

# Is bill length in curlews *Numenius* associated with foraging habitats and diet in non-breeding grounds?

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The eight members of the genus *Numenius* (curlews) show considerable intraspecific and interspecific variation in bill length (Hayman *et al.* 1986) which begs the question “can bill length be related to their respective foraging ecologies either during the breeding or non-breeding periods of their annual cycle?” Here I examine the association between bill length and foraging habitat and diet of *Numenius* curlews during non-breeding periods.

*Numenius* may be partitioned into three main groups on the basis of bill length. The first group comprising two species, *minutus* and *borealis*, which Burton (1986) argues are the ancestral type, has bill lengths of 40–50 mm. Both species in this group feed (or used to feed, *borealis* is thought to be extinct) exclusively in grasslands in the austral summer, *minutus* in NW Australia and *borealis* on the South American pampas respectively (Table 1) (Higgins & Davies 1996, Hayman *et al.* 1986). The second group of three species, *phaeopus*, *tahitiensis* and *tenuirostris*, have intermediate bill lengths of 70–90 mm and feed in both intertidal and coastal grassland areas in their non-breeding period (Hayman *et al.* 1986, Dann 1993, Cramp & Simmons 1983). The third group of three species (*arquata*, *americanus* & *madagascariensis*) have bills ranging from 120–185 mm and are found feeding in intertidal areas and coastal grasslands in non-breeding periods (Table 1) (Cramp & Simmons 1983, Grinnell 1921, Higgins & Davies 1996, Dann 2000). Of these three

species, *madagascariensis* is the least likely to be found feeding in non-tidal habitats in the non-breeding grounds and, in fact, rarely does so.

Hence there is some association between the relative lengths of bill in *Numenius* and foraging habitat in non-breeding periods (Table 1). Not surprisingly there are corresponding associations between bill length (and foraging habitat) and diet in non-breeding periods. The shorter-billed species are obligate grassland feeders in the austral summer eating mainly insects and seeds. The intermediate group frequent both coastal grasslands and intertidal habitats and consume insects in grasslands and crustaceans and molluscs in intertidal areas. The three species in the longer-billed group are either facultative grassland and intertidal feeders (*arquata* & *americanus*) or obligate intertidal feeders (*madagascariensis*). The longer-billed group feeds on crabs, shrimps, polychaetes and molluscs in intertidal habitats or, in the case of *arquata* & *americanus*, on insects or oligochaetes in grasslands. Davidson *et al.* (1986) noted that shorter bill length seemed to be associated with foraging on grasslands for two species (*minutus* and *borealis*) and also for males of one species (*arquata*). Townsend (1981) showed that it was mainly male (shorter billed sex) *arquata* that moved from mudflats to forage on pastures as temperatures fell in autumn.

Whether a relationship between morphology and foraging behaviour is adaptive can be assessed only if the evolution

**Table 1.** The bill lengths and reported diets of the eight species of *Numenius*.

Species	Bill length (mm) Male±s.d.	Bill length (mm) Female±s.d.	Diet in non-breeding period	Source
Little Curlew <i>N. minutus</i>	41.9±2.4	44.5±2.3	insects, berries and seeds <sup>h</sup>	Higgins & Davies 1996, <sup>h</sup> Jessop 2003
Eskimo Curlew <i>N. borealis</i>	42–60 <sup>a</sup>		insects <sup>b</sup> , berries	<sup>a</sup> Hayman <i>et al.</i> 1986, <sup>b</sup> Murphy 1936
Whimbrel <i>N. phaeopus</i>	76.5±3.8 78.6±3.1	84.6±3.6 <sup>j</sup> 86.9±3.9 <sup>k</sup>	molluscs, crustaceans <sup>j</sup> , insects and berries <sup>k</sup>	<sup>j</sup> Dann 1993, <sup>k</sup> Cramp & Simmons 1983
Bristle-thighed Curlew <i>N. tahitiensis</i>	85.5±10.5	90	vegetable matter, crustaceans, insects	Hayman <i>et al.</i> 1986
Slender-billed Curlew <i>N. tenuirostris</i>	72.9±2.6	89.9±4.7	polychaetes, crabs, molluscs, insects	Cramp & Simmons 1983
Eurasian Curlew <i>N. arquata</i>	121±6.6	153±7.3,	polychaetes, crabs, molluscs, insects and oligochaetes	Cramp & Simmons 1983
Long-billed Curlew <i>N. americanus</i>	132.9±3.6 <sup>c,1</sup> (s.e.)	175.8±6.1 <sup>c,1</sup> (s.e.)	crabs, shrimps, molluscs, oligochaetes, insects and berries <sup>d</sup>	<sup>c</sup> Grinnell 1921, <sup>d</sup> Wickersham 1902, <sup>d</sup> Del Hoyo <i>et al.</i> 1996, <sup>1</sup> Allen 1980
Eastern Curlew <i>N. madagascariensis</i>	150.9±7.2 <sup>f</sup> 153.0±8.1 <sup>1</sup>	183.6±8.8 <sup>f</sup> 183.1±9.7 <sup>i</sup>	crabs, shrimps <sup>e</sup> , polychaetes <sup>g</sup>	<sup>e</sup> Dann 2000, <sup>f</sup> Barter 1990, <sup>g</sup> Taylor & Mackay 1999, <sup>i</sup> Rogers 1995



of morphological traits has occurred in parallel with behavioural traits (Brooks & McLennan 1991) and this can be achieved only within a phylogenetic framework (Losos & Miles 1994). The trend within *Numenius* of increasing bill length with decreasing reliance on "surface feeding or pecking" in grasslands and increasing importance of "probing" in intertidal areas suggests that long bills are an adaptation to exploiting deeply burrowing prey in soft sediments. It parallels a phylogenetic trend noted by Barbosa & Moreno (1999) for several other groups of waders whereby longer bills appear adaptively coupled to the use of a tactile foraging strategy and shorter bills to a visual strategy. The functional requirements of a tactile foraging strategy are: a high penetration capacity and a high examination capacity (i.e. remote touch system) (Zweers 1991, Zweers & Gerritsen 1997, Zweers & Van den Berge 1997). Unfortunately, there are no studies of the remote touch capacity of *madagascariensis* (the longest-billed species) available.

Davidson *et al.* (1986) have argued that strong selection for bill length in curlews operates on the non-breeding grounds while Hale (1980) maintains that studies of morphological characters indicate that the breeding season is when competition for resources among waders is greatest. The evidence within *Numenius* supports the idea that longer bills are associated with a predominately tactile feeding strategy during non-breeding periods and thus supports the proposal of Davidson *et al.* (1986). There is a clear greater dependence on soft sediment burrowing prey in the longer-billed species which is most pronounced in *madagascariensis* (Eastern Curlew), the species with arguably the greatest sediment penetration capacity of any wader. Whether or not the available evidence supports the idea that this is an adaptation to increase their access to burrowing benthic prey in non-breeding areas remains equivocal but highly suggestive.

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