# A COMPARISON OF FUNCTIONAL AND MORPHOLOGICAL ADAPTATIONS IN THE COMMON MURRE (*URIA AALGE*) AND THICK-BILLED MURRE (*URIA LOMVIA*)

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This investigation utilizes the techniques of functional anatomy to determine adaptive differences between two closely-related species, the Common Murre (*Uria aalge*) and the Thick-billed Murre (*Uria lomvia*). While the Thick-billed Murre predominates in the far north (many breeding localities within the Arctic Circle), and the Common Murre is more successful to the south (the only breeding murre in the British Isles, the Faeroes, and along the Pacific coast of the US and British Columbia), the two species overlap broadly in their breeding and wintering ranges. And although they have been the objects of numerous ecological investigations, no consensus has developed concerning their niche differentiation. For Novaya Zemlya and Seven Islands (USSR), where both species occur, Uspenski (1956) emphasizes shortage of nesting sites rather than food as a limiting factor, thus implying that food differences are unimportant or nonexistent. Belopol'skii (1957) classifies *Uria aalge* as a "stenophage" (i.e., narrowly restricted in its food preferences) that feeds almost exclusively on pelagic fish. Conversely, he regards *Uria lomvia* as a "polyphage," capable of switching to zooplankton and bottom fish. However, Tuck (1960) on the basis of existing information concluded that there is no distinct food spectrum for either species, and felt that their diets consist of whatever small fish are available.

Lack (1966) has recently restated his views on population regulation in seabirds that have preferences for nesting on inaccessible islands and ledges. He rejects Andrewartha and Birch's (1954) emphasis on population limitation via material resource shortages that are independent of population size. Considering one such shortage, that of nest sites, he argues that without density-dependent checks, there would be a steady increase in the number of nonbreeding individuals to the point where density-dependent mortality resulted from food depletion. Even with emigration of nonbreeders, only temporary alleviation would occur and density-dependent checks would eventually operate when all possible sites were full.

If density-dependent food limitation is a reality for murre populations, differences in the diets of the two species might be expected to have evolved in their area of sympatry. However, for this to occur, two prerequisites are necessary. First, the sympatric population must be either large in comparison to the allopatric population, or isolated from it, so that selection for feeding differences in the sympatric area is not diluted by gene flow from the allopatric population. Second, the food resources in the area of sympatry must be sufficiently diverse and abundant to permit divergence to two different feeding patterns which are viable in terms of the animals' time and energy budgets. Because food limitation may only be important during part of the annual cycle, feeding similarity between two species at one time of the year may reflect temporary accommodation to a particularly abundant food source.

Existing data, particularly those of Belopol'skii (1957), show that both murres are opportunistic to the extent of feeding on a variety of pelagic fish. Probably the relative proportions in which the fish are eaten reflects their differing abundances in the feeding areas at the times of sampling. Thus, the importance of a pelagic fish species may vary from place to place throughout a murre species' range or from year to year at the same locality. Kaftanovski's (1938) data for Common and Thick-billed Murres breeding along the eastern Murmansk coast (USSR) and Tuck's (1960) data for both species wintering off Newfoundland indicate that, at certain times and places, both murres feed on much the same fish species in the same relative proportions. Since the meaning of these data in regard to niche differentiation is inconclusive,

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more food data for different times and localities are essential. Although other data are available and suggestive of certain differences (i.e., more feeding on bottom forms and pelagic invertebrates in *Uria lomvia*), the range of either species' feeding potential is still uncertain. There are essentially two methods of dealing with this uncertainty. One is continuing ecological investigation, observing the species under as great a variety of conditions as possible to determine their potentialities. The other approach involves bringing the animals into the laboratory to test their functional potentials (i.e., heat resistance, locomotor ability, feeding efficiency on a certain food, etc.). Elucidation of physiological, anatomical, and behavioral factors underlying functional differences gives additional insights into those differences. If at the same time, ecological data can be related to functional differences, a rather complete picture of adaptation emerges. Perspectives difficult if not impossible to obtain through field investigations can be developed, and it is even possible that critical field observations may be suggested.

Utilizing the latter approach, I employed a logical framework of four stages. As a first step, I photographed captive Common and Thick-billed Murres walking and swimming, and analyzed the films to determine interspecific differences. Second, I quantitatively compared the skeletal and muscular systems of the two species. Third, I correlated anatomy and function (i.e., anatomical explanations were developed to explain functional differences between the two species). As a last step, I interpreted ecological data (nesting and food data primarily) in terms of the species' differing functional abilities.

The two murre species are especially suitable material for this type of study. Their undoubtedly close evolutionary relationship assures that anatomical and functional differences cannot be explained on the basis of the two species having evolved from different ancestors. Furthermore, they are easily maintained in captivity and provide favorable anatomical material because of their large size. Ecologically they are well known, owing to their conspicuousness, abundance, and distribution over a wide area. However, they also offer one important limitation. In nature, their underwater activities are difficult to observe and foraging patterns that might readily be seen in a terrestrial situation are unobservable.

While the use of captive birds for making functional observations raises certain difficulties (i.e., their locomotor patterns might differ from those in nature), they are compensated for by two advantages. First, the use of captive birds assures clear observations and ease of photography. Second, captive animals can be subjected to conditions or stimuli that force them to engage in demonstrably inefficient activities which are seldom if ever performed in the wild. In previous work (Spring 1965), I found that by forcing various species of woodpeckers to climb vertically, different climbing efficiencies were revealed. As might be expected, the poorest climber possesses a feeding pattern in nature which employs a minimum of vertical climbing. Thus, while absence of climbing in nature suggests poor climbing ability, such a deficiency can be best confirmed under laboratory conditions. In this study, the use of small tanks has revealed a potential which I believe is meaningful. This potential might be difficult to ascertain under natural conditions, even if extensive underwater observations were possible.

## MATERIALS AND METHODS

Field observations of wintering Common Murres were made in Puget Sound around San Juan Island, Washington, and of a breeding colony of this species at Cape Lookout, Oregon. Captive birds included six Common and four Thick-billed Murres. Motion pictures of walking and swimming were taken at 32 and 64 frames/sec with a 16 mm Cine-Kodak Special No. 2 camera using Plus-X reversal and Tri-X reversal Kodak film. Both species were photographed swimming in tanks approximately 2 × 1.3 × 1.4 m filled to a depth of 1.1 m with fresh water.

Skeletal material for approximately 325 specimens of 23 Recent alcid species was examined and measured. Because of the low degree of sexual dimorphism in all alcid species, males and females were treated together. For the most part, this account utilizes skeletal data for 44 adult Common and 30 adult Thick-billed Murres. Sternal keel tracings were procured by pressing paper to the sternum's side and running a fingernail around the keel's edges. The resulting creases were outlined in pencil and the keel area obtained with a planimeter. Other bone measurements were made to the nearest 0.1 mm using dial calipers. Ratios and standard statistics were calculated with a 70-94 IBM computer. The results of a preliminary run were used to search for errors in measurement or catechization. After the final run, any additional statistics were computed with an Olivetti-Underwood Programma 101 desk computer. Drawings of bones were prepared with the aid of a Focalmatic Desk Projector and X-ray photographs.

The 8 Common and 13 Thick-billed Murres used for myological comparisons were collected near Gambell, Alaska, in July 1967. Individual pelvic and pectoral muscles were removed from both sides of these formalin-preserved birds. The muscles were then cleaned of superficial nerves, fat, and blood vessels;

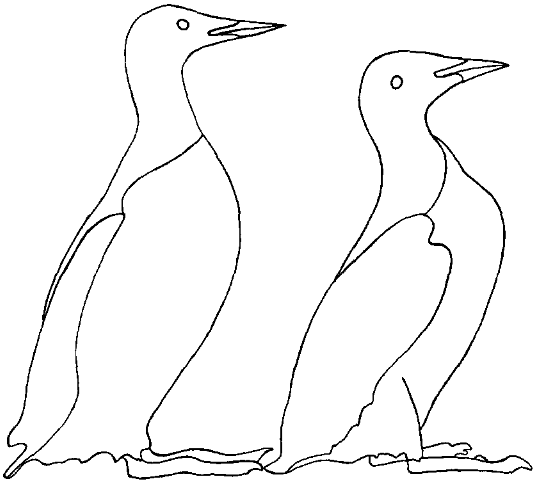


FIGURE 1. Lateral views of sitting Common Murre (left) and Thick-billed Murre (right).

their tendons trimmed away; and the remaining material dried in a 110° C oven for a minimum of 72 hr. The dried muscles were weighed to the nearest 0.1 mg and the weights used to calculate ratios.

The specimens providing myological data were also compared in terms of their palates, tongues, cranial kinetic muscles, and digestive tracts. Histological sections of formalin-fixed tongues were stained with Modified Masson Trichrome Stain. Several skeletal measurements, some of which were impossible to procure from disarticulated material, were taken from preserved specimens after muscle removal.

Angles of kinesis were determined as follows: the dried skull was placed in boiling water for 1 min to loosen joints and connective tissue; the skull was then placed in a metal clamp and the arc of movement measured to the nearest degree on a protractor suspended at the side of the skull so that its center was adjacent to the nasofrontal hinge. Skulls missing parts of the kinetic mechanism were not measured. Three or more readings were taken for each skull and the results averaged.

## RESULTS

### CHARACTERIZATION OF ACTIVITIES

*Stance and walking.* Figure 1 shows Common and Thick-billed Murres sitting in profile view. Although the Common Murre is, on the average, only two per cent heavier (data for Cape Thompson, Alaska: Schwartz 1966), it stands much taller. In addition, the Thick-billed Murre appears to have a shorter, thicker neck and a more developed breast.

The two species differ with regard to their walking abilities. Although both can shuffle about slowly with their tarsi in an essentially horizontal position, they can also raise them to a vertical orientation and walk. The Common Murre readily raises its body and walks or runs smoothly (fig. 2a). In contrast, the Thick-billed Murre either waddles slowly in a hunched position (fig. 2b) or flaps its wings during faster locomotion. Usually extension of one of the legs is coordinated with a forward wing flap (fig. 2c). Sometimes Thick-billed Murres are so rushed that the leg and wing actions become uncoordinated and the bird falls forward on its breast. Such difficulties are never encountered by Common Murres.

*Swimming.* Previous workers (Sanford and Harris 1967; Stettenheim 1959) have described most aspects of the locomotor behavior of Common Murres swimming in small tanks. In outdoor aviaries and particularly in tanks, Common Murres are more nervous and difficult to handle than thick-billeds. In comparison to thick-billeds, Common Murres are more reluctant to submerge (tending to skitter along the surface rather than dive when disturbed); stay submerged for shorter periods of time; and often leap dramatically from the water when surfacing from a dive (this being attributable to propulsion from a partial wing stroke).

As far as the basic wing stroke is concerned, there are no consistent differences between Common and Thick-billed Murres. Figure 3 illustrates the basic stroke used in underwater swimming. (This anterior view gives a particularly clear sequence of the actions involved.) Propulsion is provided in essentially two phases. The first begins with the wrist in a position which is dorsal and lateral to the shoulder joint. From there, the wing is rotated as a unit with the wrist moving through an arc of approximately 180°, coming to lie nearly directly ventral to its starting point. During this movement, the various segments of the partially folded wing (upper wing, forearm, and hand) maintain a constant relation to one another, the entire action being accomplished by anterior rotation of the humerus. From this position, the second phase of propulsion is initiated with the humerus being swung posteriorly in a horizontal plane. As a result, the forearm and hand, still immobilized about their various articulations, are swung posteromedially. Finally the forearm and hand, acting as an independent unit, swing medially.

The first phase of the stroke generates a propulsive force with posteriorly and dorsally directed components. Whether the bird maintains a level course, rises, or dives is determined in part by the relative magnitudes of these components which in turn are functions of the inclination of the wing surfaces. The second phase of the propulsive stroke generates posteriorly and medially directed com-

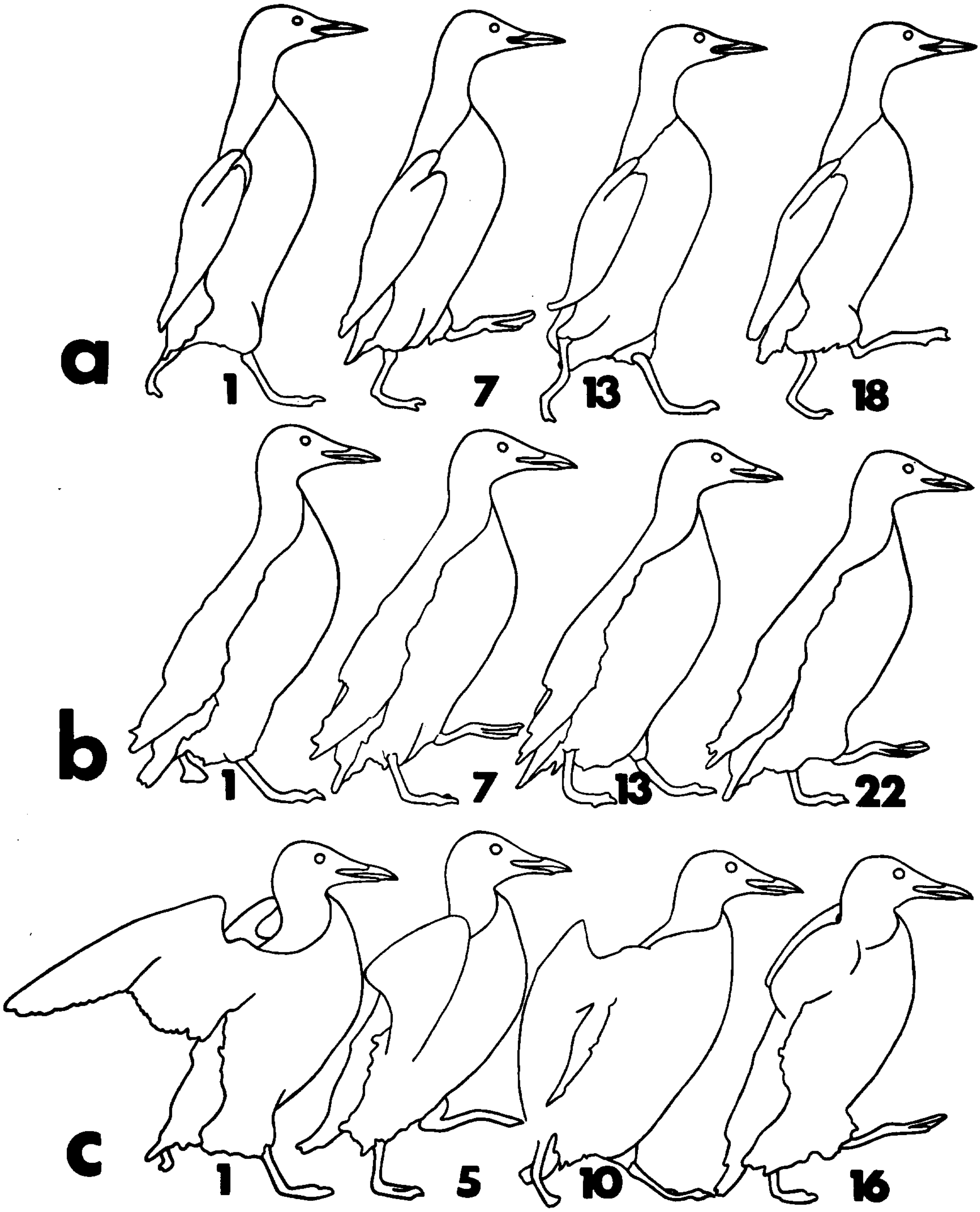


FIGURE 2. a. Walking in Common Murre; b. slow walking in Thick-billed Murre; c. fast walking in Thick-billed Murre. Numbers denote frames in sequence.

ponents. If both wings perform this phase simultaneously, the medially directed components for the two sides cancel one another while the anteriorly directed components are summed. Lack of synchrony between the two sides can result in veering.

During the propulsive stroke, the extent to which the wings are brought ventrally and then medially varies considerably. Having observed swimming in both confined and wild Common Murres, Stettenheim (1959) felt that small tanks possibly enforce a locomotory stroke in which the wings remain half open and are not pulled toward the body.

The two species are similar in their basic swimming stroke, and I could find no con-

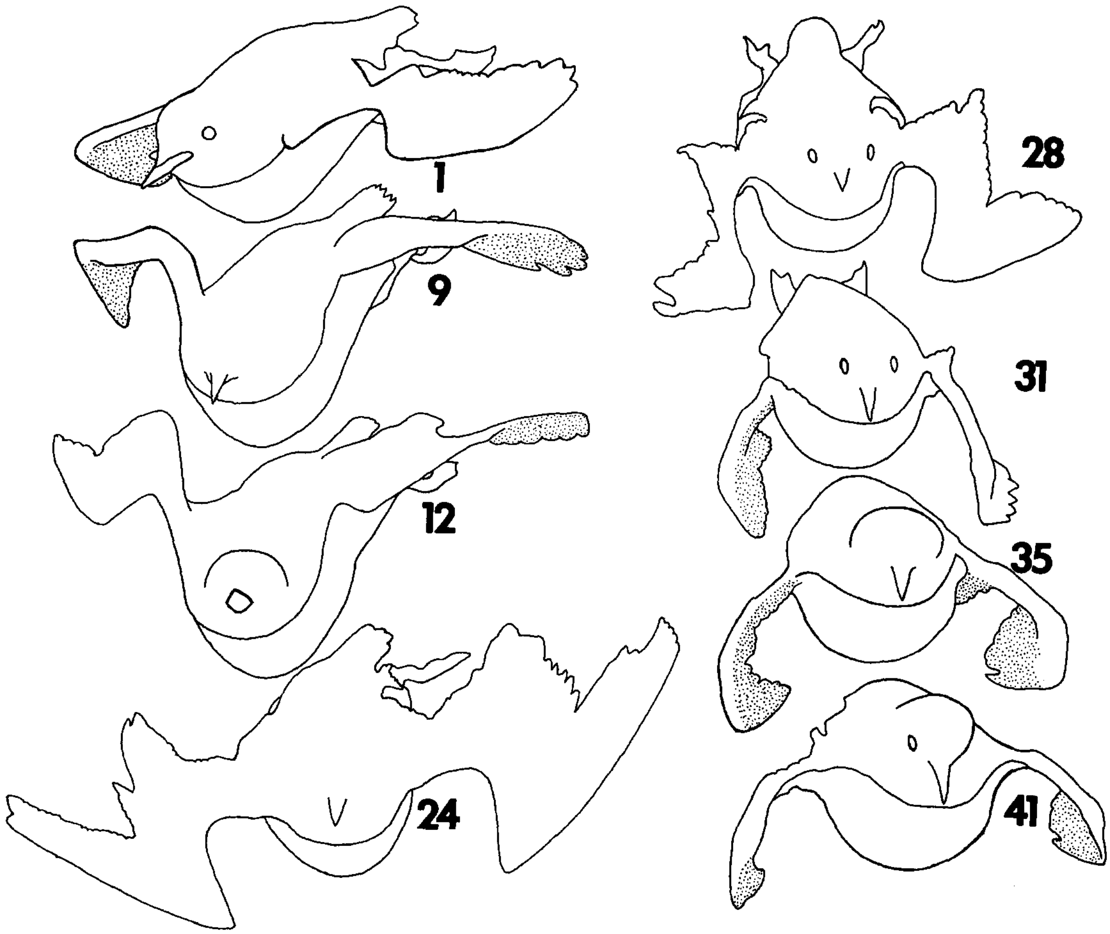


FIGURE 3. Anterior view of locomotor stroke in Thick-billed Murre. Numbers denote frames in sequence. Underwing surfaces stippled.

sistent differences between the two species with regard to other aquatic activities (mechanism of submergence, surface swimming, use of feet in underwater swimming, etc.). The one difference noted concerns the mechanism of turning (fig. 4, 5). During underwater swimming, the murres would usually make a 180° turn upon approaching a side of the tank. While the feet trail passively behind the bird in most underwater swimming, they are used in turning. The foot on the side toward which the murre is turning serves as a brake. Spreading the web of this foot, coupled with the murre's forward momentum, initiates the turn. Simultaneously, turning may be assisted by paddling of the opposite foot. Midway through the turn, further momentum is supplied by wing strokes. This stroking action may be one in which the two wings do not simultaneously engage in the same action. In figure 4I the wing on the side toward which the murre is turning remains laterally extended while that of the opposite side completes its propulsive stroke and begins another. As with the feet, one of the wings serves as a brake while the other supplies momentum for pivoting about the braked side.

Three types of turns can be described. In a Type I turn (fig. 4I), the ventral surface of the murre's body stays on an essentially even keel throughout. During a Type II turn (fig. 4II), the body is tilted about its long axis so that the extended wings are inclined at approximately 45° from the horizontal plane. For a Type III turn (fig. 4III), the long axis of the murre's trunk is oriented nearly vertically at some point in the cycle.

All film footage showing 180° turns was analyzed and each turn classified in one of five categories: Type I, II, III, intermediate between I and II, and intermediate between II and III. Figure 5 illustrates the distribution of turn types for 23 Common and 26 Thick-billed Murre turns. Of the 26 turns rated for Thick-billed Murres, 22 were of Type I. Conversely, the Common Murre showed a ma-

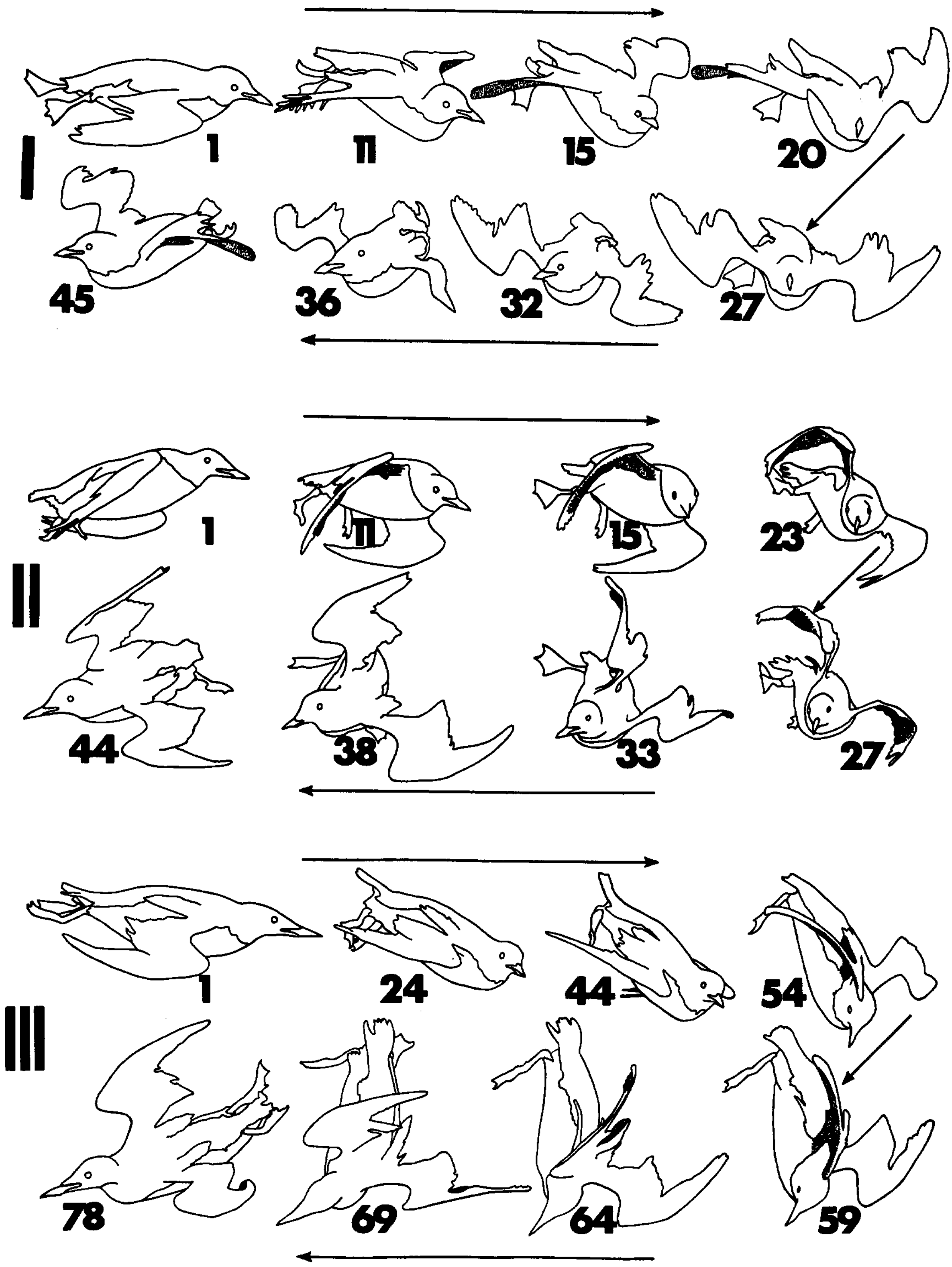


FIGURE 4. Types I, II, and III turns. Thick-billed Murre shown making Type I turn; Types II and III turns shown for Common Murre. Numbers denote frames in sequence.

jority (12 of 23 turns) of the other four categories. Thick-billed Murres showed neither Type III turns nor the category intermediate between II and III. (*P* of $\chi^2$ for the difference between the two species lies between 0.1 and 0.05.) The two Common Murre turns illustrated by Stettenheim (1959) are of the Type III category.

Stettenheim (1959) who observed the Common Murre "hovering" over the tank's bottom,

FIGURE 5. Distribution of turn Types I, II, III, and intermediates for Common ($n = 23$) and Thick-billed ($n = 26$) Murres.

described the behavior as follows. "In order to 'hover' as it does when seeking prey on the bottom, a murre holds its body at a steep angle, head downward. The wings sweep in many directions, showing the mobility of the shoulder joint. The extent to which the wings are folded varies constantly, and they move independently. Force can be exerted against the water by either the dorsal or ventral side of a wing. The result of these actions, supplemented by those of the feet, is that they counteract the bird's buoyancy without imparting propulsion." This behavior was not observed in the present study.

In conclusion, the two species show considerable overlap in those functional traits relating to aquatic performance. The difference in turning would seem to indicate greater agility or dexterity in the Common Murre. With the Common Murre being both a more proficient walker and a more dexterous swimmer, it may be asked in what activity the Thick-billed Murre excels. Besides being a more efficient aerial flier (to be discussed later), it seems to be capable of swimming greater underwater distances, possibly at higher energetic efficiency. The more persistent underwater swimming of this species is indicative. However, the more nervous behavior of the Common Murre makes it difficult to base a conclusion solely on tank performance. After examination of the anatomical data, this problem will again be considered.

## ANATOMICAL COMPARISONS

*Skeleton.* Of the various measurements taken from each skeletal specimen, 46 are included here (see table 1 for a listing and descriptions; fig. 6 for illustrations). Ratios calculated from these measurements include intramembral, functional, and dimension-trunk. Although these ratios are usually applied to situations involving lengths of limb bones, they are appropriate for dealing with other skeletal measurements.

Intramembral ratios express the bone dimension as a per cent of some other measurement within the same "functional unit." (I denote as separate "functional units" the sternum, coracoid, furcula, wing, pelvis, leg, and skull.) Intramembral ratios are not calculated where one dimension is contained directly within the other. For the pelvis, any of the width measurements expressed as a per cent of total pelvic length gives an intramembral ratio. Conversely, a functional ratio may be calculated when one measurement is expressed as a per cent of a measurement within which it is directly contained. Such a ratio is represented by the expression of the anterior or posterior pelvic length as a per cent of total pelvic length. In this case the anterior and posterior pelvic lengths contribute directly to and are necessarily highly correlated with total pelvic length.

Dimension-trunk ratios (usually referred to as limb-trunk ratios if only limb bones are being compared) express each bone dimension as a percentage of some axial skeletal measurement (in this case, the anterior back length, although the posterior back length gives very similar results). The value of the dimension-trunk ratio depends upon the assumptions that, in closely related birds, fixed distances along the dorsal skeleton are the least likely to vary adaptively from species to species and that ratio differences are likely to reflect absolute changes in skeletal proportions. The intramembral or functional ratios cannot be used to confirm or deny this assumption; they merely present different information. However, statistical treatment of the measurements (table 2) tends to confirm the dimension-trunk ratios. Of the 33 dimensions (excluding anterior and posterior back lengths) which contribute to dimension-trunk ratios that differ significantly between the two species, 23 differ significantly and in the same direction when treated only as dimensions. For the purposes of this discussion, I have included only dimension-trunk (table 3) and intramembral (table 4) ratios.

Storer's (1952) data suggest that the use of ratios is an appropriate means for comparing Common and Thick-billed Murres. Dividing the Common Murre into 12 geographical categories and the thick-billed into eight, he followed for each species trends in wing length, tarsal length, culmen, and bill depth. Using the mean wing length, tarsal length, culmen, and bill depth given for each locality,

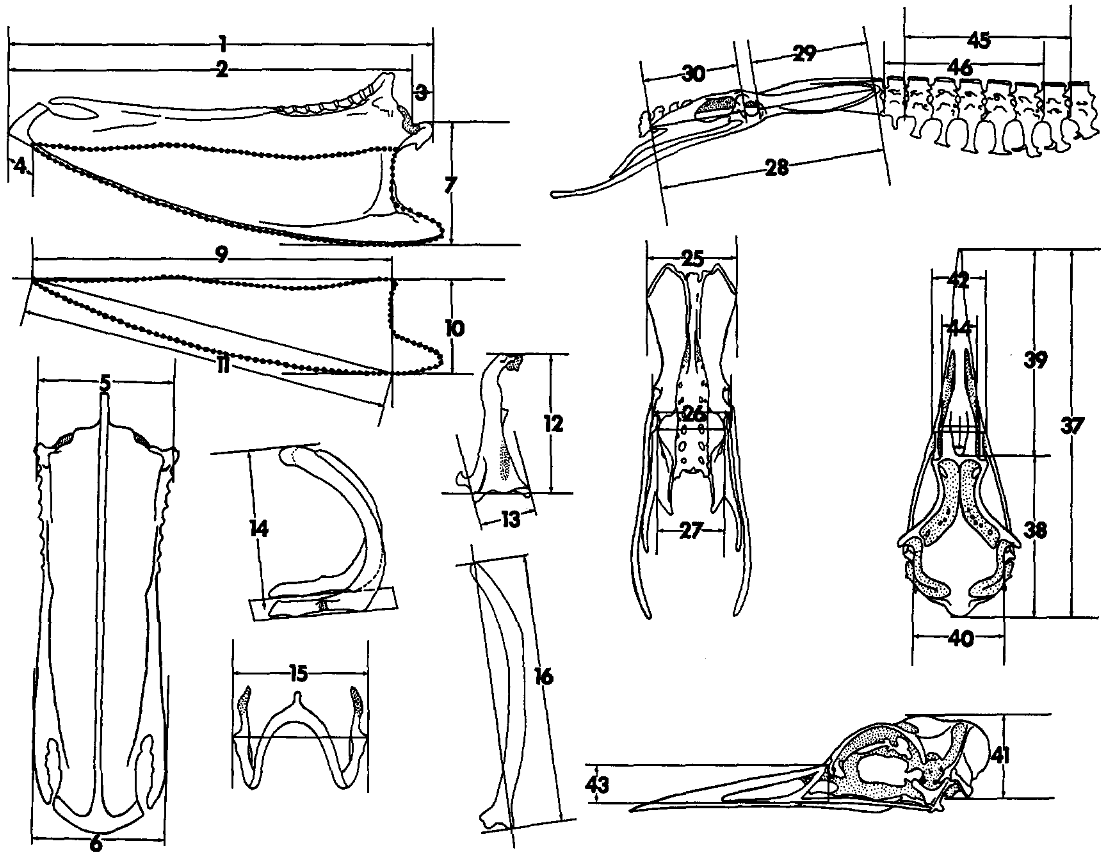


FIGURE 6. Measurements excluding those of wing and leg. Heavy dots on sternum delimit keel area, the square root of which is measurement no. 8. See table 1 for descriptions.

I have calculated correlation coefficients for each of the six possible pairings of measurements—wing length vs. tarsal length, wing length vs. culmen, etc. Uniformly high coefficients for the Thick-billed Murre strongly suggest that geographical variation in this species involves mainly total body size, with wing length, tarsal length, culmen, and bill depth maintaining a constant relation to one another. In the Common Murre bill measurements are more independent of changes in wing and tarsal length. However, a significant correlation between wing and tarsal lengths suggests that this independence may be confined to the bill. Thus there is a suggestion that the use of ratios gives results which are representative of the whole species as well as of particular populations or subspecies.

In this study all but one of the 44 Common Murre specimens came from California or Washington. Of the thick-billed 27 were taken in northern Alaska, and one each was obtained in Massachusetts, New York, and Greenland. While I have argued that ratios are at least partially refractory to intraspecific variation, raw measurement data obviously are not. Since some use is made of such data (table 2), it must be realized that, ideally, specimens from an area of sympatry should be used. While the thick-billed material is largely from such a region, the Common Murre skeletons are not. However, examination of Storer's (1952) Common Murre measurements for north Pacific populations and Swartz's (1966) measurements for Cape Thompson (northern Alaska) birds suggests that California or Washington Common Murres do not differ greatly from those in northern Alaska, the area of origin for most thick-billeds used in this study.

Figure 7 illustrates a regression line relating body weights and anterior back measurements for 19 species of alcids (see table 5 for data used). The exponential curve, $W = AL^B$ (where $W$ is weight, $L$ is the anterior back length, and $A$ and $B$ are calculated from the given $W$'s and $L$'s), is commonly used in growth studies and is appropriate to situations where closely-related species of different sizes are compared. If the data for any one species

TABLE 1. Listing and description of skeletal dimensions. (Numbers correspond to numbers of figure 6, and tables 2 and 3.)

| | |
|---|---|
| Sternum | |
| 1 | Total sternal length: anterior extremity of manubrium to posterior, medial extremity of sternum |
| 2 | Sternal length less manubrium: dorsal lip of coracoidal sulcus to posterior, medial extremity of sternum |
| 3 | Manubrium length: anterior extremity of manubrium to dorsal lip of coracoidal sulcus; equal to measurement #1 – #2 |
| 4 | Sternal length posterior to keel: posterior extremity of keel to posterior medial extremity of sternum; only measurement procured with a flexible ruler so as to take any curvature into account |
| 5 | Anterior sternal width: lateral extent of most anterior costal process on one side to comparable point on opposite side |
| 6 | Posterior sternal width: greatest width of posterior half of sternum; invariably taken at level of lateral xiphoid processes |
| 7 | Sternal height: dorsal edge of manubrium to point along ventral border of keel that is directly ventral |
| 8 | Square root of keel area: measured on keel tracing with a planimeter |
| 9 | Keel length: anterior, dorsal corner of keel to to posterior limit of keel; measured on keel tracing |
| 10 | Anterior height of keel: measured along line perpendicular to keel length (measurement #9); from anterior dorsal corner of keel to intersection of line with ventral border of keel; measured on keel tracing |
| 11 | Keel diagonal: ventral limit of measurement #10 to posterior limit of keel; measured on keel tracing |
| Coracoid | |
| 12 | Coracoid length |
| 13 | Width of coracoid base |
| Furcula | |
| 14 | Furcula height |
| 15 | Furcula width: lateral extent of coracoidal facet on one side to corresponding point on other side |
| Scapula | |
| 16 | Scapula length |
| Wing (maximal lengths in all cases except #22) | |
| 17 | Humerus |
| 18 | Ulna |
| 19 | Radius |
| 20 | Carpometacarpus |
| 21 | Pollex |
| 22 | Proximal phalanx (phalanx 1), digit 2: process projecting from distal end not included in length |
| 23 | Distal phalanx (phalanx 2), digit 2 |
| 24 | Total wing length: sum of lengths for humerus measurement (#17), ulna (#18), carpometacarpus (#20), phalanx 1 of digit 2 (#22), and phalanx 2 of digit 2 (#23) |
| Pelvis | |
| 25 | Anterior pelvic width: greatest width across anterior ilial blades |
| 26 | Medial pelvic width: lateral extent of antitrochanter on one side to corresponding point on opposite side |
| 27 | Posterior pelvic width: greatest width across posterior ilia; measured in dorsal area immediately posterior to antitrochanters |
| 28 | Total pelvic length: anterior edge of scar for "M. ilio-trochantericus posterior" to posterior extremity of ilium |
| 29 | Anterior pelvic length: anterior edge of acetabular foramen to anterior edge of scar for "M. ilio-trochantericus posterior" |
| 30 | Posterior pelvic length: posterior edge of acetabular foramen to posterior extremity of ilium |
| Leg (maximal lengths in all cases except #33) | |
| 31 | Femur |
| 32 | Tibiotarsus |
| 33 | Tibiotarsal length less cnemial crest: proximal articular surface to distal extremity |
| 34 | Cnemial crest length: measurement #32 – #33 |
| 35 | Tarsometatarsus |
| 36 | Total leg length: sum of lengths for femur (measurement #31), tibiotarsus less cnemial crest (#33), and tarsometatarsus (#35) |
| Skull | |
| 37 | Total skull length: anterior tip of premaxillaries to posterior end of cranium; taken with skull resting on flat surface |
| 38 | Cranial length: posterior limit of nasal processes of premaxillaries to posterior end of cranium |
| 39 | Upper mandible length: measurement #37 – #38 |
| 40 | Cranial width: measured across squamosal region, immediately posterior to postorbital process |
| 41 | Cranial height: maximum vertical distance in median sagittal plane between level of basitemporal plate and dorsal extent of cranial vault |
| 42 | Ventral width of upper mandible's base: from point directly lateral to apex of acute angle formed by meeting of inferior process of nasal and posterior process of maxillary, to same point on opposite side |
| 43 | Height of upper mandible's base: from apex of angle between lacrimal and inferior process of nasal to point along jugal bar which is directly ventral; taken only with quadrates in place |
| 44 | Dorsal width of upper mandible's base: maximum width of plate immediately dorsal to external nares |
| Vertebrae | |
| 45 | Anterior back length: anterior edge of centrum of vertebra #16 to posterior edge of centrum of vertebra #21 |
| 46 | Posterior back length: anterior edge of centrum of vertebra #17 to posterior edge of centrum of vertebra #22 |

TABLE 2. Skeletal dimensions for Common and Thick-billed Murres.

| | | Common Murre | | | | Thick-billed Murre | | | | |
|---|---|---|---|---|---|---|---|---|---|---|
| | Dimension[a] | $n$ | Range | $\bar{x}$ mm | SE | $n$ | Range | $\bar{x}$ mm | SE | $P$[c] |
| 1 | Total sternal l.[b] | 39 | 127.7–112.2 | 119.71 | .53 | 30 | 133.9–107.4 | 118.75 | .95 | |
| 2 | Sternal l. – manubrium l. | 39 | 118.3–104.7 | 111.75 | .48 | 30 | 125.2–100.6 | 111.15 | .92 | |
| 3 | Manubrium l. | 39 | 9.4– 6.6 | 7.96 | .10 | 30 | 8.9– 6.4 | 7.61 | .13 | * |
| 4 | L. posterior to keel | 40 | 12.0– 7.0 | 9.38 | .17 | 29 | 15.0– 6.0 | 11.76 | .36 | **** |
| 5 | Anterior sternal w. | 39 | 40.7– 36.4 | 38.52 | .19 | 29 | 46.0– 35.9 | 39.83 | .33 | **** |
| 6 | Posterior sternal w. | 39 | 44.8– 34.2 | 38.82 | .31 | 28 | 46.9– 39.3 | 43.16 | .37 | **** |
| 7 | Sternal h. | 40 | 38.5– 34.9 | 36.61 | .16 | 29 | 40.5– 35.3 | 37.50 | .21 | **** |
| 8 | Sq. root of keel area | 28 | 46.3– 40.1 | 43.37 | .24 | 27 | 47.7– 39.4 | 42.72 | .29 | |
| 9 | Keel l. | 28 | 108.2– 95.0 | 101.48 | .54 | 27 | 110.4– 87.5 | 98.51 | .89 | *** |
| 10 | Anterior keel h. | 28 | 29.1– 26.1 | 27.52 | .16 | 27 | 30.0– 25.7 | 27.81 | .19 | |
| 11 | Keel diagonal | 28 | 128.2–110.6 | 119.49 | .75 | 27 | 128.6–102.8 | 114.97 | 1.06 | **** |
| 12 | Coracoid l. | 42 | 42.1– 37.1 | 39.35 | .16 | 38 | 41.9– 37.7 | 40.45 | .17 | **** |
| 13 | Width coracoid base | 42 | 17.0– 14.6 | 15.65 | .10 | 28 | 18.2– 15.1 | 16.65 | .14 | **** |
| 14 | Furcula h. | 37 | 48.4– 40.8 | 43.92 | .27 | 28 | 46.7– 41.1 | 43.88 | .31 | |
| 15 | Furcula w. | 37 | 41.2– 32.1 | 38.55 | .35 | 29 | 44.5– 32.8 | 40.48 | .51 | *** |
| 16 | Scapula l. | 39 | 78.7– 70.1 | 74.33 | .36 | 29 | 82.6– 71.2 | 76.83 | .43 | **** |
| 17 | Humerus l. | 42 | 91.7– 82.6 | 87.68 | .31 | 30 | 93.4– 84.4 | 89.96 | .41 | **** |
| 18 | Ulna l. | 42 | 70.0– 62.9 | 66.53 | .26 | 29 | 74.0– 66.0 | 70.39 | .36 | **** |
| 19 | Radius l. | 42 | 67.1– 59.4 | 63.69 | .26 | 30 | 71.0– 63.5 | 67.50 | .33 | **** |
| 20 | Carpometacarpus l. | 42 | 46.8– 41.8 | 44.57 | .16 | 30 | 48.7– 43.3 | 46.10 | .24 | **** |
| 21 | Pollex l. | 42 | 21.0– 17.8 | 19.39 | .11 | 30 | 21.6– 17.5 | 19.00 | .18 | |
| 22 | Phalanx 1, digit 2 | 42 | 21.4– 18.6 | 20.03 | .09 | 30 | 22.9– 19.4 | 20.84 | .14 | *** |
| 23 | Phalanx 2, digit 2 | 41 | 25.1– 20.9 | 22.37 | .14 | 30 | 26.3– 22.2 | 23.66 | .18 | **** |
| 24 | Total wing l. | 41 | 251.7–227.6 | 241.42 | .86 | 29 | 264.9–237.3 | 250.92 | 1.21 | **** |
| 25 | Anterior pelvic w. | 38 | 29.1– 22.6 | 26.18 | .26 | 29 | 28.3– 23.8 | 26.10 | .25 | |
| 26 | Medial pelvic w. | 38 | 26.6– 21.4 | 22.96 | .16 | 30 | 26.4– 22.2 | 24.36 | .21 | **** |
| 27 | Posterior pelvic w. | 39 | 23.2– 18.4 | 20.25 | .20 | 30 | 23.8– 18.6 | 21.17 | .28 | *** |
| 28 | Total pelvic l. | 37 | 75.9– 68.0 | 71.78 | .36 | 30 | 72.7– 64.7 | 68.60 | .37 | **** |
| 29 | Anterior pelvic l. | 38 | 38.9– 33.9 | 36.22 | .23 | 30 | 37.9– 32.4 | 35.12 | .24 | *** |
| 30 | Posterior pelvic l. | 39 | 33.7– 28.4 | 30.73 | .21 | 28 | 31.4– 25.5 | 28.94 | .27 | **** |
| 31 | Femur l. | 42 | 50.5– 44.9 | 48.62 | .20 | 30 | 52.1– 44.0 | 47.82 | .32 | * |
| 32 | Total tibiotarsal l. | 42 | 97.8– 86.0 | 92.99 | .40 | 30 | 93.6– 80.9 | 87.94 | .52 | **** |
| 33 | Tibiotar. l. – cnemial crest | 42 | 91.3– 80.4 | 86.98 | .39 | 30 | 87.4– 75.0 | 82.12 | .50 | **** |
| 34 | Cnemial crest l. | 42 | 6.8– 4.9 | 6.01 | .07 | 30 | 6.7– 5.0 | 5.82 | .08 | |
| 35 | Tarsometatarsal l. | 40 | 41.8– 36.3 | 38.82 | .20 | 30 | 40.1– 34.2 | 37.09 | .26 | **** |
| 36 | Total leg l. | 40 | 182.7–161.6 | 174.53 | .70 | 30 | 178.6–153.2 | 167.03 | 1.00 | **** |
| 37 | Total skull l. | 34 | 110.2– 96.5 | 103.68 | .59 | 26 | 104.6– 91.6 | 97.44 | .56 | **** |
| 38 | Cranial l. | 42 | 49.1– 43.0 | 46.45 | .19 | 29 | 48.4– 43.3 | 46.08 | .24 | |
| 39 | Upper mandible l. | 34 | 62.8– 51.7 | 57.22 | .48 | 26 | 56.7– 47.7 | 51.27 | .40 | **** |
| 40 | Cranial w. | 42 | 27.3– 24.2 | 25.94 | .11 | 29 | 29.2– 26.2 | 27.53 | .16 | **** |
| 41 | Cranial h. | 42 | 23.1– 21.0 | 22.23 | .10 | 30 | 24.6– 21.5 | 23.39 | .14 | **** |
| 42 | Vt. w. upper mand. base | 43 | 16.3– 13.5 | 14.92 | .11 | 27 | 18.3– 14.4 | 16.18 | .19 | **** |
| 43 | H. upper mand. base | 40 | 14.4– 9.1 | 10.88 | .12 | 28 | 13.3– 9.5 | 11.08 | .17 | |
| 44 | D. w. upper mand. base | 43 | 12.2– 9.7 | 10.84 | .08 | 29 | 12.3– 10.3 | 11.35 | .10 | **** |
| 45 | Anterior back l. | 39 | 52.8– 45.7 | 49.45 | .29 | 28 | 50.1– 44.9 | 47.29 | .24 | **** |
| 46 | Posterior back l. | 42 | 53.8– 46.4 | 50.22 | .27 | 28 | 51.2– 45.2 | 47.99 | .25 | **** |

[a] Numbers of dimensions correspond to descriptions given in table 1.

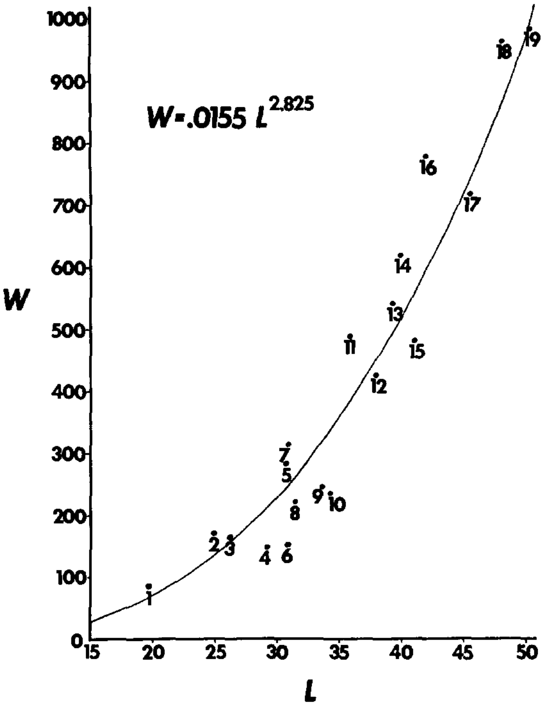
[b] l. = length; w. = width; h. = height.

[c] *, $P < 0.05$; **, $P < 0.025$; ***, $P < 0.01$; ****, $P < 0.001$. ($P$ indicates significance of difference between $\bar{x}$'s.)

are deleted from the curve fitting process, the calculated regression can be used for predicting the weight of that species from its mean anterior back length. For the Common Murre, this gives a value of 980.3 g which is quite close to the 984.6 g mean weight given by Swartz (1966) for Cape Thompson birds (northern Alaska). Conversely the predicted weight of 844.8 g for the Thick-billed Murre is much smaller than Swartz's mean weight of 964.4 grams. Thus the thick-billed is 14.3 per cent heavier for its body length, a fact suggested by its stocky build (fig. 1). A large portion of this difference is due to hyperdevelopment of the thick-billed's pectoral region, a conclusion developed below.

Dimension-trunk ratios (nos. 1, 5, 6, table 3) reveal that the sternum is relatively longer and wider in the Thick-billed Murre. While the relatively greater anterior and posterior widths involve a general broadening in both regions, the relatively greater length is due solely to an expansion of the plate-like area posterior to the sternal keel (fig. 8a, b, c). Also the square root of the keel area is relatively larger in the thick-billed, and this is due to expansion of its anterior region as reflected in ratios calculated from both the "sternal height" and "anterior keel height" (ratios nos. 7 and 10, table 3, respectively; illustrated in fig. 8d). The sternum differences between the two murres cannot be explained in terms of any one simple gradient. This is substantiated by the existence of dimension-trunk ratios where the two species do not differ, by the varying magnitudes of the statistically significant differences (see "% difference" column, table 3), and by the intramembral ratios (nos. 1–5, table 4).

Keel expansion as well as sternal widening suggest a hyperdevelopment of the muscles



←

FIGURE 7. Regression of body weight, $W$ (g), on anterior back length, $L$ (mm), for various species of alcids ($W = AL^B$). $A$ and $B$ are calculated on the basis of various values for $W$ and $L$ given in table 5; numbers below each point correspond to species numbers given in table 5.

TABLE 3. Dimension-trunk (anterior back length) ratios for Common and Thick-billed Murres.

| | | Common Murre | | | | Thick-billed Murre | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | Dimension[a] | $n$ | Range | $\bar{x}$ | SE | $n$ | Range | $\bar{x}$ | SE | $P$[b] | % diff.[c] | 95% C. I. for % diff. |
| 1 | Total sternal l.[d] | 39 | 254.7–224.3 | 238.2 | 1.2 | 28 | 265.7–228.0 | 246.2 | 1.6 | **** | 3.37 | 1.75– 5.00 |
| 2 | Sternal l. – manubrium l. | 39 | 238.4–209.3 | 222.4 | 1.1 | 28 | 247.1–213.6 | 230.4 | 1.5 | **** | 3.61 | 1.97– 5.25 |
| 3 | Manubrium l. | 39 | 17.9– 13.6 | 15.8 | 0.2 | 28 | 19.2– 13.3 | 15.8 | 0.3 | | | |
| 4 | L. posterior to keel | 40 | 25.0– 13.8 | 18.7 | 0.4 | 27 | 30.9– 12.2 | 24.2 | 0.7 | **** | 29.50 | 21.59–37.41 |
| 5 | Anterior sternal w. | 39 | 82.0– 70.7 | 76.8 | 0.4 | 27 | 91.4– 76.0 | 82.8 | 0.6 | **** | 7.77 | 5.82– 9.73 |
| 6 | Posterior sternal w. | 39 | 85.5– 67.5 | 77.3 | 0.7 | 26 | 101.3– 81.4 | 89.7 | 0.9 | **** | 16.16 | 13.21–19.10 |
| 7 | Sternal h. | 40 | 77.8– 68.3 | 72.8 | 0.4 | 27 | 83.1– 72.9 | 78.1 | 0.5 | **** | 7.32 | 5.65– 9.00 |
| 8 | Sq. root of keel area | 28 | 92.7– 81.9 | 86.2 | 0.5 | 26 | 95.4– 83.6 | 88.8 | 0.6 | *** | 2.92 | 1.06– 4.78 |
| 9 | Keel l. | 28 | 214.7–191.6 | 201.8 | 1.0 | 26 | 224.1–185.8 | 204.6 | 1.6 | | | |
| 10 | Anterior keel h. | 28 | 58.8– 51.2 | 54.7 | 0.4 | 26 | 62.8– 53.2 | 57.9 | 0.5 | **** | 5.76 | 3.48– 8.03 |
| 11 | Keel diagonal | 28 | 255.9–226.1 | 237.5 | 1.3 | 26 | 261.5–218.3 | 238.8 | 2.0 | | | |
| 12 | Coracoid l. | 42 | 83.7– 74.0 | 78.4 | 0.4 | 26 | 88.7– 80.0 | 84.3 | 0.5 | **** | 7.47 | 6.00– 8.95 |
| 13 | Width coracoid base | 42 | 34.9– 28.7 | 31.2 | 0.2 | 26 | 38.6– 31.2 | 34.6 | 0.3 | **** | 10.93 | 8.44–13.43 |
| 14 | Furcula h. | 37 | 97.0– 79.3 | 87.5 | 0.6 | 26 | 101.8– 86.4 | 91.5 | 0.8 | **** | 4.62 | 2.47– 6.77 |
| 15 | Furcula w. | 37 | 83.2– 63.8 | 76.8 | 0.7 | 27 | 92.5– 68.9 | 84.0 | 1.1 | **** | 9.47 | 6.37–12.57 |
| 16 | Scapula l. | 39 | 158.8–139.6 | 148.2 | 0.8 | 27 | 173.3–151.2 | 159.8 | 1.0 | **** | 7.84 | 6.21– 9.47 |
| 17 | Humerus l. | 42 | 186.8–163.3 | 174.7 | 0.8 | 28 | 195.9–179.9 | 187.5 | 0.7 | **** | 7.31 | 5.97– 8.66 |
| 18 | Ulna l. | 42 | 143.7–124.3 | 132.6 | 0.7 | 27 | 153.1–141.5 | 146.7 | 0.6 | **** | 10.63 | 9.20–12.06 |
| 19 | Radius l. | 42 | 138.4–119.8 | 126.9 | 0.6 | 28 | 146.6–134.9 | 140.6 | 0.6 | **** | 10.80 | 9.37–12.23 |
| 20 | Carpometacarpus l. | 42 | 93.8– 84.5 | 88.8 | 0.4 | 28 | 103.5– 93.5 | 95.9 | 0.4 | **** | 8.03 | 6.66– 9.40 |
| 21 | Pollex l. | 42 | 42.4– 36.0 | 38.6 | 0.2 | 28 | 43.7– 37.2 | 39.5 | 0.3 | * | 2.17 | 0.16– 4.19 |
| 22 | Phalanx 1, digit 2 | 42 | 44.8– 38.2 | 40.5 | 0.2 | 28 | 46.0– 41.1 | 43.4 | 0.2 | **** | 7.22 | 5.64– 8.80 |
| 23 | Phalanx 2, digit 2 | 41 | 49.3– 41.6 | 44.6 | 0.3 | 28 | 52.4– 46.8 | 49.3 | 0.3 | **** | 10.50 | 8.66–12.33 |
| 24 | Total wing l. | 41 | 520.6–453.6 | 481.1 | 2.3 | 27 | 550.5–508.6 | 522.9 | 1.9 | **** | 8.68 | 7.37–10.00 |
| 25 | Anterior pelvic w. | 38 | 60.5– 44.8 | 52.1 | 0.6 | 27 | 62.4– 50.2 | 54.5 | 0.7 | *** | 4.61 | 1.19– 8.02 |
| 26 | Medial pelvic w. | 38 | 52.3– 42.6 | 45.7 | 0.3 | 28 | 54.1– 47.0 | 50.9 | 0.4 | **** | 11.27 | 9.00–13.54 |
| 27 | Posterior pelvic w. | 39 | 46.9– 35.0 | 40.3 | 0.4 | 28 | 49.5– 37.7 | 44.3 | 0.6 | **** | 9.87 | 6.41–13.34 |
| 28 | Total pelvic l. | 37 | 152.5–133.1 | 142.7 | 0.7 | 28 | 150.8–136.6 | 142.7 | 0.7 | | | |
| 29 | Anterior pelvic l. | 38 | 78.2– 65.2 | 72.1 | 0.5 | 28 | 78.5– 67.1 | 73.0 | 0.5 | | | |
| 30 | Posterior pelvic l. | 39 | 65.9– 58.4 | 61.2 | 0.3 | 27 | 66.3– 54.4 | 60.3 | 0.5 | | | |
| 31 | Femur l. | 42 | 104.7– 91.5 | 96.9 | 0.4 | 28 | 105.4– 95.0 | 99.5 | 0.5 | **** | 2.75 | 1.41– 4.09 |
| 32 | Total tibiotarsal l. | 42 | 201.1–175.7 | 185.3 | 0.9 | 28 | 192.7–174.4 | 183.1 | 0.9 | | | |
| 33 | Tibiotar. l. – cnemial crest | 42 | 189.2–164.8 | 173.3 | 0.8 | 28 | 181.0–162.0 | 171.0 | 0.9 | | | |
| 34 | Cnemial crest l. | 42 | 14.3– 9.7 | 12.0 | 0.1 | 28 | 14.8– 10.5 | 12.1 | 0.2 | | | |
| 35 | Tarsometatarsal l. | 40 | 81.7– 72.1 | 77.3 | 0.4 | 28 | 80.0– 72.6 | 77.1 | 0.4 | | | |
| 36 | Total leg l. | 40 | 369.8–331.2 | 347.4 | 1.5 | 28 | 365.0–330.9 | 347.6 | 1.4 | | | |
| 37 | Total skull l. | 32 | 224.2–192.3 | 207.0 | 1.3 | 25 | 213.5–185.4 | 203.1 | 1.2 | * | 1.97 | 0.19– 3.74 |
| 38 | Cranial l. | 40 | 99.8– 86.3 | 92.6 | 0.5 | 27 | 104.0– 88.9 | 96.0 | 0.6 | **** | 3.74 | 1.93– 5.55 |
| 39 | Upper mandible l. | 32 | 127.6–101.9 | 114.4 | 1.0 | 25 | 115.7– 96.6 | 107.0 | 0.7 | **** | 6.92 | 4.58– 9.26 |
| 40 | Cranial w. | 40 | 56.1– 49.0 | 51.6 | 0.3 | 27 | 60.8– 53.0 | 57.5 | 0.4 | **** | 11.29 | 9.44–13.15 |
| 41 | Cranial h. | 40 | 48.1– 40.1 | 44.3 | 0.3 | 28 | 52.4– 44.7 | 48.9 | 0.4 | **** | 10.37 | 8.43–12.31 |
| 42 | Vt. w. upper mand. base | 41 | 33.3– 26.9 | 29.8 | 0.3 | 26 | 36.5– 29.1 | 33.6 | 0.4 | **** | 12.76 | 9.88–15.64 |
| 43 | H. upper mand. base | 38 | 29.6– 19.1 | 21.6 | 0.3 | 27 | 26.5– 20.0 | 23.1 | 0.4 | *** | 6.76 | 2.41–11.10 |
| 44 | D. w. upper mand. base | 41 | 23.6– 19.8 | 21.5 | 0.1 | 27 | 26.2– 22.1 | 23.6 | 0.2 | **** | 9.95 | 7.82–12.09 |

[a] Numbers of dimensions correspond to descriptions given in table 1.

[b] *, $P < 0.05$; **, $P < 0.025$; ***, $P < 0.01$; ****, $P < 0.001$.

[c] Difference expressed as per cent of smaller species; given only for ratios where there is a significant difference between the two species.

[d] l., length; h., height; w., width.

TABLE 4. Intramembral ratios for Common and Thick-billed Murres.

| | Ratio | Common Murre | | | Thick-billed Murre | | | | | 95% C. I. for % diff. |
|---|---|---|---|---|---|---|---|---|---|---|
| | | $n$ | $\bar{x}$ | SE | $n$ | $\bar{x}$ | SE | $P$[a] | % diff.[b] | |
| | Sternum | | | | | | | | | |
| 1 | Manubrium l./ant. sternal w. | 38 | 20.6 | 0.2 | 29 | 19.1 | 0.3 | **** | 7.73 | 3.98–11.49 |
| 2 | Keel l./ant. sternal w. | 27 | 263.6 | 1.2 | 26 | 245.8 | 1.5 | **** | 7.26 | 5.74– 8.79 |
| 3 | L. post. to keel/ant. sternal w. | 38 | 24.3 | 0.5 | 28 | 29.4 | 1.0 | **** | 20.95 | 12.99–28.92 |
| 4 | Posterior sternal w./ant. sternal w. | 38 | 100.8 | 0.7 | 27 | 108.3 | 1.2 | **** | 7.53 | 4.96–10.11 |
| 5 | Sternal h./ant. sternal w. | 38 | 95.1 | 0.4 | 28 | 94.1 | 0.6 | | | |
| | Coracoid | | | | | | | | | |
| 6 | W. coracoid base/coracoid l. | 42 | 39.8 | 0.3 | 28 | 41.2 | 0.4 | *** | 3.47 | 1.36– 5.58 |
| | Furcula | | | | | | | | | |
| 7 | Furcula w./furcula h. | 37 | 87.9 | 0.9 | 28 | 92.8 | 1.4 | *** | 5.65 | 1.98– 9.31 |
| | Wing | | | | | | | | | |
| 8 | Ulna l./humerus l. | 42 | 75.9 | 0.2 | 29 | 78.3 | 0.2 | **** | 3.15 | 2.49– 3.81 |
| 9 | Radius l./humerus l. | 42 | 72.6 | 0.2 | 30 | 75.0 | 0.2 | **** | 3.30 | 2.65– 3.96 |
| 10 | Carpometacarpus l./humerus l. | 42 | 50.8 | 0.1 | 30 | 51.3 | 0.2 | * | 0.83 | 0.08– 1.57 |
| 11 | Pollex l./humerus l. | 42 | 22.1 | 0.1 | 30 | 21.1 | 0.2 | **** | 4.69 | 2.80– 6.57 |
| 12 | Phalanx 1, digit 2/humerus l. | 42 | 23.2 | 0.1 | 30 | 23.2 | 0.1 | | | |
| 13 | Phalanx 2, digit 2/humerus l. | 41 | 25.5 | 0.1 | 30 | 26.3 | 0.2 | **** | 3.06 | 1.49– 4.62 |
| | Pelvis | | | | | | | | | |
| 14 | Ant. pelvic w./total pelvic l. | 37 | 36.5 | 0.4 | 29 | 38.1 | 0.4 | *** | 4.44 | 1.37– 7.50 |
| 15 | Med. pelvic w./total pelvic l. | 36 | 32.0 | 0.2 | 30 | 35.5 | 0.3 | **** | 11.00 | 8.88–13.13 |
| 16 | Post. pelvic w./total pelvic l. | 37 | 28.1 | 0.3 | 30 | 30.9 | 0.4 | **** | 9.74 | 6.55–12.94 |
| | Leg | | | | | | | | | |
| 17 | Total tibiotarsal l./femur l. | 42 | 191.3 | 0.7 | 30 | 184.0 | 0.8 | **** | 3.99 | 2.86– 5.12 |
| 18 | Tibiotarsus – cnemial crest/femur l. | 42 | 179.0 | 0.7 | 30 | 171.8 | 0.7 | **** | 4.17 | 3.01– 5.33 |
| 19 | Cnemial crest l./femur l. | 42 | 12.4 | 0.1 | 30 | 12.2 | 0.2 | | | |
| 20 | Tarsometatarsal l./femur l. | 40 | 79.8 | 0.3 | 30 | 77.6 | 0.4 | **** | 2.82 | 1.51– 4.13 |
| | Skull | | | | | | | | | |
| 21 | Upper mandible l./cranial l. | 34 | 123.2 | 1.0 | 26 | 111.1 | 0.8 | **** | 10.92 | 8.47–13.37 |
| 22 | Cranial w./cranial l. | 41 | 55.9 | 0.2 | 29 | 59.8 | 0.4 | **** | 6.98 | 5.59– 8.37 |
| 23 | Cranial h./cranial l. | 42 | 47.9 | 0.2 | 29 | 50.9 | 0.2 | **** | 6.35 | 4.98– 7.73 |
| 24 | Vt. w. upper mand. base/cranial l. | 42 | 32.1 | 0.2 | 27 | 35.1 | 0.3 | **** | 9.10 | 6.60–11.60 |
| 25 | H. upper mand. base/cranial l. | 39 | 23.2 | 0.2 | 28 | 24.0 | 0.4 | * | 3.31 | 0.15– 6.46 |
| 26 | D. w. upper mand. base/cranial l. | 42 | 23.4 | 0.2 | 29 | 24.6 | 0.2 | **** | 5.51 | 3.10– 7.91 |

[a] *, $P < 0.05$; **, $P < 0.025$; ***, $P < 0.01$; ****, $P < 0.001$.

[b] Difference expressed as per cent of smaller species; given only for ratios where there is a significant difference between the two species.

TABLE 5. Data used for calculation of regression between back length and body weight.[a]

| | Common Name | Scientific Name | Anterior back length ($\bar{x}$ mm) | $n$ | Weight ($\bar{x}$ g) | $n$ | Source of weight data |
|---|---|---|---|---|---|---|---|
| 1 | Least Auklet | *Aethia pusilla* | 19.78 | 17 | 86.3 | 26 | Bédard, 1969 |
| 2 | Cassin's Auklet | *Ptychoramphus aleutica* | 25.09 | 15 | 172.6 | 19 | Thoresen, 1964 |
| 3 | Dovekie | *Plautus alle* | 26.33 | 23 | 166.2 | 8 | Johnson, 1935 $n = 7$<br>Bédard, 1969 $n = 1$ |
| 4 | Craveri's Murrelet | *Endomychura craveri* | 29.20 | 2 | 151.1 | 8 | Bédard, 1969 |
| 5 | Crested Auklet | *Aethia cristatella* | 30.76 | 8 | 284.5 | 16 | Bédard, 1969 |
| 6 | Xantus' Murrelet | *Endomychura hypoleuca* | 30.93 | 4 | 155.9 | 7 | Bédard, 1969 |
| 7 | Parakeet Auklet | *Cyclorrhynchus psittacula* | 30.99 | 13 | 317.6 | 7 | Bédard, 1969 |
| 8 | Ancient Murrelet | *Synthliboramphus antiquus* | 31.50 | 17 | 223.6 | 5 | Bédard, 1969 $n = 2$<br>Puget Sound, Wn. $n = 3$ |
| 9 | Marbled Murrelet | *Brachyramphus marmoratum* | 33.71 | 27 | 248.5 | 14 | Bédard, 1969 $n = 3$<br>Puget Sound, Wn.[b] $n = 11$ |
| 10 | Kittlitz's Murrelet | *Brachyramphus brevirostre* | 34.25 | 2 | 237.0 | 3 | Bédard, 1969 $n = 3$ |
| 11 | Common Puffin | *Fratercula arctica* | 35.93 | 12 | 490.5 | 142 | Belopol'skii, 1957 |
| 12 | Black Guillemot | *Cepphus grylle* | 38.08 | 13 | 427.5 | 189 | Belopol'skii, 1957 $n = 120$<br>Johnson, 1944 $n = 69$ |
| 13 | Rhinoceros Auklet | *Cerorhinca monocerata* | 39.31 | 20 | 544.1 | 13 | Puget Sound, Wn. |
| 14 | Horned Puffin | *Fratercula corniculata* | 39.93 | 27 | 619.0 | 36 | Bédard, 1969 $n = 5$<br>Swartz, 1966 $n = 15$<br>Nunivak Island, Alaska[b] $n = 16$ |
| 15 | Pigeon Guillemot | *Cepphus columba* | 41.04 | 13 | 483.8 | 6 | Bédard, 1969 $n = 5$<br>Swartz, 1966 $n = 1$ |
| 16 | Tufted Puffin | *Lunda cirrhata* | 42.00 | 13 | 779.4 | 16 | Bédard, 1969 $n = 7$<br>Puget Sound, Wn.[b] $n = 5$<br>Nunivak Island, Alaska[b] $n = 4$ |
| 17 | Razorbill | *Alca torda* | 45.50 | 12 | 719.2 | 142 | Belopol'skii, 1957 |
| 18 | Thick-billed Murre | *Uria lomvia* | 47.99 | 28 | 964.4 | 139 | Swartz, 1966 |
| 19 | Common Murre | *Uria aalge* | 50.22 | 42 | 984.6 | 78 | Swartz, 1966 |

[a] See fig. 7.

[b] All or some of weights from data with skeletons loaned by University of Michigan Museum of Zoology.

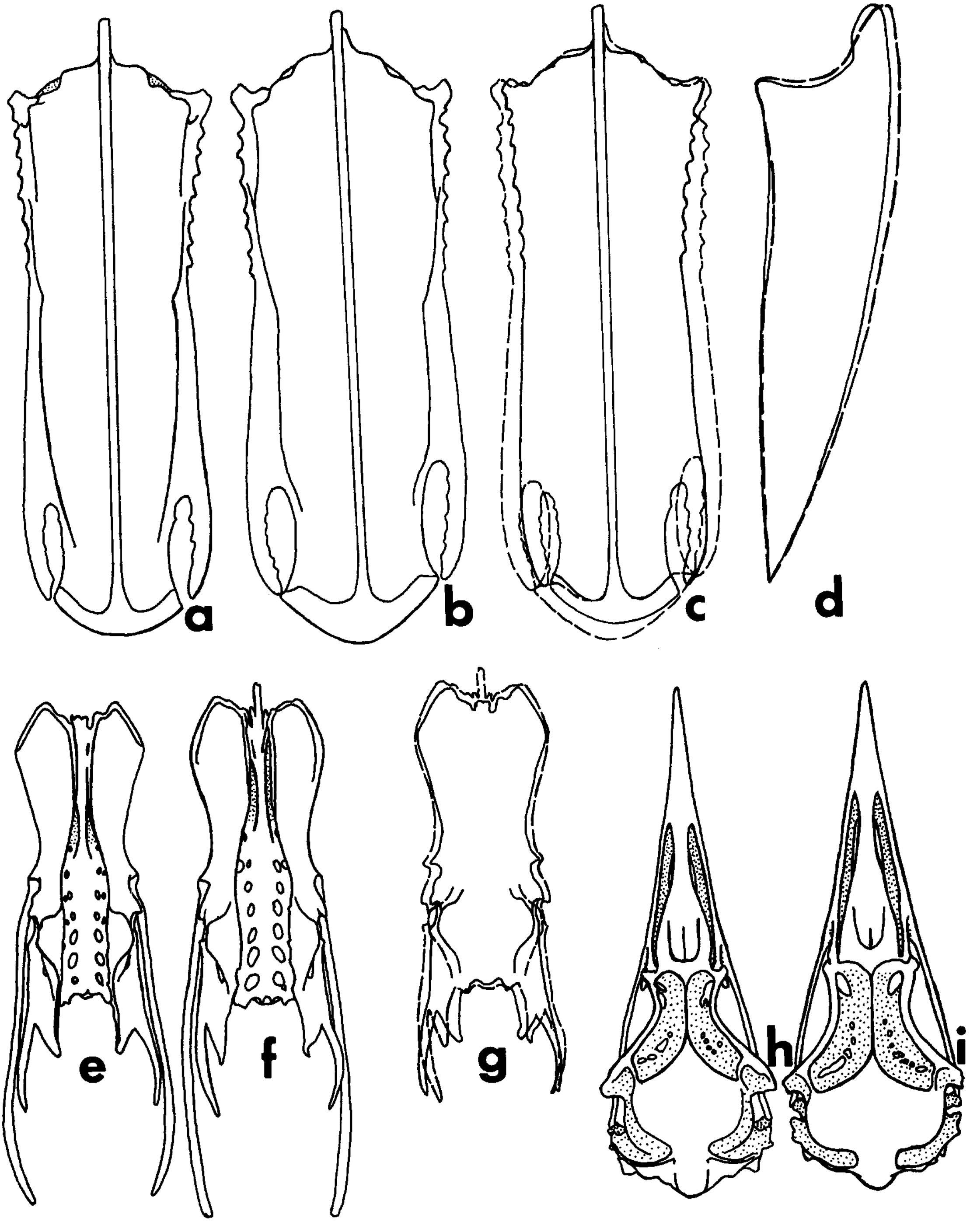


FIGURE 8. Common and Thick-billed Murre bones drawn to same relative size. Note relatively greater width in the Thick-billed Murre bones. a. ventral view of Common Murre sternum; b. ventral view of Thick-billed Murre sternum; c. Common and Thick-billed Murre sterna superimposed (solid line denotes Common Murre; broken line, Thick-billed Murre); d. keel tracings of Common and Thick-billed Murres superimposed; e. dorsal view of Common Murre pelvis; f. dorsal view of Thick-billed Murre pelvis; g. Common and Thick-billed Murre pelves superimposed; h. dorsal view of Common Murre skull; i. dorsal view of Thick-billed Murre skull.

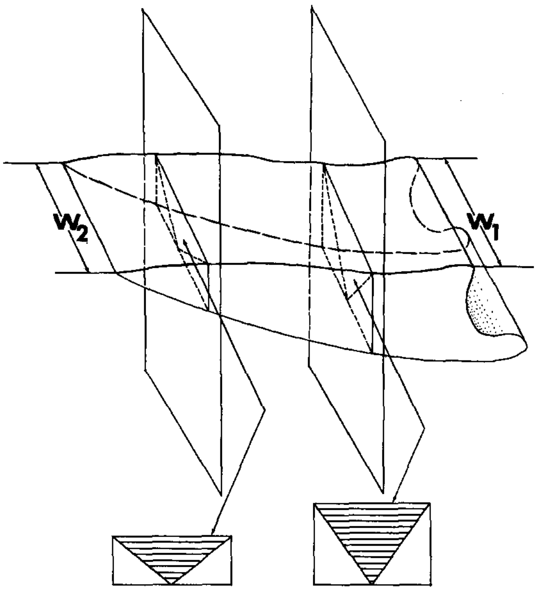


FIGURE 9. Calculation of relative volume of pectoral muscle:

$$V = \frac{A\left(\frac{W_1 + W_2}{2}\right)}{2} \div L^3$$

where $V$ = relative volume of pectoral muscle; $A$ = keel area; $W_1$ = anterior sternal width; $W_2$ = posterior sternal width; $L$ = anterior back length. Hatching designates portion of cross section which includes pectoral muscle volume.

originating from these areas, mainly the M. pectoralis thoracica and the M. supracoracoideus, the main depressor and elevator of the wing. Using the keel area, anterior sternal width, posterior sternal width, and anterior back length, it is possible to calculate a "relative volume of pectoral muscle" (fig. 9) for each specimen. While this ratio incorporates a volume which is only an approximation of the space occupied by the M. pectoralis thoracica and M. supracoracoideus (in reality the M. pectoralis thoracica bulges laterally and ventrally from this space), the ratio should nevertheless supply a valid index which can be compared with the muscle weight ratios which are presented later. The "relative volume of pectoral muscle" calculated for 23 Common and 27 Thick-billed Murres was 18.1 per cent higher in the thick-billed, a statistically significant difference ($P < .001$) which is very close to that obtained directly from muscle weights.

Three abdominal muscles attach on the plate posterior to the sternal keel: M. obliquus abdominis externus, M. rectus abdominis, and M. transversus abdominis. While the M. rectus abdominis and M. transversus abdominis insert to a limited extent on the dorsal surface of this plate (the M. rectus abdominis laterally and the M. transversus abdominis medially), the extensive insertion of the M. obliquus abdominis externus is on the ventral median portion of the plate. If this plate is indicative of relative muscle development, its greater extent in the Thick-billed Murre would seem to indicate greater development of the M. obliquus abdominis externus in that species.

The coracoid, furcula, and scapula show hyperdevelopment in the Thick-billed Murre (ratios nos. 12–16, table 3). The dimension-trunk ratios suggest and the intramembral ratios confirm that the coracoid and furcula have not hypertrophied equally in all dimensions. The width of the coracoid base has increased by a relatively greater amount than has the length. Likewise the furcula has increased in width about twice the extent that it has increased in height.

From the murres used in muscle dissection, measurements of completely articulated pectoral girdles were procured. Among the measurements taken were coracoid length, distance between coracoid bases, and distance between the distal ends of coracoids (fig. 10a). The anterior back length was also measured. From these four measurements, dimension-trunk, and intramembral ratios were calculated for 13 Thick-billed and 8 Common Murres. The three dimension-trunk ratios were all significantly greater in the Thick-billed Murre. Magnitudes of two of the three differences (6.8 per cent for distance between coracoid bases, and 10.5 per cent for distance between distal ends of coracoids) suggest that the coracoids are flared more laterally in the thick-billed. This conjecture is further supported by intramembral ratios. More laterally-pointing coracoids might account for the consistent tilt of the coracoid shaft seen in Thick-billed Murres (fig. 10b).

All wing bones, with the possible exception of the pollex, are relatively longer in the Thick-billed Murre (ratios nos. 17–23, table 3). Over-all, the wing is 8.7 per cent relatively longer. (Mean wing surface areas for four Common and two Thick-billed Murres were 519 cm$^2$ and 594 cm$^2$, respectively.) The radius, ulna, and phalanx 2 of digit 2 show the greatest increase in relative length (approximately 10.5 per cent), while the humerus, carpometacarpus, and phalanx 1 of digit 2 have increased to a lesser extent (7–8 per cent). Intramembral ratios (nos. 8–13, table 4) corroborate that a mosaic pattern exists

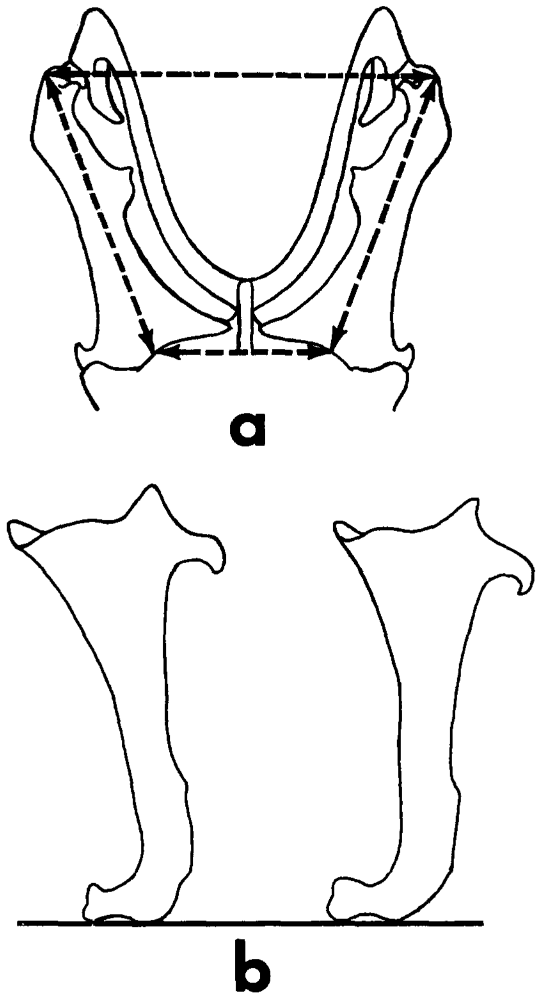


FIGURE 10. a. Ventral view of furcula, coracoids, and anterior sternum in an intact murre. Broken lines denote measurements taken. b. Lateral views of right coracoids from Thick-billed (left) and Common (right) Murres (both resting on distal tuberosities). Note tilt of shaft in Thick-billed Murre.

for the wing regarding magnitudes of increase in relative bone lengths.

The similarity in relative pollex length may reflect two statistically significant ($P < 0.01$) correlation coefficients which were calculated from means for 22 alcid species. Relative pollex length is positively correlated with anterior back length ($r = 0.63$) and relative length of the carpometacarpus ($r = 0.68$). Thus, the similarity in pollex length is possibly reflective of opposition between these two factors (thick-billeds have shorter anterior back lengths but longer relative carpometacarpus lengths).

In regard to the relative dimensions of their pelves and leg bones (ratios nos. 25–36, table 3; fig. 8e, f, g), the two species are more similar. Only the three pelvic widths plus the length of the femur are relatively larger in the Thick-billed Murre. The greater anterior pelvic width implies that the M. ilio-trochantericus posterior which originates over most of the surface of the anterior ilial blades is more massively developed in the thick-billed. A much smaller muscle, the M. gluteus medius et minimus, originates medial to the antitrochanters where the medial pelvic width was measured. However, a relatively greater width in this region may simply be indicative of wider spacing of the legs. Because of their close proximity, the relative medial and posterior pelvic widths are highly correlated ($r = 0.97$ for 21 alcid species). This is not true for either the anterior vs. medial width or the anterior vs. posterior width. While the legs are 11.3 per cent farther apart in the thick-billed, the femora are only 2.8 per cent longer.

In regard to the skull, Common Murres have a relatively longer upper mandible (and possibly total skull length). However, all other skull dimensions are relatively larger in the thick-billed (fig. 8h, i). The statistical techniques of linear regression and correlation are most useful in interpreting differences in skull proportions between the murre species. Linear regressions were determined from data for 21 species of alcids where species means for each of the skull's dimension-trunk ratios (nos. 37–44, table 3) were regressed against mean anterior back lengths. Negative regressions, significant at the 0.01 level, were obtained for three of the eight ratios—those involving relative cranial length, cranial width, and cranial height. A significant positive correlation was found for the relative length of the upper mandible.

The tendency for larger alcids to possess relatively longer upper mandibles (as is the case for Common vs. Thick-billed Murres) is probably correlated with a shift from feeding on invertebrates to feeding on fish. Negative regressions for relative cranial length, width, and height (separately calculated correlation coefficients = –0.68, –0.79, and –0.78, respectively) follow a rule which is generally valid for the whole animal kingdom, namely that within any closely related group, the larger species have relatively smaller central nervous systems. Thus, the larger relative size of the Thick-billed Murre's braincase is explicable, at least in part, by its smaller body size (as expressed by anterior back length) in comparison to the Common Murre.

The calculation of correlation coefficients for different pairs of dimension-trunk ratios

TABLE 6. Functional ratios (dry weight of muscle/total dry weight of pelvic muscles) for pelvic muscles.

| | | Common Murre[b] | | | Thick-billed Murre[c] | | |
|---|---|---|---|---|---|---|---|
| | Muscle[a] | Range | $\bar{x}$ | SE | Range | $\bar{x}$ | SE |
| 1 | M. ilio-trochantericus posterior | 7.67– 6.54 | 6.89 | .13 | 7.88– 5.79 | 6.89 | .14 |
| 2 | M. ilio-trochantericus anterior*** | 2.09– 1.71 | 1.87 | .04 | 2.56– 1.77 | 2.18 | .07 |
| 3 | M. gluteus medius et minimus | 0.40– 0.18 | 0.25 | .02 | 0.52– 0.19 | 0.32 | .02 |
| 4 | M. iliacus | 0.31– 0.19 | 0.24 | .01 | 0.32– 0.17 | 0.23 | .01 |
| 5 | M. sartorius | 8.44– 6.91 | 7.60 | .19 | 7.94– 5.13 | 7.11 | .20 |
| 6 | M. ilio-tibialis** | 3.33– 2.73 | 3.00 | .08 | 3.35– 2.10 | 2.58 | .11 |
| 7 | M. femori-tibialis externus and medius | 9.17– 7.42 | 8.17 | .22 | 8.75– 7.36 | 8.03 | .12 |
| 8 | M. femori-tibialis internus | 1.61– 1.33 | 1.45 | .05 | 1.63– 1.18 | 1.37 | .04 |
| 9 | M. piriformis: pars caudi-femoralis* | 1.95– 1.46 | 1.69 | .05 | 2.19– 1.37 | 1.93 | .08 |
| 10 | M. piriformis: pars ilio-femoralis | 1.71– 0.95 | 1.23 | .08 | 1.77– 0.82 | 1.34 | .07 |
| 11 | M. semitendinosus | 3.65– 2.84 | 3.29 | .10 | 3.72– 2.72 | 3.20 | .07 |
| 12 | M. semimembranosus | 3.36– 2.01 | 2.71 | .17 | 3.62– 2.38 | 2.94 | .11 |
| 13 | M. biceps femoris | 6.62– 5.32 | 5.71 | .14 | 6.54– 4.89 | 5.66 | .15 |
| 14 | M. ischio-femoralis | 1.92– 1.60 | 1.75 | .04 | 1.94– 1.22 | 1.61 | .05 |
| 15 | M. obturator-internus | 1.44– 0.97 | 1.25 | .05 | 1.36– 0.85 | 1.15 | .04 |
| 16 | M. obturator-externus | 0.52– 0.33 | 0.40 | .02 | 0.54– 0.28 | 0.41 | .02 |
| 17 | M. adductor longus et brevis | 9.88– 6.97 | 8.50 | .29 | 9.78– 7.33 | 8.58 | .23 |
| 18 | M. tibialis anterior | 7.43– 6.24 | 6.59 | .15 | 8.00– 5.79 | 6.74 | .18 |
| 19 | M. extensor digitorum longus* | 3.13– 2.79 | 2.99 | .06 | 4.32– 2.59 | 3.38 | .14 |
| 20 | M. peronaeus longus | 1.76– 0.78 | 1.17 | .10 | 1.48– 0.66 | 1.05 | .07 |
| 21 | M. peronaeus brevis | 0.31– 0.21 | 0.27 | .01 | 0.40– 0.20 | 0.31 | .02 |
| 22 | M. gastrocnemius | 18.27–16.35 | 17.11 | .23 | 18.12–16.20 | 16.93 | .15 |
| 23 | M. plantaris | 0.51– 0.33 | 0.42 | .02 | 0.62– 0.23 | 0.40 | .02 |
| 24 | M. flexor perforatus digiti II | 0.83– 0.67 | 0.75 | .02 | 0.95– 0.55 | 0.77 | .03 |
| 25 | M. flexor perforatus digiti III | 2.63– 2.24 | 2.41 | .05 | 2.55– 1.58 | 2.21 | .07 |
| 26 | M. flexor perforatus digiti IV | 4.17– 3.78 | 4.00 | .06 | 4.64– 3.40 | 4.05 | .10 |
| 27 | M. flexor perforans et perforatus digiti II and III | 5.27– 4.37 | 4.84 | .11 | 5.56– 4.34 | 4.98 | .10 |
| 28 | M. flexor digitorum longus | 3.61– 2.90 | 3.24 | .09 | 4.67– 2.77 | 3.44 | .13 |
| 29 | M. popliteus | 0.28– 0.17 | 0.20 | .01 | 0.27– 0.17 | 0.23 | .01 |

[a] Sequence and terminology follow that of Hudson 1937. *, $P < 0.05$; **, $P < 0.025$; ***, $P < 0.01$. ($P$ indicates significance of difference between $\bar{x}$'s.)

[b] $n = 8$ (except muscles# 24 and #25 where $n = 7$).

[c] $n = 13$.

revealed several positive correlations significant at the 0.01 level. Very high coefficients were obtained for the three pairwise comparisons among cranial length, cranial width, and cranial height ratios ($r$'s equaled 0.91, 0.96, and 0.95). These high correlations, as opposed to the statistically significant but lower coefficients between each of these ratios and body size (as expressed by anterior back length), suggest that evolutionarily the braincase has responded as a single unit, while the magnitude of the response has depended to a large extent on changes in body size.

Along with other positive correlations of dimension-trunk ratios were those for ventral width of upper mandible's base vs.: cranial width ($r = 0.70$), height of upper mandible's base ($r = 0.82$), and dorsal width of upper mandible's base ($r = 0.86$). Also, the height of the upper mandible's base was correlated with its dorsal width ($r = 0.87$). The latter three correlations concern only dimensions around the upper mandible's base. As in the case of the three braincase dimensions, these ratios appear to be responding as a unit. The functional reasons as to why these ratios are linked as a unit are unclear. However, the significant but lower correlation for cranial width vs. ventral width of the upper mandible's base, and a lack of significant correlation for cranial width vs. dorsal width of upper mandible's base and cranial height vs. height of upper mandible's base suggest little dependence between evolutionary changes in the unit comprising the braincase and changes in the unit comprising the base of the upper mandible.

In addition to the above measurements, others were taken. The cranial kinetic angles did not differ significantly between the two species: 38° in the Common Murre ($n = 5$) and 39° in the thick-billed ($n = 14$). Although the Common Murre appears to have a relatively longer neck than the thick-billed, I was unable to demonstrate a statistically significant difference. Since neck length is impossible to measure on disarticulated skeletons, the preserved birds were utilized. The measurement was taken from the posterior dorsal edge of the foramen magnum to the posterior extremity of the neural crest of the thirteenth vertebra. Actually this might sometimes have

TABLE 7. Functional ratios for pelvic muscle action groups.

| | | Common Murre[b] | | | Thick-billed Murre[c] | | |
|---|---|---|---|---|---|---|---|
| | Action group[a] | Range | $\bar{x}$ | SE | Range | $\bar{x}$ | SE |
| 1 | Pulls femur forward (4), (5) | 8.65– 7.12 | 7.83 | .19 | 8.19– 5.36 | 7.35 | .20 |
| 2 | Pulls femur backward 9, 10, (14), 17 | 14.18–12.32 | 13.17 | .23 | 14.64–12.23 | 13.45 | .21 |
| 3 | Rotates femur forward and inward 1, 2 | 9.38– 8.30 | 8.76 | .11 | 10.02– 7.68 | 9.07 | .17 |
| 4 | Rotates femur backward and inward (14), 15, 16 | 3.81– 3.03 | 3.40 | .09 | 3.59– 2.70 | 3.17 | .07 |
| 5 | Adducts femur (4) | 0.31– 0.19 | 0.24 | .01 | 0.32– 0.17 | 0.23 | .01 |
| 6 | Abducts femur 3 | 0.40– 0.18 | 0.25 | .02 | 0.52– 0.19 | 0.32 | .02 |
| 7 | Extends tibiotarsus* (5), 6, 7 | 20.39–17.51 | 18.77 | .37 | 19.23–14.68 | 17.72 | .29 |
| 8 | Flexes tibiotarsus 11, 12, 13 | 12.79–10.67 | 11.72 | .27 | 13.58–10.74 | 11.79 | .22 |
| 9 | Rotates head of tibiotarsus inward 8 | 1.61– 1.33 | 1.45 | .05 | 1.63– 1.18 | 1.37 | .04 |
| 10 | Draws fibula toward tibia 29 | 0.28– 0.17 | 0.20 | .01 | 0.27– 0.17 | 0.23 | .01 |
| 11 | Extends tarsometatarsus (20), 22, 23 | 20.46–17.85 | 18.70 | .30 | 19.68–17.64 | 18.38 | .15 |
| 12 | Flexes tarsometatarsus 18 | 7.43– 6.24 | 6.59 | .15 | 8.00– 5.79 | 6.74 | .18 |
| 13 | Abducts tarsometatarsus 21 | 0.31– 0.21 | 0.27 | .01 | 0.40– 0.20 | 0.31 | .02 |
| 14 | Extends digits* 19 | 3.13– 2.79 | 2.99 | .06 | 4.32– 2.59 | 3.38 | .14 |
| 15 | Flexes digits (20), 24, 25, 26, 27, 28 | 17.61–15.73 | 16.43 | .22 | 18.52–14.41 | 16.51 | .33 |

[a] Numbers after each action group indicate muscles (see table 6) included; parentheses indicate that muscle is listed in another action group. *, $P < 0.05$. ($P$ indicates significance of difference between $\bar{x}$'s.)

[b] $n = 8$.

[c] $n = 13$.

been the fourteenth, since all murres were assumed to have 22 presynsacral vertebrae (although they often have 23) and the "thirteenth" vertebra was determined by counting from the synsacrum forward. Although the dimension-trunk ratio for neck length was larger in the Common Murre, the difference was significant at only the 0.1 level ($df = 17$). Probably a significant difference could be demonstrated if larger samples were available.

Kuroda (1954) has characterized the ventral vertebral processes or hypapophyses (see presynsacral vertebrae illustrated in fig. 6) as being particularly well developed in the alcid genera *Uria, Synthliboramphus,* and *Brachyramphus.* These processes serve as origins for the M. longus colli ventralis (also called M. longus colli "anterior" or "anticus") which straightens the neck and consequently flicks the skull forward. Using skeletal specimens, the nine presynsacral vertebrae of each bird were serially articulated by stringing them on to pipe cleaners via their neural canals. The preparations were X-rayed in lateral view and the X-ray negatives inserted into a photographic enlarger so that all specimens could be drawn to the same relative size. Comparing tracings for seven Common and seven Thick-billed Murres revealed that in every one of the thick-billed preparations, the hypapophyses projected farther ventrally than in any of the Common Murres.

*Muscles.* The pelvic muscles removed are listed in table 6, the pectoral muscles, in table 8. In both cases the muscles were treated both individually (tables 6, 8) and as action groups (tables 7, 9). Since often a muscle can engage in at least two different actions, many are included in two groups; this is especially true for the pectoral muscles. Deletion of such muscles from the action groups does not alter the conclusion reached below.

The pelvic muscles are compared in terms of functional ratios where the weight of each muscle or action group is expressed as a per cent of the total weight for all pelvic muscles dissected (tables 6 and 7). Because of the skeletal similarity in pelves and hind limbs between the two species, I am wary of the few differences which are significant at the 0.05 level. On the basis of chance, approximately two of the 37 ratios calculated would be expected to differ at the 0.05 level.

Of the 15 action groups designated in table 7, ratios for two are significantly different ($P < 0.05$), the tibiotarsal extensors and digital extensor. The former are larger in the Common Murre, the latter in the thick-billed. Of the three muscles contributing to the tibiotarsal group, the M. sartorius, M. ilio-tibialis, and M. femori-tibialis (externus and medius), only the M. ilio-tibialis is significantly larger ($P < 0.025$) on an individual basis, although the means for all three are larger in the Common Murre. The M. piriformis: pars caudifemoralis, is relatively larger ($P < 0.05$) in the Thick-billed Murre. However, this is not reflected in the functional group of which it is a part.

The earlier suggestion that the thick-billed's relatively wider anterior pelvis is due to hyperdevelopment of the M. ilio-trochantericus posterior is not substantiated. The mean ratios

TABLE 8. Ratios (dry weight of individual muscle/total dry weight of pelvic muscles) for pectoral muscles.

| | Muscle[a] | Common Murre | | | Thick-billed Murre | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|
| | | $n$ | $\bar{x}$ | SE | $n$ | $\bar{x}$ | SE | $P$[b] | % diff.[c] | 95% C. I. for % diff. |
| 1 | M. latissimus dorsi anterior | 8 | 0.89 | 0.04 | 13 | 1.05 | 0.04 | * | 18.10 | 2.42–33.79 |
| 2 | M. latissimus dorsi posterior | 7 | 8.74 | 0.45 | 11 | 10.54 | 0.45 | ** | 20.60 | 4.42–36.77 |
| 3 | M. rhomboideus superficialis and profundus | 8 | 6.42 | 0.26 | 13 | 7.60 | 0.23 | *** | 18.37 | 6.62–30.12 |
| 4 | M. serratus profundus | 8 | 2.70 | 0.10 | 13 | 3.39 | 0.10 | **** | 25.58 | 14.31–36.86 |
| 5 | M. serratus superficialis anterior | 8 | 1.99 | 0.12 | 13 | 2.33 | 0.10 | * | 16.78 | 0.01–33.54 |
| 6 | M. serratus superficialis posterior | 7 | 1.40 | 0.07 | 11 | 1.71 | 0.06 | *** | 22.31 | 7.51–37.11 |
| 7 | M. scapulohumeralis anterior | 8 | 0.28 | 0.01 | 13 | 0.41 | 0.03 | **** | 48.41 | 22.29–74.53 |
| 8 | M. scapulohumeralis posterior | 8 | 11.98 | 0.54 | 13 | 15.95 | 0.60 | **** | 33.10 | 17.68–48.52 |
| 9 | M. pectoralis thoracica | 8 | 255.32 | 13.17 | 13 | 299.62 | 13.24 | * | 17.35 | 1.08–33.61 |
| 10 | M. pectoralis propatagialis | 8 | 0.97 | 0.06 | 13 | 1.08 | 0.09 | | | |
| 11 | M. supracoracoideus | 8 | 69.98 | 4.84 | 12 | 80.35 | 3.43 | | | |
| 12 | M. coracobrachialis anterior | 8 | 0.46 | 0.05 | 13 | 0.56 | 0.03 | | | |
| 13 | M. coracobrachialis posterior | 8 | 5.35 | 0.19 | 13 | 6.77 | 0.37 | ** | 26.54 | 6.90–46.19 |
| 14 | M. sternocoracoideus | 8 | 2.19 | 0.13 | 13 | 2.76 | 0.11 | *** | 25.94 | 9.27–42.61 |
| 15 | M. subcoracoideus and subscapularis | 8 | 10.84 | 0.62 | 13 | 12.42 | 0.42 | * | 14.60 | 0.61–28.58 |
| 16 | M. propatagialis longus and brevis | 8 | 5.60 | 0.23 | 13 | 6.78 | 0.32 | ** | 21.03 | 4.30–37.77 |
| 17 | M. deltoideus major | 8 | 1.92 | 0.11 | 13 | 2.83 | 0.11 | **** | 47.48 | 29.75–65.22 |
| 18 | M. deltoideus minor | 8 | 4.99 | 0.25 | 12 | 5.87 | 0.20 | ** | 17.57 | 4.30–30.85 |
| 19 | M. triceps brachii scapularis | 8 | 5.57 | 0.29 | 13 | 6.84 | 0.20 | *** | 22.90 | 10.16–35.63 |
| 20 | M. triceps brachii humeralis | 8 | 7.44 | 0.31 | 13 | 9.11 | 0.35 | *** | 22.33 | 7.87–36.78 |
| 21 | M. biceps brachii | 8 | 0.73 | 0.03 | 12 | 1.21 | 0.06 | **** | 65.58 | 43.11–88.06 |
| 22 | M. brachialis | 8 | 0.38 | 0.03 | 13 | 0.52 | 0.03 | ** | 36.23 | 9.42–63.03 |
| 23 | M. pronator sublimis | 8 | 0.62 | 0.05 | 13 | 0.83 | 0.07 | * | 33.88 | 1.74–66.03 |
| 24 | M. pronator profundus | 8 | 1.25 | 0.10 | 13 | 1.63 | 0.09 | ** | 30.70 | 6.90–54.51 |
| 25 | M. flexor carpi ulnaris | 8 | 0.78 | 0.05 | 13 | 1.03 | 0.07 | ** | 32.21 | 7.26–57.16 |
| 26 | M. flexor digitorum profundus | 8 | 0.52 | 0.03 | 13 | 0.72 | 0.04 | *** | 38.92 | 13.79–64.05 |
| 27 | M. ulnimetacarpalis ventralis | 8 | 0.51 | 0.04 | 13 | 0.67 | 0.04 | ** | 31.21 | 7.88–54.53 |
| 28 | M. extensor metacarpi radialis | 8 | 1.95 | 0.12 | 13 | 2.73 | 0.14 | *** | 40.16 | 18.00–62.33 |
| 29 | M. supinator | 8 | 0.28 | 0.02 | 13 | 0.31 | 0.02 | | | |
| 30 | M. extensor digitorum communis | 8 | 0.45 | 0.03 | 13 | 0.52 | 0.04 | | | |
| 31 | M. extensor carpi ulnaris | 8 | 1.17 | 0.08 | 13 | 1.59 | 0.09 | *** | 36.17 | 12.46–59.88 |
| 32 | M. anconaeus | 8 | 0.68 | 0.06 | 13 | 0.83 | 0.04 | * | 22.32 | 1.74–42.89 |
| 33 | M. extensor pollicis longus | 8 | 0.11 | 0.01 | 13 | 0.11 | 0.01 | | | |
| 34 | M. extensor indicis longus | 8 | 0.32 | 0.02 | 13 | 0.46 | 0.02 | *** | 42.23 | 19.34–65.12 |
| 35 | M. ulnimetacarpalis dorsalis | 8 | 0.21 | 0.02 | 13 | 0.29 | 0.02 | ** | 42.79 | 9.46–76.11 |

[a] Sequence and terminology follow that of Hudson and Lanzillotti 1955.

[b] *, $P < 0.05$; **, $P < 0.025$; ***, $P < 0.01$; ****, $P < 0.001$.

[c] Difference expressed as per cent of smaller species; given only for ratios where there is a significant difference between the two species.

for this muscle are identical in both species (no. 1, table 6). Rather, width expansion of the anterior ilial blades seems to be a response to the M. ilio-trochantericus anterior which arises from the lateral edge of the anterior ilium. Of all ratios calculated for pelvic muscles, the two species differ significantly at the 0.01 level only in this instance.

In the case of the pectoral muscles, each muscle and action group weight was expressed as a per cent of the total weight for all pelvic muscles dissected (tables 8 and 9). Because of the great similarity between the pelvic muscles of the two species, the use of "total pelvic muscle weight" as a basis for pectoral muscle comparisons should give results which approximate the dimension-trunk ratios of the skeletal comparisons. Because of hypertrophy of the pectoral skeletal elements in the Thick-billed Murre, one would predict that most of its separate muscles and action groups would be relatively larger.

Of the ratios calculated, the means for the thick-billed were all higher except for one case where they were equal. Of a total of 52 ratios, 7 were not statistically different, 9 differed at the 0.05 level, 12 at the 0.025 level, 15 at the 0.01 level, and 9 at the 0.001 level. Possibly all of these ratios would differ at a high level of significance if sample sizes comparable to those for the skeletal data were available. The magnitude of the values of "per cent difference" (table 8) is high enough in some instances to suggest that certain muscles are more hyperdeveloped than others, i.e., M. scapulohumeralis anterior, M. deltoideus major, and M. biceps brachii. The greater hyperdevelopment of these muscles cannot be predicted from the ratio data for bone dimensions.

If the weights of the M. pectoralis thoracica and M. supracoracoideus are combined and this weight expressed as a per cent of the total weight of all pelvic muscles, the per cent difference between the Thick-billed and Common Murre is significant ($P < 0.05$). This difference (17.8 per cent) is very close to the 18.1 per cent difference in "relative volume of pectoral muscle" calculated from the sternal measurements. In both species, approximately 78 per cent of the pectoral muscle mass is composed of these two muscles. For all pectoral muscles dissected, the thick-billed is 18.4 per cent relatively larger.

The cranial kinetic muscles of three Common and three Thick-billed Murres were examined. No consistent differences between the species were observed. Both murres have strong mandibular levators. This is particularly true of the various portions of the M.

TABLE 9. Ratios (dry weight of action group/total dry weight of pelvic muscles) for pectoral muscle action groups.

| | | Common Murre | | | Thick-billed Murre | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|
| | Action group[a] | $n$ | $\bar{x}$ | SE | $n$ | $\bar{x}$ | SE | $P$[b] | % diff.[c] | 95% C. I. for % diff. |
| 1 | Elevates humerus (1), (2), (8), (11), (17) | 7 | 93.31 | 6.55 | 10 | 110.45 | 4.73 | * | 18.36 | 0.42–36.31 |
| 2 | Depresses humerus (9), (13) | 8 | 260.67 | 13.27 | 13 | 306.38 | 13.46 | * | 17.54 | 1.37–33.70 |
| 3 | Pulls humerus posteriorly (1), (2), 7, (8), (15), (17) | 7 | 34.81 | 1.74 | 11 | 42.84 | 1.58 | *** | 23.07 | 8.31–37.82 |
| 4 | Pulls humerus anteriorly 12, (18) | 8 | 5.46 | 0.27 | 12 | 6.42 | 0.20 | *** | 17.56 | 4.90–30.21 |
| 5 | Rotates humerus upward (11), (13), (17), (18) | 8 | 82.24 | 5.17 | 13 | 95.16 | 3.66 | | | |
| 6 | Rotates humerus downward (8), (9), (15) | 8 | 278.14 | 14.03 | 13 | 327.99 | 13.93 | * | 17.92 | 2.16–33.68 |
| 7 | Tenses and supports propatagium (10), (16) | 8 | 6.58 | 0.26 | 13 | 7.86 | 0.35 | ** | 19.51 | 3.76–35.26 |
| 8 | Extends forearm 19, 20 | 8 | 13.01 | 0.39 | 13 | 15.95 | 0.52 | **** | 22.57 | 10.70–34.44 |
| 9 | Flexes forearm (10), (16), 21, 22, (28), (30) | 8 | 10.09 | 0.35 | 12 | 12.90 | 0.51 | **** | 27.89 | 13.53–42.25 |
| 10 | Raises distal radius (29) | 8 | 0.28 | 0.02 | 13 | 0.31 | 0.02 | | | |
| 11 | Depresses distal radius (23), (24) | 8 | 1.87 | 0.14 | 13 | 2.47 | 0.15 | ** | 31.76 | 6.40–57.12 |
| 12 | Pulls radius to humeral condyle (23), (24), (29) | 8 | 2.15 | 0.16 | 13 | 2.78 | 0.17 | ** | 29.11 | 4.84–53.38 |
| 13 | Raises distal ulna 32 | 8 | 0.68 | 0.06 | 13 | 0.83 | 0.04 | * | 22.32 | 1.74–42.89 |
| 14 | Elevates manus (31) | 8 | 1.17 | 0.08 | 13 | 1.59 | 0.09 | *** | 36.17 | 12.46–59.88 |
| 15 | Extends manus (28), 33, (34) | 8 | 2.38 | 0.14 | 13 | 3.30 | 0.17 | *** | 38.57 | 17.22–59.92 |
| 16 | Flexes manus (26), (27), (30), (31), (35) | 8 | 2.86 | 0.19 | 13 | 3.80 | 0.20 | *** | 32.97 | 11.13–54.81 |
| 17 | Pronates manus (27) | 8 | 0.51 | 0.04 | 13 | 0.67 | 0.04 | ** | 31.21 | 7.88–54.53 |
| 18 | Draws pollex toward metacarpal #2 (30) | 8 | 0.45 | 0.03 | 13 | 0.52 | 0.04 | | | |
| 19 | Extends digit #2 (26), (34) | 8 | 0.84 | 0.05 | 13 | 1.18 | 0.06 | *** | 40.19 | 17.92–62.45 |
| 20 | Slides and rocks coracoid (14) | 8 | 2.19 | 0.13 | 13 | 2.76 | 0.11 | *** | 25.94 | 9.27–42.61 |
| 21 | Stabilizes scapula 3, (4), (5), (6) | 7 | 12.57 | 0.48 | 11 | 15.33 | 0.41 | **** | 21.97 | 11.04–32.89 |
| 22 | Expands rib cage (4), (5), (6), (14) | 7 | 8.30 | 0.36 | 11 | 10.34 | 0.27 | **** | 24.58 | 13.15–36.00 |
| 23 | Affects wing feathers 25, (35) | 8 | 0.98 | 0.06 | 13 | 1.32 | 0.08 | *** | 34.43 | 10.87–57.99 |

[a] Numbers after each action group indicate muscles (see table 8) included; parentheses indicate that muscle is listed in another action group.

[b] *, $P < 0.05$; **, $P < 0.025$; ***, $P < 0.01$; ****, $P < 0.001$.

[c] Difference expressed as per cent of smaller species; given only for ratios where there is a significant difference between the two species.

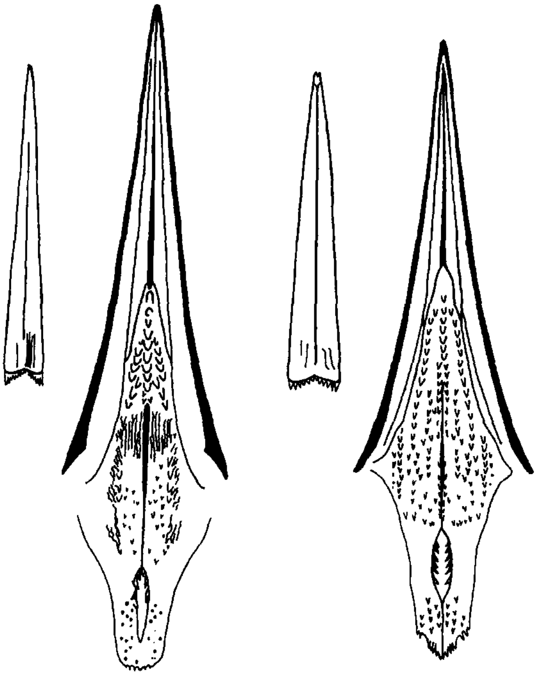


FIGURE 11. Palates and tongues (dorsal view) of the Common (left) and Thick-billed (right) Murres (life size).

adductor mandibulae and the M. pseudotemporalis superficialis. The M. protractor pterygoidei ("sensu stricto" and protractor quadrati) is small in both species. There may be quantitative differences between the two species, as suggested by the skull ratios, but demonstrating them would involve the removal, drying, and weighing of separate muscles.

Other than the relative weight differences discussed above for pelvic and pectoral muscles, no further differences (e.g., degree of pinnation, points of tendon insertion, etc.) were noted between the two species. Although such differences possibly exist, quantitative methods would probably be required for their demonstration.

*Tongue, palate, and gut.* Palates and tongues of the two murres are illustrated in figure 11. Kuroda (1954) characterized *Uria aalge* as having a slender, corneous tongue resembling that of the murrelets (*Synthliboramphus* and *Brachyramphus*). He found *Uria lomvia's* tongue to be wider and less corneous, like those of *Cepphus, Cerorhinca, Fratercula,* and *Lunda.* These differences agree with my observations for eight *Uria aalge* and thirteen *Uria lomvia.*

Fig. 12 illustrates histological cross sections of tongues from the two species (taken midway along their length). The broader tongue of the thick-billed can be derived by lateral expansion of the tissues and structures present in the Common Murre. Also, the intermediate layers of the stratified squamous epithelium are more developed on the dorsal side of the thick-billed's tongue. The more corneous nature of the Common Murre's tongue is probably due to the outer keratinized layer contributing proportionally more to its cross-sectional area. If the thickness of this layer remains constant while the tongue's total

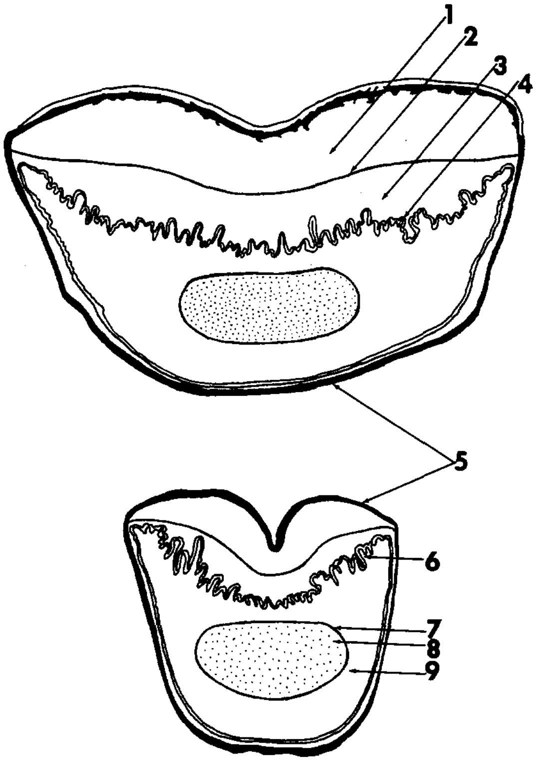


FIGURE 12. Cross sections of Thick-billed (above) and Common Murre (below) tongues. Both taken midway along length of tongue (14.5×). 1–5. Stratified squamous epithelium consisting of a basal layer (4), two thick intermediate layers (1 and 3), a narrow transitional zone (2), and a heavily keratinized outer layer (5); 6. dermal papillae; 7. perichondrium; 8. hyaline cartilage (paraglossum); 9. space between paraglossum and epithelium which contains fibrous connective tissue, blood vessels, nerves, and bundles of striated muscle.

cross-sectional area diminishes, there is an automatic increase in the layer's relative contribution to cross-sectional area.

Bédard (1969), noting the tongue differences, has also found that the horny palate of the two species differs. The palate's small, horny protuberances or "denticles" are more numerous in the thick-billed. The condition illustrated for the Common Murre (fig. 11) is not constant. Of eight specimens examined, four had denticles like those illustrated, while the others were more similar to those of the thick-billed in which the denticles anterior to the choanal slit were small. Counts of the total number of denticles confirm that the thick-billed's are more numerous but only on a statistical basis, since there is wide overlap between the two species. Contrastingly, the width of the denticle-bearing portion of the palate anterior to the choanal slit appears consistently wider in the thick-billed.

The guts of all specimens were removed and the gross structure of their esophaguses, stomachs, intestines, and intestinal caecae examined. Kuroda (1954) illustrated esophaguses and gizzards from Common and Thick-billed Murres which differed in size and configuration, although he cautioned that the difference might be individual. I found approximately the same range of variation in both species. Possibly this variation is determined to a greater extent by the amount of food present (or recently present) in the various parts of the digestive tract than by any other factor.

## CORRELATION OF FUNCTION AND ANATOMY

I have assumed that if the relative weights of the same muscle or action group differ significantly between the two species, the larger will produce relatively more tension. ("Relative" refers to the basis of muscle comparison; for both the individual muscles and the action groups, it is the total weight of all pelvic muscles dissected.) This is an oversimplification since the tension-producing properties of a muscle are also related to such other factors as the physiological characteristics of its constituent fibers and the arrangement of these fibers relative to tendons. Gans and Bock (1965) have emphasized and quantified the importance of muscle fiber arrangement on the tension-producing properties of muscle. It is unknown whether muscles in the Thick-billed Murre contain fibers which differ physiologically from fibers found in comparable muscles of the Common Murre. However, no differences in the degree of pinnateness and general muscle proportions were observed between the two species.

The walking difficulties of the Thick-billed Murre are attributable to hyperdevelopment of its pectoral girdle and wings. The probable reasons for its hunched posture and greater tendency to fall forward can be seen with the aid of a simple mechanical model. With the femoral heads serving as pivots, the muscles running between the posterior pelvis and femora or tibiotarsi will be mainly responsible for pulling the trunk into and holding it in an upright position. If the torque anterior to the femoral heads is equal to that posterior, the system will remain in equilibrium.

However, because of its heavier pectoral region, relative to the pelvic muscles, the Thick-billed Murre will experience relatively greater anterior torque. At any speed, its tendency to fall forward will be greater. With increasing speed and hence greater anterior torque because of forward momentum, the torque from the pelvic muscles is probably inadequate to maintain the trunk in an upright posture. The Thick-billed Murre flaps its wings to produce a backward directed component that helps to prevent it from falling on its breast. Since the moment of greatest instability is during leg extension, a forward wing flap at that instant is most favorable for maintaining the body in an upright position. Even when waddling about with their tarsi on the ground (the usual form of terrestrial locomotion), Common Murres should be able to move with greater speed and agility than thick-billeds walking in a similar manner.

The Thick-billed Murre has evolved some compensations for the walking difficulties created by hyperdevelopment of its pectoral girdle and wings. Wider spacing of the femora, as indicated by the 11.3 per cent relatively larger "medial pelvic width," has widened the body's base of support. Concomitantly, an increase in the relative size of the M. ilio-trochantericus anterior, a muscle for rotating the femur forward and inward, helps maintain the legs under the weight which they support.

With its longer wings of larger area and its slightly smaller total weight, the Thick-billed Murre should be a more energetically efficient, although possibly less maneuverable flier than the Common Murre. Since lift-destroying turbulence is especially strong at the wing tips, longer wings result in a greater length and relatively larger area of wing being devoted to lift production. The Thick-billed Murre's larger wing surface, accompanied by an increase in wing muscle weight, should result in greater propulsive force per wing beat. Thus, for any speed at which both species can fly, the Common Murre will have to beat its wings at a faster rate than the Thick-billed Murre.

In water as in air, the Thick-billed Murre should be able to exert greater propulsive force per wing beat than the Common Murre. Thus, for any long underwater distance, the thick-billed should traverse it in fewer wing strokes. However, a greater concentration of mass in the ventral pectoral region and more massive wings inhibit tilting and twisting of the sort seen in Type II and III turns (fig. 4). Probably any deviation from a straight line course could be managed more quickly by the Common Murre. Thus, the anatomical evidence indicates that the Thick-billed Murre is a swimmer of low agility, but one capable of moving over longer distances, possibly at higher energetic efficiency. If it "hovers" over the bottom in a manner similar to Stettenheim's (1959) observations of the Common Murre, the thick-billed should be a more stable "hoverer" because of its larger wings. Likewise, the thick-billed should be capable of maintaining a more stable semi-stationary position at any water level between the surface and bottom.

Hyperdevelopment of some of the Thick-billed Murre's respiratory muscles is suggestive of superior diving ability. Inspiratory muscles are relatively larger on both an individual (nos. 4, 5, 6, 14, table 8) and action group basis (no. 22, table 9). Hyperdevelopment of the M. obliquus abdominis externus, an expiratory muscle, is suggested by expansion of the plate posterior to the sternal keel. Hyperdevelopment of these muscles may be linked to an increase in the relative volume of the thoracic cavity and air sacs.

Head differences which can be functionally interpreted include those concerned with the bill, tongue, and horny palate. Bédard (1969) has found that those alcids with short, broad bills; fleshy, poorly cornified tongues; and numerous palatal denticles eat more invertebrates. These characters tend to be linked as an adaptive unit. With increasing ichthyophagy, the bill becomes longer and narrower, the tongue more cornified, and the palatal denticles fewer and more sharply pointed. Thus, the Thick-billed Murre should be equipped to feed more efficiently on invertebrates and less efficiently on fish than the Common Murre.

Higher values for the Thick-billed Murre in the relative sizes of the three skeletal dimensions around the upper mandible's base (ventral width, height, and dorsal width of base) are probably all concerned with the breadth of the bill's base. While the ventral width of the upper mandible's base is a direct expression of this feature, the relative lengths of all three dimensions are linked as a unit. Thus a change in the relative ventral width of the upper mandible's base will be accompanied by changes in the other two dimensions, these probably being more directly concerned with maintaining the strength and/or efficiency of the cranial mechanism.

How the Thick-billed Murre's bill, palate, and tongue structure is more adaptive to invertebrate feeding is unclear. Although speculations are suggested, they are probably best deferred until careful observations are made on the feeding behavior of either the two murres or other alcid species comparable in bill, palate, and tongue structure.

## CORRELATION OF FUNCTIONAL-ANATOMICAL DATA WITH ECOLOGY

The functional-anatomical data can be correlated with such aspects of the natural history and ecology of murres as incubation stance, nest site distribution, food eaten by adults and fed to young, and length of foraging and migratory flights. I will devote attention to correlating ecological data from several sources in an attempt to develop generalizations relevant to the functional and anatomical information.

Both murre species incubate with the egg lying on the outstretched membranes of their webbed feet. However, Thick-billed Murres usually brood in a prone position, while Common Murres assume an upright stance (Sergeant 1951; Tuck 1960). Hyperdevelopment of the thick-billed's pectoral region probably makes it more difficult for this species to maintain an upright stance.

Where both murres occur as breeding birds, the Common Murre usually occupies the longer, broader ledges (Uspenski 1956; Belopol'skii 1957; Tuck 1960; Swartz 1966). Similarly, Sergeant (1951) observed on Bear Island that Thick-billed Murres occurred in thin bands along the edges of flat clifftops; inward from these bands, the tops were occupied exclusively by Common Murres. Murre breeding aggregations are often very dense (up to 34 birds/m$^2$ for Common Murres, Tuck 1960) and the denser coloniality seen in the Common Murres (Kaftanovski 1951; V. S. Uspenski 1941) might be facilitated by its superior walking ability and upright stance.

Three lines of evidence suggest that ledge segregation depends on Common Murres actively excluding thick-billeds. First, in the northern, allopatric portion of its breeding range, the Thick-billed Murre nests on all types of ledges (Sergeant 1951; Tuck 1960). Second, Belopol'skii (1957) documents two instances (both near the Murmansk coast, USSR) where increases in Common Murre numbers have resulted in the thick-billed being pushed first to the edges of the larger ledges and then to narrower, more peripheral sites. If the murre population is low relative to the number of nesting sites, both species will often breed in close proximity on the same broad ledges. Third, the Thick-billed Murre should prefer nesting on the broader ledges because of the lower egg and chick mortality incurred there. In this connection, S. M. Uspenski (1956) found that egg falls for the Thick-billed Murre varied from 35 to 70 per cent, depending on the slope and broadness of the nesting ledges. The lowest losses occurred on nonsloping ledges more than 50 cm wide. Likewise there should be fewer chick falls from broad ledges, although S. M. Uspenski gives no exact data on this point. Kaftanovski (1938) found that egg and chick losses to gulls (*Larus argentatus* and *Larus marinus*) varied drastically with nesting density. For very dense aggregations, predation did not exceed 7 per cent; in the case of more dispersed breeders (as tends to occur on narrow ledges) predation attained 80–100 per cent.

The exact means by which Common Murres exclude thick-billeds is unclear. S. M. Uspenski (1956) and Belopol'skii (1957) imply that interspecific conflicts occur, although they give no direct observations. General belligerence (such as jostling and pecking) among birds first settling on the nesting ledges is documented by Pennycuick (1956), Tuck (1960), and Swartz (1966). Swartz's observations are unspecified as to species, while Tuck observed intraspecific conflict in the Common Murre, and Pennycuick in the Thick-billed Murre. Extreme intraspecific aggression is suggested by Tuck's (1960) observations at Quaker Hat, Labrador. On each of several ledges, he found nine or ten dead Thick-billed Murres. They appeared to have been killed by "sharp jabs on the head," probably delivered by members of the same species, since only thick-billeds were nesting on these small ledges.

Thus, present evidence does not confirm that physical belligerence occurs between the species. It seems likely, but more careful, systematic observations are required. If interspecific fighting is involved, the taller, more mobile, and agile Common Murre would be at a definite advantage on the broad ledges, possibly even if it was not the aggressor.

As indicated earlier, food data for the Common and Thick-billed Murre suggest opportunism in their feeding habits. It is presumably this opportunism which results in both murres eating the same fish species in approximately the same relative proportions at certain times and places. However, the functional-anatomical data indicate that the two species are adapted to potentially different means of feeding. These potentials might be expected to be occasionally reflected in dietary differences. The Thick-billed Murre's low agility, long-distance swimming adaptations, and presumed ability to maintain a stable, semi-stationary, underwater position appear potentially adaptive to two environmental conditions: one where a low-mobility, pelagic food source is available, or one where the low-mobility food source is on or near the bottom, possibly far from the water's surface. Conversely, the Common Murre appears better adapted to catching mobile pelagic fish.

Swartz's (1966) data for Cape Thompson, Alaska, are important not only because they show food differences between the murre species but also because some information is available on the distribution and abundances of the food utilized at this site. Of the 66 food-containing Common Murre stomachs examined by Swartz, 95.5 per cent contained fish. Conversely, fish were more poorly represented in the 133 food-containing stomachs of Thick-billed Murres (63.9 per cent) and invertebrates were found in 33.8 per cent of them. My somewhat arbitrary division of the invertebrates into pelagic vs. bottom dwellers reveals a higher occurrence of the bottom forms. The two fish most frequently present in murre stomachs, polar cod (*Boreogadus saida*) and lance (*Ammodytes hexapterus*), occur near the surface.

In an exploratory fishery investigation conducted off Cape Thompson and Point Hope (Alverson and Wilimovsky 1966), pelagic and bottom fish were found to be low in number. Continuous echo soundings (August 5–31) indicated no concentrations of schooling subsurface fish, and the standing crop of bottom fish was characterized as "extremely low" in comparison with areas where commercial trawling occurs.

In sharp contrast to the fish, the benthonic invertebrate fauna in the Cape Thompson region is rich both in number of species and standing crop (Sparks and Pereyra 1967). But Sparks and Pereyra estimated that because of inshore scouring by ice, significant benthonic invertebrate populations could not be established in the area between the beach and approximately 20-ft water depth. For Point Barrow, MacGinitie (1955) estimated that the bottom was "rubbed or gouged" by ice to a depth of 90–100 ft. Because of the gradual underwater slope at Cape Thompson, ice scouring probably has a detrimental effect out to several miles from shore.

Around the Cape Thompson region, Swartz (1967) found that the majority of Common Murres do not venture offshore more than five miles. In contrast, Thick-billed Murres reach their peak at approximately 20 miles from shore. Thus, it appears possible that the Thick-billed Murres fly farther out to dive for invertebrates, an abundant food source but one far from shore in deeper water. *Boreogadus* and *Ammodytes* are probably maneuverable enough swimmers to make it difficult for the Thick-billed Murre to catch them. If these fish are in low density, it is probably more efficient in terms of the Thick-billed Murre's time and energy budget to feed on bottom invertebrates even if the bird must fly farther out to dive for them. In terms of its adaptations, the Common Murre appears to operate most efficiently by remaining closer to shore and catching pelagic fish.

Further expression of the Thick-billed Murre's potential for bottom exploitation is shown by Tuck and Squire's (1955) data for Akpatok Island. Located south of Baffin Island, Akpatok Island has only Thick-billed Murres. Foraging no farther than 10 miles from their colony within an area where the bottom ranged to 60 fathoms, they reached their greatest concentration one to five miles offshore.

Because of strong winds around the nesting ledges, adults frequently dropped food being brought to their young. From 9–25 August, Tuck and Squires collected fish along a one-mile strip below the nesting ledges. As at Cape Thompson, pelagic fish (represented by *Mallotus villosus*, *Boreogadus* sp., and *Ammodytes americanus*) are probably present at low densities in the waters around this area. Of the total number of food items, 56.5 per cent were fish which occur on or near the bottom. In sharp contrast, stomach contents for 34 adults consisted of 85 per cent zooplankton in the form of hyperid and gammarid amphipods.

Thus, Thick-billed Murres at Akpatok Island appear to use their bill and mouth adaptations and ability to maintain a stable, semi-stationary underwater position, to feed on zooplankton. But adult murres, like other large alcids, are committed to feeding their young chiefly on fish. At low pelagic fish densities, the Thick-billed Murre is capable of obtaining bottom fish, probably by utilizing its long-distance swimming adaptations to get to the bottom and then its stable "hovering" ability to seek out bottom fish. The fact that adults feed largely on zooplankton suggests that feeding on bottom fish is a higher energy- and time-consuming activity in terms of the energy obtained.

S. M. Uspenski's (1956) and Belopol'skii's (1957) data for Novaya Zemlya offer yet another perspective. In 1942, 1947, 1948, and

1949, Thick-billed Murres (Common Murres constitute less than one per cent of the population and are localized in distribution.) fed almost entirely on pelagic fish. However, in 1950, the temperature of Novaya Zemlya's coastal waters was higher than in any of the previous 50 years. *Boreogadus saida*, which prefer low temperatures, were scarce. And for some unknown reason, the cod (*Gadus morrhua*) also appeared in low numbers. As a result, many stomachs lacked fish, the birds were light in weight (956.6 g vs. 1014.2 g for the other four years), and more bottom fish were taken. S. M. Uspenski (1956) reports that in 1950 large numbers of murres remained near their colonies and searched the bottom in a manner similar to guillemots (*Cepphus*).

Thus, the long-term success of the Thick-billed Murre at Novaya Zemlya is probably related in part to its ability to exploit bottom fish. In most years pelagic fish probably appear in sufficient quantities to render bottom feeding unnecessary.

In addition to some of the food data discussed above, other data stress the importance of invertebrate feeding in the Thick-billed Murre, particularly in the spring. In April and May, Demme (1934) collected 17 Thick-billed Murre stomachs at Franz Joseph Land. Crustacea occurred in eight, fish in seven, polychaetes in two, and molluscs in one. For Thick-billed Murres taken in the eastern Murmansk region, USSR, crustaceans decreased from an absolute occurrence of 10 per cent in April, May, and June to 6.7 per cent in July and August (Belopol'skii 1957). Likewise, in the Common Murre they dropped from 3.4 to 1.3 per cent. For molluscs, occurrence in the Thick-billed Murre went from 5.0 to 2.2 per cent; while comparable figures for the Common Murre were 1.7 and 0 per cent. These trends generally correlate with a spring increase in plankton followed by a summer encroachment of fish. In comparison with the situation farther south, the appearance of fish near northern breeding localities is usually later in occurrence, involves fewer individuals and species, and is more uncertain in occurrence. (Belopol'skii's comparison of Novaya Zemlya and the Murmansk coast would be a clear illustration of these differences.)

Swartz's (1967) observations on the distribution of Common and Thick-billed Murres at sea are the only data available which suggest that thick-billeds may fly farther to sea for food. Because annual bottom scouring by ice is a widespread phenomenon within the thick-billed's breeding range, its flying ability should be generally adaptive in the way suggested for Cape Thompson thick-billeds. Also, the thick-billed, because of its extensive occurrence as a breeder in pack ice areas, will generally have to engage in more extensive migratory movements than the Common Murre.

## DISCUSSION

For the world, Tuck (1960) estimates there are 56 million murres, with thick-billeds predominating three to one. Between Europe and North America, the Thick-billed Murre reaches its greatest abundance in the southern portion of the arctic and northern portions of the subarctic marine zones (the definition of subarctic followed here is that of Dunbar 1955). The Common Murre appears adapted to more southerly conditions. Dunbar (1955) has characterized the fish fauna of the arctic marine zone as follows. "The fishes of the marine arctic zone are few in number of species. For some reason, perhaps connected with the comparatively recent freeing of the arctic waters from the Pleistocene glaciation, the fishes as a group have not yet managed to invade the coldest waters with any success. Moreover, such fish as are found in the arctic waters are benthonic forms, that is, living close to the bottom. Even the little polar cod (*Boreogadus saida*), although it is occasionally seen at the surface among the ice floes, cannot be considered a true pelagic fish. The lack of pelagic fish is the more surprising since the plankton of the arctic water, though less abundant than that in the subarctic, is nevertheless considerable, as witness the number of seals and whales that depend on it." Even in the area immediately south of this zone, the pelagic fish which do appear in summer may be low in number and uncertain in appearance.

The Thick-billed Murre appears to be adapted to conditions similar to those described by Dunbar. Three major adaptations have been suggested in this study. First, the Thick-billed Murre is structurally adapted for feeding on invertebrates. Second, it has morphological (and possibly physiological) adaptations for diving to the ocean bottom and feeding there. (These modifications may be particularly important for providing chicks with their necessary fish food.) Third, increased flying efficiency has also been attained. This may be important for foraging in areas far from the nesting colony and in moving to and from the breeding colonies in the spring and fall as pack ice melts and is reformed. While the foregoing adaptations appear mutually compatible and may even enhance one another, they are not reconcilable with efficient walking and maneuverable swimming.

In contrast to the Thick-billed Murre, the Common Murre is adapted to conditions where pelagic fish are numerous and form a stable food source. Adaptations for invertebrate feeding, bottom exploitation, and flying over distances in search of food or to reach breeding sites have been sacrificed for adaptations contributing to the efficient pursuit and capture of pelagic fish. These adaptations are compatible with walking proficiency. Correlated with its walking ability and upright incubation stance is a tendency to nest in very dense aggregations and to exclude Thick-billed Murres from the more favorable nesting sites.

It must be emphasized that the adaptations discussed are not absolute. Common Murres can and do feed on invertebrates and bottom fish. Thick-billed Murres can and do feed on pelagic fish. The invertebrate and bottom feeding adaptations of the Thick-billed Murre can be considered potentials whose expression is dependent on environmental conditions. If pelagic fish are available in high numbers, the Thick-billed Murre may get more food per unit energy expenditure by pursuing pelagic fish in lieu of searching for invertebrates or feeding on the bottom. As pelagic fish become fewer, both the Thick-billed and Common Mures will have to expend greater energy per unit food if they continue to rely on pelagic fish. But because of its more maneuverable swimming ability, the Common Murre should probably expend less energy per unit food at all pelagic fish concentrations. If only pelagic fish are considered, the Common Murre should be able to subsist and feed young at fish concentrations where the Thick-billed Murre will be unable to succeed. The thick-billed's success is dependent on its ability to switch to zooplankton and bottom forms. At more northerly, subarctic localities (like Cape Thompson, Alaska), the Thick-billed Murre begins switching to bottom and invertebrate feeding, while the Common Murre continues feeding largely on pelagic fish. At arctic localities, the pelagic fish are probably so low in density and/or uncertain in occurrence that the Common Murre cannot sustain itself as a breeding bird. Thus the inability of the Common Murre to succeed in the arctic is related to its inability to utilize alternative food sources in the absence of pelagic fish (Belopol'skii 1957).

While both murres occur as sympatric breeders at the southern limit of their western Atlantic breeding range, the thick-billed stops far short of the Common Murre's southern limit in the eastern Atlantic and north Pacific. Thick-billed Murres fledge at higher weights on the eastern Murmansk coast (Kharlov Island) than at Novaya Zemlya (246 vs. 152 g) (Kaftanovski 1941; S. M. Uspenski 1956). The lighter weights of Novaya Zemlya fledgings is also correlated with slower rates of wing and tarsal growth( Belopol'skii 1957). But in comparison with Novaya Zemlya where they compose over 99 per cent of the murre population, Thick-billed Murres contribute 5–30 per cent of the population at various sites along the Murmansk coast. At Murmansk, as in other more southern regions where fish occur in large quantities, the low proportion of Thick-billed Murres may be due to Common Murres excluding them from most of the suitable nesting sites. However, this appears inadequate to explain the thick-billed's absence as a breeding bird from much of the boreal marine zone (which lies immediately south of subarctic marine zone). Possibly both lower pelagic fish and bottom animal populations are excluding factors.

Interspecific competition does not necessarily have to be invoked to explain the origin or maintenance of the adaptive differences between Thick-billed and Common Murres. The majority of the world's population of Thick-billed Murres breed at sites where they are allopatric. In the north Atlantic particularly, selection in the southern, sympatric area of the thick-billed's range might be expected to be diluted by gene flow from the extensive northern areas where it is allopatric (the north Atlantic and adjacent Arctic populations have been assigned to one subspecies, *Uria lomvia lomvia*, by Storer 1952). However, in the north Pacific, most Thick-billed Murres breed in proximity to Common Murres.

Since the majority of the Common Murre's breeding population occurs sympatrically with Thick-billed Murres, interspecific competition may have had more of an effect on the development of some of its characters, particularly those concerned with its success at excluding Thick-billed Murres from the more suitable nesting sites. On the other hand, the Common Murre's walking ability, upright incubation stance, and denser coloniality may have been facilitated by adaptations concomitant with pelagic fish feeding, and may have originally evolved in geographical isolation from the Thick-billed Murre.

## SUMMARY

Differences in walking and swimming between the Common Murre (*Uria aalge*) and Thick-billed Murre (*Uria lomvia*) are described and compared using films of captive birds. While the Common Murre is a more proficient walker and a more agile swimmer, the Thick-billed Murre swims with greater stability and should be capable of moving over greater underwater distances.

Skeletal and muscular modifications are correlated with the differences in locomotor performance. The Thick-billed Murre's walking difficulty is attributable to a greater tendency to fall forward because of its enlarged wings and pectoral muscles. Wider spacing of the legs and enlargement of one of the femur rotating muscles are compensations for this difficulty. In underwater swimming, the Thick-billed Murre's longer wings and ventrally bulging pectoral region reduce tilting around and twisting of the trunk's long axis; but more propulsive force should be produced by each wing stroke, thus giving it a greater capacity for traveling over long distances. In air, the Thick-billed Murre should be an energetically more efficient flier.

Enlargement of some of the expiratory muscles and suggested enlargement of at least one of the inspiratory muscles are possibly correlated with greater diving ability in the Thick-billed Murre. Bill, tongue, and palate modifications are indicative of greater ichthyophagy in the Common Murre and more invertebrate feeding in the thick-billed.

Differing aspects of the two murres' natural history and ecology are related to their functional and anatomical modifications. Because of its enlarged pectoral region, the Thick-billed Murre usually assumes a prone egg incubation position, while the Common Murre has an upright stance. The taller stance and superior walking ability of the Common Murre correlate with its potential for excluding thick-billeds from the broader, more suitable nesting ledges. The Common Murre's maneuverable swimming ability is associated with its nearly exclusive dependence on pelagic fish. The Thick-billed Murre's more stable underwater swimming and capacity for moving over long underwater distances correlate with its ability to feed on pelagic invertebrates, bottom invertebrates, and bottom fish. However, it will sometimes feed almost exclusively on pelagic fish. Thus the Thick-billed Murre's invertebrate or bottom feeding may be viewed as potentials dependent on ecological conditions. Such feeding potentials are adaptive to conditions found in the arctic marine zone and areas immediately south. There, the pelagic fish are few in species and low in density; they may also vary drastically in numbers from year to year. At low fish densities, the Thick-billed Murre can switch to invertebrate and bottom feeding. Exploitation of bottom fish may be necessary to feed their chicks. The Thick-billed Murre's greater flying efficiency may be correlated with greater distances between the breeding and wintering grounds, and long flights for food from the breeding colonies.

Although a mechanism appears to exist for avoiding interspecific competition, interspecific competition does not have to be invoked to explain either the evolution or the maintenance of the adaptive differences between these two birds.

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