

A NEW SPECIES OF LARGE AUK FROM THE PLIOCENE OF BELGIUM

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Abstract : A new species of fossil auk, *Alca stewarti* from the Kattendijk Sands Formation (early Pliocene) of Belgium is described. Preserved elements of this new species include humeri and ulnae, all of which are longer than those of the largest auk currently known, the recently extinct Great Auk (*Pinguinus impennis*). The relative proportions and structure of these wing elements, together with our estimates of body mass and wing loading suggest that this new species was capable of flapping flight. We consider the biomechanical implications for a large flighted auk, and speculate on the lifestyle and appearance of this new species. We also estimate the likely flight speed and flapping frequency of *Alca stewarti*.

Keywords : Auk, Belgium, Pliocene, Flight

Une nouvelle espèce de grand pingouin du Pliocène de Belgique

Résumé : Nous décrivons une nouvelle espèce de pingouin fossile, *Alca stewarti*, provenant de la Formation des Sables de Kattendijk (Pliocène inférieur) en Belgique. Le matériel inclut des humerus et des ulnas qui tous sont plus longs que ceux du grand pingouin (*Pinguinus impennis*), un genre récemment éteint. Les proportions relatives et la structure de ces composants des ailes, comparées avec la masse estimée de l'animal et la portance des ailes, suggèrent que cette nouvelle espèce était capable d'un vol battu. Nous examinons les implications biomécaniques d'un grand pingouin volant et spéculons sur le mode de vie et l'apparence de cette nouvelle espèce. Nous estimons également la vitesse probable du vol d'*Alca stewarti* et la fréquence de ses battements d'aile.

INTRODUCTION

The auks (Alcidae) have a relatively rich fossil history; it has been suggested that the Eocene *Hydrotherikornis* Miller (1931) is the earliest representative of the family, although there is some debate concerning the exact affinities of this genus (Olson, 1985). The earliest unequivocal alcids date from the Middle Miocene and include *Miocepphus* from Maryland (Olson, 1985) and *Alcodes* from California (Howard 1968). By the Pliocene, the alcids had radiated to dominate many seabird communities throughout the Holarctic (Gaston & Jones, 1998). All alcids

are wing-propelled divers and, in some cases, further specialisation to this mode of locomotion resulted in their becoming large and secondarily flightless. In the Pliocene, flightless genera included *Mancalla* spp. (Howard, 1970), and *Pinguinus* spp. (Olson, 1977). The avifauna also included the flighted *Australca* (Brodkorb, 1955), as well as representatives of many modern genera (Olson, 1985).

The vast majority of auks presently described from the Pliocene are from the coasts of North America (e.g. Olson, 1985; Chandler, 1990; Emslie, 1995). In this paper we describe a new auk from Belgian deposits, which has larger wing elements

than any other known alcid. We also evaluate the probable locomotory strategy utilised by this new species.

All specimens examined are held in the departments of Palaeontology (BMNH A) and Zoology (BMNH S) of the Natural History Museum, London. The specimen numbers of comparative specimens are as follows; *Alca torda*; BMNH S/1975.44.4; *Pinguinus impennis*; BMNH S/1864.12.10.1; *Uria aalge*; BMNH S/1985.71.11.1. The anatomical nomenclature follows Baumel & Witmer (1993); systematic relationships follow Wetmore (1960).

SYSTEMATIC PALAEOLOGY

AVES Linnaeus, 1758

CICONIIFORMES (Garrod, 1874)

ALCIDAE Linnaeus, 1758

ALCA Linnaeus, 1758

Alca stewarti sp. nov.

Figs. 1, 2; tabs. 1, 2.

Derivation of name

Named in honour of J. R. Stewart, who first brought the specimen to the attention of CAW.

Holotype

BMNH A 7050, a complete left ulna (figs. 1, 2; tabl. 1) collected from Kallo sometime between 1970 and 1978 by J. Herman and donated to the Natural History Museum, London in 1986.

Paratypes

BMNH A 7051, distal end of left ulna and portion of shaft (fig. 2B; tabl. 1), collected from Kallo by J. Herman and donated to the Natural History Museum in 1986; BMNH A 7052, cast of complete right humerus (figs. 1, 2D; tabl. 2). The original was collected in Kallo by J-P. Luyaerts, and retained in his collection in Belgium; BMNH A 7053, proximal end of right humerus and shaft (fig. 2E; tabl. 2), collected from Kallo by J-P. Luyaerts and donated to the Natural History Museum in 1986; BMNH A 7054, distal end of left humerus and portion of shaft (fig. 2F; tabl. 2), collected from Kallo by W. In 'Tout and donated to the Natural History Museum in 1989; BMNH A 7055, distal end of left humerus and portion of shaft (fig. 2G; tabl. 2), collected from Kallo by J. Herman and donated to the Natural History Museum in 1986.

Referred specimen

BMNH A 7056, rostral portion of maxilla (figs. 1, 2A; tabl. 1), collected from Kallo by J. Herman and

donated to the Natural History Museum in 1986. This specimen is referred to *A. stewarti* through size comparisons with the holotype and paratypes, and on the basis of comparisons with *A. torda*.

Type locality, deposit and age

All material is from the Kattendijk Sands Formation, at Kallo, near Antwerp, Belgium. These sands were deposited in a cold water marine environment during the early Pliocene (De Heinzelin, 1955; Herman *et al.*, 1974). The material described here is part of a rich fossil avifauna from this locality, comprising several other auks, as well as ducks (Anatidae), and a small passerine (Dyke & Walker, in prep.).

Diagnosis : A large alcid, osteologically very similar to the extant razorbill (*Alca torda*), but at least one third larger in size. Both this new species and *Alca torda* are distinguished osteologically from the other large alcids alcid genera *Uria* and *Pinguinus* in the possession of a slender and curved ulna having a rounded and proximally elevated cotyla dorsalis. An additional autapomorphy of this new species may be a flatter and less hooked rostral margin of the maxilla (although this is broken on the referred specimen).

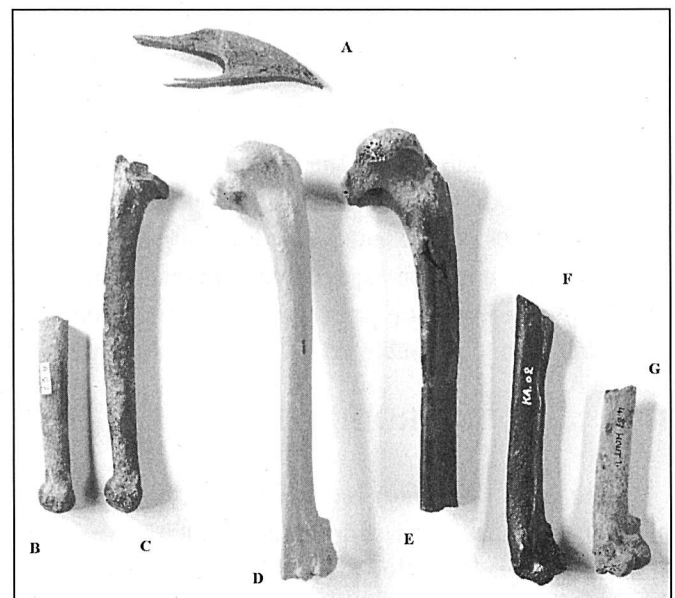


Figure 2: The holotype, paratypes and material referred to *Alca stewarti*. From the Kattendijk Sands Formation, near Kallo, Antwerp, Belgium. A. Referred maxilla, BMNH A 7056. B. Paratype distal end of right ulna, BMNH A 7051. C. Holotype complete right ulna, BMNH A 7050. D. Paratype cast of complete right humerus, BMNH A 7052. E. Paratype proximal end and shaft of right humerus, BMNH A 7053. F. Paratype distal end of right humerus, BMNH A 7054. G. Paratype distal end of right humerus, BMNH A 7055. Magnification x 0.52.

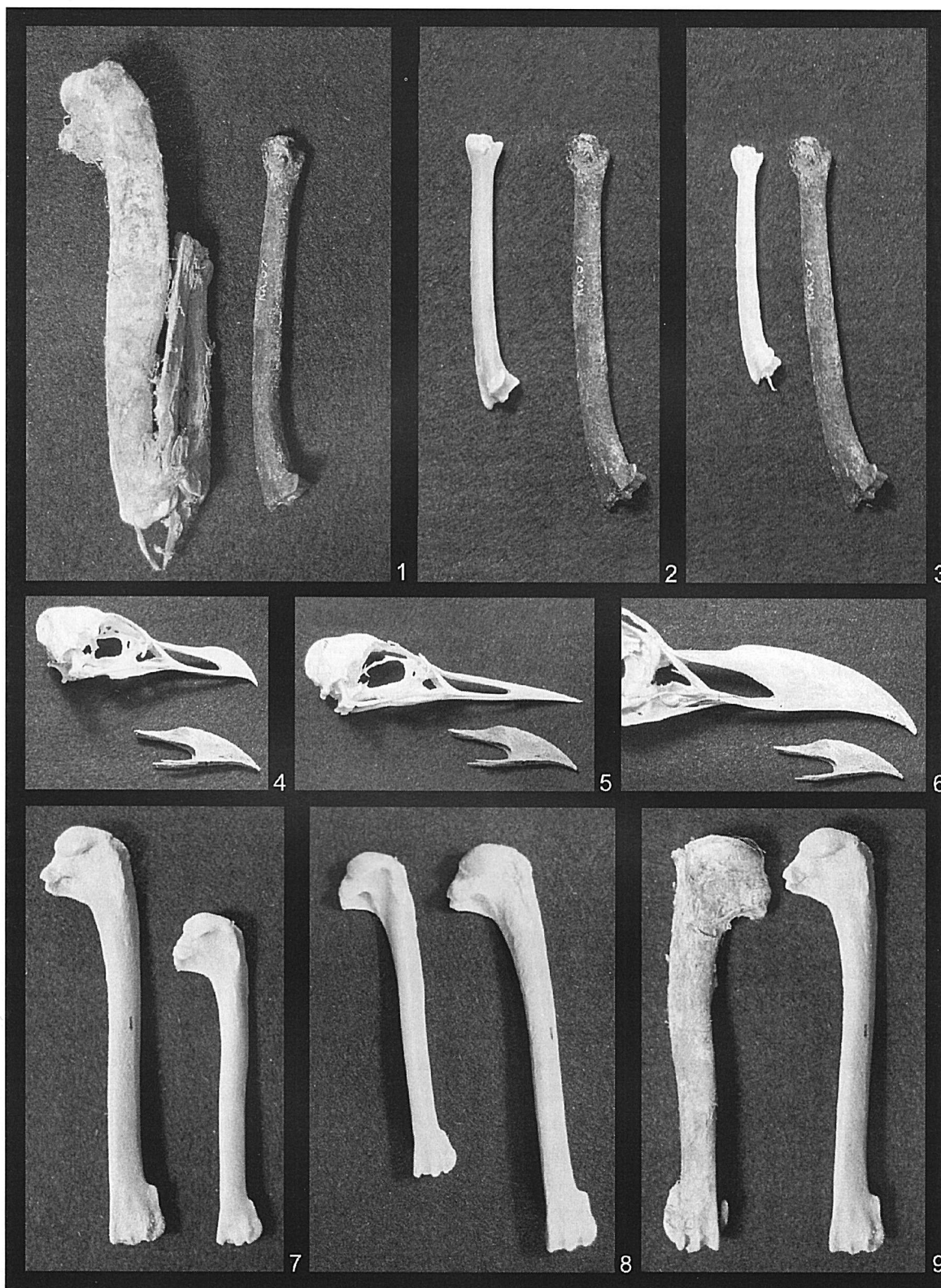


Figure 1: 1-3. *Alca stewarti*, BMNH A 7050. Kattendijk Sands Formation, near Kallo, Antwerp, Belgium. Holotype; right ulna (BMNH A 7050) with; 1, Ulna of *Pinguinus impennis*, BMNH S/1864.12.10.1; 2, Ulna of *Uria aalge*, BMNH S/1985.71.11.1; 3, Ulna of *Alca torda*, BMNH S/1975.44.4; x 0.66. 4-6. *Alca stewarti*, BMNH A 7050, locality and horizon as above. Referred maxilla (BMNH A 7056) with; 4, Skull of *Alca torda*, BMNH S/1927.2.11.2; 5, Skull of *Uria aalge*, BMNH S/1985.71.11.1; 6, Skull of *Pinguinus impennis*, BMNH S/1864.12.10.1; x 0.45. 7-9. *Alca stewarti*, BMNH A 7050, locality and horizon as above. Cast of paratype; right humerus (BMNH A 7052) with; 7, Humerus of *Alca torda*, BMNH S/1975.44.4; 8, Humerus of *Uria aalge*, BMNH S/1985.71.11.1; 9, Humerus of *Pinguinus impennis*, BMNH S/1864.12.10.1; x 0.62.

DESCRIPTION

The ulna (figs.1, 2BC; tabl. 1) of *A. stewarti* is gently curved medially and is shorter than the humerus. Overall, with the exception of relative size, the morphology of this element is very similar to that of *A. torda*. The shaft of the ulna is broad and sub-circular in outline. It is, however, somewhat more robust than the corresponding element in the extant alcids, and is not as dorso-ventrally compressed as the ulnae of *Pinguinus*, *Mancalla* or *Praemancalla*. The depressio radialis and sulcus intercondylaris are shallow in comparison to other alcids; the olecranon is pointed and pronounced and the cotyla ventralis is flat and cup-like in outline. The paratype ulna is morphologically identical to the holotype, differing slightly in size (table 1), but falls within the range of individual and sexual variation within the alcids.

All of the corresponding ulnae and humeri included within this taxon can be articulated together. On the proximal end of the humerus (figs.1, 2D-G; tabl. 2), the caput humeri is rounded but turned over somewhat distally; the incisura capitis is shallow and appears broader than that of Recent alcids. As in Recent taxa, the tuberculum ventrale is pronounced, and the fossa dorsalis is turned obliquely with respect to the plane of the shaft. On the distal end, the epicondylus ventralis is pronounced and extends proximally along the shaft; the lateral margin of this structure is flat, whilst in Recent alcids it is hooked proximally, lateral to the processus flexorius. Unlike *Pinguinus*, *Mancalla* or *Praemancalla*, the ectepicondylar process is located close to the condyles.

The rostral portion of the referred maxilla (figs.1, 2A; tabl. 1) is broken rostral to the ascending process of the os nasale (not preserved). On the dorsal margin of the maxilla, the contact with the premaxilla is raised and prominent, as is the case in extant alcids. The symphysal region is narrow, and deeper than in any extant alcid. The maxillary symphysis is shorter and considerably narrower than in *Pinguinus*. The rostral border of the os nasale is rounded and smoothed internally; in Recent alcids, this border is narrower, and often sub-circular in outline. On the surface of the rostrum maxilla, a number of deep, circular neurovascular foramina are preserved. Rostrally, the margin of the maxilla is gently curved caudally; in both *A. torda* and *Pinguinus*, the beak is much more

pronounced and rather hooked.

A. stewarti differs from the Pliocene *Australca* in many aspects of the preserved morphology. The humerus of *A. stewarti* is longer, and the crista deltopectoralis is less rounded. The tuberculum ventrale is downturned in *A. stewarti*, whilst it is flat and smoothly rounded in *Australca*. Also, a longitudinal ridge is present on the bone, located laterally but rather indistinct in *A. stewarti*, whilst it is central and prominent in *Australca*. The crus dorsale fossa is more obliquely positioned in *A. stewarti*. Distally, the ectepicondylar prominence extends further along the shaft in *A. stewarti*, but it is narrower and less robust; also, the sulcus humeralis tricipitalis is wider in *A. stewarti*.

Characteristic	Holotype; right ulna (BMNH A 7050)	Paratype; right ulna (BMNH A 7051)	Referred maxilla (BMNH A 7056)
Total preserved length ..	91.0	47.2	47.0
Breadth proximal end ..	12.0		
Breadth distal end	10.2	9.9	
Mid-shaft width	6.8		
Max. width narial opening			7.5
Max width mandibular symphysis			4.0
Dorsoventral height distal to narial opening .			13.5

Characteristic	Paratype; right humerus (BMNH A 7052)	Paratype; right humerus (BMNH A 7053)	Referred maxilla (BMNH A 7056)	Paratype right humerus (BMNH A 7055)
Total preserved length	110.4	94.2	45.2	71.6
Breadth proximal end	23.3	25.4		
Breadth distal end	15.8		14.2	14.9
Mid-shaft width	8.6	9.1		
Proximal end to ectepi. proc. ...	95.1			

THE FLIGHT CAPABILITY OF *A. STEWARTI*

Determination of flight capability

The wing bones of *A. stewarti* are longer than those of any other known auk. Many of the larger auks were flightless, and consequently it is important to determine whether *A. stewarti* was volant. One of the principal anatomical differences between volant and flightless auks is the relative length of the ulna and humerus. It is well documented that specialization for wing-propelled diving leads to a relative shortening of the ulna, compared to fully volant forms (e.g. Storer, 1960; Pennycuick, 1975; Raikow *et al.*, 1988).

Using previously published data, we determined the mean ulna:humerus ratio for the following alcid; *Alle alle*, *Uria lomvia*, *Cerorhinca monocerata*, *Fratercula arctica* (from Lockwood, 1995), *Uria aalge*, *Alca torda*, *Cepphus grylle*, *Pinguinis impennis* (from Livezey 1988), *Praemancalla wetmorei*, *Mancalla diagenese*, *Mancalla milleri* (from Howard, 1970), and *Mancalla cedrocensis* (from Howard, 1971).

The mean value of this ratio for *A. stewarti* is 0.52, whereas in flightless alcid it is 0.44 ± 0.02 (95% confidence limit = 0.07), and in flighted alcid 0.79 ± 0.02 (95% confidence limit = 0.03). A two-sample *t*-test showed that flightless and flighted auks differed significantly in terms of this ratio ($t = 1.94$, $p < 0.001$). There is no significant difference between the ulna:humerus ratios of flighted auks and *A. stewarti* ($t_s = 0.88$, $p > 0.4$, 6 d.f.), whilst there is a significant difference between those of *A. stewarti* and the flightless auks ($t_s = 6.01$, $p < 0.01$, 4 d.f.) (*t*-test comparison of single observation with sample mean; Sokal & Rohlf, 1995). This demonstrates that although *A. stewarti* was a wing-propelled diver, the relative proportions of the wing bones were markedly different to those of the flightless auks, suggesting that *A. stewarti* was fully volant. Osteological evidence supports this suggestion; for example, the ectepicondylar prominence is located close to the distal end of the humerus, at a similar relative distance along the shaft as that of *A. torda* and *U. aalge*, but more distally than either *Pinguinus* or *Mancalla*. In flightless auks there is a tendency for this muscle

attachment to move proximally along the bone shaft (Livezey, 1988). Also *A. stewarti*, in common with volant auks, exhibits a lesser degree of dorsoventral flattening of the wing bones than the flightless alcid.

Estimation of the body mass

When estimating the body mass from bone dimensions, it is essential to use those bones which in some way support the mass *i.e.* wing or leg bones. Using previously published data (Kuroda, 1967; Livezey, 1988; Dunning, 1993; Lockwood, 1995), we derived a relationship between mass and humerus length for 9 species of auk (fig. 3). Best fit for these data was provided by the following regression equation :

$$\log \text{ mass} = 2.787 \log \text{ humerus length} - 2.406 \quad (r^2 = 0.99, p < 0.01) \quad (1)$$

Substituting into the equation (1), we derived an estimated body mass of 1.941 kg for *A. stewarti*. This is almost twice as heavy as the largest extant auks (the similarly-sized *U. aalge* and *U. lomvia*) and more than three times more massive than the nearest relative of this species, *A. torda* (Dunning, 1993). However, the mass of *A. stewarti* was less than that of any of the extinct flightless auks (Livezey, 1988).

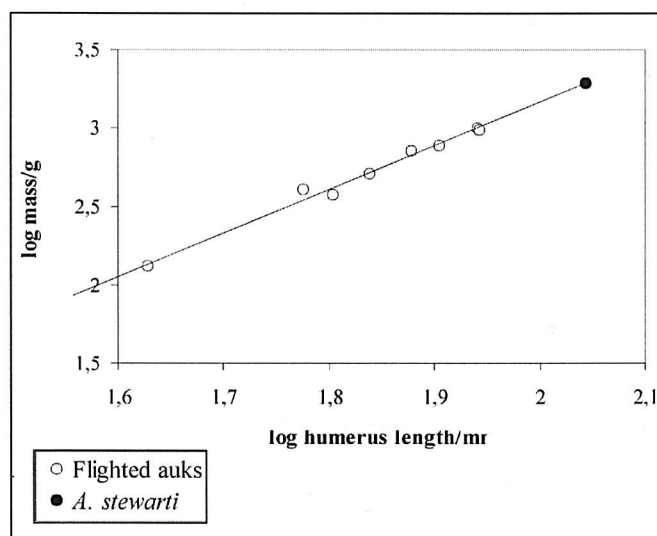


Figure 3: The relationship between log humerus length and log body mass in Recent flighted alcid. The regression equation is: $\log \text{ mass} = 2.787 \log \text{ humerus length} - 2.406$ ($r^2 = 0.99$, $p < 0.01$). The log humerus length of *A. stewarti* is 2.043; this generates an estimated body mass of 1.941 kg. The regression line has been extended to include *A. stewarti*.

Wing beat frequency and flight speed

Pennycuick (1996) suggests that a good approximation of the wing beat frequency f (Hz) of a bird in steady cruising flight can be derived from

$$f = m^{3/8} g^{1/2} b^{-23/24} S^{-1/3} rd^{-3/8} \quad (2)$$

Where m = mass (kg), g is the acceleration due to gravity (9.81 ms^{-2}), b is the wing span (m), S is the wing area (m^2), and rd is the air density (1.21 kg m^{-3}). Curves of log wing area and log wing span against log humerus length were generated for five extant species of volant alcid, using previously published data (Pennycuick, 1990, Lockwood, 1995) (fig. 4). The following relationships were derived to predict the wing span and area of *A. stewarti*;

$$\log \text{ wing area} = -4.600 + 1.720 \log \text{ humerus length} \quad (r^2 = 0.98, p < 0.01) \quad (3)$$

$$\log \text{ wing span} = -1.720 + 0.812 \log \text{ humerus length} \quad (r^2 = 0.82, p < 0.05) \quad (4)$$

From these equations, the wing area was predicted to be 0.082 m^2 and the wing span, 0.869 m .

When these values were substituted into the equation (2), we derived an estimated wingbeat frequency of 9.85 Hz for *A. stewarti* during cruising flight. This is very high when compared to most birds, but agrees well with published values of extant auks (Pennycuick, 1990).

The flight speed of *A. stewarti* can be estimated using Pennycuick's (1997) model. This gives an approximate value for the minimum power speed, ($V_{\text{mp}} \text{ ms}^{-1}$) where:

$$V_{\text{mp}} = [0.807 k^{1/4} (mg)^{1/2} / [rd^{1/2} b^{1/2} (S_b C_{\text{Db}})^{1/4}]] \quad (5)$$

Where k is the induced power factor (1.2) and C_{Db} is the body drag coefficient (0.1) (other variables as above). The body frontal area S_b (m^2) is derived from the mass; Pennycuick *et al.* (1988) show that for wildfowl and raptors,

$$S_b = 8.13 \times 10^{-3} m^{0.666} \quad (6)$$

giving us a value of 0.01265 m^2 for *A. stewarti*. Substituting into equation 5, V_{mp} is estimated to be 18.9 ms^{-1} . Pennycuick (1997) included data from three species of alcid in his analysis; *U. aalge*, *A.*

torda and *F. arctica*. Their predicted velocities were 16.5 , 14.8 and 14.0 ms^{-1} respectively. Field data, however, show that cruising speeds for these species are, on average, 16.5% higher; this points to a probable flight speed of around 22 ms^{-1} for *A. stewarti*.

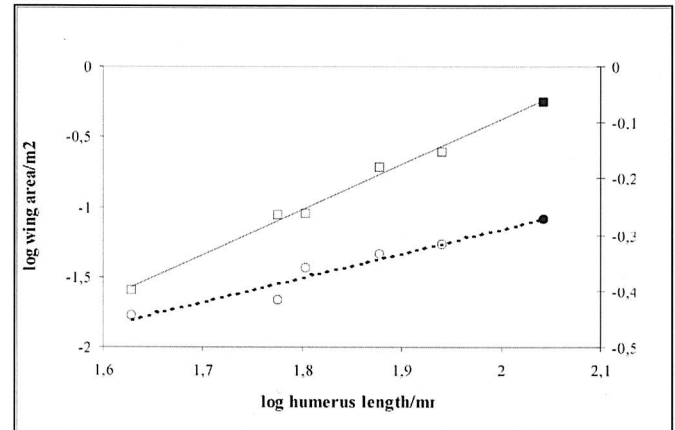


Figure 4: The relationship between log wing area (dashed line), log wing span (solid line) and log humerus length in five species of extant alcids (open symbols). The regression equations are:

$$\log \text{ wing area} = -4.600 + 1.720 \log \text{ humerus length} \quad (r^2 = 0.98, p < 0.01)$$

$$\log \text{ wing span} = -1.720 + 0.812 \log \text{ humerus length} \quad (r^2 = 0.82, p < 0.05)$$

From these equations, approximate values for the wing area (0.082 m^2) and the wing span (0.869 m) of *A. stewarti* were generated. The regression lines have been extended to show the values of *A. stewarti* (filled symbols). Using these figures, the mean wingbeat frequency was estimated to have been around 9.85 Hz .

DISCUSSION

Our analysis shows suggests that *A. stewarti* was a large, fully flighted auk, and like other alcids it was a wing-diving specialist. Although this was a big bird larger than the extant alcids, weighing an estimated 2 kg , it was considerably less massive than the 5 kg *Pinguinus* (given by Livezey, 1988), despite the fact that its wing elements are larger in absolute terms. As a group, the Alcidae exhibit very high wing loading (mass divided by wing area) (e.g. Rayner, 1988; Lockwood, 1995), as a result of the morphological compromises imposed by aerial and submarine flight; this necessitates fast flight, with a high wingbeat frequency and a correspondingly high power output (Rayner, 1988). We have shown that both the

wing beat frequency (9.85 Hz) and the minimum power speed (16.8 ms^{-1}) of *A. stewarti* were very high; flight was energetically expensive for these birds. The high wing loading of alcids also results in low aerial manoeuvrability (Andersson & Norberg, 1981; Norberg & Rayner, 1987). Using our estimates of bodymass and wing area, *A. stewarti* had a wing loading of approximately 2.36 g cm^{-2} ; this is exceptionally high for any flighted bird (Livezey, 1986), but is close to the 2.30 g cm^{-2} estimated by Livezey (1988) for an auk of this size. However, it has been suggested that the highest theoretical wing loading that would still permit flight is around 2.50 g cm^{-2} (Meunier, 1951; Livezey, 1988). This implies that *A. stewarti* was able to conduct powered flight, albeit with limited manoeuvrability. Manoeuvrability does not seem to be an evolutionarily-constraining factor in seabirds, where the environment is generally clutter-free, and aerial predators are few. This, however, may have rendered *A. stewarti* prone to attack from kleptoparasitic seabirds, as are many modern alcids (O'Donald, 1983; Gaston & Jones, 1998).

The Pliocene alcid avifauna included a variety of large, flighted auks; in addition to *A. stewarti*, there were also at least two species of *Australca* (Brodkorb, 1955; Olson, 1985), both of which failed to survive into the Pleistocene. It is possible that these large species were displaced by the relatively recent arrival of the Pacific genus *Uria* into Atlantic waters (Olson, 1985; Moum *et al.*, 1994). The larger Recent genera feed almost exclusively on fish and squid (Bédard, 1969; Gaston & Jones, 1998); there is no reason to suggest that *A. stewarti* was any different. Swennen & Duiven (1977) showed that there is a great deal of overlap in the size of prey taken by piscivorous alcids; it appears that different auk species select prey on the basis of diameter, rather than length. Also, Watanuki & Burger (1999) show that maximum dive duration in alcids increases as $3.612 m^{0.735}$. This gives a maximum dive duration of *A. stewarti* of around 5.8 minutes, compared to only 3.2–3.3 minutes for the largest extant species, *U. lomvia*. However, feeding time during diving increases as $1.094 m^{0.391}$, giving an approximate value of 1.4 minutes. This is within the reported range (0.9–1.6 minutes) for *U. lomvia*, suggesting that larger auks must work relatively harder in order to feed themselves and their young.

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