

THE RELATIONSHIP BETWEEN PRECOCITY AND BODY COMPOSITION IN SOME NEONATE ALCIDS¹

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The family Alcidae contains species whose young hatch with an unusual variety of developmental types providing the opportunity to examine the influence of precocity among similar species in which potentially confounding factors such as phylogenetic and ecological differences are reduced. Alcids range from precocial species whose young leave the nest within a few days of hatching (*Synthliboramphus* spp.), to semiprecocial species whose young are fed at the nest until nearly adult size (puffins, guillemots, and many auklets), with

a few species intermediate between these two types in which the young leave the nest site when 20 to 25% of adult size (Sealy 1973).

The eggs of precocial alcids are proportionately larger than those of semiprecocial and intermediate species (21 to 25% vs. 14 to 19% of adult body mass) (Jehl and Bond 1975; Sealy 1975; Birkhead and Harris 1985; H. Hasegawa, in litt.). In addition, the eggs of Ancient Murrelets (*S. antiquus*), a precocial alcid, contain a greater proportion of lipid-rich yolk than do those of other, less precocial alcids (Birkhead and Gaston, unpubl.). Birds with precocial young generally lay eggs with relatively large yolks and thus higher overall energy content than those of altricial species (Sotherland and Rahn 1987). Larger eggs and more yolk are presumed to provide additional energy and materials for increased hatchling, and possibly embryonic, requirements (e.g., Sealy 1975, Vleck et al. 1980). Much of the initial energy content of a fresh egg is retained in the hatchling since embryonic development uses only

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TABLE 1. Mass of chicks and yolk sacs (g), proportionate mass of yolk sacs and legs, and water index (g water/g lean dry mass) of various species of alcids ($\bar{x} \pm SE$).

Species	n	Chick	Yolk sac	Yolk sac as % of chick	Legs as % of carcass ¹	Water index of chick
Ancient Murrelet	8	32.9 ± 0.7	3.41 ± 0.27 ²	10 ²	27	4.55 ± 0.13
Thick-billed Murre	7	71.8 ± 1.3	12.04 ± 0.64	17	21	4.69 ± 0.21
Rhinoceros Auklet	3	56.2 ± 2.8	3.77 ± 1.07	7	20	5.33 ± 0.20
Pigeon Guillemot	4	38.8 ± 1.7	3.68 ± 0.38	9	20	5.33 ± 0.14
Cassin's Auklet	2	20.1 ± 1.3	1.55 ± 0.85	8	18	5.65 ± 0.45

¹ Carcass = chick (plucked) minus yolk sac.

² n = 7.

TABLE 2. Lipid and lean mass (g) and lipid index (g lipid/g lean dry mass) of carcasses, yolk sacs, and whole bodies of neonates of various species of alcids ($\bar{x} \pm SE$).

Species	n	Carcass ¹			Yolk sac
		Lipid	Lean	Lipid index	Lipid
Ancient Murrelet	8	2.96 ± 0.10	4.60 ± 0.07	0.64 ± 0.02	0.97 ± 0.08
Thick-billed Murre	7	2.65 ± 0.25	8.47 ± 0.24	0.31 ± 0.03	3.11 ± 0.34
Rhinoceros Auklet	3	2.72 ± 0.07	7.41 ± 0.33	0.36 ± 0.01	0.86 ± 0.20
Pigeon Guillemot	4	1.07 ± 0.08	4.87 ± 0.22	0.22 ± 0.01	0.90 ± 0.13
Cassin's Auklet	2	0.59 ± 0.01	2.61 ± 0.08	0.23 ± 0.01	0.26 ± 0.13

¹ Carcass = whole body (plucked) minus yolk sac.

about one third of an egg's energy (Sotherland and Rahn 1987). However, data on energy reserves of neonate birds are few and a relationship between precocity and hatchling energy content has not been established.

Data which purportedly show that precocial hatchlings have relatively large yolk sacs have been cited as evidence that precocial neonates have a higher energy content than do altricial ones (Ar and Yom-Tov 1978, Vleck et al. 1980, Carey 1983). However, all these studies cite Schmekel (1960), despite the fact that Schmekel herself considered her data insufficient to conclude that the size of the yolk sac was related to developmental type. Moreover, yolk sacs often contain only a minor proportion of a hatchling's energy reserves (Sotherland and Rahn 1987) and the relative size of yolk sacs is not indicative of the total lipid content of hatchlings (Duncan 1988).

METHODS

We examined neonates from five species of alcids to determine whether the body composition varies with developmental precocity. The species examined were: precocial Ancient Murrelets; semiprecocial Pigeon Guillemots (*Cepphus columba*), Rhinoceros Auklets (*Cerorhinca monocerata*), and Cassin's Auklets (*Ptychoramphus aleuticus*); and intermediate Thick-billed Murres (*Uria lomvia*). The lipid and water contents, and relative sizes of yolk sacs and legs of these hatchlings were compared.

Chicks were collected in 1986 and 1987 from eggs that had been incubated and hatched naturally, with the exception of one Cassin's Auklet. This egg was deserted in the late stages of hatching and had to be artificially warmed for 2 hr to enable the chick to emerge from the shell. Eggs were not hatched in an incubator because artificial conditions may greatly alter the speed of hatching and size of the yolk sac (Romanoff 1944). Only chicks that were still damp from hatching or known to be less than 6 hr old were used to ensure accurate representation of conditions at hatching. Ancient Murrelets and Cassin's Auklets were collected from Reef Island in the Queen Charlotte Islands, British Columbia, Canada. Rhinoceros Auklets and Pigeon Guillemots were collected from Seabird Rocks near Barkley Sound on Vancouver Island, British Columbia. Thick-billed Murres were obtained from Coats Island in northern Hudson Bay, Northwest Territories, Canada.

Fresh weights of the chicks and their yolk sacs were obtained, the chicks were plucked (feathers were discarded), and the material was preserved in 9% formalin. Storage in formalin has little effect on lipid con-

tent or extractability (Heslinga and Deiekauf 1962). The lipids were extracted after about 4 months of storage. Prior to lipid extraction, the entire legs of the chicks were severed from the pelvic girdle to determine the mass of the legs relative to the rest of the carcass. The entire carcasses were chopped and all material was dried to constant weight at 70°C. The material was then ground and the lipid extracted with petroleum ether in a Soxhlet apparatus. Entire yolk sacs and aliquots of 75 to 100% of the carcasses were used for the extractions.

The term carcass herein refers to the body of the chick without the yolk sac and feathers. Lipid content is expressed as a lipid index (L.I., grams lipid/grams lean dry mass) and water content as a water index (grams water/grams lean dry mass). Statistical analyses were performed with the significance level set at 0.05. Multiple comparisons were made using Kruskal-Wallis rank sums analysis. Where there were significant overall differences, individual comparisons were made using Mann-Whitney *U*-tests.

RESULTS AND DISCUSSION

Relative leg mass differed among species (Table 1, $P < 0.001$) with Ancient Murrelets having proportionately heavier legs than each of the other species ($P < 0.05$). Previous researchers noted that the tarsometatarsi of newly hatched precocial alcids are similar in length to that of the adults (Sealy 1976, Murray et al. 1983). Increased leg size in Ancient Murrelet chicks has apparently been selected for in response to the locomotory demands of running from their nest burrows and swimming out to sea 2 days after hatching (Sealy 1976).

Lipid indices of the carcasses and whole bodies differed among species (Table 2, $P < 0.001$). The L.I.s of both the carcasses and whole bodies of Ancient Murrelets were higher than those of each of the other species ($P < 0.05$). There was no indication of an allometric relationship of lipid content among species; mean L.I. of both carcasses and whole bodies was not correlated with mean hatchling mass (Spearman's $\rho = 0.1, 0.4, P > 0.05, n = 5$, respectively). The higher lipid content in Ancient Murrelets supports the prediction that precocial chicks are endowed with greater energy reserves and reinforces the trend observed among other species of birds (Ricklefs 1967, Duncan 1988). The lipid content of Ancient Murrelets is one of the highest reported and is greater than that of numerous species of ducks (cf. Duncan 1988). Greater lipid reserves in Ancient Murrelets probably serve to provide increased energy for thermoregulatory and locomotory needs. Semiprecocial alcids have poor coordination and are not highly mobile in the first few days after hatching (Gaston 1985). Eppley (1984) found that precocial alcid chicks had a high energy demand and attributed it to their small size and the apparent lack of brooding after they leave the burrow. The effect of being in cold water did not appear to be important because by 3 days of age, chicks lost no more heat in water than in air of the same temperature (Eppley 1984). Although it has been suggested that large energy reserves in precocial chicks might be an adaptation for tolerating food shortages caused by being self-feeding, this does not apply to

TABLE 2. Extended.

Lean	Yolk sac		Whole body
	Lipid index		Lipid index
0.96 ± 0.09	1.03 ± 0.07		0.71 ± 0.02
3.15 ± 0.35	1.00 ± 0.07		0.49 ± 0.02
0.85 ± 0.38	1.21 ± 0.24		0.43 ± 0.01
0.92 ± 0.17	1.03 ± 0.18		0.34 ± 0.02
0.38 ± 0.13	1.57 ± 1.01		0.29 ± 0.01

alcids because precocial alcid chicks appear to be fed by their parents (DeWeese and Anderson 1976; Eppley, in litt.). Williams et al. (1982) suggested that variation in hatchling energy reserves might be related to the time between hatching and first feeding. Such could be the case here because Ancient Murrelet chicks are not fed until they are at sea, more than 2 days after hatching (Sealey 1976), whereas nonprecocial alcids are fed at the nest site, usually within 24 hr of hatching (Gaston 1985).

Comparing the four nonprecocial species, the L.I.s of the whole bodies of Thick-billed Murres was higher than that of Pigeon Guillemots and Cassin's Auklets ($P < 0.05$), and that of Rhinoceros Auklets was greater than that of Pigeon Guillemots ($P < 0.05$). Mean L.I. increased linearly with mean body mass among these species (Spearman's $\rho = 1$, $P = 0.05$, $n = 4$) (i.e., lipid scaled allometrically). The absence of such a relationship when Ancient Murrelets were included (see above) illustrates the overwhelming influence of precocity on lipid reserves.

The size of the yolk sac in proportion to the body differed among species (Table 1, $P < 0.01$) with Thick-billed Murres having relatively larger yolk sacs than each of the other species ($P < 0.05$). Thus, size of the yolk sac was not related to precocity of the chick. The large yolk sacs in Thick-billed Murres may be related to their larger body size as chicks of larger species have proportionately larger yolk sacs among domestic birds (Romanoff 1944). The lipid in the yolk sacs of the different species constituted various proportions of the hatchlings' total lipid content; from 24 to 25% in Rhinoceros Auklets and Ancient Murrelets, to 54% in Thick-billed Murres. The importance of yolk as a lipid reserve in Thick-billed Murres was a result of their comparatively large yolk sacs.

Within both the Thick-billed Murres and Ancient Murrelets (the species with largest sample sizes), mass of the hatchlings was not correlated to mass of the yolk sacs (Spearman's $\rho = -0.36$, 0.69 , $P > 0.05$, $n = 7$, 7 , respectively) or to overall L.I.s of the chicks (Spearman's $\rho = -0.60$, 0.29 , $P > 0.05$, $n = 7$, 8 , respectively). This suggests that within species, heavier hatchlings do not have proportionately higher fat reserves and that yolk sacs are not a primary determinant of differences in hatchling weight, contrary to Birkhead and Nettleship's (1984) conclusion about Thick-billed Murres. The discrepancy between studies may have resulted from Birkhead and Nettleship's use of embryos from piped eggs rather than hatchlings because yolk is rapidly catabolized and assimilated between the late embryo stage and newly hatched chicks.

The L.I.s of yolk sacs did not differ among species (Table 2, $P > 0.05$), and was at the high end of the range in various other birds, similar to that of ducklings (cf. Duncan 1988). Lipid content in the yolk of fresh eggs is similar among birds, including alcids (Birkhead and Nettleship 1984; Sotherland and Rahn 1987; Birkhead and Gaston, unpubl.).

Water content differed among species (Table 1, $P < 0.05$). Ancient Murrelets had lower water indices than Pigeon Guillemots, Rhinoceros Auklets and Cassin's Auklets ($P < 0.05$), and Thick-billed Murres contained proportionately less water than Pigeon Guillemots (P

< 0.05). Thus, the water content of newly hatched alcids appeared to be inversely related to their precocity as it is among other birds (Ar and Yom-Tov 1978, Ar and Rahn 1980, Duncan 1988). Ar and Yom-Tov (1978) suggested that additional water in altricial hatchlings might be adaptive because they are fed dry food. Ricklefs (1979) suggested that lower water content in precocial young could result from the increased maturity of their skeletal muscle because functionally mature tissues appear to contain less water. Alternatively, differences in water content of neonate birds might simply be a by-product of the initial differences in the composition of eggs. The water content of fresh eggs varies inversely with precocity of the hatchling and is very similar to that of the hatchling (Ar and Rahn 1980, Sotherland and Rahn 1987). Hence water content of hatchlings will also vary inversely with precocity.

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LITERATURE CITED

- AR, A., AND H. RAHN. 1980. Water in the avian egg: overall budget of incubation. *Am. Zool.* 20:373-384.
- AR, A., AND Y. YOM-TOV. 1978. The evolution of parental care in birds. *Evolution* 32:655-669.
- BIRKHEAD, T. R., AND D. N. NETTLESHIP. 1984. Egg size, composition and offspring quality in some Alcidae (Aves: Charadriiformes). *J. Zool. (Lond.)* 202:177-194.
- BIRKHEAD, T. R., AND M. P. HARRIS. 1985. Ecological adaptations for breeding in the Atlantic Alcidae, p. 205-231. *In* D. N. Nettleship and T. R. Birkhead [eds.], *The Atlantic Alcidae*. Academic Press, London.
- CAREY, C. 1983. Structure and function of avian eggs, p. 69-103. *In* R. F. Johnston [ed.], *Current ornithology*. Vol. 1. Plenum Press, New York.
- DEWEESE, L. R., AND D. W. ANDERSON. 1976. Distribution and breeding biology of Craveri's Murrelet. *Trans. San Diego Soc. Nat. Hist.* 18:155-168.
- DUNCAN, D. C. 1988. Body reserves of neonate Northern Pintails. *Can. J. Zool.* 66:811-816.
- EPPLEY, Z. A. 1984. Development of thermoregulatory abilities in Xantus' Murrelet chicks *Synthliboramphus hypoleucus*. *Physiol. Zool.* 57:307-317.
- GASTON, A. J. 1985. Development of the young in the Atlantic Alcidae, p. 319-354. *In* D. N. Nettleship and T. R. Birkhead [eds.], *The Atlantic Alcidae*. Academic Press, London.
- HESLINGA, F.J.M., AND F. A. DEIEKAUF. 1962. The

- action of formaldehyde solutions on human brain lipids. *J. Histochem. Cytochem.* 10:704-709.
- JEHL, J. R., JR., AND S. I. BOND. 1975. Morphological variation and species limits in the murrelets of the genus *Endomychura*. *Trans. San Diego Soc. Nat. Hist.* 18:9-24.
- MURRAY, K. G., K. WINNETT-MURRAY, Z. A. EPPLEY, G. L. HUNT, JR., AND D. B. SCHWARTZ. 1983. Breeding biology of Xantus' Murrelet. *Condor* 85: 12-21.
- RICKLEFS, R. E. 1967. Relative growth, body constituents, and energy content of nestling Barn Swallows and Red-winged Blackbirds. *Auk* 84: 560-570.
- RICKLEFS, R. E. 1979. Patterns of growth in birds. V. A comparative study of development in the Starling, Common Tern and Japanese Quail. *Auk* 96: 10-20.
- ROMANOFF, A. L. 1944. Avian spare yolk and its assimilation. *Auk* 61:235-241.
- SCHMEKEL, L. 1960. Daten über das Gewicht des Vogeldottersackes vom Schlupftag bis zum Schwinden. *Rev. Suisse Zool.* 68:103-110.
- SEALY, S. G. 1973. Adaptive significance of post-hatching developmental patterns and growth rate in the Alcidae. *Ornis Scand.* 4:113-121.
- SEALY, S. G. 1975. Egg size of murrelets. *Condor* 77: 500-501.
- SEALY, S. G. 1976. Biology of nesting Ancient Murrelets. *Condor* 78:294-306.
- SOTHERLAND, P. R., AND H. RAHN. 1987. On the composition of bird eggs. *Condor* 89:48-65.
- VLECK, C. M., D. VLECK, AND D. F. HOYT. 1980. Patterns of metabolism and growth in avian embryos. *Am. Zool.* 20:405-416.
- WILLIAMS, A. J., W. R. SIEGFRIED, AND J. COOPER. 1982. Egg composition and hatching precocity in seabirds. *Ibis* 124:456-470.

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EMBRYONIC VOCALIZATIONS AND THE REMOVAL OF FOOT WEBS FROM PIPPED EGGS IN THE AMERICAN WHITE PELICAN¹

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Key words: American White Pelican; embryonic vocalizations; incubation; foot webs; communication; development.

The American White Pelican (*Pelecanus erythrorhynchos*) normally incubates a clutch of two eggs under the foot webs (Schaller 1964, Knopf 1979, pers. observ.). This mode of incubation is similar to that employed by several other members of the Pelecaniformes, including the Brown Pelican (*P. occidentalis*, Schreiber 1977), gannets, and boobies (Sulidae, Nelson 1978). In the Sulidae, Nelson has noted that with the onset of pipping, the incubating parent moves the webs below the eggs, presumably so the embryo will not be injured by the parent should weight be applied to the cracked and weakened shell. White pelicans also remove their foot webs from the eggs when they pip (pers. observ.).

Pelicans, along with sulids and presumably other members of the order, although altricial, are able to vocalize strongly during the pipped egg stage. This raises the possibility (Nelson 1978) that embryonic calls may play a functional role in bringing about the removal of the webs from newly pipped eggs. An exper-

imental test of this hypothesis for the American White Pelican was the objective of this study.

METHODS

Pelicans were observed at a colony of over 1,000 nests located on an island in East Shoal Lake, Manitoba, Canada. A blind was erected about 5 m from the edge of the colony 1 week before the onset of pipping. Nests within viewing range of the blind were examined quickly each morning and a sample of those containing either two unpipped eggs or one pipped and one unpipped egg were marked with small color-coded plastic flags. A miniature microphone (Realistic, Model 33-1052) was enclosed in thin plastic and laid between the eggs on the nest floor at four nests containing one pipped and one unpipped egg. Microphone leads were run back to the blind for subsequent monitoring with a Uher 4000 Report tape recorder. The nests were monitored, both visually and audibly, for a total of 5.33 hr.

To test experimentally for effects of pipped egg vocalizations on parental incubation behavior, a small (9.5 cm diameter) loudspeaker covered with plastic and a protective screen was buried immediately under the center of the nest cup and covered with about 1 cm of nest material, usually a mixture of fine gravel and dead vegetation. Nests ($n = 10$) selected for playbacks contained two unpipped eggs, but were always within a portion of the colony showing evidence of actual or

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