AN APPROACH TO THE FUNCTIONAL ANALYSIS OF BILL SHAPE

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OF the many features characterizing birds, none is more diagnostic than the bill. Although several other groups within the vertebrates, such as the turtles, have acquired a beak-like structure that is superficially similar to the avian bill, the internal morphology and presumably the functional properties of these convergent structures are quite different. Students of avian anatomy have been intrigued by the jaw apparatus ever since the earliest days of ornithology, and have seized upon the bill as a favorite subject for studies of functional, phylogenetic, and evolutionary morphology. Moreover, in spite of the demonstration that the bill is an extremely plastic feature in evolution, it still possesses value as a taxonomic character. Several higher taxa, such as the parrots, the waterfowl, flamingos, pelicans, and various other groups, can be recognized most easily by the configuration of their bill. At the lower end of the taxonomic scale, species and genera of birds frequently may be separated on the basis of precise differences in the sizes and shapes of their bills. These small differences reflect the minor divergences in the adaptiveness of the closely related forms; the difference in adaptiveness may generally be related to a difference in food preference. Generally, however, the value of the bill in systematic studies is in providing evidence of the degree of evolutionary divergence between groups rather than providing clues to relationships. Yet, it may be hoped that, with sufficient study, the bill will prove to be of value in establishing affinities between groups of birds.

Although the bill continues to be of great interest to students of avian systematics and evolution, studies in these areas are hampered by an insufficient appreciation of the many functional properties of the bill, in spite of our very detailed knowledge of the morphology of the entire jaw apparatus and of our reasonable knowledge of the feeding habits of many birds. It is not possible, at present, to separate the adaptive features from the nonadaptive features of bill structure; the nonadaptive features are largely associated with the historical factors influencing bill structure, and are those features most useful in demonstrating relationships. The problem may be stated as one of separating the factors and features important in horizontal comparison versus those important in vertical comparisons. Perhaps the most outstanding problem in understanding the functional properties of the avian bill is the analysis of the several factors that influence the size and the shape of the bill. In this

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paper I wish to outline several methods that are useful in clarifying the correlations of these several factors with the size and shape of the bill, with special emphasis being placed upon the question of bill shape.

Because the avian bill is a three-dimensional structure, functional investigations must eventually include all dimensions. Yet for the present, a good foundation for future functional studies can be established by considering the bill as a two-dimensional feature. Thus, for the purposes of this paper, the silhouette of the bill may be taken as its shape and will serve as the object under analysis. The shape of the silhouette of the bill may be described in terms of a number of different measures. One commonly used measure is the curvature of the culmen and of the tomium for the upper jaw and the curvature of the tomium and of the gonys for the lower jaw. It is possible to reduce the analysis of bill shape to that set of factors influencing the curvatures of the culmen, tomium, and gonys. Such a simplification has many decided advantages, but it also obscures certain aspects of bill shape. Another set of useful measures is the moment arms of the force vectors and the angle between the force vector and a set of x–y axes at the center of rotation of the jaw; this set of measures will be used in the analysis of the magnitude of the forces acting on the bill.

All the factors influencing bill shape may be classified into historical and nonhistorical factors. All historical factors, whether these are accidental or not, will be excluded from this study. Inclusion of these factors would simply make the analysis inordinately complex without achieving significant gains at this time.

The major nonhistorical factors affecting the shape of the bill are: (a) the demands for a specific structure because of the particular feeding method and other uses of the bill, (b) the forces acting on the bill, (c) the necessary size of the bill, and (d) the weight of the bill. These factors are not independent of one another, but are all closely interrelated. The first factor, that of the necessary shape of the bill for the particular feeding method, places definite limitations on the other factors. The remaining factors, in turn, restrict the possible influence of the first. Moreover, the factors of force, size, and weight are so closely interrelated that it is scarcely possible to consider one without the others. This interrelationship between these factors will be come increasingly clear throughout the paper. Much of the previous work has concentrated on the influence of the particular mode of feeding; the general correlation between bill shape and feeding method is reasonably well established. I would like, in this paper, to concentrate attention on the factors of force, size, and weight which are still little understood.

ACKNOWLEDGMENTS

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STRUCTURE OF THE BILL

The Common Crow (*Corvus brachyrhynchos*), which possesses a generalized bill structure, has been chosen as the basis for analysis. Most of the bewildering array of bill types seen in the class Aves is correlated with the different methods of feeding and hence with the first of the above-listed factors; almost all of this variation may be ignored in the formulation of general methods to evaluate the factors of forces, size, and weight. A detailed description of the jaw apparatus will not be given; the reader should refer to such general papers on the structure of the avian bill as Hofer (1945), Jollie (1957), and Bock (1964), for details of cranial morphology and for references to the earlier literature.

The most significant aspect of cranial morphology for the present investigation is the nature of the kinetic hinge present in the upper jaw (see Bock, 1964, for a description of the structure and mechanism of cranial kinesis in birds). The position of the kinetic hinge, or the region of bending in the upper jaw, is most pertinent. Only birds possessing a rigid upper jaw with a prokinetic or a secondary prokinetic hinge will be considered. Special difficulties arise in the analysis of the rhynchokinetic skull, i.e., one in which the region of bending lies more anteriorally along the dorsal bar of the upper jaw, because the jaws are flexible. The method of torque analysis requires rigid structures as a basic condition.

The upper jaw (Figure 1) is attached to the rigid brain case at the nasal-frontal hinge or kinetic hinge. Because the nasal-frontal hinge is the pivot for all movements of the upper jaw, it is the center of rotation from which all moment arms in the upper jaw will be measured.

The upper jaw is a hollow structure with an internal network of bony trabeculae; the exact distribution of the trabeculae will be discussed below (p. 37; see also Figures 8 and 10). The position and structure of the nasal-frontal hinge can be appreciated readily in these sections of

[1] The acknowledgment to Dr. Gans in my earlier study on cranial kinesis (Bock, 1964: 30) should be modified into a more general statement. Dr. Gans and I discussed this possible shock-absorbing mechanism along with a number of other points. However he did not suggest, and is not responsible for, the exact mechanism proposed, as might be interpreted from my acknowledgment to him.

the jaw. The compact bone of the dorsal bar of the upper jaw narrows until only a single, thin, flexible sheet of bone exists at the nasal-frontal hinge (see Figure 8). (The thinness of this bony sheet is shown clearly in Figures 10j and 10j[a].) Only this thin sheet of bone connects the upper jaw to the brain case. It is, as will be shown below, the weakest point in the upper jaw and the point that limits the size of the forces acting upon the upper jaw. The series of figures illustrating the transverse sections demonstrates that the upper jaw is basically a flattened tube with most of its bone comprising the walls of the tube. These walls are reinforced by a complex system of bony struts running in all three directions. This type of construction results in a very rigid structure, one in which very little bending occurs under normal loads. Hence, the upper jaw may be characterized as a rigid structure in which no bending occurs except at the flexible nasal-frontal hinge that connects the upper jaw to the brain case.

The force of the several muscles operating the upper jaw is transmitted to the jaw through the bony palate and the jugal bars. To simplify the analysis, only one transmitter, the bony palate, will be considered. This simplification will not lead to any great error because in many birds the jugal bars are too thin to be efficient transmitters of either pulling or pushing forces and because in those birds having stout jugal bars, both the bony palate and the jugal bars attach to the upper jaw so close together that the differences in their vector directions and in their moment arms are negligible. The force vector of the muscle force (MF) along the bony palate and its moment arm are shown in Figure 1.

The lower jaw (Figure 1) may also be considered as a solid, single piece structure; the vertical hinge near the midpoint of each ramus in some birds (Bock, 1964: 8–9) has little influence on the forces acting in the dorsal–ventral plane. The mandible is articulated to the quadrate near its posterior end; this articulation may be taken as the pivot around which the mandible rotates. The possible shift of the pivot from the articular–quadrate hinge to the point of insertion of the postorbital ligament under certain conditions (Bock, 1964: 19–20) may be overlooked because this shift of pivots does not alter substantially the lengths of the various moment arms in the lower jaw.

Several muscles attach to the mandible; all are concentrated along the posterior segment of the mandibular ramus. Most of these muscles have broad areas of insertion, either fleshy or by many tendons. *M. pseudotemporalis superficialis* in most birds is a notable exception as it inserts by means of a single narrow tendon. However, to simplify the analysis, the forces produced by these muscles have been reduced to three force vectors; one represents the major depressor (not shown), one represents the

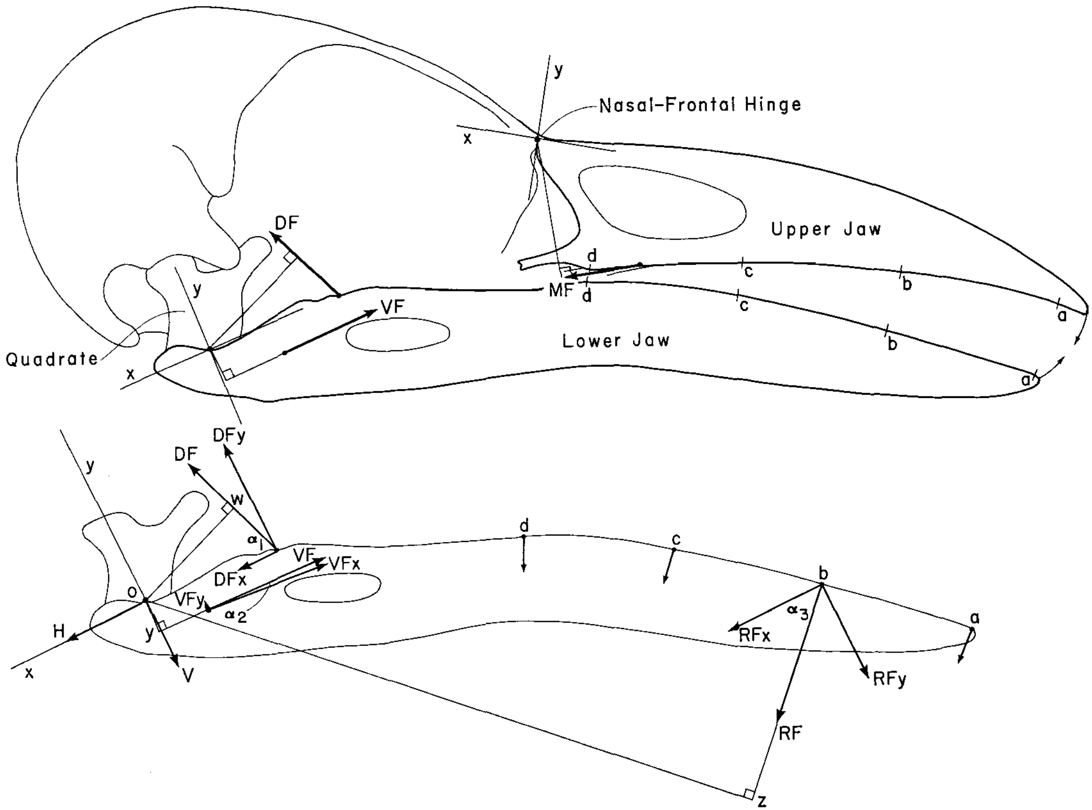


Figure 1. (Upper) Lateral view of the skull of a crow. The x and y axes pass through the centers of rotation of the jaws. These axes are so oriented that one axis is along the longitudinal axis of the nasal-frontal hinge or of the quadrate. The moment arms of the vectors of the muscle forces (MF, DF, and VF) are the perpendiculars from the center of rotation to the force vector. The points, a, b, c, and d, along the tomium of each jaw, are the sites at which will be placed the resultant forces acting on the jaws.

(Lower) The lower jaw of a crow taken from Figure 1 (Upper), presented to show the arrangement of all external forces acting on it when the bird is biting on an object held at point b. Force vectors **DF** and **VF** represent the force of the dorsal and the ventral sets of adductor muscles of the mandible; their moment arms are ow and oy. Force vector **RF** represents the resultant force exerted by the object on the mandible; its moment arm is oz. The H and V forces along the x–y axes at the quadrate are the forces exerted by the quadrate on the mandible; they are the forces equal and opposite to the stresses exerted by the lower jaw on the quadrate-mandibular hinge. The resultant forces act at points a, c, and d and are also shown.

set of dorsal adductors (DF); and one, *M. pterygoideus* (VF), the ventral adductors. The force vectors (DF and VF) and moment arms of the adductor masses are shown in Figure 1. Changes in the direction of the force vectors and hence in the length of their moment arms as the mandible rotates about its quadrate articulation should be included in any analysis.

Rotation of the quadrate about its squamosal articulation in a forward-backward plane as the bill opens and closes will shift the position of the pivot of the mandible. These shifts will affect the lengths of the moment arms of the forces acting on the lower jaw and hence their torques. They will also affect the direction of the x and y axes plotted on the quadrate and hence the magnitude of the forces acting on the quadrate. These changes are small and will be ignored in this study, but they probably will have to be included in any exact investigations of the forces acting on the mandible and quadrate in actual cases.

The Strength of Bone

Bone has quite high strength to resist tension and compression, and lower, but still high, strength to resist shear (see Evans, 1957, for a general discussion of strength of bone). The figures given for human compact bone (Koch, 1917: 214) are from 13,000 to 17,700 pounds per square inch for tension, from 18,000 to 24,000 pounds per square inch for compression, and from 7,150 to 11,800 pounds per square inch for shear. I am unaware of any figures for the strength of avian bones so that these figures for human bone will have to be used for the present. Basically bone can resist the same amounts of compression and tensile stresses, but only about one-third to one-half the amount of shear. Thus, if the strength of bone under one type of stress can be measured, its resistance to the other types can be estimated. But, of most significance to this study, is the fact that the resistance of bone to shear is much lower then to tension and compression. This means that one limiting factor to the size of the forces acting on the upper jaw may be the resistance of the bone at the nasal-frontal hinge to shearing stresses.

Using the figures given by Koch and a rough estimate of the cross-sectional area of the bone at the nasal-frontal hinge (about 1/600 square inches), the nasal-frontal hinge of the crow would resist a compression of 30 to 40 pounds, a tension of 20 to 30 pounds, and a shear of 15 to 20 pounds. A simple experiment demonstrated that the nasal-frontal hinge of a cleaned and long-dried crow skull resists a tensile stress of at least 35 pounds. Rupture of the bone occurred when a stress between 35 and 40 pounds was applied. The bone ruptured exactly along the junction of the upper jaw with the brain case. No part of the upper jaw (i.e., the nasal-frontal hinge) was left attached to the brain case after the jaw broke away from the rest of the skull, indicating that the nasal-frontal hinge is the weakest point in the upper jaw.

ANALYSIS OF EXTERNAL FORCES

Both upper and lower jaws of birds may be treated as rigid structures which can rotate about a fixed pivot. The rotary effort, relative to the pivot, of a force acting on a rigid structure depends upon the magnitude of the force and upon the length of the moment arm of the force; the product of the force and the length of the moment arm is the moment of the force or the torque. The units of a torque, therefore, include a force and a distance, and for the purposes of this paper all torques will be in units of the pound-inch. The reader should consult Koch (1917) or any general textbook of college physics for additional details of torque analysis. The method developed in this study is identical with the concept of the "free-body diagram" advocated by Dempster (1961) although Dempster's paper was read after this manuscript was completed. The reader is urged to consult Dempster's excellent paper as general background for the approach used in the present investigation.

A word of warning should be inserted regarding certain limitations of the free-body diagram or torque method. Free-body diagrams may be applied only when the mechanical system is completely determined, that is when all force vectors and all movements of parts are known exactly. In particular, the hinge about which the parts rotate should be one that does not store any energy and no friction forces should exist between the rotating structure and the objects against which it pushes. Moreover, the individual structures must be rigid and the loading must be symmetrical; these conditions have been assumed although it should be noted that generally the loading on the bill is asymmetrical, e.g., the seed is held on one side of the bill when it is being shelled. The prokinetic upper jaw has several features which make it somewhat undetermined. The nasal-frontal hinge is not an idealized pin hinge (like a door hinge) as shall be assumed throughout this study. Rather the nasal-frontal hinge in most prokinetic birds is formed by a short, flexible strip of bone. The bone bends as the upper jaw rotates; the bending of the bone requires force which is then stored in the hinge and released later. This force must be accounted for in actual studies although it does not appear in the analysis presented below. Presumably the force stored in the hinge is quite small compared with the total force acting on the bill, as may be estimated from the very small force required to rotate the upper jaw to its upper limit. Any frictional forces between the jaw and the object held in the jaws would reduce the perpendicular force exerted by the jaw on the object; the forces exerted by the jaws were assumed to be exactly perpendicular to the curvature of the tomium. The magnitude of the frictional forces is not known and cannot be estimated at this time. These still undetermined parts of the jaw system do not affect the formulation of the theoretical method for the external forces on the jaws, but they would affect the application of the method to actual cases. Exclusion of the rhynchokinetic bill from analysis is because of its highly undetermined nature.

The torques produced by the forces acting upon the jaws, no matter whether these forces originate from muscular action or from external forces acting upon the bill, may cause the jaws to rotate about their pivots or may cause the jaws to exert pressures against some object. In this analysis, I will consider only static conditions in which the jaws are not moving. Further, I will consider only the case when the jaws are closing against an object. The condition in powerful gapers in which the bill is forced open while inserted in a tough object will be excluded because few birds are powerful gapers and because the same principles will apply to the jaws when gaping as when crushing an object between the jaws. I would like to emphasize at this point that, although the jaws are not moving, the entire analysis and the general conclusions to be presented depend upon the kinetic nature of the avian skull. If birds possessed an akinetic skull, the entire analysis would be different.

The analysis of dynamic conditions is being carried out currently and will be presented separately.

If a structure is subjected to several forces acting at different distances from the center of rotation and is in static rotational equilibrium (i.e., at rest) then the following conditions must be met:

(a) The sum of the torques must be equal to zero;

(b) The sum of the forces in the x direction must be equal to zero; and

(c) The sum of the forces in the y direction must be equal to zero.

The choice of the x axis is arbitrary; the y axis is perpendicular to the x axis.

The upper jaw is the easier to analyze and will serve as the example of how the forces acting on a jaw may be studied with the help of torque analysis (Figure 2). Consider the case in which the upper jaw is pressing against an object, such as a seed, which is resisting the force being applied to it. The muscular force (of *M. pterygoideus*) transmitted to the upper jaw through the bony palate is shown by the vector MF. The moment arm (ow) of vector MF is the perpendicular dropped from the center of rotation (o) at the nasal-frontal hinge. Thus the torque of the vector

MF is the product of the force and the moment arm (MF × ow) and acts in a clockwise direction which shall be designated as a positive torque. The upper jaw exerts a force on an object at point b. This force is not shown in Figure 2; instead, the equal and opposite force (RF) being exerted by the object on the jaw is shown. All RF forces acting on the bill will be assumed to act perpendicular to the curvature of the tomium. The moment arm of vector RF is oy and its torque is (RF × oy) which is in a counterclockwise direction and hence designated as a negative torque. No other torque-producing forces are acting on the upper jaw. Because the upper jaw is in static rotational equilibrium, the torques (MF) (ow) and (RF) (oy) must be equal, hence:

$$\Sigma\, T\ (\text{tau}) = (MF)\ (ow) - (RF)\ (oy) = 0;\ \text{or:}$$
$$(MF)\ (ow) = (RF)\ (oy)$$

If we know the magnitude of MF and the lengths of the moment arms of the force vectors MF and RF, then the resulting force on the object may be found easily. Likewise, if we know RF and the length of the moment arms, the size of the force along the bony palate can be calculated and from this, the strength of *M. pterygoideus* may be estimated. In practice, it would be far easier to measure the RF force than the MF force. From a simple inspection of Figure 2, one can appreciate that the force RF will have to be less than the force MF applied to the upper jaw because the moment arm oy is longer than the moment arm ow. Moreover, the resulting force RF will increase as the object is held closer to the base of the bill and will be greatest when the object is held at the base of the bill (at point d). The minimum resulting force would be at the tip of the bill. In a similar fashion, it can be appreciated that the torque of the muscular force, MF, will increase as the bill becomes deeper at its base and thereby increases the length of the moment arm of the force vector MF; the resulting force on an object would automatically increase.

Determination of the torques about the nasal-frontal hinge shows how much force is applied by the upper jaw upon an object being held in the bill, but it does not describe all the forces acting on the jaw. The torques do not provide any indication of the magnitude of the force acting on the nasal-frontal hinge. These forces may be found by adding the forces along some chosen set of x–y axes. Since the choice of the x and y axes is arbitrary, I shall place the x axis along the longitudinal axis of the thin layer of bone forming the nasal-frontal hinge. Thus the force along the x axis will be either compression or tensile stress on the bone of the nasal-frontal hinge. The force along the y axis will be a shearing stress. The x forces (= horizontal forces) acting to the right and the y forces (=

vertical forces) acting upwards will be considered positive. It should be noted that the bone is thinnest and hence weakest at the point where the jaw meets the brain case at the nasal-frontal hinge. The resistance of the bone to various stresses at this point constitutes the limiting factor for the size of the forces the bill can withstand, as will be shown below.

The forces, MF and RF, acting on the upper jaw, may be resolved into their rectangular components; these components are parallel to the x and y axes. These components are:

(a) For the force MF, $MF_x = MF \cos \alpha_1$
$MF_y = MF \sin \alpha_1$; and

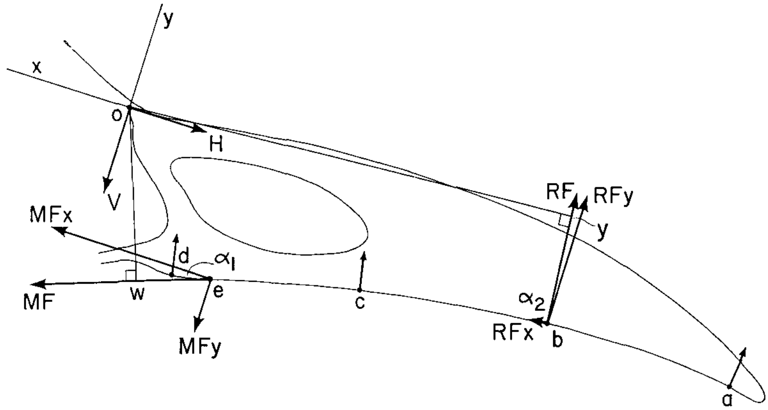
(b) For the force RF, $RF_x = RF \cos \alpha_2$
$RF_y = RF \sin \alpha_2$

The forces along the x axis and the y axis may be added algebraically, hence:

$$\Sigma F_x = -MF \cos \alpha_1 - RF \cos \alpha_2 + H = 0, \text{ or}$$
$$MF \cos \alpha_1 + RF \cos \alpha_2 = H; \text{ and}$$
$$\Sigma F_y = -MF \sin \alpha_1 + RF \sin \alpha_2 - V = 0, \text{ or}$$
$$MF \sin \alpha_1 - RF \sin \alpha_2 = V$$

Since the values for the two components of the forces acting on the bill, MF and RF, are known, the equations can be solved easily; the solutions give the forces at the nasal-frontal hinge. The forces H and V have been drawn in Figure 2 as the equal and opposite forces exerted by the brain case on the upper jaw. Hence if H is positive, a compression stress exists on the bone of the hinge and if V is positive, a shearing stress exists on the hinge with the upper jaw tending to move downwards relative to the brain case. If these forces are negative just the opposite is true—a tensile stress and a shear with the upper jaw tending to move upwards exist on the hinge. The magnitude of these forces must be below the ultimate strength of the bone at the nasal-frontal hinge or the bill will rupture at this point.

The forces acting on the lower jaw may be analyzed exactly the same as in the upper jaw (Figure 1, lower) using the same conventions for the direction of the forces. Again the lower jaw is a rigid structure and is in a condition of static rotational equilibrium. The force vectors of the dorsal adductors have been condensed into a single vector DF, and the force vectors of *M. pterygoideus* have been condensed into a single vector VF. These vectors represent a great oversimplification, which cannot be done in the analysis of specific cases because the position and direction of the vectors in both dorsal and ventral sets of adductors are diverse and because the several jaw muscles probably contract at different times as the bill is being closed. The center of rotation for the mandible was placed at the midpoint of the articular-quadrate articulation. The x–y axes were



$$\text{Torque} = (MF)(ow) - (RF)(oy) = 0$$

$$\Sigma Fx = -MF\cos\alpha_1 - RF\cos\alpha_2 + H = 0$$

$$\Sigma Fy = -MF\sin\alpha_1 + RF\sin\alpha_2 - V = 0$$

Figure 2. The upper jaw of a crow taken from Figure 1 (Upper), to show the arrangement of all external forces acting upon it when the bird is biting on an object held at point b. Force vector MF represents the retractor force of *M. pterygoideus*; its moment arm is ow. Force vector RF represents the resultant force exerted by the object on the upper jaw; its moment arm is oy. The H and V forces along the x–y axes at the nasal-frontal hinge are the forces exerted by the brain case on the upper jaw; they are the forces equal and opposite to the stresses exerted by the upper jaw on this hinge. The formulae for static rotational equilibrium are given. The resultant forces at points a, c, and d are also shown.

placed so that the y axis lies parallel to the longitudinal axis of the quadrate. Thus, the formulae for static rotational equilibrium for the mandible are:

(a) $\Sigma T = -(DF)(ow) - (VF)(oy) + (RF)(oz) = 0$, or
$(DF)(ow) + (VF)(oy) = (RF)(oz)$;

(b) $\Sigma X = -DF\cos\alpha_1 + VF\cos\alpha_2 - RF\cos\alpha_3 - H = 0$, or
$DF\cos\alpha_1 - VF\cos\alpha_2 + RF\cos\alpha_3 = H$; and

(c) $\Sigma Y = DF\sin\alpha_1 + VF\sin\alpha_2 - RF\sin\alpha_3 - V = 0$, or
$DF\sin\alpha_1 + VF\sin\alpha_2 - RF\sin\alpha_3 = V$

Several points become immediately clear from these equations and Figure 1, Lower. First, the VF force has a very short moment arm and hence contributes much less to the counterclockwise torque than does the DF force, assuming that these forces are equal. The torque produced by the VF force could be increased by increasing the depth of the mandible and by the insertion of *M. pterygoideus* as close as possible to the ventral rim of the mandible. The moment arm of the RF force is several times longer than the combined moment arms of the muscle forces; hence the magnitude of the RF force is several times smaller than the combined strength of the muscle forces. The forces along the x and y axes are shown as the equal and opposite forces exerted by the quadrate on the mandible. The force along the y axis represents compression on the quadrate if V is negative. This force could be quite large without causing damage to the quadrate, because this is a thick, heavy-walled bone. The forces along the x axis would tend to rotate the quadrate forward or backward about its squamosal articulation, depending upon the direction of H. This force could act to disarticulate the mandible or could act to disrupt the proper operation of the kinetic mechanism if it became too large. But, as can be seen on the diagram the DF_x, VF_x, and RF_x forces are so arranged that they would tend to cancel each other out, leaving a small H force.

The above qualitative analysis of the forces acting on the upper and lower jaws presents a complete picture of the force vectors, but it does not give any real impression of the magnitude of the forces involved. The lengths of the vectors on the figures, for example, are not drawn proportionally to the size of the force. Several sets of calculations were made using hypothetical but realistic forces. All calculations are based upon the vectors of the muscle forces and the x–y axes shown in Figures 1 and 2, with the several resultant forces at points a, b, c, and d shown on both jaws.

Consider first an object held in the bill of a crow at point b with force applied to it. What are the magnitudes of the force, RF_b, at point b and of the forces along the x and y axes at the nasal-frontal hinge as the muscle force, MF, increases from 10 pounds to 100 pounds in 10-pound steps? The force vector MF has a moment arm of 0.4736 inches and intersects the x axis at an angle of 19°. The force vector RF_b has a moment arm of 1.2631 inches and intersects the x axis at an angle of 86°. The results are shown in Table 1. Inspection of this table shows that the force applied to the object held at point b is slightly more than one-third the size of the muscle force because its moment arm is almost three times longer than the moment arm of vector MF. The force at the nasal-frontal hinge along the x axis becomes large quite rapidly because the MF_x and the RF_x forces are acting in the same direction. Thus a large compression stress is present on the bone of the nasal-frontal hinge; this force is represented as the equal and opposite reaction force in Figure 2. The maximum ability of the bone to resist compression is probably reached when the muscle force is around 50 pounds (see p. 15 for the strength of the nasal-frontal hinge). If this is the case, then the maximum force a crow can exert on an object at point b in its bill is just over 18 pounds.

TABLE 1
FORCES (POUNDS) ACTING ON THE UPPER JAW OF A CROW

MF	*Torque*[1]	RF_b	*H*[2]	*V*[2]
10	4.736	3.75	9.72	–0.49
20	9.472	7.50	19.43	–0.97
30	14.208	11.25	29.15	–1.45
40	18.944	15.00	38.87	–1.94
50	23.680	18.75	48.58	–2.42
60	28.416	22.50	58.30*	–2.91
70	33.152	26.25	68.02*	–3.39
80	37.888	30.00	77.73*	–3.88
90	42.624	33.75	87.45*	–4.36
100	47.360	37.50	97.17*	–4.85

[1] The torque is the same for the MF and RF_b forces, only opposite in sign.
[2] The H (compression) and V (shear) forces act along the x–y axes at the nasal-frontal hinge.
* Forces that are probably larger than the strength of the bone at the nasal-frontal hinge.

Note that the shearing stress, again shown as the equal and opposite force in Figure 2, is still below the ultimate strength of the bone when the muscle force is 100 pounds.

Assuming the same conditions as above, consider an object held in the bill of a crow at a series of points, a, b, c, and d, with force applied to it. What are the sizes of the forces, RF, at these several points and of the forces along the x and y axes at the nasal-frontal hinge as the muscle force, MF, increases from 20 pounds to 100 pounds in 20-pound steps? The force vector MF is the same as above. The force vector RF_a has a moment arm of 1.8289 inches and intersects the x axis at an angle of 81°, while the comparable values for vector RF_b are 1.2631 inches and 86°, for vector RF_c are 0.6974 inches and 79°, and for vector RF_d are 0.1711 inches and 80°. The results are given in Tables 2 and 3. The resultant forces acting on the object increase, as one would expect, from point a to point d, but the rate of increase is very great. The force at point d is about 11 times greater than the force at point a, reflecting the difference in their moment arms. The compression at the nasal-frontal hinge approaches the maximum strength of this bone at different magnitudes of the muscle force when the object is held at the several points along the bill. Therefore a crow can exert a force of up to 20 pounds at point a, up to 22 pounds at point b, up to 40 pounds at point c, and up to 110 pounds at point d according to the limits definitely determined by compression on the kinetic hinge. The values for the shearing stress set even lower limits at some points. Note that greater shearing stresses exist when an object is held at point a than at point b; this depends upon the difference in the curvature of the bill which results in a smaller angle between the force vector and the x axis at b than at a. The shearing stress on the nasal-frontal hinge exceeds the ultimate strength of the bone when

TABLE 2
FORCES (POUNDS) ACTING ON THE UPPER JAW OF A CROW

MF	*Torque*[1]	RF_a[2]	RF_b[2]	RF_c[2]	RF_d[2]
20	9.472	5.18	7.50	13.58	55.36
40	18.944	10.36	15.00	27.16	110.72
60	28.416	15.54	22.50	40.75	166.08
80	37.888	20.72	30.00	54.33	221.44
100	47.360	28.90	37.50	67.91	276.80

[1] The torque is the same for the MF and each RF force, only opposite in sign.
[2] Resultant forces at points a, b, c, and d shown on the upper jaw in Figure 2.

the force exerted at point c is 40 pounds or more, and far exceeds the ultimate strength of the bone when the force exerted at point d is 48 pounds, which occurs with a muscle force of 20 pounds. From these figures, it is obvious that the muscle and resultant forces in the crow bill are not arranged to permit the crow to exert large biting forces without causing damaging stresses at the nasal-frontal hinge.

The same analyses may be made for the mandible. An object is held at point b with force applied to it. What are the magnitudes of the force, RF_b, at point b and of the forces along the x and y axes on the quadrate as the muscle forces, DF and VF, increase from 10 pounds each to 100 pounds each in 10-pound steps? Convenience was the only reason for setting the force DF equal to the force VF. The force vector DF has a moment arm of 0.4211 inches and intersects the x axis at an angle of 71° while the force vector VF has a moment arm of 0.1184 inches and intersects the x axis at an angle of 1°. The force vector RF_b has a moment arm of 2.1447 inches and intersects the x axis at an angle of 46°. The results are shown in Table 4. The first point of interest is that the force VF contributes about one-fifth of the total counterclockwise torque; the other four-fifths come from force DF, although the sizes of these forces are equal. Second, the force applied to the object

TABLE 3[1]
FORCES (POUNDS) ACTING ON THE NASAL-FRONTAL HINGE OF A CROW

MF	RF_a		RF_b		RF_c		RF_d	
	H[2]	*V*[2]	*H*[2]	*V*[2]	*H*[2]	*V*[2]	*H*[2]	*V*[2]
20	18.10	–1.40	19.43	–0.97	21.50	–6.82	28.52	–48.01*
40	36.20	–2.79	38.87	–1.94	43.00	–13.64	57.04*	–96.01*
60	54.30	–4.19	58.30*	–2.91	64.50*	–20.46*	85.56*	–144.02*
80	72.40*	–5.59	77.75*	–3.88	85.98*	–30.28*	114.08*	–192.02*
100	90.50*	–6.98	97.17*	–4.85	107.51*	–34.10*	142.60*	–240.03*

[1] These forces correspond to those in Table 2.
[2] The H (compression) and V (shear) forces act along the x–y axes at the nasal-frontal hinge.
* Forces that are probably larger than the strength of the bone at the nasal-frontal hinge.

TABLE 4
FORCES (POUNDS) ACTING ON THE LOWER JAW OF A CROW

Force[1]	*Torque, DF*	*Torque, VF*	*Total torque*[2]	RF_b	H[3]	V[3]
10	4.211	1.184	5.395	2.52	–4.99	–7.82
20	8.422	2.368	10.790	5.03	–9.99	–15.64
30	12.633	3.552	16.185	7.55	–14.98	–23.46
40	16.844	4.736	21.580	10.06	–19.98	–31.28
50	21.055	5.590	26.645	12.58	–25.97	–39.10
60	25.266	7.104	32.370	15.09	–29.97	–46.92
70	29.477	8.288	37.765	17.61	–34.96	–54.94
80	33.688	9.472	43.160	20.12	–39.96	–62.56
90	37.899	10.656	48.555	22.64	–44.95	–70.38
100	42.110	11.840	53.950	25.16	–49.95	–78.20

[1] The forces DF and VF are equal as indicated by the single force column.
[2] The total torque is the sum of the torques of the DF and VF forces and is equal to, but opposite in sign to, the torque of RF_b.
[3] The H (shear) and V (compression) forces act along the x–y axes at the quadrate articulation.

at point b is only slightly more than one-eighth of the sum of the two muscle forces acting to close the mandible. The forces along the x axis are so arranged that the horizontal component of the DF and RF forces cancel out much of the large horizontal component of the VF force. The remaining force would tend to swing the quadrate forward, which would oppose the desired backward movement of the quadrate when the jaws close. This indicates that the decision to set the VF force equal to the DF force is not justified; more likely the DF force is larger than the VF force. The large vertical component of the DF force is only slightly cancelled by the vertical component of the RF force, which results in a large compression stress on the quadrate shown as the equal and opposite reaction force in Figure 3. Although this stress is quite large, it is probably below the ultimate strength of the thick-walled bone of the quadrate.

If the same conditions are assumed, consider an object held in the bill of a crow at a series of points, a, b, c, and d, with force applied to it. What are the sizes of the forces, RF, at these several points and of the forces along the x and y axes on the quadrate as the muscle forces, DF and VF, increase from 20 pounds to 100 pounds each in 20-pound steps? The force vectors, DF and VF, are the same as above. The force vector RF_a has a moment arm of 2.6052 inches and intersects the x axis at an angle of 42°, while the comparable values for vector RF_b are 2.1447 inches and 46°, for vector RF_c are 1.6711 inches and 46°, and for vector RF_d are 1.2500 inches and 59°. The results are given in Tables 5 and 6. The RF forces, as expected, decrease from point d out to point a. Each RF force is smaller than the RF force at the comparable point on the upper jaw. At point a, the difference is relatively little, while at point c, the force exerted by the upper jaw is just over twice that exerted by the

TABLE 5

FORCES (POUNDS) ACTING ON THE LOWER JAW OF A CROW

Forces[1]	*Total torque*[2]	RF_a[3]	RF_b[3]	RF_c[3]	RF_d[3]
20	10.790	4.14	5.03	6.46	8.63
40	21.580	8.28	10.06	12.91	17.26
60	32.370	12.42	15.09	19.37	25.90
80	43.160	16.57	20.12	25.83	34.53
100	53.950	20.71	25.16	32.28	43.16

[1] Force of each muscle vector, DF and VF.

[2] Total torque produced by the muscle forces; it is equal to, but opposite in sign to, the torque of each RF force.

[3] Resultant forces at points a, b, c, and d shown on the lower jaw in Figure 1 (Upper).

lower jaw. The difference at point d is huge, the force of the upper jaw being six to seven times greater than that of the lower jaw. What is most interesting is that the stresses on both the x and the y axes decrease from point a to point d in spite of the increase in the RF force from point a to point d. The reason for this decrease in stresses on the quadrate lies in the fact that the largest components of the external forces tend to cancel each other; as the RF force increases, its x and y components increase and thus cancel more of the x and y components of the DF and the VF forces, which are constant.

Up to this point, this quantitative analysis has started with assumed values for the muscle force, after which the force exerted by the bill and the stresses at the pivot were calculated. A shortcoming of this approach is that the forces exerted by the upper jaw and by the lower jaw at the same spot differ. If the jaws are in a static state of rotational equilibrium when large forces are exerted on an object held in the bill, then the forces exerted by both jaws at comparable points along the tomium have to be equal. Otherwise the entire jaw apparatus would rotate either upward or downward around the nasal-frontal hinge and would quickly place

TABLE 6[1]

FORCES (POUNDS) ACTING ON THE QUADRATE ARTICULATION OF A CROW

Force[2]	RF_a		RF_b		RF_c		RF_d	
	H[3]	*V*[3]	*H*[3]	*V*[3]	*H*[3]	*V*[3]	*H*[3]	*V*[3]
20	−10.41	−16.49	−9.99	−15.64	−9.00	−14.62	−9.04	−11.86
40	−20.81	−32.98	−19.98	−31.14	−18.00	−29.23	−18.08	−23.72
60	−31.22	−49.47	−29.97	−46.92	−27.00	−43.85	−27.12	−35.58
80	−41.63	−65.96	−39.96	−62.56	−36.00	−58.62	−36.15	−47.44
100	−52.02	−82.44	−49.94	−78.21	−45.00	−73.08	−45.19	−59.30

[1] The forces correspond to those in Table 5.

[2] Force of each muscle vector, DF and VF.

[3] The H (shear) and the V (compression) forces act along the x–y axes at the quadrate articulation.

TABLE 7

FORCES (POUNDS) ACTING ON BOTH JAWS OF A CROW

Upper Jaw

RF_b[1]	*Torque*[2]	*MF*[2]	*H*[2]	*V*[2]
10	12.631	26.67	25.91	–1.29
20	25.262	53.34	51.83*	–2.58
30	27.893	81.05	77.74*	–3.88
40	50.524	106.68	103.66*	–5.17
50	63.155	133.35	129.57*	–6.49

Lower Jaw

RF_b[1]	*Total torque*[4]	*DF*[4]	*Torque DF*[4]	*VF*[3, 4]	*Torque VF*[4]	*H*[4]	*V*[4]
10	21.447	47.18	19.868	13.34	1.579	–8.98	–37.65
20	42.894	93.47	39.362	26.67	3.158	–17.66	–74.46
30	64.341	141.54	59.604	40.01	4.737	–27.02	–112.95
40	85.788	188.73	79.473	53.34	6.316	–35.91	–150.60
50	107.235	237.91	99.341	66.68	7.893	–44.88	–188.25

[1] The RF_b force on the upper jaw is equal to the RF_b force on the lower jaw.
[2] These forces are the same as in Table 1.
[3] The force VF is set equal to one-half the force MF.
[4] These forces are the same as in Table 4.
* Forces that are probably larger than the strength of the bone at the nasal-frontal hinge.

damaging stresses on this hinge. Consider, then, an object held in the bill of a crow at point b with force applied to it. What are the sizes of the MF, DF, and VF forces and of the forces along the x and y axes at the nasal-frontal hinge and on the quadrate as the RF force at point b on both the upper and the lower jaws increases from 10 pounds to 50 pounds in 10-pound steps? The moment arms and the angles of intersect with the x–y axes of the vectors are the same as above. Because *M. pterygoideus* attaches to the bony palate at one end and to the mandible at the other end, contraction of this muscle produces both the MF and the VF forces. A relationship must be established between these forces, and for this I shall assume that VF = ½ MF. The justification for this assumption is that part of *M. pterygoideus* inserts on the basitemporal plate and on the internal process of the mandible in such a way that none of its force contributes to the VF force and that the fibers of *M. pterygoideus* insert on the mandible at a greater angle than on the palate and hence a smaller amount of the force would contribute to the VF force than to the MF force. The results are given in Table 7. The figures in this table may be compared with those in the preceding tables. Note that for the upper jaw, when the RF_b force is 20 pounds, the compression stress (the H force) is probably at the ultimate strength of the bone at the nasal-frontal hinge or slightly past it. Thus, this would limit the

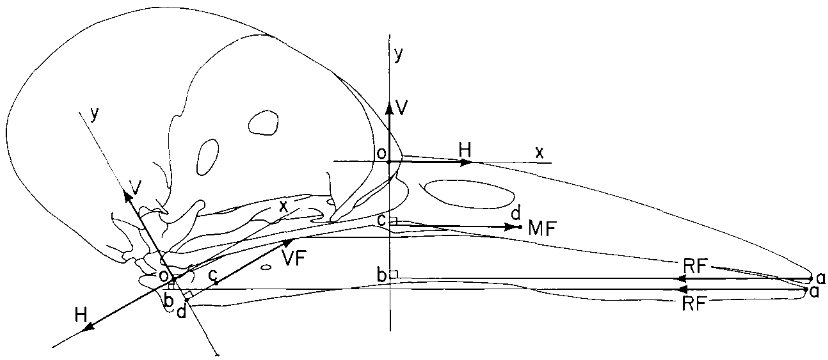


Figure 3. The skull of a woodpecker, presented to show the forces acting on the bill when the bird is pounding on a tree. Note that the MF force is a protractor force rather than a retractor force. The DF force on the mandible has been omitted from analysis. The forces along the x–y axes at the nasal-frontal hinge are shown as the actual stresses on this bone, although vector V is equal to zero because no stress exists along the y axis. The forces along the x–y axes at the quadrate are shown as the actual stresses on the quadrate. The analysis for the upper jaw was done separately from that for the lower jaw, hence the double use of the same lettering.

force a crow could exert on an object held at point b even if all other stresses—the shear at the nasal-frontal hinge and the stresses on the quadrate—were below the strength of the bones to withstand them. Note again that the VF force contributes so little to the total counterclockwise torque on the mandible that even if it were set equal to the MF force or twice the MF force, the major contribution to the torque would still come from the DF force.

The analysis starting at the forces exerted by the bill has a great advantage because these forces would be the easiest to measure experimentally. A series of experiments could be devised by which one could ascertain the contribution of the individual muscles throughout the cycle of closing the bill to the force exerted by the bird upon its food item.

SPECIAL EXAMPLES

The general validity of the torque method in analyzing the forces acting on the avian bill may be tested by applying it to several special examples. A woodpecker was chosen as an extreme case of a bird having a straight bill on which the normal forces are large forces acting directly on the tip. A finch was chosen as an extreme case of a bird having a decurved bill on which the normal forces are large biting forces.

The straight woodpecker bill.—The Red-headed Woodpecker (*Melanerpes erythrocephalus*) was chosen to represent the straight bill construction (Figure 3); this bird was considered by Burt (1930) to be a moderately specialized woodpecker. A discussion of a possible shock-absorbing mechanism in woodpeckers is given in Bock (1964: 29–30). I shall not include all of the subtle points suggested in that paper in the present analysis. In particular, no effort was made to consider the bill in a protracted position the instant it contacts the tree. In Figure 3, the analyses for both jaws were combined on the same drawing, hence the overlap in lettering. These can easily be separated by considering only one jaw at a time while examining the figure.

When a woodpecker pounds against a tree, the major forces will act directly at the squared tip (points a) and in a direction closely paralleling the longitudinal axis of the jaws. The RF forces, the MF force, and the VF force matched the x–y coordinates so closely, that I lined them up as shown on Figure 3. This simplification does not affect the general conclusions. The force of the dorsal adductors of the mandible, DF, was omitted because these muscles may not have a large role when the woodpecker is pounding on a tree; this assumption is discussed more fully below. The RF force on each jaw is set at 50 pounds.

The upper jaw shall be considered first. The vector RF has a force of 50 pounds and a moment arm (ob) of 0.3388 inches; hence it exerts a clockwise torque of 16.94 pound-inches on the upper jaw. The vector MF, which is the force produced by the very large *Mm. protractor pterygoidei,* has a moment arm (oc) of 0.1869 inches, hence its force is 90.64 pounds. The forces at the nasal-frontal hinge are a tension of 46.64 pounds exerted by the upper jaw on the hinge and no shear along the y axis, as both RF and MF forces are parallel to the x axis. Note that the force on the nasal-frontal hinge is a tensile stress, as indicated by the vector H, in this case the actual force exerted by the upper jaw on the hinge. Most workers have assumed that a large compression stress would be present at the nasal-frontal hinge and that this compression passes into the brain case. It should be noted, however, that a rather large tension does exist; this force can be reduced by flattening the bill and having the upper jaw positioned so that the moment arm of the vector RF is almost equal to the moment arm of the vector MF, i.e., these vectors act along the same path but in opposite directions. This condition is achieved in the more highly specialized woodpeckers.[1]

[1] The upper jaw of the woodpecker is, very probably, fully protracted when the bird strikes the tree with its bill. Moreover, the force and torque produced by *Mm. protractor pterygoidei* are very large, as shown by the calculations above. This large counterclockwise torque acts on the upper jaw before the bill strikes the tree, and hence this torque acts before it is balanced by the clockwise torque produced by the tree on the bill. Before the moment of impact, the counterclockwise torque would tend to rotate the upper jaw upwards and would probably force the upper jaw beyond the breaking point of the nasal-frontal hinge unless the upward rotation of the upper jaw was checked by some mechanical stop. Burt (1930) described an

The vector RF on the lower jaw has a force of 50 pounds and a moment arm (ob) of 0.0234 inches, hence it exerts a clockwise torque of 1.17 pound-inches on the mandible. The vector VF has a moment arm (od) of 0.0701 inches; hence its force is 16.69 pounds. Vector RF intersects the x axis at an angle of 30° while the vector VF is parallel to the x axis. The forces on the quadrate are a horizontal force of 26.61 pounds acting in the direction shown by vector H, and a vertical force of 25.00 pounds acting in the direction shown by vector V which is comprised entirely of the vertical component of force RF. Several interesting points become clear from these results. The first concerns the position of the quadrate. It is apparent that, as the quadrate has an increasingly horizontal orientation, the smaller will become the force along the x axis and the larger will become the compression stress along the y axis. The quadrate can withstand the large compression forces. This is exactly what one finds in the highly specialized woodpeckers, in which the quadrate is almost horizontal. Both the large VF force produced by *M. pterygoideus* and the large force along the x axis are disadvantageous. These forces would retract the palate and thereby oppose the pull of *Mm. protractor pterygoidei.* The size of the force shown by the vector H will be reduced as the quadrate lies in a more horizontal position. The size of the VF force can be reduced by having its role assumed by one of the dorsal adductors, one that would have as small a negative x component as possible. *M. pseudotemporalis superficialis* may have the role of producing the counterclockwise torque that balances the clockwise torque of the RF force. This would eliminate *M. pterygoideus* and its very disadvantageous hindrance to *Mm. protractor pterygoidei.* These calculations indicate that the above assumption to include the VF force and to exclude the DF force in the analysis was not a valid assumption. The opposite assumption appears to be the correct one.

The decurved finch bill.—The Cardinal (*Richmondena cardinalis*) was chosen to represent the decurved bill construction (Figure 4). The analysis of the biting forces will be only for the static condition of rotational equilibrium and will follow closely the analysis above of the crow skull. If a seed is held at several different points along the tomium, points a, b, c, and d, what are the magnitudes of the resultant forces at each one of

overhang of the frontal bone over the nasal-frontal hinge and has shown that the development of this overhang is correlated with the degree of specialization of the woodpecker for pounding. I would suggest that this overhang of the frontal bone is an adaptation to prevent rupture of the nasal-frontal hinge by the large protractor forces, and that the development of this overhang would be directly correlated with the magnitude of the protractor force which is, in turn, directly correlated with the degree of specialization of the woodpecker for drilling into wood.

these points and of the stresses on the nasal-frontal hinge and on the quadrate for fixed muscle forces, MF, DF, and VF? The vectors have the following dimensions. For the upper jaw, the vector MF has a moment arm of 0.30 inches and intersects the x axis at an angle of 19°; the moment arms and angle of intersection with the x axis for the resultant forces are: for the vector RF_a, 0.3786 inches and 67°, for the vector RF_b, 0.3000 inches and 68°, for the vector RF_c, 0.2143 inches and 72°, and for the vector RF_d, 0.0714 inches and 89°. For the lower jaw, the vector DF has a moment arm of 0.3857 inches and intersects the x axis at an angle of 78°, while the comparable figures for the vector VF are 0.1785 inches and 35°. The moment arms for the resultant forces are 0.6928 inches for vector RF_a, 0.6214 inches for vector RF_b, 0.5642 inches for vector RF_c, and 0.5285 inches for vector RF_d; all vectors intersect the x axis at an angle of 45°. For both jaws, the vectors H and V represent the forces being exerted on the jaw at the center of rotation.

Given the above conditions, what are the forces acting on the upper jaw if the muscle force MF is 50 pounds and what are the forces acting on the lower jaw if each muscle force, DF and VF, is 50 pounds? The results are shown in Table 8. In both jaws the resultant force increases, as expected, from the tip of the bill to the base. In the upper jaw, the compression stress on the nasal-frontal hinge is probably below the ultimate strength of the bone at that point, but the shearing stress along the y axis becomes large very rapidly and almost certainly represents a limiting factor. The force of 50 pounds along the y axis for RF_c may be above the maximum strength of the bone at the hinge, and the force of 193 pounds for RF_d certainly must be. These observations allow two predications. The first is that the seed is held in the bill anterior to the heavy lateral bar formed by the nasal and maxillary bones, that is, the seed is held in the decurved part of the bill between points c and a. Observations of Cardinals and Rose-breasted Grosbeaks (*Pheucticus ludovicianus*) cracking sunflower seeds confirm this predication. The seeds were held in the bill below the anterior end of the external naris. The second predication is that the decurved bill in finches is an adaptation to allow the bird to exert large biting forces without excessive shearing forces acting on the nasal-frontal hinge. More highly adapted finches would have a more strongly decurved bill. Some calculations pertaining to this predication will be presented below. The last point that should be noted is the depth of the bill at its base. No matter what direction the vector MF has, the deeper the bill at its base the greater will be the moment arm of the vector and hence its torque. In finches, which require large biting forces, the increase in the torque of the vector MF is advantageous. Hence, the relatively great depth of finch bills would be an adaptation

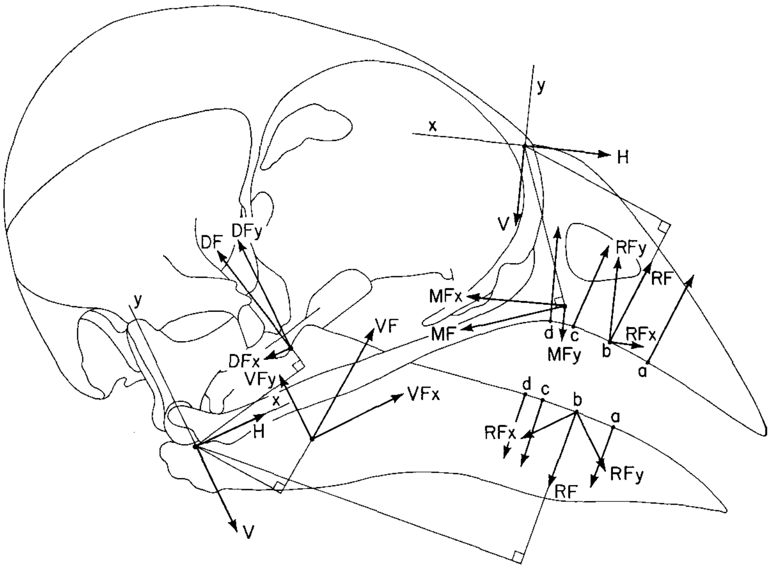


Figure 4. The skull of a Cardinal, presented to show all external forces acting on the bill when the bird is crushing a seed. The force vectors and moment arms are shown for a seed held at point b. The force vectors are also shown for the points a, c, and d. The forces along the x and y axes at the nasal-frontal hinge and at the quadrate are shown as the forces equal and opposite in reaction to the stresses on these bones.

to increase the torque of the muscle force. The orientation of the vector MF should also be such that its moment arm is maximum; this will be analyzed below.

The general conclusions that may be drawn from the lower jaw are simpler than those for the upper jaw. The relatively greater length of the moment arm of vector RF to the moment arms of the vectors DF and VF, compared with the lengths of the moment arms in the upper jaw, means that the resultant forces are less than in the upper jaw in spite of the combined muscle forces being two times greater. Thus the adductors of the mandible must be more powerful than the retractors of the upper jaw. The increased depth of the mandible and the shift in the direction of the vector VF has resulted in a far greater contribution to the total counterclockwise torque by this force. The increased depth of the mandible also provides sites of attachment for larger muscles. A most important aspect of the finch mandible, which is not shown in the figure, is that the strong adductors of the lower jaw insert far forward on the bill. This anterior insertion would reduce the ratio of the lengths of the moment arms. The stresses on the quadrate are small compared with the stresses on the nasal-frontal hinge. This is accounted for partly by the

TABLE 8

FORCES (POUNDS) ACTING ON BOTH JAWS OF A CARDINAL

Upper Jaw

RF Vector[1]	*Torque*[2]	*Force*[3]	*H*[4]	*V*[4]
RF_a	15.00	39.62	31.80	–20.19
RF_b	15.00	50.00	28.55	–30.08
RF_c	15.00	69.99	25.65	–50.30
RF_d	15.00	210.03	43.60	–193.70

Lower Jaw

RF Vector[5]	*Torque*[6]	*Force*[7]	*H*[8]	*V*[8]
RF_a	28.210	40.72	10.51	–61.07
RF_b	28.210	45.40	13.82	–57.76
RF_c	28.210	50.00	17.07	–54.51
RF_d	28.210	53.38	19.46	–52.12

[1] The force MF is set at 50 pounds for all RF vectors.
[2] The torque is the same for the MF and RF forces, only opposite in sign.
[3] The force of the RF vector.
[4] The H (compression) and V (shear) forces act along the x–y axes at the nasal-frontal hinge.
[5] The forces DF and VF are both set at 50 pounds for all RF vectors.
[6] The total torque produced by both muscle forces; it is equal to, but opposite in sign to, the torque of each RF vector.
[7] The force of the RF vector.
[8] The H (shear) and V (compression) forces act along the x–y axes at the quadrate articulation.

smaller resultant forces and partly by the arrangement of the forces so that the horizontal and vertical components tend to cancel each other.

The following comparisons were made to test the hypothesis that the decurved bill is an adaptation to allow large biting forces without an excessive shearing stress on the nasal-frontal hinge. Using the dimensions of the Cardinal bill (Figure 4) and holding the vector MF constant, the tomium of the upper jaw was decurved to position 2, position 3, and position 4 (Figure 5). A vector perpendicular to the curvature of the tomium was drawn at point c. The moment arm and angle of intersection with the x axis for each vector are: for vector C_1, 0.2143 inches and 72°, for vector C_2, 0.3214 inches and 46°, for vector C_3, 0.3571 inches and 27°, and for vector C_4, 0.3714 inches and 17°. What are the resultant forces and the stresses on the nasal-frontal hinge for each vector if the force MF is 50 pounds? The results are given in Table 9. The size of the resultant force decreases, which results from the increased length of the moment arm. The size of the forces on the nasal-frontal hinge, however, drops markedly. This drop is partly due to the decrease in the resultant force but is mainly due to the fact that the MF and RF forces are arranged so that their horizontal and vertical components tend more and more to cancel each other. Note the small size of the H and V forces when the bill is the most decurved, but the resultant force is just one-half of

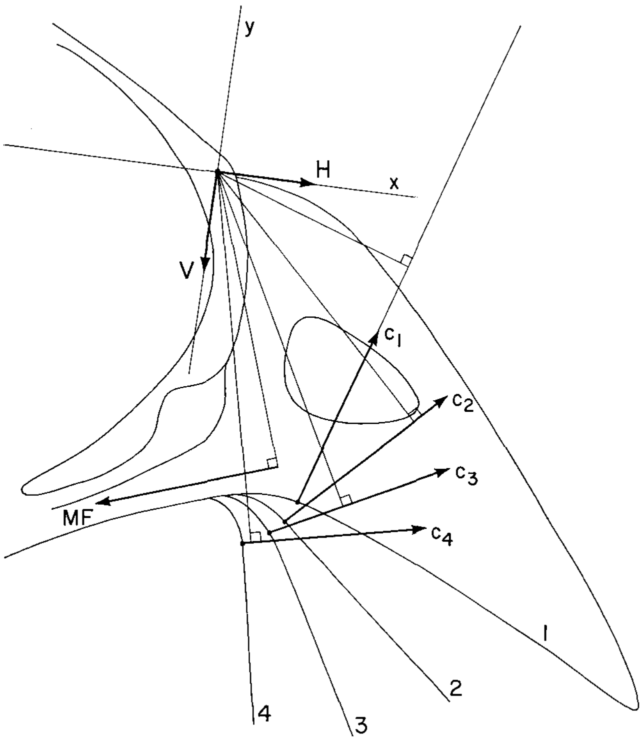


Figure 5. The upper jaw of a Cardinal, presented to show the influence of the decurved tomium on the forces acting on the jaw. Tomium 1 and vector C_1 are taken from Figure 4. Tomia 2, 3, and 4 with their corresponding vectors represent an increasingly decurved bill. The vector force MF is taken from Figure 4 and is held constant.

the resultant force in the least decurved bill. If MF is increased to 100 pounds, then the resultant force at C_4 is 80 pounds with the shearing stress at the nasal-frontal hinge still only 9 pounds.

The importance of the direction of the vector MF can be shown by rotating this vector to a more vertical direction about a pivot at the base of the bill (Figure 6). These shifts will have two important effects. The first is a change in the moment arm and the second is a change in the angle of intersection with the y axis and hence in the x and y components of its force. The moment arms and angle of intersection with the x axis of the several MF forces are: for vector MF_1, 0.3000 inches and 19°, for vector MF_2, 0.2714 inches and 39°, for vector MF_3, 0.2286 inches and 50°, and for vector MF_4, 0.2000 inches and 58°. If a force of 50 pounds is assigned to each vector, what are the resultant forces at point c and the stresses on the nasal-frontal hinge for each of the several curvatures of the upper jaw shown in Figure 5? The dimensions for the sev-

TABLE 9
FORCES (POUNDS) ACTING ON THE UPPER JAW OF A CARDINAL

C Vector[1]	*Torque*[2]	*Force*[3]	*H*[4]	*V*[4]
C_1	15.00	70.00	25.65	–50.29
C_2	15.00	46.67	14.85	–17.29
C_3	15.00	42.01	9.85	–2.79
C_4	15.00	40.39	8.65	+4.47
C_4	30.00	80.68	17.10	+9.17

[1] The C vectors are for increasingly decurved tomia as shown in Figure 5; the muscle force MF is set at 50 pounds for each C vector, and also for 100 pounds for vector C_4.
[2] The torque is the same for the MF and C vectors, only opposite in sign.
[3] Force at the C vector.
[4] The H (compression) and V (shear) forces act along the x–y axes at the nasal-frontal hinge.

eral C vectors are given above. This comparison tests each of the directions of the MF vector against each of the curvatures of the upper jaw and hence directions of the C vector. The results are given in Table 10. The angle between the vectors MF and RF is included.

For any fixed curvature of the bill, say the curvature giving vector C_1, the resultant force decreases as the MF vector has a more vertical direction; this results simply from the decrease in the moment arm of the MF vector and hence its torque. The combination of increasingly vertical MF vector and increasing curvature of the bill results in ever-decreasing resultant forces as well as changes in the stresses on the nasal-frontal hinge. The compression force decreases to a very small force as the x components of the MF and RF vectors cancel each other more and more, and in the final combination of vectors MF_4 and C_4, the force is reversed and a tensile stress acts on the nasal-frontal hinge. The pattern of shearing stresses is more obscure; no simple correlation with the stress along the horizontal axis or with the angle between the MF and RF vectors appears to exist. It is only possible to examine the table for combinations of the MF and C vectors in which the RF force is large with small compression and shearing stresses. The four most favorable combinations are MF_1 and C_4, MF_2 and C_2, MF_3 and C_1, and MF_4 and C_1. This table does demonstrate that, given a certain MF force, the size of the RF force depends only on the relative lengths of the moment arms while the sizes of the stresses at the pivot depends upon both the relative lengths of the moment arms (this could also be expressed in terms of the vector forces) and the directions of the vectors (which can be expressed in terms of the angle of intersect with the x axis). Neither the RF force nor the stresses on the nasal-frontal hinge depends upon the angle between the MF and the RF vectors.

The forces acting on the upper jaw of an Evening Grosbeak (*Hesperiphona vespertina*) were analyzed. This bird is certainly one of the most

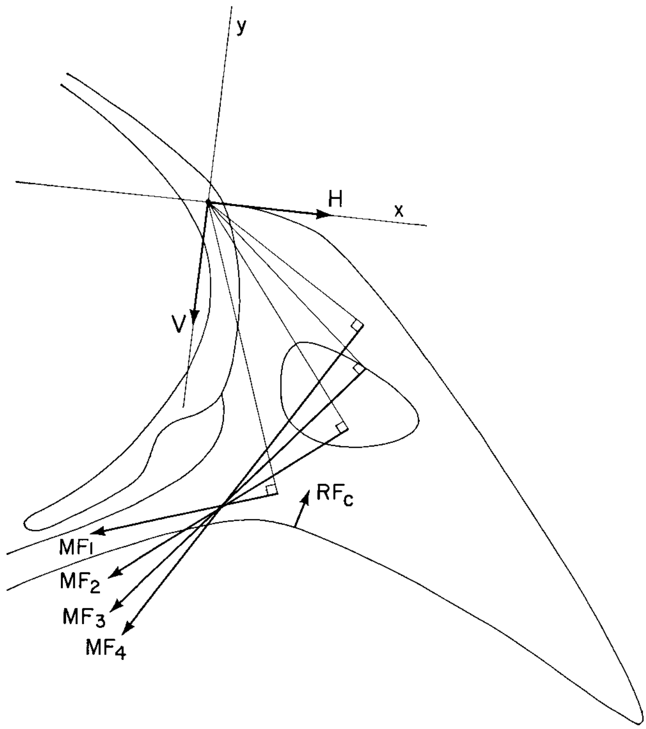


Figure 6. The upper jaw of the Cardinal, presented to show the influence of the direction of the MF vector. Vector MF_1 is taken from Figure 4; vectors MF_2, MF_3, and MF_4 represent an increasingly angled bony palate. The several MF vectors were tested against the RF_c vector (from Figure 4) shown in the figure and against the several C vectors shown in Figure 5.

highly specialized finches and is capable of exerting large biting forces. Its close relative, the Hawfinch (*Coccothraustes coccothraustes*) is able to crack open cherry stones and olive stones which requires forces of 60 to 125 pounds in testing devices (Sims, 1955: 391–392). The dimensions of the vectors are, for the MF vector, a relative moment arm of 1.65 and an intersect with the x axis of 40°; and, for the RF vector, a relative moment arm of 2.45 and an intersect with the x axis of 67°. The RF vector was placed at the anterior edge of the thick rhamphothecal pad on the upper jaw, this being where the finches observed held sunflower seeds to be cracked. Assuming an RF force of 50 pounds, what are the MF force and the stresses at the nasal-frontal hinge? The MF force is 74.25 pounds, which reflects the large difference in the moment arms. The forces on the nasal-frontal hinge are a compression of 39.34 pounds and a shear of 0.65 pounds, with the upper jaw tending to move downward relative to the brain case. Hence in the Evening Grosbeak, a rea-

TABLE 10
FORCES (POUNDS) ON THE UPPER JAW OF A CARDINAL

Vector[3]	*Force*[4]	*H*[4]	*V*[4]	*Angle*[5]
$MF_1 = 50$[1]	Torque = 15.00[2]			
C_1	69.99	25.65	–50.29	53°
C_2	63.32	19.29	–28.76	27°
C_3	53.36	15.65	–12.45	8°
C_4	46.66	12.08	–1.98	2°
$MF_2 = 50$[1]	Torque = 13.57[2]			
C_1	46.67	14.85	–17.29	33°
C_2	42.22	9.52	+1.09	7°
C_3	35.56	7.43	+12.72	12°
C_4	31.11	4.88	+20.02	22°
$MF_3 = 50$[1]	Torque = 11.43[2]			
C_1	42.01	9.85	–2.79	22°
C_2	38.00	4.99	+14.21	2°
C_3	32.01	3.62	+23.77	23°
C_4	28.00	1.54	+29.69	33°
$MF_4 = 50$[1]	Torque = 10.00[2]			
C_1	40.39	8.65	+4.47	14°
C_2	36.54	3.92	+20.78	12°
C_3	30.78	2.71	+29.30	31°
C_4	26.93	–1.25	+34.52	41°

[1] The MF vector shifts to an increasingly vertical direction as shown in Figure 6; each MF force is set at 50 pounds.
[2] The torque is the same for the MF and each C vector, only opposite in sign.
[3] The C vectors are from Table 9 and Figure 5.
[4] These forces are the same as in Table 9.
[5] The angle between the MF and C vectors.

sonably large compression exists at the nasal-frontal hinge, but almost no shear.

The ideal conditions for a decurved finch bill are not as simple to deduce as the ideal conditions for a straight woodpecker bill. The best conditions for the upper jaw appear to be having the length of the moment arms as equal as possible; the angles of intersect with the x axis close, but with the RF vector having the larger intersect; and the angle of intersect of the MF vector with the x axis being close to 45°. These conditions will result in almost equal y components (shearing stress) although the MF force is greater than the RF force.

Summary.—A few summarizing statements on torque analysis and the external forces on the bill may be offered. The directions of the MF and RF vectors depend upon the configuration of the bill. The MF vectors depend upon the angle at which the bony palate attaches to the upper jaw; the DF and VF vectors depend upon the angle of insertion of the adductors of the mandible. The direction of the RF vectors depends upon the curvature of the tomium, if we assume that the force acts normally to the curvature of the bone. The relative sizes of these forces depend only upon the relative lengths of their moment arms and upon their direction of rotation when more than two opposing forces are present. The stresses at the pivots depend upon the sizes of the vector forces and their angles to the x–y axes. Whether these stresses are or are not excessive depends upon the strength of the bone and other structures at the pivots. A large compression, for example, may be perfectly harmless if the bone is thick enough. These forces do not, however, depend upon the entire shape of the jaws. The curvature of the culmen and of the gonys has not been mentioned once in the above analysis; these curvatures have no influence on the sizes of the forces acting on the jaws. If the position, direction, and force of the MF and RF vectors are held constant, then the resulting stresses on the nasal-frontal hinge would remain the same, no matter what the shape of the upper jaw. All of these properties are dependent upon the upper jaw being kinetic even though no movement of the jaws takes place, this being a primary basis for the analysis. An akinetic skull could not be analyzed with these methods.

ANALYSIS OF THE INTERNAL FORCES

Although the general conclusion reached in the torque analysis is that over-all bill shape does not influence the sizes of the forces acting on the bill, it would be foolish to claim that bill shape is of no importance. It is essential to realize that torque analysis provides a clue as to how the factors of force and, to some extent, of size influence the shape of the bill. Torque analysis provides no clue to the distribution of forces within the bill itself and how this distribution of forces affects the weight of the bill. It is reasonable to suggest that the weight is closely associated with the over-all shape of the bill and that an analysis of the internal forces must be coupled with the analysis of the external forces. If the jaws were constructed of solid bone, they could easily withstand the forces placed upon them, but the weight would be excessive. Birds, being flying creatures, must be as light as possible and hence must be built according to the maximum-minimum principle, that is, maximum strength for minimum material. The problem is how much bone can be removed, and how the remaining bone should be arranged to insure maximum strength of the jaws. This problem may be attacked with the help of trajectorial analysis. General background information of the trajectorial theory may be found in Koch (1917), Murray (1936), and in the recent papers of Kummer (1959a, b, 1961), who gives an extensive bibliography including the papers of Pauwels.

If a solid, rigid object is subjected to an external force, the distribution of forces within the object will be along lines of trajectories. Basically the trajectories correspond to the two principle stresses on the object and thus the trajectories representing one principle stress cross the trajectories representing the other principle stress at right angles. The closer the trajectories lie to one another, the greater is the stress in that region. If no trajectories are present in a part of the structure, then the stress on that region is small or even absent. The material comprising the structure, in our case bone, along these lines of force serves to resist the stress and prevents the structure from being excessively deformed. Material may be removed from the areas between the trajectories without reducing the strength of the structure because the material in these areas is not contributing to the resistance against the deforming forces. Hence the weight of the entire structure may be reduced without weakening the structure.

If a certain structure, a bridge, a crane, a femur, or an avian bill, must have certain dimensions and resist certain forces without being deformed, the minimum weight may be obtained by arranging the material so it corresponds to the trajectories in the most optimal fashion. Material is arranged where it resists the internal forces to its maximum extent. If the material is not or cannot be arranged in the most optimal positions, then more material is required and the weight of the structure will increase. As applied to bones, the trajectorial theory has it that the trabeculae of spongy bone lie along the lines of trajectories. The trabeculae would be stressed and would resist the stress the same as would homogeneous bone. Where the trajectories crowd close together, as along the outer walls of long bones, compact bone will be found. In these regions, the stress would be so great that solid bone is required to resist it. Conversely, where the trajectories are far apart or absent, cavities develop in the bone, as for example the hollow centers of long bones. It must be emphasized that the bony trabeculae do not lie exactly along the calculated lines of trajectories, partly because other structures may interfere, partly because biological systems are rarely perfect, and partly because most bones are subject to a number of different deforming forces and the pattern of trabeculae within a bone would be a compromise between several systems of trajectories acting within the bone at the same or different times.

That the trabeculae seen in spongy bone and the placement of compact bone correspond to the lines of trajectories in a bone is supported by a considerable mass of evidence. The reader is referred to the above-cited papers for discussion; I shall accept the trajectory theory of bone structure as sufficiently well demonstrated for the purposes of this study, and I

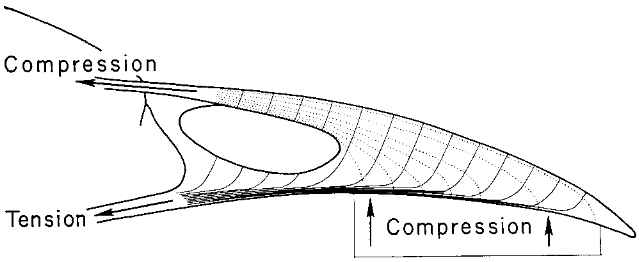


Figure 7. The upper jaw of a crow, presented to show the arrangement of trajectories within the jaw when the bird closes its bill against an object. The solid lines represent the trajectories of tension and the dotted lines represent the trajectories of compression. The illustrated pattern of trajectories is schematic and serves only to give an impression of the arrangement of the trajectories within the upper jaw.

shall consequently accept the observed pattern of bony trabeculae and compact bone in the avian bill as the pattern of trajectories within these structures. I shall concentrate discussion on the upper jaw and on the forces encountered when the bird exerts a large biting force on an object.

When an object is crushed between the jaws of a bird, a retracting force is transmitted through the bony palate to rotate the upper jaw downward. This force places a tensile stress on the upper jaw; this stress is distributed in the jaw as shown in Figure 7. The object held in the bill is subjected to a crushing force. An equal and opposite force (to the crushing force on the object) is exerted by the object on the jaw, which places a compression stress on the jaw. This compression is distributed through the jaw as shown in Figure 7; it becomes concentrated along the

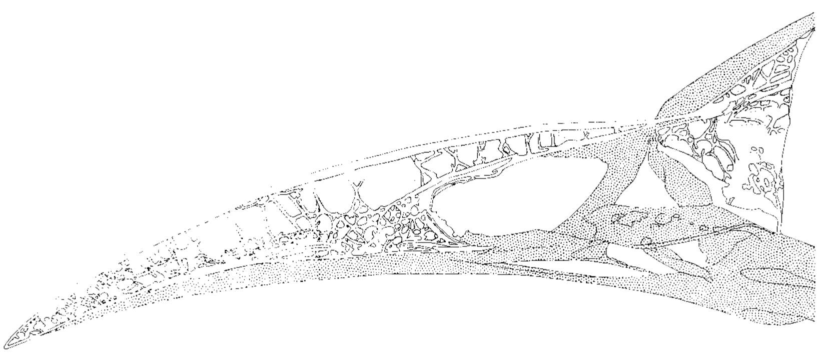


Figure 8. A mid-sagittal section of a crow skull, presented to show the arrangement of the trabeculae within the upper jaw. The deeper, nontrabecular areas of the jaw are shown in fine stippling while the other bone is shown in larger stippling. Note how the bone of the dorsal surface narrows to a thin sheet of compact bone at the nasal-frontal hinge. Compare the arrangement of the trabeculae with the pattern of trajectories shown in Figure 7.

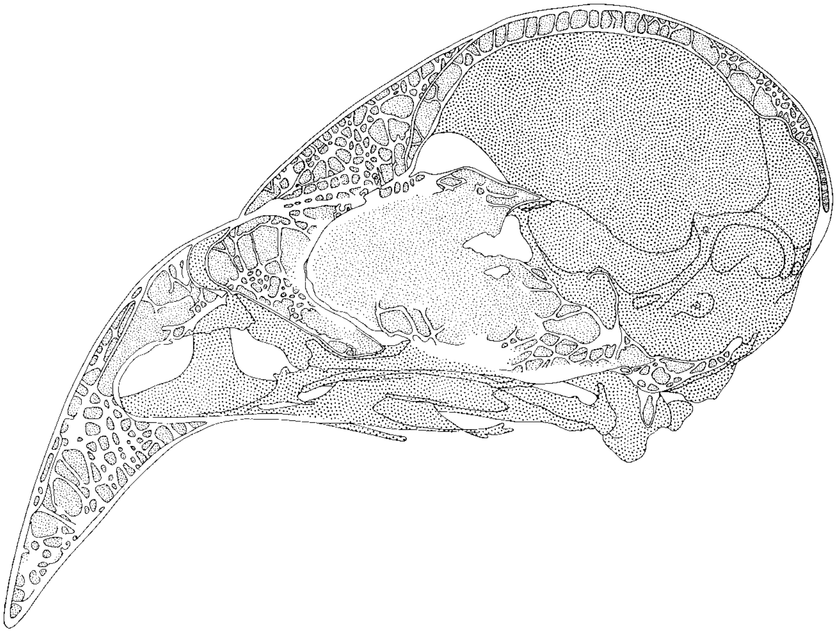


Figure 9. A mid-sagittal section of a Cardinal skull, presented to show the arrangement of the trabeculae within the upper jaw. The deeper, nontrabecular areas of the jaw are shown in fine stippling while the other bone is shown in larger stippling. Note the arrangement of the bone of the brain case at the nasal-frontal hinge. The bone of the upper jaw appears to be continuous with the trabeculae within the region of the forehead; this may help to distribute the compression stress acting on the nasal-frontal hinge.

upper edge of the jaw close to the nasal-frontal hinge. The area at the base of the bill, between the dorsal edge with its concentration of compression trajectories and the ventral edge with its concentration of tensile trajectories, is subjected to lower stress; this would be more apparent in a three-dimensional picture of the trajectories.

The longitudinal sections of the crow skull (Figure 8) and of the Cardinal skull (Figure 9) show the arrangement of the bony trabeculae and compact bone in the upper jaw. If attention is concentrated on the region just anterior to the nasal cavity, a pattern of downward-curving trabeculae may be discerned; these trabeculae run perpendicularly into the bone of the ventral edge of the jaw. Near the upper corner of the anterior edge of the nasal cavity, these trabeculae concentrate rapidly into the compact bone of the dorsal edge of the nasal cavity and of the dorsal surface of the jaw. Close to the base of the upper jaw, the bone becomes the thin flexible sheet of compact bone that forms the nasal-frontal hinge. Another set of trabeculae that curves upward to run perpendicularly into the bone of the upper surface of the jaw may be seen along the entire length of the upper jaw. In the area anterior to the nasal cavity this set of trabeculae crosses the first set at roughly right angles. In the anterior half of the jaw these trabeculae appear to lie normal to both upper and lower surfaces of the jaw, but close inspection reveals that they curve backward just before reaching the ventral surface. The first set of trabeculae would correspond to the compression trajectories while the second set would correspond to the tensile trajectories. In the anterior part of the bill, especially in the Cardinal bill, the trabeculae may correspond to both compression and tensile trajectories, which curve so sharply from the edges of the jaw that they share a common path in the central region.

No attempt will be made to show the three-dimensional arrangement of the trabeculae. Some hint of this may be obtained from the transverse sections (Figures 10 and 11). These sections do show that the trabeculae concentrate along the lateral parts of the jaw; the central core of the jaw is relatively free of trabeculae. This is especially true in the base of the skull, where much of the stress is concentrated ventrally and dorsally, allowing for the presence of the large nasal cavity. The stresses at the lateral sides of the base of the upper jaw are concentrated in the heavy lateral bar that forms the posterior wall of the external naris (Figure 12).

The curvature of the entire dorsal surface of the upper jaw is most probably correlated with the requirements imposed by the maximum-minimum principle (weight reduction) that act through the trajectory system of bone construction. The compact bone of the outer wall of the jaw carries most of the stress to the base of the jaw; the trabeculae within the jaw transmit forces from the points where they act on the bill to the major load-bearing bone of the outer wall. The compression force that acts on the ventral surface of the upper jaw of the Cardinal is transmitted to the dorsal surface by the set of trabeculae lying anterior to the nasal cavity. Therefore, the shape of the outer surface of the upper jaw, and especially of the dorsal surface, must correspond to those outer trajectories of the greatest stress. These would be the compression trajectories for the dorsal surface. Thus the upper jaw will curve from its tip and lateral edges toward the nasal-frontal hinge, the exact curvature depending upon the necessary size of the bill and the pattern and size of the forces acting upon it. In general the shape of the upper jaw would correspond to the trajectories of compression in a cantilever beam shown in Figure 13. Any material outside the last trajectory (in shaded area) is not needed as it does not contribute to the strength of the jaw. This

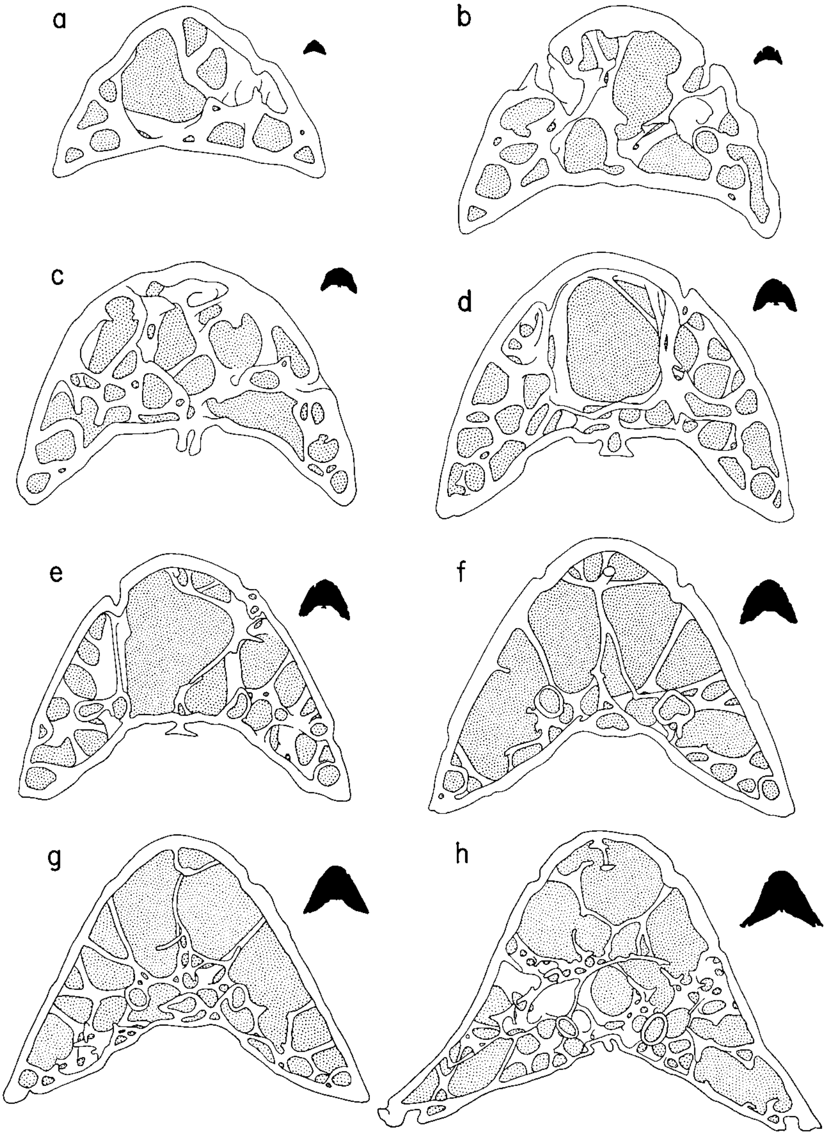


Figure 10, part. Transverse sections of a crow skull, showing the trabeculae of the upper jaw. Each view is of the posterior face of the jaw at each cut shown in Figure 11, except view j(a), opposite, which shows the anterior face of the bone at this cut. The jaw was cut as close as possible to the true transverse plane; the angle of cut j makes little difference because only the dorsal part of the section is pertinent. The small silhouettes give the absolute size of each section. Note that the trabeculae tend to be less concentrated in the center of the section. The thinness of the bone at the nasal-frontal hinge is shown clearly in sections j and j(a).

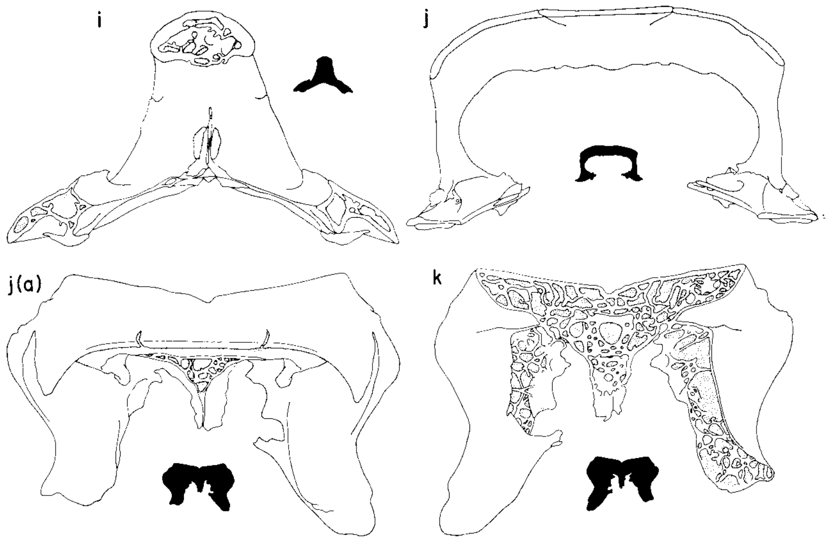


Figure 10, continued.

material represents only excess weight and would be eliminated. Hence, birds do not have squared upper jaws.

In summary, it can be shown by an analysis of trajectories that the weight of a bird's bill is reduced by eliminating unneeded bone within the bill and that the outer shape of the jaw (discussed only for the upper jaw) corresponds to the curvature of the outermost set of trajectories carrying large stresses to the base of the bill. It is still necessary to determine by experimental means the precise pattern of trajectories for bills of particular sizes and loading and to ascertain whether the distribution of the trabeculae and compact bone corresponds to this pattern.

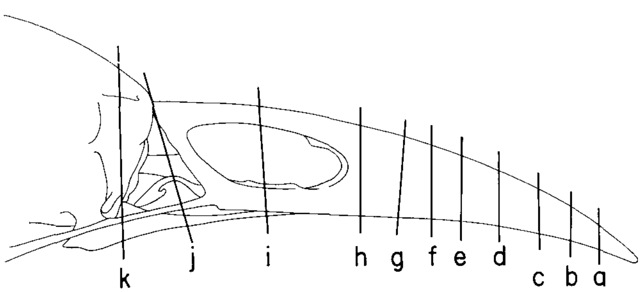


Figure 11. The bill of a crow, presented to show the position of the transverse cuts illustrated in Figure 10.

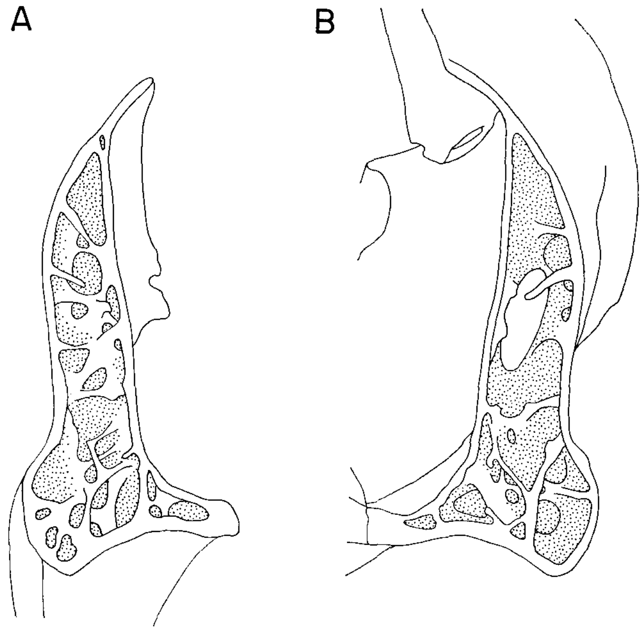


Figure 12. The trabeculae seen within the lateral bar of a Cardinal skull; the bone was cut transversely. Note that the trabeculae run mainly across the cut, and that most of the bone is concentrated in the walls. A shows the anterior face of the cut; B shows the posterior face of the cut.

The Hofer-Bowman Analysis

The present study was initiated because of the necessity to understand the functional significance of bill curvature in conjunction with my review (Bock, 1963) of Bowman's (1961) monograph on the Galápagos finches. In the latter (pp. 141–155) Bowman presented a method by which the functional significance of bill curvature could be ascertained and by which the curvature of the bill in the different species of geospizines could be compared; this method was based upon one suggested by Hofer (1945: 74–85) to analyze the stresses on the tip of the bill. In both earlier studies, bill curvature was construed as the silhouette, as in the present study. Bowman (1961: 136–139, 155–156) used the results of the comparisons of bill curvature as the primary basis on which he established generic limits in the Geospizinae. In my review (p. 204) I deferred detailed discussion of Bowman's analysis of bill curvature to the present study. The methods of torque analysis and trajectory analysis described above, even if they may prove to be completely sufficient to explain the functional significance of bill curvature, provide no basis on which to judge the Hofer-Bowman method. These methods certainly do

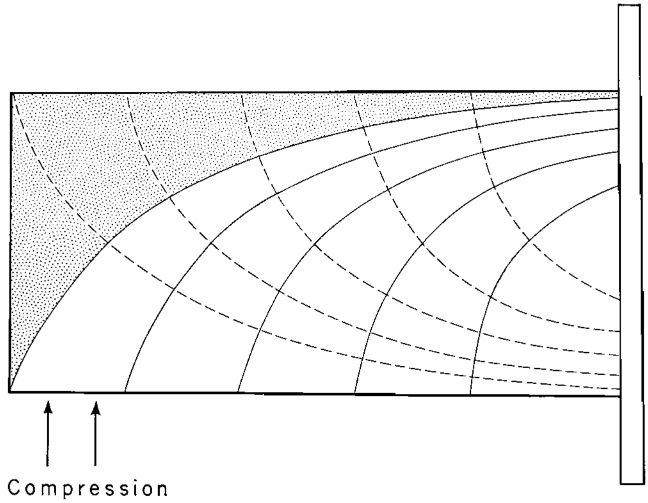


Figure 13. The trajectorial diagram of a beam attached at one end and loaded, but drawn upside down. The area outside the outer trajectory is shaded. The remaining area of the beam is similar to the general shape of the upper jaw. (Redrawn after Koch, 1917: figure 12a.)

not invalidate the Hofer-Bowman method; the latter method may also be correct, being a different approach to the same problem. I shall present the details of the Hofer-Bowman method briefly and then discuss the essential points.

Hofer (1945: 74–79) outlined a method to illustrate how the forces acting upon the tip of the bill can be subdivided into various components, basing his analysis on earlier work by von Kripp (1935). The basic assumption used by Hofer is that the main forces acting on a bill result either from pecking or from biting, and that these forces act on the tip of the bill (Figure 14). Thus, a force P acts on the tip of the upper jaw as a result of pecking (Figure 14, B) in a direction approximately parallel to the longitudinal axis of the bill. This force is resolved into *two* sets of vectors, one based upon the curvature of the culmen and the other based upon the curvature of the maxillary tomium. Considering the culmen, the component m lies tangential to the curve of the culmen at the tip of the bill. This component of force P proceeds along the culmen and is the compression stress on the culmen. The component n, which acts at a right angle to component m, pulls the tip of the bill downward and backward, and is the force tending to fracture or disrupt the culmen. It represents the fracture-risk component (the shearing stress) on the culmen. A second and similar parallelogram of forces is constructed for the tomium, with component m′ lying tangentially to the curve of the maxillary

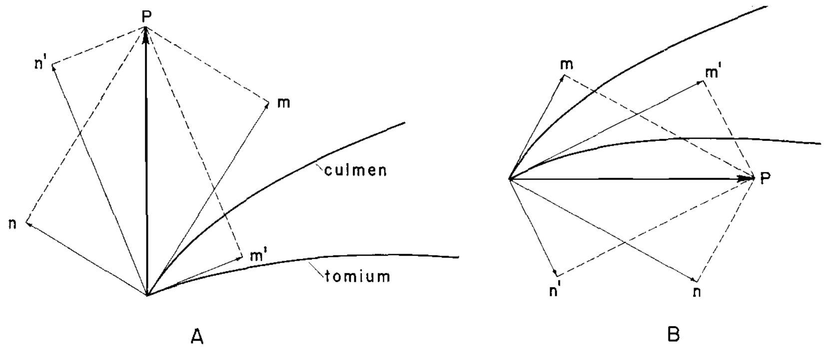


Figure 14. Analysis of the forces acting on the tip of the upper jaw. A represents the force resulting from biting and B represents the force resulting from pecking. In each, the force P is resolved into two sets of vectors. Component m is tangential to the culmen, and component n at right angles to it. Components m′ and n′ are drawn relative to the tomium. The components m and m′ represent compression forces, and components n and n′ represent "fracture-risk" forces. The figures are modified from Hofer (1945: figures 19 and 20) and from Bowman (1961: figure 35).

tomium at the tip and representing the compression stress on the tomium. Component n′ represents the fracture-risk force on the maxillary tomium. When the bird is biting, a force P acts on the tip of the upper jaw in a direction roughly normal to the longitudinal axis of the bill (Figure 14, A); this force may be resolved into two sets of vectors according to the method just described for the pecking force. Hofer claims, on the basis of von Kripp's work, that the forces acting on the culmen and tomium produce strains within the bone and rhamphotheca of the bill, and that the evolved shape of the bill is such that these strains are reduced to a minimum or eliminated completely. The compression components, m and m′, are not thought to be dangerous and can be increased without danger to the bill. The components n and n′ represent the fracture-risk force which is the dangerous component; they must be reduced as much as possible. On the basis of his analysis, Hofer claims that a straight bill is more suitable for those birds experiencing large forces resulting from pecking or probing since the components n and n′ will be reduced to a minimum and the m and m′ increased. A strongly decurved bill is most suitable for those birds experiencing large biting forces as the components n and n′ will again be minimal.

Hofer further (1945: 79–85) considered the consequences of a series of forces, neither purely biting nor purely probing forces, acting on the tip of the upper jaw (Figure 15). These forces, P_1, P_2, P_3 . . . P_n, act on the tip of the upper jaw in slightly different directions; all forces are equal in size and are separated by equal distances along the arc. These forces are assumed to travel through the upper jaw without being altered,

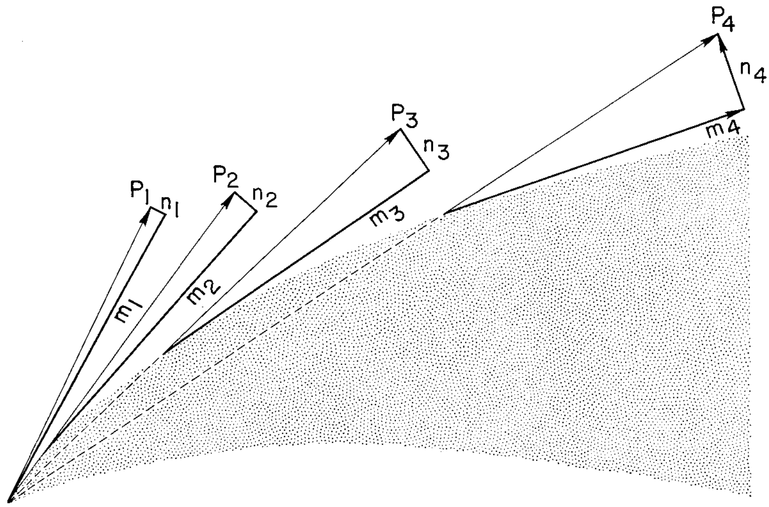


Figure 15. Analysis of a series of forces, which result from a combination of pecking and biting, acting on the tip of the upper jaw. The forces are equal in size and are separated by equal angles. The forces are resolved into compression and "fracture-risk" forces where they emerge from the culmen; the compression forces are tangential to the curvature of the culmen. Modified from Hofer (1945: figure 21).

either in size or direction, and emerge at various points along the culmen. At the point where the forces leave the upper jaw, they are resolved into sets of components. For each force vector, component m lies tangentially to the curve of the culmen while the component n lies normal to component m. The series of m components (m_1, m_2, m_3 . . . m_n) passes along the culmen as compression stresses, while the series of n components (n_1, n_2, n_3 . . . n_n) acts to pull the bill upward and poses the dangerous fracture-risk stresses. Hofer argues from this analysis that the curvature of the culmen should be one that would reduce the angle between the force line P and the vector m to a minimum; hence the stress represented by the component n would be minimal. Consequently, those bills in which the curve of the culmen parallels the direction of the vector P at the point where P emerges from the bill would be most efficiently constructed to resist these forces.

Hofer's analysis was designed to handle forces acting on the tip of the bill. Bowman (1961: 141–149) accepted Hofer's method in his analysis of the tip curvature of the bill in the geospizines. However, Bowman, being also interested in the analysis of the force acting along the length of the tomium when the bird is crushing seeds, modified Hofer's basic method in the following way. A series of forces, P_1, P_2, P_3 . . . P_n, of equal magnitude and separated by equal distances, acts on the tomium at

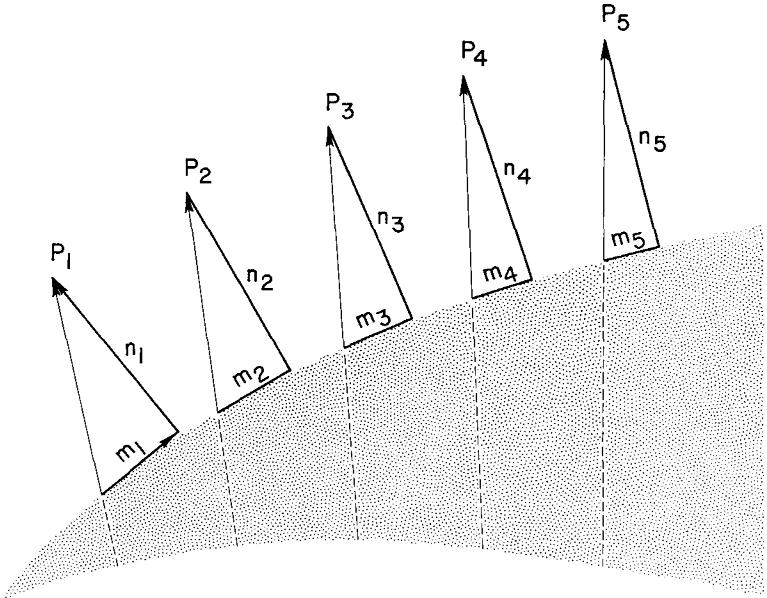


Figure 16. Analysis of a series of forces which result from biting. The forces are equal in size and are separated by equal distances along the tomium. The forces are resolved into compression and "fracture-risk" forces where they emerge from the culmen; the compression forces are tangential to the curvature of the culmen. Modified from Bowman (1961: figure 39).

right angles to its curve as a result of the bird biting on some object (Figure 16). These forces pass unmodified through the upper jaw and emerge from the culmen. At the point where each force intersects the culmen, it can be resolved into a parallelogram of forces, component m running tangentially to the curve of the culmen at the point of intersection and component n being at right angles to vector m. The series of m components is transmitted along the culmen as compression stress, while the series of n components tends to pull the jaw upwards. The n components are the fracture-risk forces on the bill and must be resisted by the strength of the bony matrix and horny rhamphotheca. From this analysis, it can be seen that when the curvature of the culmen is large at the point of intersection with vector P (the angle between the vector and the tangent to the curvature approaching 0°), the compression component m is large and the fracture-risk component n is small. As the curvature of the culmen decreases, the fracture-risk component increases, and where the culmen lies at right angles to force P, all of this force is fracture-risk. Thus, Bowman concludes (1961: 150): "the fracture component may be lessened either by a more convex curvature or by thickening of the bony support of the bill."

Bowman extends this analysis to the lower jaw, but since the principles involved are the same, I shall exclude the lower jaw from discussion.

The Hofer-Bowman analysis appears to be very straightforward, but it rests upon an inadequate foundation of morphology and physics. The major problems are:

(a) The assumption that the force vectors acting on the tip of the bill or along the tomium travel through the jaw without modification in direction or magnitude is not justified. This assumption would require that the bill be a solid structure of homogeneous material. And, even if the bill were of solid construction, the external forces acting on it would be dispersed into a pattern of trajectories, and would not pass through the bill along the original path of the vector.

(b) The resolution of the force P acting on the tip of the bill into two sets of vectors, one depending upon the curvature of the culmen and one depending upon the curvature of the maxillary tomium, is obscure. Neither Hofer nor Bowman state clearly whether or not the two parallelograms of force are considered together. If the two sets of vectors are considered simultaneously, one must begin with a force of 2P acting on the tip of the upper jaw, otherwise the sum of the forces in the two sets of components would be double the original force.

No explanation is given in support of the assumption that the compression component, m, lies tangentially to the curvature of the jaw at its intersection with vector P, after which this compression force runs along the curvature of the jaw. Note that the vector force P is assumed to continue along its original straight path through the jaw while component m proceeds along the curvature of the jaw. The vector P might be resolved into a different set of components, rather than those based upon the curvatures of the jaw or, most likely, the vector P divides into a series of components as shown by the lines of trajectories.

(c) No reason is given why only the n components are considered fracture-risk forces, and why only these should be reduced. All stresses on the bill, whether compression, tension, or shear, are dangerous if they become too large and exceed the strength of the bone to resist them as demonstrated in some of the above calculations.

(d) Little consideration is given to the entire morphology of the jaw and to all of the forces acting on the bill. The kinetic mechanism is never mentioned, nor are the muscular forces that act on the bill.

These objections lead me to doubt that the method suggested by Hofer and Bowman for analyzing bill curvature is valid, and to feel that the conclusions based upon it are subject to question.

Summary

Several methods are suggested by which the influence of force, size, and weight on the shape of the avian bill can be analyzed.

Torque analysis allows determination of the external forces acting on the bill, including the stresses on the nasal-frontal hinge and on the quadrate. This method allows inquiry into the factors of external force and size on the shape of the bill. Using torque analysis, the forces on a woodpecker bill and on a finch bill are described.

Trajectory analysis allows investigation of the distribution of forces within the bill and how the bone is arranged best to withstand these stresses. It is suggested that the curvature of the dorsal surface of the upper jaw corresponds to the lines of trajectory. This method allows insight into the factor of weight, assuming that bone is present where stress is greatest, and into the outer shape of the bill.

The analysis of external forces suggests that the kinetic structure of the avian skull may have some important functional properties that are not associated with movement of the upper jaw. One of these properties may be distribution of the major stresses on the upper jaw to the ventral part of the brain case rather than to the dorsal and lateral parts, as would be the case in the akinetic condition. The heavy bone of the base of the brain case can resist larger stresses than could the thin roof and sides of the brain case. This distribution of stress to the base of the brain case may also have an important part in the shock absorbing function of the kinetic mechanism.

Note added in proof.—Lowell W. Spring's excellent paper "Climbing and pecking adaptations in some North American woodpeckers" (Condor, 67: 457–488, 1965) and the proofs of this paper arrived simultaneously. I agree completely with Spring that the combination of cranial kinesis and *Mm. protractor pterygoidei* serve primarily to distribute the force on the bill resulting from pounding on a tree to the base of the skull (as discussed above), and that it does not serve to absorb this force by stretching as I proposed earlier (1964: 29–30). Spring's conclusion that stretch of *M. protractor pterygoidei* would decrease the force of impact of the bill against the tree is correct; I overlooked this important point in my earlier analysis. Only a few differences remain between Spring's and my analysis (above, not in Bock 1964) of the mechanics of the woodpecker skull. These include: whether the bill is in the resting position as implied by Spring (p. 482) or fully protracted (above, pp. 28–29, footnote) at the moment of impact; the mechanism by which *Mm. protractor pterygoidei* remains in isometric contraction (Spring, p. 486); and the importance of the reported reduction in mobility of the upper jaw. These points are quite minor compared with the area of agreement; their resolution will probably require difficult experimentation. Lastly I would like to note that Beecher's term "resilient rigidity" may be the most apt description of the mechanism of shock-absorption by the redistribution of force.

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