last depending on the length of the breeding season. With all these advantages, they enjoy the highest recruitment rates of any of the three groups considered here and thus can sustain populations even with substantial adult mortality rates of about 50 percent annually. It seems quite possible that the northern breeding limits of grebes may well be affected by such considerations as opportunities for re-nesting or double brooding, whereas southern breeding limits in loons seem to be influenced by the distribution of large oligotrophic lakes offering adequate food supplies. Such lakes are virtually all of glacial origin (Dunker 1974), thus restricting the loons to northerly distributions and re-nesting opportunities that range from limited to nil.