Chapter 3

Comparative Reproductive Ecology of the Auks (Family Alcidae) with Emphasis on the Marbled Murrelet

Toni L. De Santo[1, 2] **S. Kim Nelson**[1]

Abstract: Marbled Murrelets (*Brachyramphus marmoratus*) are comparable to most alcids with respect to many features of their reproductive ecology. Most of the 22 species of alcids are colonial in their nesting habits, most exhibit breeding site, nest site, and mate fidelity, over half lay one egg clutches, and all share duties of incubation and chick rearing with their mates. Most alcids nest on rocky substrates, in earthen burrows, or in holes in sand, around logs, or roots. Marbled Murrelets are unique in choice of nesting habitat. In the northern part of their range, they nest on rocky substrate; elsewhere, they nest in the upper canopy of coastal coniferous forest trees, sometimes in what appear to be loose aggregations. Marbled Murrelet young are semi-precocial as are most alcids, yet they hatch from relatively large eggs (relative to adult body size) which are nearly as large as those of the precocial murrelets. They also share with precocial murrelets an early age of thermoregulation, as indicated by a short brooding period. Hatching success in monitored Marbled Murrelets nests was somewhat lower and fledging success was markedly lower than for other alcids. The lower rate of reproduction was attributed in part to egg and chick predation. Marbled Murrelet young raised in forest nests may incur additional mortality on their trips from inland nest sites to the ocean. El Niño effects may also decrease productivity in this species. To document murrelet reproduction more fully, further study of individually marked, breeding Marbled Murrelets and their young conducted during periods without El Niño influences is needed.

The family Alcidae is composed of 22 living species of marine diving birds representing 12 genera (*table 1*). These birds, commonly referred to as auks, murres, guillemots, murrelets, auklets, and puffins, inhabit oceans of the Northern Hemisphere (Nettleship and Evans 1985; Udvardy 1963). Although seabird research is logistically difficult, much information has been gathered on the reproductive biology of alcids. Such research has been facilitated by the colonial nature of most species and by the accessibility of some breeding areas to scientists (Birkhead 1985). Thorough reviews have been published on nearly half of the species. For instance, Birkhead (1985), Gaston (1985), Harris and Birkhead (1985), Hudson (1985), and Nettleship and Evans (1985) present reviews of the reproductive biology of Atlantic alcids (Dovekie, Razorbill, Common Murre, Thick-billed Murre, Black Guillemot, Atlantic Puffin, and the extinct Great Auk [*Plautus impennis*]). Reviews of four auks that breed on the Farallon Islands in the Pacific Ocean (Common Murre, Pigeon Guillemot, Cassin's Auklet, Rhinoceros Auklet, and Tufted Puffin) are presented by Ainley (1990), Ainley and others (1990a, b, c) and Boekelheide and others (1990). Four inshore fish feeding alcids of the northern Pacific Ocean (Kittlitz's Murrelet, Pigeon Guillemot, Spectacled Guillemot, and Marbled Murrelet) are reviewed by Ewins and others (1993) (also see Marshall 1988a for a review of the Marbled Murrelet). The Ancient Murrelet, another inhabitant of the northern Pacific Ocean, has been reviewed by Gaston (1992).

Alcids that nest in small, loosely-aggregated colonies, as isolated pairs, or in areas less accessible to researchers, have not been well studied. For instance, the reproductive biology of Craveri's and Kittlitz's murrelets and Spectacled Guillemots is largely unknown. Although Marbled Murrelets have received considerable attention during the last two decades, the reproductive ecology of this species is not well understood. Unlike many other alcids, Marbled Murrelets do not nest in conspicuous colonies on cliffs, in rock crevices, or in burrows in the ground. Instead, this species nests on the alpine tundra or in the upper canopy of old-growth coniferous trees (Hamer and Nelson, this volume b; Marshall 1988a). Additionally, Marbled Murrelets are secretive around their nests and active during low light periods at dawn and dusk. Consequently, few nests have been located and observed, and few quantitative data have been collected.

This paper summarizes the reproductive ecology of the auk family and specifically compares Marbled Murrelets to the other alcids. Such a comparison may allow for a better understanding of the reproductive strategy of Marbled Murrelets and should provide useful information for conservation and management of this species.

Nest Sites and Coloniality

The nest sites of all alcids have been described, although few nests of some species have been located (e.g., Kittlitz's and Marbled murrelets). Murres and Razorbills nest primarily on cliff ledges or in crevices or caves. The nests of Common and Thick-billed murres are in the open whereas those of Razorbills are typically partially or fully enclosed (Byrd and others 1993; Harris and Birkhead 1985). Puffins and Rhinoceros Auklets nest in burrows they excavate. Additionally, nests of these species are found in rock crevices (Tufted and Horned, on the level ground of forested islands (Rhinoceros Auklet), and among boulders and rocks of islands lacking soft substrate for burrowing (Atlantic Puffin) (Byrd and others 1993; Hatch and Hatch 1983). The guillemots nest in cracks and crevices of cliffs, among stones or boulders, in

[1] Research Wildlife Biologists, Oregon Cooperative Wildlife Research Unit, Oregon State University, Nash 104, Corvallis, OR 97331-3803

[2] Current address: Postdoctoral Research Associate, Pacific Northwest Research Station, USDA Forest Service, 2770 Sherwood Lane, Suite 2A, Juneau, AK 99801-8545

Table 1—Extant members of the family Alcidae

Common name(s)	Scientific name[a]
Dovekie (Little Auk)	*Alle alle*
Razorbill (Razorbill Auk)	*Alca torda*
Common Murre (Common Guillemot)	*Uria aalge*
Thick-billed Murre (Brunnich’s Guillemot)	*Uria lomvia*
Black Guillemot	*Cepphus grylle*
Spectacled Guillemot (Sooty Guillemot)	*Cepphus carbo*
Pigeon Guillemot	*Cepphus columba*
Marbled Murrelet	*Brachyramphus marmoratus*
Kittlitz’s Murrelet	*Brachyramphus brevirostris*
Xantus’ Murrelet	*Synthliboramphus hypoleucus*
Craveri’s Murrelet	*Synthliboramphus craveri*
Ancient Murrelet	*Synthliboramphus antiquus*
Japanese Murrelet (Crested Murrelet)	*Synthliboramphus wumizusume*
Crested Auklet	*Aethia cristatella*
Least Auklet	*Aethia pusilla*
Whiskered Auklet	*Aethia pygmaea*
Cassin’s Auklet	*Ptychoramphus aleuticus*
Parakeet Auklet	*Cyclorrhynchus psittacula*
Rhinoceros Auklet (Horn-billed Puffin)	*Cerorhinca monocerata*
Tufted Puffin	*Fratercula cirrhata*
Horned Puffin	*Fratercula corniculata*
Atlantic Puffin	*Fratercula arctica*

[a]Nomenclature according to American Ornithologists’ Union (1983)

abandoned burrows, on covered ledges, or in self-excavated holes (Ewins and others 1993; Harris and Birkhead 1985). Nests of Dovekies are found most often in cracks in cliffs and among boulders (Harris and Birkhead 1985). Parakeet, Crested, Whiskered, and Least auklets nest under rocks in talus fields, whereas Cassin’s Auklets excavate burrows in the soil (Springer and others 1993). The Synthliboramphus murrelets (Xantus’, Craveri’s, Ancient, and Japanese) nest in existing holes and hollows around tree roots, logs, or under rocks, or in crevices. Additionally, Japanese and Ancient murrelets may nest in self-excavated holes (Springer and others 1993). Kittlitz’s Murrelets nest in the open on rocky ground. Marbled Murrelets nest in the open on rocky ground in the northern part of their range. In the southern part of their range, they nest on the large limbs of old-growth coniferous trees in forests up to 40 km from the ocean (Hamer and Nelson, this volume b; Marshall 1988a).

Alcids are highly social birds, and most species are colonial in their nesting habits (*table 2*). Nineteen of the 22 species can be found nesting in colonies consisting of 10 to several thousand pairs. Craveri’s Murrelets probably nest in loose aggregations and as scattered pairs. The Kittlitz’s Murrelet is the only species considered to be truly non-colonial (i.e., nesting only as isolated pairs).

Marbled Murrelets have been described as solitary (Gaston 1985) and loosely colonial (Divoky and Horton, this volume), and may nest solitarily in some areas, but in loose aggregations in others. Simons (1980) reported a ground nest that appeared to be a solitary nest. There is also strong indirect evidence that murrelets nest in loose aggregations. In Washington and Oregon, two concurrently active nests were located 100 and 30 m apart, respectively, within a forest stand (Hamer and Cummins 1991; Nelson, pers. obs.). In addition, in Oregon, multiple nests have been found in each of three trees located in different stands, and four trees within a small area (40-m radius) were found to contain nests (Nelson and others 1994). It is not known, however, if these nests were active concurrently.

Breeding Site, Nest Site, and Mate Fidelity

Studies of individually marked birds have provided information on the degree of breeding site and mate fidelity exhibited by alcids. Strong breeding site fidelity has been documented in the 15 species of alcids for which this aspect of reproductive ecology has been adequately investigated (Divoky and Horton, this volume) (*table 2*). For example, 96 percent of Common Murres at one colony returned to breed at the same colony site the following year, and 90 percent used the same nest site (Birkhead 1976 as cited by Hudson 1985). Similarly, Ashcroft (1979) as cited by Harris and Birkhead (1985) reported that 92 percent of Atlantic Puffins

Table 2—Breeding site fidelity, mate fidelity, and degree of coloniality in the alcids

Species	Breeding site fidelity	Mate fidelity	Degree of coloniality
Dovekie[1]	yes	yes	small to large colonies, scattered pairs
Razorbill[2]	yes	probably	small to large colonies
Common Murre[3]	yes	probably	small to large colonies
Thick-billed Murre[4]	probably	?	small to large colonies
Black Guillemot[5]	yes	yes	small to large colonies, loose aggregations, scattered pairs
Spectacled Guillemot[6]	?	?	small to medium colonies, solitarily
Pigeon Guillemot[7]	yes	probably	small, loose aggregations, medium colonies, isolated pairs
Marbled Murrelet[8]	probably	?	probably in loose aggregations; probablysolitarily
Kittlitz's Murrelet[9]	possibly	?	solitarily
Xantus' Murrelet[10]	yes	yes	small to large colonies
Craveri's Murrelet[11]	probably	probably	probably in loose aggregations and scattered pairs
Ancient Murrelet[12]	yes	possibly	small to large colonies
Japanese Murrelet[13]	?	?	small to medium colonies
Crested Auklet[14]	yes	yes	small to large colonies
Least Auklet[15]	yes	yes	small to large colonies
Whiskered Auklet[16]	?	?	small to medium colonies
Cassin's Auklet[17]	yes	probably	small to large colonies
Parakeet Auklet[18]	yes	?	small, loose to large colonies
Rhinoceros Auklet[19]	yes	?	small to large colonies, solitarily
Tufted Puffin[20]	yes	?	small to large colonies
Horned Puffin[21]	yes	?	large colonies
Atlantic Puffin[22]	yes	yes	small to large colonies

[1]Reviewed by Birkhead (1985), Freethy (1987), Harris and Birkhead (1985), Nettleship and Evans (1985); Evans (1981), Norderhaug (1968)

[2]Reviewed by Birkhead (1985), Freethy (1987), Hudson (1985), Nettleship and Evans (1985); Lloyd (1976)

[3]Reviewed by Birkhead (1985), Freethy (1987), Harris and Birkhead (1985), Hudson (1985), Nettleship and Evans (1985); Sowls and others (1980), Speich and Wahl (1989)

[4]Reviewed by Birkhead (1985), Harris and Birkhead (1985), Hudson (1985), Nettleship and Evans (1985)

[5]Reviewed by Birkhead (1985), Freethy (1987), Harris and Birkhead (1985), Hudson (1985), Nettleship and Evans (1985)

[6]Reviewed by Birkhead (1985), Ewins and others (1993)

[7]Reviewed by Birkhead (1985), Emms and Verbeek (1989), Ewins (1993); Ainley and others (1990b), Sowls and others (1980), Speich and Wahl (1989)

[8]Reviewed by Birkhead (1985), Ewins and others (1993); Divoky and Horton (this volume), Nelson and others (1994), Simons (1980), Strong and others (in press)

[9]Reviewed by Birkhead (1985); Day and others (1983), Naslund and others (1994)

[10]Reviewed by Birkhead (1985); Carter and McChesney (1994), Murray and others (1983), Sowls and others (1980), Springer and others (1993)

[11]Reviewed by Birkhead (1985); DeWeese and Anderson (1976)

[12]Reviewed by Birkhead (1985), Gaston (1992); Gaston (1990), Springer and others (1993)

[13]Reviewed by Birkhead (1985); Springer and others (1993)

[14]Reviewed by Birkhead (1985), Freethy (1987); Bédard (1969b), Jones (1993a), Konyukhov (1990a), Sealy (1968), Springer and others (1993)

[15]Reviewed by Birkhead (1985); Bédard (1969b), Jones I. (1992, 1993b), Jones and Montgomerie (1991), Roby and Brink (1986), Sealy (1968), Springer and others (1993)

[16]Reviewed by Birkhead (1985); Byrd and Gibson (1980), Byrd and others (1993), Springer and others (1993)

[17]Reviewed by Birkhead (1985); Ainley and others (1990a), Emslie and others (1992), Sowls and others (1980), Speich and Manuwal (1974), Speich and Wahl (1989), Springer and others (1993), Vermeer and Lemon (1986)

[18]Reviewed by Birkhead (1985), Freethy (1987); Bédard (1969b), Sealy (1968), Springer and others (1993)

[19]Reviewed by Ainley and others (1990c), Birkhead (1985); Byrd and others (1993), Sowls and others (1980), Speich and Wahl (1989), Wehle (1980)

[20]Reviewed by Ainley and others (1990c), Birkhead (1985), Byrd and others (1993); Sowls and others (1980), Speich and Wahl (1989), Wehle (1980)

[21]Reviewed by Birkhead (1985), Byrd and others (1993); Wehle (1980)

[22]Reviewed by Birkhead (1985), Harris and Birkhead (1985), Nettleship and Evans (1985)

returned to breed in the same burrow in consecutive years. Two studies reported at least 70 percent of Black Guillemots returned to use the same nest sites within the same nest colonies year after year (Asbirk [1979] and Petersen [1981], as cited by Harris and Birkhead 1985). Murray and others (1983) observed that 64 percent of Xantus' Murrelets retained the same nest sites for two years, and Roby and Brink (1986) found that 91 percent of Least Auklets used the same nest entrance in two consecutive years.

At least six alcids show mate fidelity (*table 2*). Divorce rates have been reported to be approximately 24 percent for Crested Auklets (Jones 1993a) and approximately 7 percent for Black Guillemots and Atlantic Puffins. These figures were confirmed by Harris and Birkhead (1985). Emslie and others (1992) have shown that mate retention has a positive influence on reproduction of Cassin's Auklets; both fledging and breeding success were higher for pairs that practiced mate retention.

No studies have been conducted on individually marked, breeding Marbled Murrelets, but indirect evidence suggests that they show both mate and breeding site fidelity. Murrelets are primarily observed in groups of two throughout the year, and many groups include a male and female (Carter 1984, Sealy 1975c). Strong and others (1993) observed at-sea groups of murrelets in spring and summer and reported that of 4918 groups, 55 percent consisted of pairs. The possibility exists that these twosomes were mated pairs, although without observations of marked birds this is speculative. Marbled Murrelet activity has been documented in the same forest stands for periods up to 18 years (Divoky and Horton, this volume), and murrelet nests have been found in the same trees (Nelson and others 1994; Nelson and Peck, in press; Singer and others, in press), and on the same general location of tundra (Simons 1980), in consecutive years. These observations suggest breeding site fidelity. Reuse of nests has recently been documented for the ground nesting Kittlitz's Murrelet, a close relative of the Marbled Murrelet (Naslund and others 1994).

Adult Life History Characteristics

Historically, the Great Auk, which became extinct in the 1800s, was the largest member of the Alcidae, ca. 5 kg (Harris and Birkhead 1985). At present, the murres are the largest alcids (ca. 1 kg). Fifteen alcids are small by comparison, having body masses less than half that of the murres (*table 3*). The Marbled Murrelet has a mass of 220 g, approximately 22 percent that of the murres.

Adult annual survival has been estimated for ten species (*table 3*). The lowest estimates of this population parameter are 75 percent reported for both the Least Auklet, the smallest alcid (ca. 85 g), and 77 percent for the Ancient Murrelet, a relatively small alcid (ca. 200 g), (*fig. 1*, $r^2 = 0.45$, $P < 0.05$). The larger alcids, Common and Thick-billed murres, Razorbills, and Atlantic Puffins (ca. 1004, 941, 620, and 460 g, respectively), have higher survival estimates ranging from 89 to 94 percent.

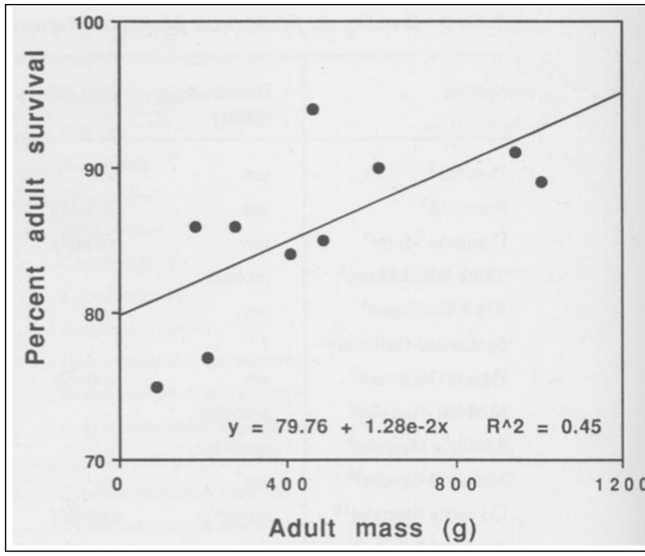

Figure 1—Relationship between mean adult body mass and percent annual adult survival for ten alcids (see *table 3* for values).

Adult annual survival has not been measured for Marbled Murrelets. However, based on the relationship between adult body mass and annual survival (*fig. 1*), Marbled Murrelets (ca. 220 g) are predicted to have an annual adult survival of 83 percent, comparable to alcids of similar size (i.e., the Ancient Murrelet, ca. 206 g, 77 percent survival, or the Crested Auklet, 272 g, 86 percent survival).

Alcids are considered long-lived although this life history aspect has not been well studied. Longevity of several individuals of several species has been documented from recovery of marked birds or their bands. Values range from 5 years for an Ancient Murrelet to 32 years for a Common Murre (*table 3*). Values determined from band returns may be indicative of band longevity, not bird longevity. These values should, therefore, be considered minimums (see Clapp and others 1982 for discussion). It is not known how long Marbled Murrelets live; no reports of recovered banded birds have been made.

Alcids exhibit deferred maturity with most species beginning to breed between 2 and 8 years of age (*table 3*). It is not known at what age Marbled Murrelets begin to breed, but an estimate of 2 to 4 years is reasonable based on information available for other alcids.

At least several alcid species breed annually once they reach sexual maturity (*table 3*). For example, over 80 percent of Least Auklets (Jones 1992) and 90 percent of Xantus' Murrelets (Murray and others 1983) bred in consecutive years. Cassin's Auklet is the only alcid known to lay a second clutch following the rearing of their first brood (Ainley

Table 3—Size, survival, longevity, age of first reproduction, and breeding frequency of adult alcids

Species	Mean body mass (g)[a]	Annual Survival of adults (pct.)	Longevity (yr)[b]	Age first reproduction	Breeding frequency
Dovekie[1]	164	?	?	?	1/season
Razorbill[2]	620	90	6, 6, 30	4-6	1/season
Common Murre[3]	1004	89	20, 26, 32	4-6	1/season
Thick-billed Murre[4]	941	91	22	?	?
Black Guillemot[5]	406	84	12, 20	2-8+	most annually and 1/season
Spectacled Guillemot[6]	490	?	?	?	50 pct. annually
Pigeon Guillemot[7]	487	80-90	9, 11, 14+	3-4	1/season and probably not every year
Marbled Murrelet[8]	221	?	?	?	?
Kittlitz's Murrelet[9]	224	?	?	?	?
Xantus' Murrelet[10]	167	?	9	?	most annually and probably 1/season
Craveri's Murrelet[11]	151	?	?	?	?
Ancient Murrelet[12]	206	77	5	3-4	1/season
Japanese Murrelet[13]	183	?	?	?	?
Crested Auklet[14]	272	86	?	possibly 3	1/season
Least Auklet[15]	86	75	4.5 predicted	3	most annually and 1/season
Whiskered Auklet[16]	121	?	?	?	1/season
Cassin's Auklet[17]	177	86	5, 10, 20	2-4	1-2/season
Parakeet Auklet[18]	297	?	?	?	1/season
Rhinoceros Auklet[19]	533	?	6, 7	?	probably 1/season
Tufted Puffin[20]	773	?	6	?	?
Horned Puffin[21]	612	?	?	?	?
Atlantic Puffin[22]	460	94	13, 20	3-8+ (most at 5)	probably breed annually and 1/season

[a]Adult mass prior to chick rearing used for Ancient Murrelet, Crested Auklet, Least Auklet, Cassin's Auklet, and Atlantic Puffin; includes both males and females

[b]Observed longevity of ringed or banded birds unless otherwise stated

[1]Reviewed by Harris and Birkhead (1985); Norderhaug (1980)

[2]Harris and Birkhead (1985), Hudson (1985); Clapp and others (1982), Freethy (1987), Klimkiewicz and Futcher (1989), Lloyd (1979)

[3]Reviewed by Harris and Birkhead (1985), Hudson (1985); Boekelheide and others (1990), Clapp and others (1982)

[4]Reviewed by Harris and Birkhead (1985), Hudson 1985); Clapp and others (1982)

[5]Reviewed by Hudson (1985); Ainley and others (1990b), Clapp and others (1982), Cairns (1981, 1987), Divoky (1994, pers. comm.)

[6]Reviewed by Dunning (1992); Kitaysky (1994)

[7]Reviewed by Ewins (1993), Kuletz (1983); Ainley and others (1990b), Clapp and others (1982), Klimkiewicz and Futcher (1989), Nelson (1987), Ewins and others (1993)

[8]Sealy (1975a,c)

[9]Sealy (1975b)

[10]Klimkiewicz and Futcher (1989), Murray and others (1983)

[11]Reviewed by Dunning (1992)

[12]Clapp and others (1982), Gaston (1990), Gaston and Jones (1989), Jones (1990), Sealy (1975c, 1976), Vermeer and Lemon (1986)

[13]Kuroda (1967), Ono (1993)

[14]Bédard (1969b), Jones (1992, 1993a), Piatt and others (1990)

[15]Bédard (1969b), Jones (1992, 1993b, 1994), Piatt and others (1990), Roby and Brink (1986)

[16]Reviewed by Dunning (1992); Ainley and others (1990a), Knudtson and Byrd (1982)

[17]Ainley and others (1990a), Clapp and others (1982), Jones P. (1992), Gaston (1992), Klimkiewicz and Futcher (1989), Manuwal (1979), Speich and Manuwal (1974), Thorensen (1964), Vermeer and Cullen (1982)

[18]Ainley and others (1990a), Bédard (1969b), Sealy (1972)

[19]Ainley and others (1990c), Clapp and others (1982), Klimkiewicz and Futcher (1989)

[20]Klimkiewicz and Futcher (1989), Sealy (1972), Vermeer and Cullen (1979)

[21]Sealy (1973c)

[22]Reviewed by Harris and Birkhead (1985), Hudson (1985); Barrett and Rikardsen (1992), Clapp and others (1982), Harris and Hislop (1978), Klimkiewicz and Futcher (1989), Kress and Nettleship (1988), Nettleship (1972)

and others 1990a; Manuwal 1979). Within and between year breeding frequencies for Marbled Murrelets are unknown.

The Egg and Incubation

Most alcids, including Marbled Murrelets, lay a clutch consisting of one egg (*table 4*). The guillemots and the *Synthliboramphus* murrelets typically have clutch sizes of two.

Alcid eggs range in size from less than 20 g to over 100 g (*table 4*) and vary in proportion to adult mass (*fig. 2*, r^2 = 0.92, $P < 0.001$). Alcid egg masses typically represent between 10 and 23 percent of the laying female's body mass (*table 4*) with the precocial species laying the heaviest eggs relative to adult body size. Marbled Murrelet eggs (ca. 35 g) at 18 percent of adult body mass are also large.

The duties of incubation are shared by both members of the breeding pair (*table 5*). Incubation shifts can be as short as several hours (e.g., Pigeon and Black guillemots) or as lengthy as several days (e.g., Xantus', Ancient, and Japanese murrelets) (*table 5*). Incubation is completed within 27 and 45 days (*table 5*). Overall, there is no significant correlation between incubation period and egg mass (*fig. 3*, r^2 = 0.10, P = 0.21). The eggs of four of the larger alcids (Rhinoceros Auklet and Tufted, Horned, and Atlantic puffins), however, require up to 45 days of incubation, while the small eggs of the Least Auklet are incubated for a much shorter period of time (ca. 30 days).

Nine species of alcids are known to leave their eggs unattended for periods of 1 to 19 days, particularly during the early stages of incubation (*table 5*). Egg neglect is common in Xantus' (Murray and others 1983) and Ancient murrelets (Gaston and Powell 1989) occurring at nearly half of the nests studied. Egg neglect can lengthen the period from laying to hatching (Gaston and Powell 1989; Murray and others 1983; Sealy 1984), but can decrease the total number of days of actual incubation necessary (see Murray and others 1983).

Compared to other alcids, Marbled Murrelets have a short incubation period (ca. 27-30 days) (*table 5*). Parents exchange incubation duties every 24 hours (*table 5*), typically during pre-dawn hours (Naslund 1993a, Nelson and Hamer, this volume a; Nelson and Peck, in press; Simons 1980). Simons (1980) noted a one-day period of egg neglect early in incubation at an exposed ground nest of a Marbled Murrelet. Additionally, at three tree nests, eggs were left unattended for up to 4 hours during the day and evening (Naslund 1993a; Nelson and Hamer, this volume a; Nelson and Peck, in press). It is not known if egg neglect occurs commonly at Marbled Murrelet nests, but other alcid species which lay their eggs in open nests (e.g., Common and Thick-billed murres; see Gaston and Nettleship 1981) do not frequently leave their nests unattended.

Average hatching success exceeds 70 percent for over half of the 19 alcids for which this parameter has been measured (*table 6*). The lowest value (33 percent) was reported for Xantus' Murrelets nesting on islands with high rates of mouse predation (Murray and others 1983). Avian and mammalian predation have been cited as a cause for clutch loss in other studies as well (Birkhead and Nettleship 1981; Drent and others 1964; Emms and Verbeek 1989; Evans 1981; Ewins and others 1993; Gilchrist 1994; Harfenist 1994; Jones 1992; Piatt and others 1990; Sealy 1982; Thorensen 1964; Vermeer and Lemon 1986). Additional causes of hatching failure include infertility and embryo death (Evans 1981; Knudtson and Byrd 1982; Thorensen 1964), mechanical destruction of eggs or nests (Birkhead and Nettleship 1981; Thorensen 1964), and adverse weather (reviewed by Harris and Birkhead 1985).

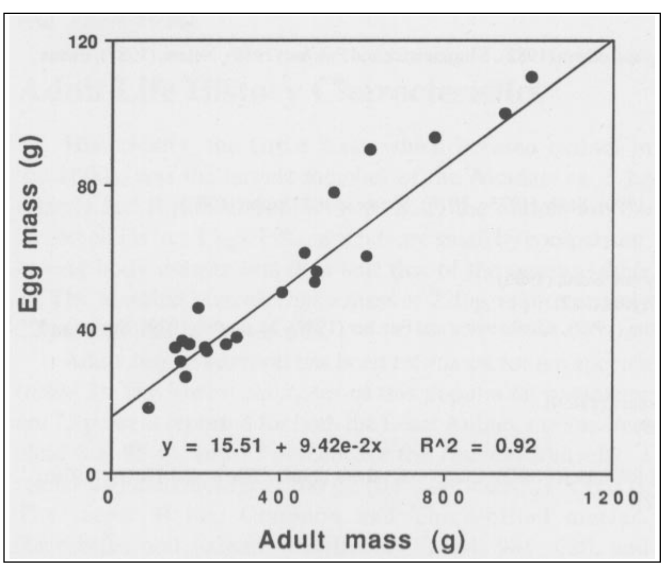

Figure 2—Relationship between mean adult body mass and mean egg mass for 21 alcids (see *tables 3* and *4* for values).

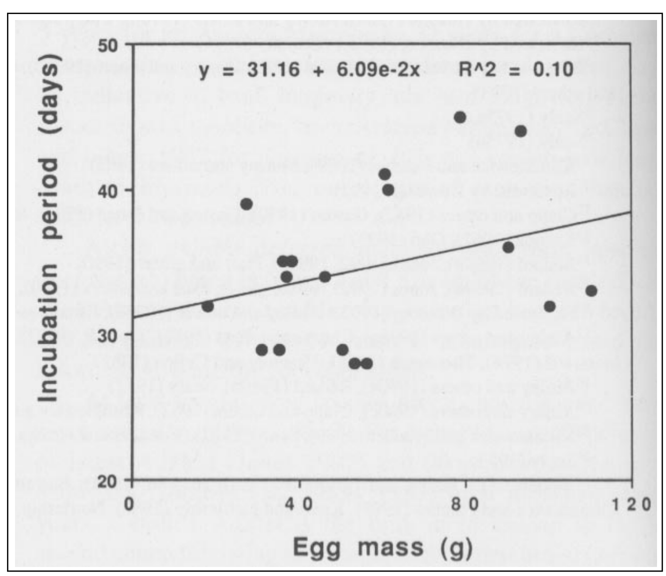

Figure 3—Relationship between mean egg mass and incubation period for 19 alcids (see *tables 4* and *5* for values).

Table 4—Egg size, relationship of egg mass to adult body mass and clutch size of alcids

Species	Mean egg mass (g)	Egg mass as pct. adult body mass	Clutch size range (average)
Dovekie[1]	31 (calculated)	19	1
Razorbill[2]	90	14	1
Common Murre[3]	ca. 110	12	1
Thick-billed Murre[4]	100	10-12	1
Black Guillemot[5]	50	12-13	1-2 (1.83)
Spectacled Guillemot[6]	56	11	1-2 (1.60)
Pigeon Guillemot[7]	53	11	1-2 (1.76)
Marbled Murrelet[8]	35	18	1
Kittlitz's Murrelet[9]	34	15	1
Xantus' Murrelet[10]	37	22	1-2 (1.70)
Craveri's Murrelet[11]	35	23	1-2 (1.88)
Ancient Murrelet[12]	46	22	1-2 (1.99)
Japanese Murrelet[13]	36	22	1-2 (1.80)
Crested Auklet[14]	36	14	1
Least Auklet[15]	18	22	1
Whiskered Auklet[16]	?	?	1
Cassin's Auklet[17]	27	16	1
Parakeet Auklet[18]	38	ca. 14	1
Rhinoceros Auklet[19]	78	ca. 15	1
Tufted Puffin[20]	93	12	1
Horned Puffin[21]	ca. 60	ca. 10	1
Atlantic Puffin[22]	61	ca. 13	1

[1]Reviewed by Harris and Birkhead (1985), Evans (1981)
[2]Reviewed by Harris and Birkhead (1985)
[3]Reviewed by Harris and Birkhead (1985)
[4]Reviewed by Harris and Birkhead (1985)
[5]Reviewed by Harris and Birkhead (1985); Cairns (1987), Divoky and others (1974)
[6]Reviewed by Ewins and others (1993); Kitaysky (1994), Thorensen (1984)
[7]Reviewed by Ewins (1993), Ewins and others (1993); Kuletz (1983), Nelson (1987)
[8]Hirsch and others (1981), Nelson and Hamer (this volume a), Sealy (1974, 1975b), Simons (1980)
[9]Reviewed by Day and others (1983); Sealy (1975b)
[10]Murray and others (1983)
[11]DeWeese and Anderson (1976), Schönwetter (1963)
[12]Reviewed by Gaston (1992); Gaston (1990), Gaston and Jones (1989), Jones (1992), Sealy (1975b, 1976), Vermeer and Lemon (1986)
[13]Ono (1993), Ono and Nakamura (1993), Schönwetter (1963)
[14]Reviewed by Jones (1993a); Bédard (1969b)
[15]Jones (1993b), Piatt and others (1990), Roby and Brink (1986)
[16]Freethy (1987), Williams and others (1994)
[17]Ainley and others (1990a), Manuwal (1979), Vermeer and Lemon (1986)
[18]Sealy (1972), Bédard (1969b)
[19]Ainley and others (1990c), Freethy (1987), Sealy (1972), Wilson and Manuwal (1986)
[20]Reviewed by Boone (1986); Ainley and others (1990c), Sealy (1972)
[21]Freethy (1987), Sealy (1972)
[22]Reviewed by Harris and Birkhead (1985)

Table 5—Incubation patterns of the alcids

Species	Incubating parent[a]	Incubation shift (hours)	Mean duration of incubation (days)[a]	Egg neglect
Dovekie[1]	both	12	29	?
Razorbill[2]	both	12-24	36	?
Common Murre[3]	both	12-24	33	probably not
Thick-billed Murre[4]	both	12-24	32	very infrequently
Black Guillemot[5]	both	ca. 1-3	29	yes
Spectacled Guillemot[6]	?	?	ca. 28	?
Pigeon Guillemot[7]	both	2-4 but up to 17	28	yes
Marbled Murrelet[8]	both	ca. 24	27-30 (probable range)	yes for several hrs to 1 day
Kittlitz's Murrelet[9]	?	?	?	?
Xantus' Murrelet[10]	both	24-144, most at 72	34	yes for 1-19 days
Craveri's Murrelet[11]	both	?	?	?
Ancient Murrelet[12]	both	48-120	34	yes for 1-3 days
Japanese Murrelet[13]	both	24-72	?	yes for 5 days
Crested Auklet[14]	both	?	35	possibly
Least Auklet[15]	both	24	32	yes
Whiskered Auklet[16]	both	24	ca. 35	?
Cassin's Auklet[17]	both	24	39	very infrequently
Parakeet Auklet[18]	both	?	35	?
Rhinoceros Auklet[19]	both	24	45	yes for 1-3 days
Tufted Puffin[20]	both	?	44	?
Horned Puffin[21]	?	?	41	?
Atlantic Puffin[22]	both	2-50	range 35-45	yes frequently

[a]Incubation refers to the period from clutch completion to egg hatching except for the Spectacled Guillemot for which this information was unavailable

[1]Reviewed by Harris and Birkhead (1985)

[2]Reviewed by Harris and Birkhead (1985)

[3]Reviewed by Harris and Birkhead (1985), Boekelheide and others (1990), Hatch and Hatch (1990a)

[4]Reviewed by Harris and Birkhead (1985), Hatch and Hatch (1990a)

[5]Reviewed by Harris and Birkhead (1985)

[6]Ritaysky (1994), Kondratyev (1994)

[7]Reviewed by Harris and Birkhead (1985), Ewins (1993); Ainley and others (1990b), Drent and others (1964)

[8]Carter (1984), Hirsch and others (1981), Naslund (1993a), Nelson and Hamer (this volume a), Nelson and Peck (in press), Sealy (1974, 1975a), Simons (1980), Singer and others (1991, in press)

[9]No information located

[10]Murray and others (1983)

[11]Reviewed by DeWeese and Anderson (1976)

[12]Reviewed by Gaston (1992); Gaston and Jones (1989), Gaston and Powell (1989), Sealy (1976, 1984)

[13]Ono and Nakamura (1993)

[14]Reviewed by Freethy (1987); Jones (1993a), Piatt and others (1990), Sealy (1984)

[15]Bédard (1969b), Knudtson and Byrd (1982), Piatt and others (1990), Roby and Brink (1986), Sealy (1984)

[16]Reviewed by Freethy (1987); Knudtson and Byrd (1982), Williams and others (1994)

[17]Reviewed by Manuwal and Thorensen (1993); Ainley and others (1990a), Manuwal (1974, 1979)

[18]Bédard (1969b), Sealy and Bédard (1973)

[19]Leschner (1976), Wilson and Manuwal (1986)

[20]Reviewed by Freethy (1987); Ainley and others (1990c), Boone (1986)

[21]Ainley and others (1990c), Leshner and Burrell (1977), Sealy (1973c)

[22]Reviewed by Harris and Birkhead (1985)

Table 6—Hatching and fledging success, number of young produced per breeding pair and juvenile survival for alcids

Species	Mean hatching success [a]	Mean fledging success[a,b]	Juvenile survival
	---percent---		
Dovekie[1]	65	77	?
Razorbill[2]	78	93	32
Common Murre[3]	79	88	30
Thick-billed Murre[4]	73	85	34
Black Guillemot[5]	66	68	27
Spectacled Guillemot[6]	?	?	?
Pigeon Guillemot[7]	70	67	?
Marbled Murrelet[8]	67	45	?
Kittlitz's Murrelet[9]	?	?	?
Xantus' Murrelet[10]	33	?	?
Craveri's Murrelet[11]	?	?	?
Ancient Murrelet[12]	91	>90	ca. 50
Japanese Murrelet[13]	50	76	?
Crested Auklet[14]	63	66	?
Least Auklet[15]	82	81	?
Whiskered Auklet[16]	86	100	?
Cassin's Auklet[17]	75	80	65
Parakeet Auklet[18]	65	?	?
Rhinoceros Auklet[19]	81	69	?
Tufted Puffin[20]	63	70	?
Horned Puffin[21]	76	70	?
Atlantic Puffin[22]	72	73	0.4-13.3 observed, 15-36 calculated

[a]Includes replacement eggs for Common Murre, Razorbill, Thickbilled Murre, and Pigeon Guillemot, and possibly for Black Guillemot, and Atlantic and Horned puffins; does not include second broods

[b]Fledging is defined as departure from the nest to the ocean

[1]Reviewed by Harris and Birkhead (1985); Evans (1981), Stempniewicz (1981)

[2]Reviewed by Harris and Birkhead (1985), Hudson (1985)

[3]Reviewed by Harris and Birkhead (1985), Hudson (1985); Ainley (1990), Boekelheide and others (1990), Murphy (1994); Hatch and Hatch (1990b); also see Byrd and others (1993)

[4]Reviewed by Harris and Birkhead (1985), Hudson (1985); Hatch and Hatch (1990b); also see Byrd and others (1993)

[5]Reviewed by Harris and Birkhead (1985), Hudson (1985); Cairns (1981), Divoky (1994, pers. comm.)

[6]No information located

[7]Reviewed by Ewins and others (1993); Ainley and others (1990b), Kuletz (1983), Nelson (1987); also see summary by Ewins (1993)

[8]Nelson and Hamer (this volume b)

[9]No information located

[10]Drost (1994), Murray and others (1983)

[11]No information located

[12]Gaston (1990, 1992), Rodway and others (1988), Vermeer and Lemon (1986)

[13]Ono (1993), Ono and Nakamura (1993)

[14]Knudtson and Byrd (1982), Piatt and others (1990), Sealy (1982); also see Jones (1993a)

[15]Jones (1992), Piatt and others (1990), Roby and Brink (1986), Sealy (1982); also see Jones (1993b)

[16]Knudtson and Byrd (1982), Williams and others (1994)

[17]Ainley and others (1990a), Manuwal (1979), Thorensen (1964), Vermeer and Cullen (1982), Vermeer and Lemon (1986)

[18]Sealy (1984)

[19]Vermeer and Cullen (1979), Watanuki (1987), Wilson and Manuwal (1986)

[20]Reviewed by Byrd and others (1993)

[21]Reviewed by Byrd and others (1993)

[22]Reviewed by Barrett and Rikardsen (1992), Harris and Birkhead (1985), Hudson (1985); Barrett and Rikardsen (1992), Nettleship (1972)

There is some indication that hatching success of the Marbled Murrelet is low compared to other alcids (Nelson and Hamer, this volume b). Combining observations throughout the range of the Marbled Murrelet, 67 percent (n = 20) of the eggs of 30 monitored nests successfully hatched. Egg predation was documented or strongly suspected to be the cause of failure for five of the 11 (45 percent) hatching failures (Nelson and Hamer, this volume b).

When the clutches of alcids are lost or fail to hatch, some species (e.g., Razorbills, Common and Thick-billed murres, Atlantic Puffins, and Black Guillemots [see Harris and Birkhead 1985 for review], Pigeon Guillemots [Ainley and others 1990b], Cassin's Auklets [Ainley and others 1990a; Manuwal 1979], Horned Puffins [Wehle 1983]) lay replacement eggs. Egg replacement in murres has been reported to be between 15 and 43 percent (reviewed by Boekelheide and others 1990; Byrd and others 1993). Ten percent of Cassin's Auklet pairs replaced naturally lost eggs, and 54 percent replaced eggs removed by researchers (Manuwal 1979). Hatching and fledging success of replacement clutches was often lower than first clutches (Ainley and others 1990a; Byrd and others 1993; Manuwal 1979; Murphy 1994). The incidence of egg replacement is low for Least and Crested auklets (Piatt and others 1990) and Xantus' Murrelets (Murray and others 1983) and apparently does not occur in Ancient Murrelets (Sealy 1976). Cassin's Auklet is the only alcid known to lay a second clutch following the rearing of their first brood (Ainley and others 1990a; Manuwal 1979). Hatching and fledging success of second clutches were usually lower than those of first clutches (Ainley and others 1990a). It is not known if Marbled Murrelets lay replacement eggs or if they attempt to raise more than one brood per season.

Development and Survival of the Young

Newly hatched alcids are downy (*table 7*) and are brooded by their parents for 1 to 10 days (*table 8*) until homeothermy has been achieved (*table 7*). Body mass of hatchling alcids is proportional to egg mass (*fig. 4*, r^2 = 0.98, P < 0.001) and adult body mass (*fig. 5*, r^2 = 0.91, P < 0.001). Alcid chicks are between 6 and 15 percent adult size at hatching (*table 7*). Newly hatched Marbled Murrelet chicks at 15 percent adult body mass, are large in comparison to the other alcid chicks (*tables 7-9*).

Most alcid chicks are semi-precocial (*table 7*). Parents feed their semi-precocial young at the nest for 27-52 days until they reach at least 60 percent adult mass. Kittlitz's Murrelet may be an exception; the body mass of one fledgling was reported to be 40 percent that of an adult (Day and others 1983) (*table 9*). For most semi-precocial species, the young reach independence at the time of fledging (*table 8*).

The *Synthliboramphus* murrelets have precocial young. For up to 2 days after hatching, precocial alcid chicks are brooded but are not fed at the nest. Following this time, they depart the nest at only 12-14 percent adult size and accompany their parents to the sea where they receive additional care until reaching independence at approximately 4 weeks of age (*tables 7, 8, and 9*).

Murres and Razorbills are intermediate to these two patterns of development (Gaston 1985; *table 7*). Their young leave the nest at about 20 days of age, earlier than semi-precocial species, but much later than precocial species (*table 9*). At fledging, murre and Razorbill chicks are around 20 to 30 percent adult mass, lighter than semi-precocial young, yet heavier than precocial young (*table 9*). The chicks accompany their male parents to the sea

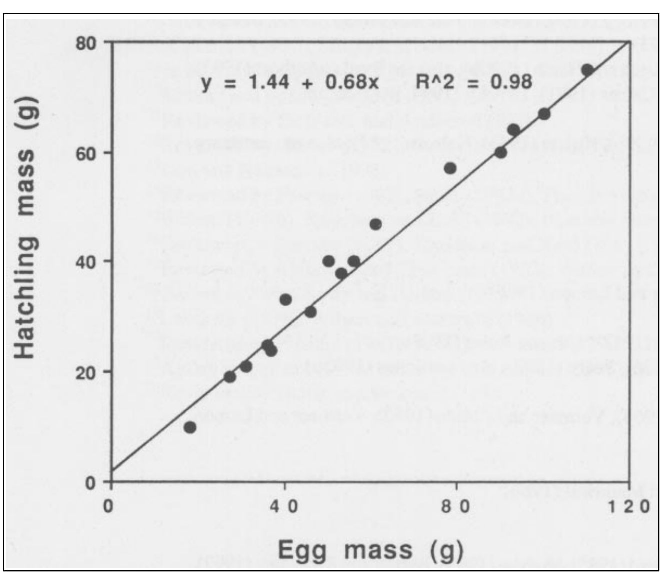

Figure 4—Relationship between mean egg mass and mean hatchling mass for 18 alcids (see *tables 4* and *7* for values).

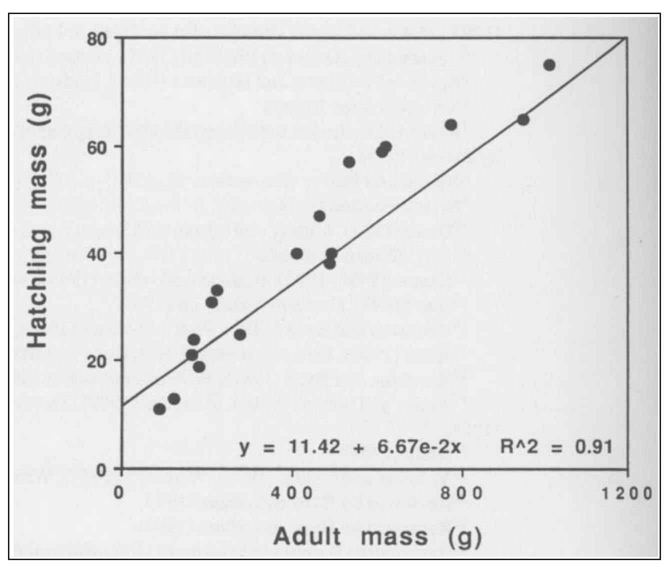

Figure 5—Relationship between mean adult mass and mean hatchling mass for 18 alcids (see *tables 3* and *7* for values).

Table 7—Condition of alcid chicks at hatching and age at which homeothermy (uniform body temperature maintained nearly independent of environment) is achieved

Species	Developmental stage at hatching	Plumage	Mean body mass (g)	Pct. adult mass at hatching	Age (days) of homeothermy
Dovekie[1]	semi-precocial	downy	21	13	2-5
Razorbill[2]	intermediate	downy	ca. 60	9-10	9-10
Common Murre[3]	intermediate	downy	55-95 (range)	6-10	10
Thick-billed Murre[4]	intermediate	downy	ca. 65	7	9-10
Black Guillemot[5]	semi-precocial	downy	ca. 40	ca. 10	1-4
Spectacled Guillemot[6]	semi-precocial	downy	40 (n=1)	8	?
Pigeon Guillemot[7]	semi-precocial	downy	38	8	1
Marbled Murrelet[8]	semi-precocial	downy	33	15	probably 1-2
Kittlitz's Murrelet[9]	semi-precocial	downy	?	?	?
Xantus' Murrelet[10]	precocial	downy	24	15	probably 1-2
Craveri's Murrelet[11]	precocial	downy	?	?	?
Ancient Murrelet[12]	precocial	downy	31	13	2
Japanese Murrelet[13]	precocial	downy	?	?	?
Crested Auklet[14]	semi-precocial	downy	ca. 25	10	probably 4-5
Least Auklet[15]	semi-precocial	downy	11	12-14	probably 5
Whiskered Auklet[16]	semi-precocial	downy	13	11	probably by 7
Cassin's Auklet[17]	semi-precocial	downy	19	11	3-4
Parakeet Auklet[18]	semi-precocial	downy	?	?	?
Rhinoceros Auklet[19]	semi-precocial	downy	57	10	?
Tufted Puffin[20]	semi-precocial	downy	64	8	?
Horned Puffin[21]	semi-precocial	downy	59	10	?
Atlantic Puffin[22]	semi-precocial	downy	47	11	6-7

[1]Reviewed by Gaston (1985), Harris and Birkhead (1985), Ydenberg (1989); Evans (1981), Konarzewski and others (1993), Norderhaug (1980)
[2]Reviewed by Gaston (1985), Harris and Birkhead (1985), Ydenberg (1989)
[3]Reviewed by Gaston (1985), Harris and Birkhead (1985), Ydenberg (1989); Birkhead (1976), Johnson and West (1975)
[4]Reviewed by Gaston (1985), Harris and Birkhead (1985), Ydenberg (1989); Birkhead and Nettleship (1981), Johnson and West (1975)
[5]Reviewed by Gaston (1985), Harris and Birkhead (1985), Ydenberg (1989); Cairns (1981, 1987)
[6]Kitaysky (1994), Thorensen (1984)
[7]Reviewed by Freethy (1987), Gaston (1985), Ydenberg (1989); Ainley and others (1990b), Drent (1965)
[8]Reviewed by Gaston (1985), Ydenberg (1989); Hirsch and others (1981), Sealy (1975c), Simons (1980)
[9]Reviewed by Freethy (1987), Ydenberg (1989)
[10]Reviewed by Freethy (1987), Gaston (1985), Ydenberg (1989); Murray and others (1983)
[11]Reviewed by Gaston (1985), Ydenberg (1989); DeWeese and Anderson (1976)
[12]Reviewed by Gaston (1985, 1992), Ydenberg (1989); Sealy (1976), Vermeer and Lemon (1986)
[13]Reviewed by Gaston (1985)
[14]Reviewed by Freethy (1987), Gaston (1985), Ydenberg (1989); Sealy (1968), Jones (1993a), Piatt and others (1990)
[15]Reviewed by Freethy (1987), Gaston (1985), Ydenberg (1989); Jones (1993b), Piatt and others (1990), Roby and Brink (1986)
[16]Reviewed by Byrd and Williams (1993); Williams and others (1994)
[17]Reviewed by Gaston (1985), Ydenberg (1989); Ainley and others (1990a), Manuwal (1979), Thorensen (1964), Vermeer and Lemon (1986)
[18]Reviewed by Gaston (1985), Ydenberg (1989)
[19]Reviewed by Freethy (1987), Gaston (1985), Ydenberg (1989); Wilson and Manuwal (1986)
[20]Reviewed by Freethy (1987), Gaston (1985), Ydenberg (1989); Boone (1986), Vermeer and others (1979)
[21]Reviewed by Freethy (1987), Gaston (1985), Ydenberg (1989); Sealy (1973c)
[22]Reviewed by Gaston (1985), Harris and Birkhead (1985), Ydenberg (1989); Barrett and Rikardsen (1992)

Table 8—Parental care in alcids

Species	Brooding parent	Period of brooding (days)	Feeding parent	Time at which young reach independence
Dovekie[1]	both	2-7	both at nest; probably neither at sea	at fledging
Razorbill[2]	both	5-10	both at nest; male at sea	several weeks following fledging
Common Murre[3]	both	until fledging	both at nest; male at sea	70-85 days
Thick-billed Murre[4]	both	until fledging	both at nest; male at sea	?
Black Guillemot[5]	both	3-5	both at nest; neither at sea	at fledging
Spectacled Guillemot[6]	?	?	?	?
Pigeon Guillemot[7]	both	at least 3	both at nest; neither at sea	at fledging
Marbled Murrelet[8]	both	0.5-3.0	both at nest; probably neither at sea	at fledging
Kittlitz's Murrelet[9]	?	?	both at nest	?
Xantus' Murrelet[10]	both	1-2	neither at nest; both at sea	?
Craveri's Murrelet[11]	?	?	both at sea	?
Ancient Murrelet[12]	both	2	neither at nest; both at sea	42-56 days
Japanese Murrelet[13]	?	?	neither at nest; both at sea	?
Crested Auklet[14]	both	7	both at nest; neither at sea	at fledging
Least Auklet[15]	both	7	both at nest; neither at sea	at fledging
Whiskered Auklet[16]	?	probably 7	both at nest	probably at fledging
Cassin's Auklet[17]	both	3-5	both at nest; neither at sea	at fledging
Parakeet Auklet[18]	both	?	both at nest	?
Rhinoceros Auklet[19]	both	4	both at nest	probably at fledging
Tufted Puffin[20]	?	?	?	?
Horned Puffin[21]	?	?	?	?
Atlantic Puffin[22]	both	9	both at nest; neither at sea	at fledging

[1]Reviewed by Gaston (1985), Harris and Birkhead (1985)
[2]Reviewed by Gaston (1985), Harris and Birkhead (1985)
[3]Reviewed by Gaston (1985), Harris and Birkhead (1985); Boekelheide and others (1990); also see Bayer and others (1991)
[4]Reviewed by Gaston (1985), Harris and Birkhead (1985)
[5]Reviewed by Gaston (1985), Hudson (1985)
[6]No information located
[7]Reviewed by Ewins (1993), Freethy (1987), Gaston (1985)
[8]Naslund (1993a), Nelson and Hamer (this volume a), Nelson and Hardin (1993a), Nelson and Peck (in press), Simons (1980), Singer and others (1992, in press)
[9]Naslund and others (1994)
[10]Reviewed by Freethy (1987); Murray and others (1983)
[11]DeWeese and Anderson (1976)
[12]Reviewed by Gaston (1990, 1992); Sealy (1976)
[13]Ono and Nakamura (1994)
[14]Reviewed by Freethy (1987), Gaston (1985); Jones (1993a), Piatt and others (1990)
[15]Reviewed by Gaston (1985); Jones (1993b), Piatt and others (1990), Roby and Brink (1986), Sealy (1973a)
[16]Reviewed by Byrd and Williams (1993), Freethy (1987)
[17]Ainley and others (1990a), Manuwal (1979), Vermeer (1981)
[18]Bédard (1969b)
[19]Reviewed by Vermeer and Cullen (1982); Wilson and Manuwal (1986)
[20, 21]No information located
[22]Reviewed by Gaston (1985), Harris and Birkhead (1985)

Table 9—Condition of alcid young at time of fledging from the nest

Species	Mean fledging age (days)	Mean body mass at fledging (g)	Mean pct. adult mass
Dovekie[1]	27	120	67-80
Razorbill[2]	18	ca. 170	20-30
Common Murre[3]	21	170-270 (range)	18-28
Thick-billed Murre[4]	22	180	19
Black Guillemot[5]	37	356	86
Spectacled Guillemot[6]	ca. 33	545 (1 obs.)	111
Pigeon Guillemot[7]	38	460	95
Marbled Murrelet[8]	probably 27-40	149	67
Kittlitz's Murrelet[9]	29	possibly 90 (1 obs.)	possibly 40
Xantus' Murrelet[10]	1-2	24	14
Craveri's Murrelet[11]	2-4	?	?
Ancient Murrelet[12]	2	26	12-13
Japanese Murrelet[13]	1-2	?	?
Crested Auklet[14]	33	ca. 245	80-100
Least Auklet[15]	29	87	104
Whiskered Auklet[16]	probably 39-42	106	92
Cassin's Auklet[17]	43	153	90
Parakeet Auklet[18]	35	235	79
Rhinoceros Auklet[19]	52	329	61
Tufted Puffin[20]	49	490	69
Horned Puffin[21]	38	400	65
Atlantic Puffin[22]	46	271	69

[1]Reviewed by Gaston (1985), Harris and Birkhead (1985); Evans (1981)
[2]Reviewed by Gaston (1985), Harris and Birkhead (1985); Lloyd (1979)
[3]Reviewed by Gaston (1985), Harris and Birkhead (1985); Hatch and Hatch (1990a)
[4]Reviewed by Gaston (1985), Harris and Birkhead (1985), Hudson (1985); Birkhead and Nettleship (1981), Hatch and Hatch (1990a)
[5]Reviewed by Gaston (1985), Harris and Birkhead (1985), Hudson (1985); Cairns (1981, 1987)
[6]Kitaysky (1994), Kondratyev (1994), Thorensen (1984)
[7]Reviewed by Ewins (1993), Gaston (1985); Ainley and others (1990b), Drent and others (1964), Kuletz (1983)
[8]Reviewed by Gaston (1985); Hirsch and others (1981), Nelson and Hamer (this volume a), Nelson and Hardin (1993a), Nelson and Peck (in press), Sealy (1974, 1975a), Simons (1980), Singer and others (1992, in press)
[9]Day and others (1983), Naslund and others (1994)
[10]Reviewed by Gaston (1985); Murray and others (1983)
[11]Reviewed by DeWeese and Anderson (1976), Gaston (1985)
[12]Gaston (1992), Jones and Falls (1987), Sealy (1976), Vermeer and Lemon (1986)
[13]Reviewed by Gaston (1985), Ono and Nakamura (1993)
[14]Reviewed by Gaston (1985); Jones (1993a), Piatt and others (1990)
[15]Reviewed by Gaston (1985); Piatt and others (1990), Roby and Brink (1986)
[16]Reviewed by Byrd and Williams (1993); Williams and others (1994)
[17]Reviewed by Gaston (1985); Ainley and others (1990a), Manuwal (1979), Thorensen (1964), Vermeer and Cullen (1982), Vermeer and Lemon (1986)
[18]Sealy and Bédard (1973)
[19]Reviewed by Byrd and others (1993), Gaston (1985); Ainley and others (1990c), Leschner (1976), Vermeer (1980), Vermeer and Cullen (1979), Wilson and Manuwal (1986); also see Bertram (1988)
[20]Reviewed by Gaston (1985); Ainley and others (1990c), Boone (1986), Vermeer and Cullen (1979), Wehle (1980)
[21]Reviewed by Gaston (1985), Wehle (1983); Sealy (1973c)
[22]Reviewed by Gaston (1985), Harris and Birkhead (1985); Barrett and Rikardsen (1992), Harris and Hislop (1978), Nettleship (1972)

where they receive additional care for several weeks until independent (*table 8*).

Marbled Murrelet chicks are semi-precocial and remain in the nest where they are cared for by both parents until fledging at 27 to 40 days of age (*tables 7 and 8*). The chick is apparently able to thermoregulate at an early age as continuous brooding by the parents ceases after 1–3 days (Naslund 1993a; Nelson and Hamer, this volume a; Nelson and Peck, in press; Simons 1980; S.W. Singer, pers. comm.). The period of continuous brooding is shorter than most alcids raised in the nest (semi-precocial and intermediate species) and is comparable to that of the precocial murrelets (*table 7*). Growth data have been collected for only four nestlings, the preliminary data suggest murrelets grow more rapidly than comparable alcids (Hamer and Cummins 1991; Hirsch and others 1981; Simons 1980).

The incubation and nestling periods of semi-precocial alcids are related (*fig. 6*, $r^2 = 0.68$, $P < 0.001$), however, the precocial and intermediate species do not fit this pattern. (The relationship between the incubation and the nestling period including the alcids with precocial and intermediate developmental modes is not significant [$r^2 = 0.19$, $P < 0.07$]).

Lengthy incubation and nestling periods have been attributed to slow rates of development (Manuwal 1979). In contrast, Marbled Murrelets appear to have a relatively short incubation and nestling period indicating a rapid rate of development. However, the nestling stage of the Marbled Murrelet can vary between 27 and 40 days and the extended growth period may reflect parental difficulty in provisioning the nestling (Nelson and Hamer, this volume a; Nelson and Hardin 1993a). Barrett and Rikardsen (1992) reported lengthy nestling periods of Atlantic Puffins during years of food shortages when parents delivered less food to their young.

Estimates of mean fledging success range from 66 percent for Crested Auklets to over 90 percent for the Ancient Murrelets and Wiskered Auklet (*table 6*). Causes of pre-fledgling mortality include mammalian, avian, and reptilian predation (Emms and Verbeek 1989; Evans 1981; Ewins and others 1993; Gaston 1994; Jones 1992; Manuwal 1979; Sealy 1982; Thorensen 1964), food shortages or starvation (Ainley and Boekelheide 1990; Barrett and Rikardsen 1992; Manuwal 1979; Vermeer 1980), adverse weather (reviewed by Harris and Birkhead 1985), and injury inflicted by adult conspecifics (Birkhead and Nettleship 1981).

Fledging success of Marbled Murrelets has been estimated to be 45 percent, a value lower than those of other species (*table 6*). Chicks in 19 nests were monitored in Alaska, California, Oregon, Washington, and British Columbia (Nelson and Hamer, this volume b). Nearly 25 percent of these young were documented or strongly suspected to have been taken by predators, three others fell from their nest trees, and one died of unknown causes.

Although juvenile survival is difficult to observe and measure, banding studies have provided estimates of survival for seven alcid species ranging from below 1 percent for Atlantic Puffins to a high of 65 percent for Cassin's Auklets

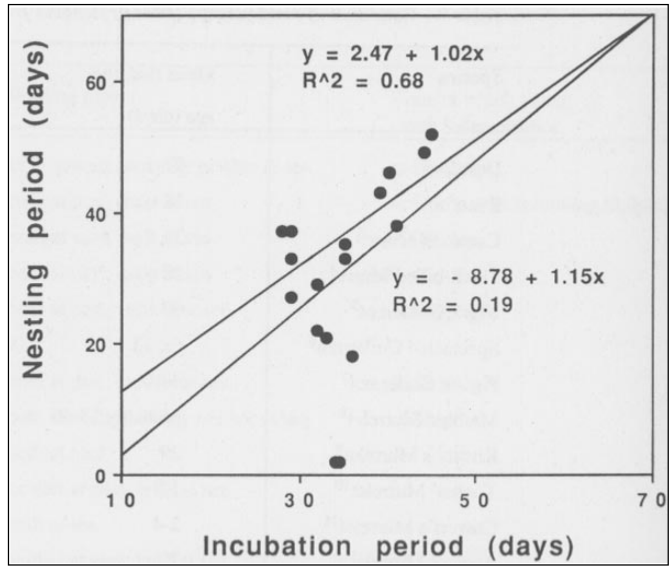

Figure 6—Relationship between incubation and nestling periods for 19 alcids (see *tables 5* and *9* for values).

(*table 6*). Juvenile survival has not been estimated for Marbled Murrelets. It is likely that recently fledged Marbled Murrelets experience some mortality on their trip from inland nest trees to the ocean. Forty-six juveniles in postfledging plumage have been found on the forest floor or in parking lots, presumably following unsuccessful attempts at fledging from inland nests (see Nelson and Hamer, this volume b). An indication of low fledgling success is also reflected in at-sea surveys conducted in California, Oregon, and Alaska in which only 1 to 5 percent of birds on the water were observed to be recently fledged young (Nelson and Hardin 1993a; Ralph and Long, this volume; Strong and others, in press; Strong and others, this volume; Varoujean and Williams, this volume).

Although the average number of young produced by alcid pairs can be high in some years, it is common for productivity to be variable among years, and extremely low reproductive rates are not uncommon. For example, over a 12-yr period on the South Farallon Islands, Common Murre pairs produced an average of 0.86 young per season, but values over this time fluctuated from a high of 0.9 to a low of 0.1 fledglings (Boekelheide and others 1990). Complete nesting failures have been documented as well (Bergman 1971).

Summarizing the available information on the reproduction of Marbled Murrelets, it appears that this alcid has a low reproductive rate. This species lays only one egg, has relatively low hatching success and fledgling survival, and a low rate of recruitment of young into the population. However, some of the Marbled Murrelet reproductive data were collected during El Niño periods (Ainley 1990). Because reproduction of other alcids has been documented to be low during such times (Boekelheide and others 1990), values reported for Marbled Murrelets may reflect a similar depression. Reproduction in "good" years may be higher. On the other hand, reproduction of the Marbled Murrelet is not likely to exceed that of other alcids with comparable reproductive traits. See Beissinger (this volume) for a discussion on the possible reproductive rates of Marbled Murrelets using general reproductive parameters.

If the Marbled Murrelet does have a low rate of reproduction, then it is quite possible that this species will have difficulty recovering from significant population declines, and steps should be taken to minimize the impact of human activity on the production of murrelet young. To completely address this issue, however, thorough study of the reproductive biology of this species is needed. Long-term studies of individually marked, nesting Marbled Murrelets and their young need are required. Effects of natural and human-induced perturbations on the reproductive ecology of this species can then be better understood.

Acknowledgments

George Divoky, Harry Carter, Steve Singer, Barney Dunning, and Scott Hatch assisted us in locating information and references for this review. We thank Bob Peck, Dave D'Amore, George Divoky, Jeff Grenier, Scott Hatch, and George Hunt for reviewing earlier drafts of this manuscript. Support for preparation of this manuscript was provided by the Oregon Department of Fish and Wildlife, USDA Forest Service, USDI Bureau of Land Management, and U.S. Fish and Wildlife Service. Support for preparation of this manuscript was provided by the Oregon Department of Fish and Wildlife, USDA Forest Service, USDI Bureau of Land Management, and U.S. Fish and Wildlife Service. This is Oregon State University Agricultural Experiment Station Technical Paper number 10,539.