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Oystercatchers' bill shapes as a proxy for diet specialization: more differentiation than meets the eye

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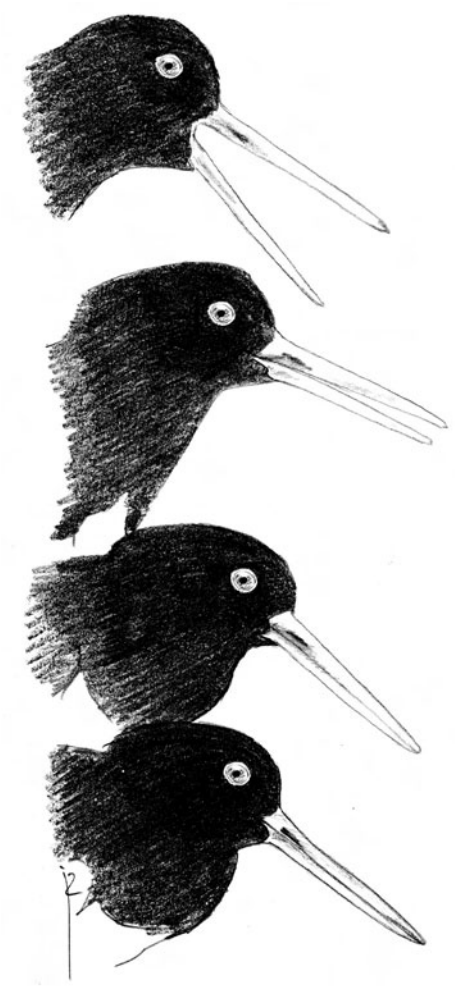

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Eurasian Oystercatchers *Haematopus ostralegus ostralegus* are a classic example of individual feeding specialization. Feeding specialization causes morphological differentiation in Oystercatchers' bill shapes due to varying degrees of abrasion associated with specific handling techniques for each prey species. Consequently, the Oystercatcher's bill shape has been used as a proxy for diet specialization, as it provides a quick and easy way to assess the diet choice of this marine top-predator. However, bill shapes of Oystercatchers are categorized visually in distinct types, while it has been argued that the relevant variation is continuous. Also, it is unclear how comparable the bill-shape classification is among studies and between the sexes and how universal bill shape–diet relationships are. Here we investigate the usefulness of bill-shape types as a proxy for diet choice in Oystercatchers, using four new and two published datasets. We show that quantitative bill-morphometrics provide no evidence that bill-shape types are discrete entities. Additionally, the dimensions of the same bill-shape type differ across studies. This difference is unlikely to be caused by methodology and might reflect subtle additional feeding specialization among birds with the same bill-shape type. Moreover, we show that the tip of the bill of males is typically 7% higher than that of females with the same bill-shape type. A higher – and probably stronger – bill tip in males may explain why males had more shellfish in their diet than females with the same bill-shape type. Finally, a literature-review shows that the exact bill shape–diet relationship differs between studies and the sexes. We conclude that the interpretation of bill-shape type as a proxy for diet choice in Oystercatchers is context dependent. We propose that quantitative bill dimensions are a better proxy for feeding specialization than bill-shape types.

Key words: *Haematopus ostralegus,* bill damage, bill morphology, prey choice, sexual dimorphism, sex-dependent diet choice, shellfish, trophic polymorphism

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INTRODUCTION

In many bird, fish, reptile, mammal and insect species some individuals only use a subset of the resources available to the whole population (Partridge & Green 1985, Bolnick *et al.* 2003). Eurasian Oystercatchers *Haematopus ostralegus ostralegus* are one of the best known and thoroughly studied cases of feeding specialization (reviewed by Sutherland *et al.* 1996, Hulscher 1996). Individual Eurasian Oystercatchers specialize on

eating specific prey species and also specialize in how they handle these prey items, as also observed in other oystercatcher species (e.g. Hockey & Underhill 1984, Nol & Humprey 1994, Laura & Nol 1995). Eurasian Oystercatchers' feeding specialization is sex-dependent (Hulscher & Ens 1992, Durell *et al.* 1993) and is learned from the parents (Norton-Griffiths 1967), with juveniles becoming more specialized towards adulthood (Goss-Custard & Durell 1983). Furthermore, feeding specialization in Oystercatchers is environment-dependent, with individuals switching specialization as a function of food availability (Swennen *et al.* 1983, Hulscher 1985) and density of competitors (Goss-Custard & Durell 1988). The ecology of this marine top-predator is closely linked to that of its macro-benthic food sources, and therefore the development, ecology and evolution of Oystercatchers' feeding specialization are of interest from both a pure and applied science perspective (Sutherland *et al.* 1996, Hulscher 1996, Verhulst *et al.* 2004).

It has been known for a long time that three distinct feeding techniques can be observed in wild Eurasian Oystercatchers (e.g. Dewar 1908, Drinnan 1957, Tinbergen & Norton-Griffiths 1964). Swennen *et al.* (1983) first described how these three feeding techniques are related to three types of bill shapes (Fig. 1), although earlier studies had already recognized a subset of bill-types and their link to prey choice and handling technique (Salomonsen 1930, White & Gittins 1964, Hulscher 1982). Swennen *et al.* (1983) showed that birds with a pointed bill shape typically probe into the substrate in search for worms (e.g. Ragworm *Nereis diversicolor* and Lugworm *Arenicola marina*) and deep-buried bivalves (e.g. Soft-shell Clam *Mya arenaria* and Peppery Furrow Shell *Scrobicularia plana*). Birds with a chisel bill shape typically stab between the gaping shells of surface-living or superficially-buried bivalves to cut the adductor muscle that keeps the shells together, which allows them to eat the shellfish meat. In contrast, birds with a blunt bill shape hammer the shells, and then cut the adductor muscle through the fractured shell. Stabbing and hammering representing two different techniques to open the same bivalve species (e.g. Baltic Tellin *Macoma Balthica*, Mussel *Mytilus edule* and Cockles *Cerastoderma edule*). Swennen *et al.* (1983) also identified three intermediate types of bill-shape types (pointed-chisel, pointed-blunt, chisel-blunt) which are thought to result from using either a mixture of two feeding techniques, or from a transient switching-between-specializations-stage.

Using experimental diet manipulations, Swennen *et al.* (1983) showed that diet causes the aforementioned

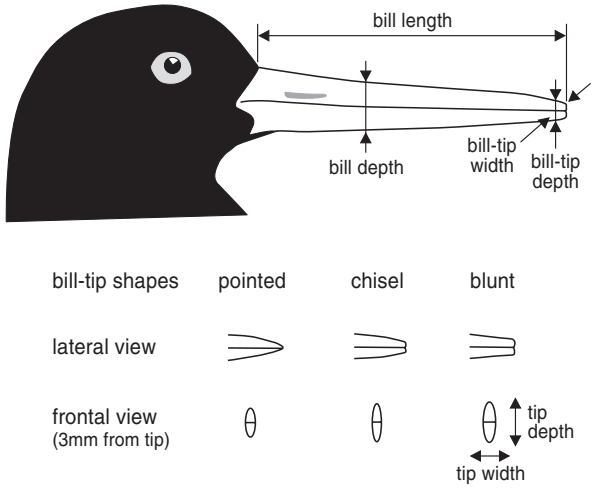

Figure 1. Overview of the three main types of Oystercatcher's bill shapes and the bill measurements. Figure adapted from Swennen *et al.* (1983) and Zwarts *et al.* (1996).

differentiation in bill shape, and not the other way around. Hulscher (1985) subsequently showed that differential rates of abrasion are the mechanism causing the bill-shape types. Abrasion of the horny rhamphotheca is highest in areas of the bill tip that are used predominantly in each feeding technique. Probing causes wear all around the distal part of the bill and thus result in a pointed bill shape, stabbing primarily causes wear at the lateral sides of the tip resulting in a chisel bill shape, and hammering causes wear to be most intense at the frontal edge resulting in a blunt bill shape (Hulscher 1985, Fig. 1). The hardness of bivalves' shells probably further affects the rate of abrasion, with stabbing and hammering hard-shelled bivalves (Cockles and Mussels) causing more abrasion than stabbing and hammering soft-shelled bivalves (Baltic Tellin, Soft-shell Clam and Peppery Furrow Shell) (Sutherland *et al.* 1996, Hulscher 1996). Diet choice and bill shape positively reinforce each other and thereby further facilitate specialization (Hulscher & Ens 1991, Sutherland *et al.* 1996). For example, probing for worms results in a pointed bill shape, which is thought to be a poor tool to hammer Cockles and Mussels due to a high risk of bill-tip damage and a low intake rate (Hulscher & Ens 1991, Rutten *et al.* 2006). As plastically changing bill shape is both time-consuming (2–3 weeks) and costly (Hulscher 1982, 1985), most individuals do not alter their bill shape within and between seasons (~30% change annually) and are quite consistent in their diet (Hulscher & Ens 1991).

The causal link between feeding specialization and bill abrasion suggests that bill-shape type can be used as a proxy for what an Oystercatcher eats, which is very useful as it takes much less effort to catch many Oystercatchers and determine their bill-shape types than to do time-consuming behavioural observation on the diet choice of individually marked Oystercatchers. Using bill shape as a proxy potentially allows one to quickly gain insights into the natural and anthropogenic factors affecting the feeding ecology of this estuarine indicator species. For example, Verhulst *et al.* (2004) used the bill-shape types of Oystercatchers caught in either protected or unprotected areas to infer that closing areas for mechanical shellfisheries results in more shellfish in the diet of the Oystercatchers living there.

Bill-shape types are visually determined by characterizing the shape of the tip using both a lateral, dorsal and frontal view (Fig. 1). The question whether trophic and morphological polymorphisms are discrete in nature or are primarily perceived as discrete in the eye of human observers, is relevant to many cases of feeding specialization (Bolnick *et al.* 2003). Many discrete polymorphisms later turn out to be less discrete than previously thought, and arguably individual variation and polymorphism are ends of a continuum of variation that vary from a unimodal to a multimodal distribution (Bolnick *et al.* 2003). A critical question thus is whether Oystercatchers' bill morphs are really discrete and if not, whether more continuous and quantitative bill-morphometrics are a more suitable proxy for diet choice than a visual categorization of bill shape. Moreover, it is still unknown how universal – and thereby comparable between studies – the bill shape–diet choice relationship is, or whether the relationship varies in space, time or between the sexes. Answering these questions is crucial for establishing whether bill-shape types are a reliable proxy for diet choice in Eurasian Oystercatchers. More fundamentally, it may provide insights into how polymorphisms differ between the sexes or depend on the environment.

In this study, we compare whether the quantitative dimensions of visually categorized bill-shape types are comparable among studies/areas and between the sexes based on four new and two published datasets. Using a within-observer between-studies comparison we disentangle methodological from biological differences, to show that there is actually more differentiation in bill-shape types than meets the eye. Subsequently, we review the literature to show that the exact bill shape–diet relationship also differs among studies and between the sexes. Finally, we discuss the usefulness of bill-shape types and other quantitative morphometrics as a proxy for diet choice in Eurasian Oystercatchers.

METHODS

Study characteristics

We collated data on quantitative dimension of the tip of the bill of Eurasian Oystercatchers with different bill shapes from two published datasets (Swennen *et al.* 1983, Durell *et al.* 1993) and four new datasets (henceforth called 'Friesland', 'Schiermonnikoog', 'Texel' and 'Wadden Sea' dataset) that differ in season, years, and/or location of sampling (Table 1). We considered only adults (≥ 3 years) for which all relevant bill-measurements were taken. The sex of birds was determined in only three datasets (Table 1). Studies comprised birds caught while living in coastal areas and feeding on inter-tidal flats, with the exception of the Friesland dataset that also included some birds breeding inland where they fed on agricultural land. Birds were caught on the nest with a walk-in cage or on roosts using cannon nets and mist nets; the Friesland dataset included some freshly found frost victims. For the Friesland dataset we were unable to retrieve all the raw data, but with the help of Leo Zwarts we were able to reconstruct aggregate statistics of bill morphology measurements for both sexes combined.

Bill measurements

The literature on Oystercatchers' bill morphology has been substantially convoluted by the fact that several studies (e.g. Hulscher 1985, Zwarts *et al.* 1996, van de Pol *et al.* 2009) have continued to use an alternative bill shape classifications and terminology than Swennen *et al.* (1983). These studies often classified bill shapes in the field as described by Swennen *et al.* (1983), but presented their results using the simpler classification of White & Gittins (1964). White & Gittins classified bill shapes using only a lateral view, and consequently only categorized variation in bill-tip depth (Fig. 1). To make matters worse, White & Gittins (1964) and Swennen *et al.* (1983) partly used the same terminology to describe different bill-shape types (Table 2). By ignoring variation in bill-tip width, White & Gittins (1964) had effectively grouped chisel, blunt and chisel-blunt bills into one group called 'blunt' bills. Similarly, they had grouped pointed-chisel and pointed-blunt bills into one group called 'intermediate' bills. Note that Swennen *et al.* (1983) refers to pointed-blunt, pointed-chisel and chisel-blunt bills as 'intermediates'.

In the new datasets we followed the methodology and terminology of Swennen *et al.* (1983), as this description is most complete. Bill-tip depth and width were measured at 3 mm from the tip of the bill (Fig. 1) using sliding callipers with 3-mm thick jaws (accuracy of 0.1 mm). Bill-tip depth and width were highly repeatable between observers (both $r > 0.8$, $n = 87$). In the Schiermonnikoog and Wadden Sea datasets it was recorded whether the bill-tip was damaged, i.e. a difference of >1 mm in length between the upper and lower mandible. Bill-tip damage is caused by breaking off of part of the bill tip as a result of eating (too) large hard-shelled bivalves (e.g. Rutten *et al.* 2006). In the Friesland, Schiermonnikoog and Texel dataset the vast majority of measurements were taken by a small group of scientists involved in the studies for several years. One observer (KO) measured a large number of birds in the Schiermonnikoog and Texel dataset, as well as all birds in the Wadden Sea dataset, allowing us to disentangle observer effects from biological among-study differences.

Statistics

Statistical analyses were performed in R (R Development Core Team 2007); all test are two-tailed. In combined analyses of datasets we used one-way ANOVA's with summary statistics as input (Larson 1992) as Swennen *et al.* (1983) and Durell *et al.* (1993) did not present the raw data and we only have aggregate statistics for these studies and the Friesland dataset. The occurrence of bill-tip damage was treated as a binary variable and analyzed using a GLM with a logit-link function.

Review of bill-shape type and diet choice relationship

Swennen *et al.* (1983) and Hulscher (1985) manipulated the diet of captive birds to study how bill-shape type depends on diet (e.g. a diet of only worms or Mussels). To determine whether bill shape can be used as a proxy for diet choice in the wild, we reviewed the literature for bill shape–diet association in free-living Oystercatchers. Of the five studies that reported bill shape–diet relationship in the wild (Table 2), two studies used the Swennen *et al.* (1983) and three the White & Gittins (1964) classification. It appeared, but was not stated explicitly, that in all studies bill-shape type and diet of the same individuals were both characterized within a relatively short time span (< 2 months), such that plasticity was unlikely. Of these studies, Hulscher (1985) and Swennen (1990) only provided verbal descriptions of the association between bill-shape type and diet, while Durell *et al.* (1993), Ens *et al.* (1996) and Hulscher & Ens (1991) also provided quantitative data. Durell *et al.* (1993) presented data about how an Oystercatcher's bill-shape type was associated with the prey type 'predominantly' eaten by that individual. Specialization was very strict in the Durell *et al.* study, especially during the main feeding period of low tide in mid-winter (pers. comm. S. Durell). Ens *et al.* (1996) ignored minor prey species in diets (< 30%) and only reported quantitative data on the predominant prey

Table 1. Overview of the two published and four new datasets for which data on bill measurements were available.

Type	Name	Area	Habitat	Season	Years	Sample size	Method sexing	More details in
Published datasets	Durell *et al.* (1993)	Exe estuary, United Kingdom	coastal	winter	1986–1991	212	biometric	Durell *et al.* (1993)
	Swennen *et al.* (1983)	Dutch Wadden Sea, island of Vlieland	coastal	winter (January)	1982	293	not sexed	Swennen *et al.* (1983)
New datasets	Friesland	Dutch Wadden sea and mainland Friesland	coastal & inland	year-round	1973–1993	1255	not sexed	Zwarts *et al.* (1996)
	Schiermonnikoog	Dutch Wadden sea, island of Schiermonnikoog	coastal	summer (March–August)	1993–2008	1429	62% DNA, 38% by sex of partner	van de Pol *et al.* (2009)
	Texel	Dutch Wadden sea, island of Texel	coastal	year-round	1996–2008	677	not sexed	Oosterbeek *et al.* (2006)
	Wadden sea	Dutch Wadden sea, seven different sites	coastal	winter (November–March)	2002–2003	515	40% DNA, 60% biometric	Rutten *et al.* (2006)

Table 2. An overview of bill shape–diet relationships in free-living birds. Swennen (1990) and Durell *et al.* (1993) followed the bill shape classification of Swennen *et al.* (1983), while Hulscher (1985), Ens *et al.* (1996) and Hulscher & Ens (1991) followed the classification of White & Gittins (1964). Samples sizes refer to the number of individuals observed, which were typically followed for hours.

Bill shape categories		**Diet**					
Swennen *et al.* (1983)	White & Gittins (1964)	Swennen (1990) wintering coastal birds	Durell *et al.* (1993) wintering coastal birds	Hulscher (1985) wintering coastal birds	Hulscher (1985) inland breeders	Ens *et al.* (1996) coastal year-round	Hulscher & Ens (1991) coastal breeders
Pointed	Pointed	-	91% worms[a] and Peppery Furrow Shell, 9% Mussel (n = 35)	'predominantly' Ragworm, Lugworm	'predominantly' earthworms, leatherjackets, caterpillars	'predominantly' shellfish[c] of which: 90% Cockle, 10% Mussel (n = 3)	62% Ragworm, 2% Lugworm, 11% Soft-shell Clam, 23% Baltic Tellin, 1% Mussel, 1% Cockle (n = 15)
Pointed-blunt	Intermediate	-	-	'predominantly' Baltic Tellin, Soft-shelled Clam, Peppery Furrow Shell	-	'predominantly' shellfish[c] of which: 74% Cockle, 26% Mussel (n = 6)	39% Ragworm, 1% Lugworm, 8% Soft-shell Clam, 46% Baltic Tellin, 4% Mussel, 2% Cockle (n = 61)
Pointed-chisel		'predominantly' Giant Bloody Cockle	worms[a], Peppery Furrow Shell, Mussel (n = 2)				
Chisel	Blunt	-	93% Mussel, 7% Cockle (n = 54)	'predominantly' Mussel, Cockle	-	'predominantly' shellfish[c] of which: 57% Cockle, 43% Mussel (n = 9)	23% Ragworm, 1% Lugworm, 4% Soft-shell Clam, 60% Baltic Tellin, 10% Mussel, 2% Coclke (n = 68)
Chisel-blunt		-	-				
Blunt		-	94% Mussel, 5% Cockle, 1% snails[b] (n = 66)				

Note: Durell *et al.* (1993) refer to percentage of birds that predominantly fed on a specific species, while Ens *et al.* (1996) and Hulscher & Ens (1991) refer to the percentage of a specific species in the diet of birds. [a]Mainly Ragworm, some lug- and catworm (*Nephtys* spp.) (pers. comm. S. Durell) [b]*Littorina* spp. [c] Baltic Tellins, Ragworms, Lugworms and shorecrabs *Carcinus* spp. were also in the diet (<30%), but quantitative data was unavailable.

species Cockles and Mussels, during two years in which these species were very abundant. Hulscher & Ens (1991) presented detailed data about within-individual variation in summer diet, but data only included diet data for Oystercatchers foraging in their territory (constituting 70% of their time budget; Kersten 1996).

RESULTS

Bill shape: discrete or continuous trait?

There were no indications that the univariate distribution of bill-tip depth (Fig. 2A), bill-tip width (Fig. 2B) and the bivariate distribution of bill-tip width-depth (Fig. 2C) were multimodal in three of the new datasets (similar results were obtained for Schiermonnikoog, Texel and Wadden Sea datasets separately, not shown). All distributions were quite smoothly unimodal, suggesting these traits or trait combinations are part of a continuum of trait values. When comparing the bivariate distribution to the average bill-tip dimensions of the bill-shape types, we see that there is a steep ridge in the bill-tip width-depth plane on which the pointed, pointed-chisel and chisel shaped bill are situated (mean values for bill types given as symbols in Fig. 2C). Bill-tip width–depths combinations typically associated with pointed-chisel bills were most common in the combined dataset, suggesting that the bill shape of many individuals is actually a compromise between two different feeding specializations. Since blunt, chisel-blunt and pointed-blunt shapes were rare in the three datasets, there are no ridges visible on the bill-tip width-depth plane between blunt and pointed (or chisel) bills (Fig. 2C).

Bill-differences among studies

Within each of the six datasets, the three main and three intermediate bill-shape types differed in their average bill-tip width and depth (Fig. 3A-F). On average, pointed bills had a lower bill-tip width and depth than blunt bills. Chisel bills typically had a higher bill depth than pointed bills, but still slightly lower than the average blunt bill. Furthermore, chisel bills were much narrower than blunt bills and generally also slightly narrower than pointed bills, with the exception of the Friesland and Schiermonnikoog dataset (Fig. 3C,D).

Although bill-shape types differed in bill-tip width and depth within studies, the absolute dimensions of the same type of bill shape varied among studies (Fig. 3I). For example, chisel bills in the Friesland and Schiermonnikoog datasets had a similar bill-tip width and depth as pointed-blunt bills in the Texel and Wadden Sea dataset. As another example, pointed-chisel bills in the Texel and Wadden Sea datasets had a similar bill-tip width and depth as chisel bills in most

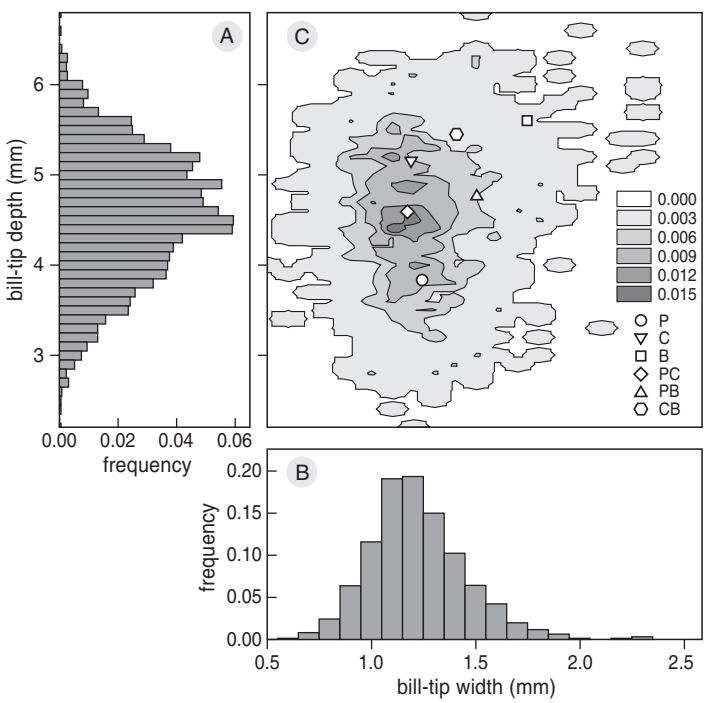

Figure 2. Univariate frequency distributions of (A) bill-tip depth, (B) bill-tip width and (C) their bivariate distribution. In (C) the different shades of grey represent the frequency of bill-tip width/depth combinations (see legend); the mean values of the three main (P = pointed, C = chisel, B = blunt) and three intermediate (PC = pointed-chisel, PB = pointed-blunt, CB = chisel-blunt) bill-shape types are presented by white symbols. Data from Schiermonikoog, Texel, and Wadden Sea datasets combined (n = 2518).

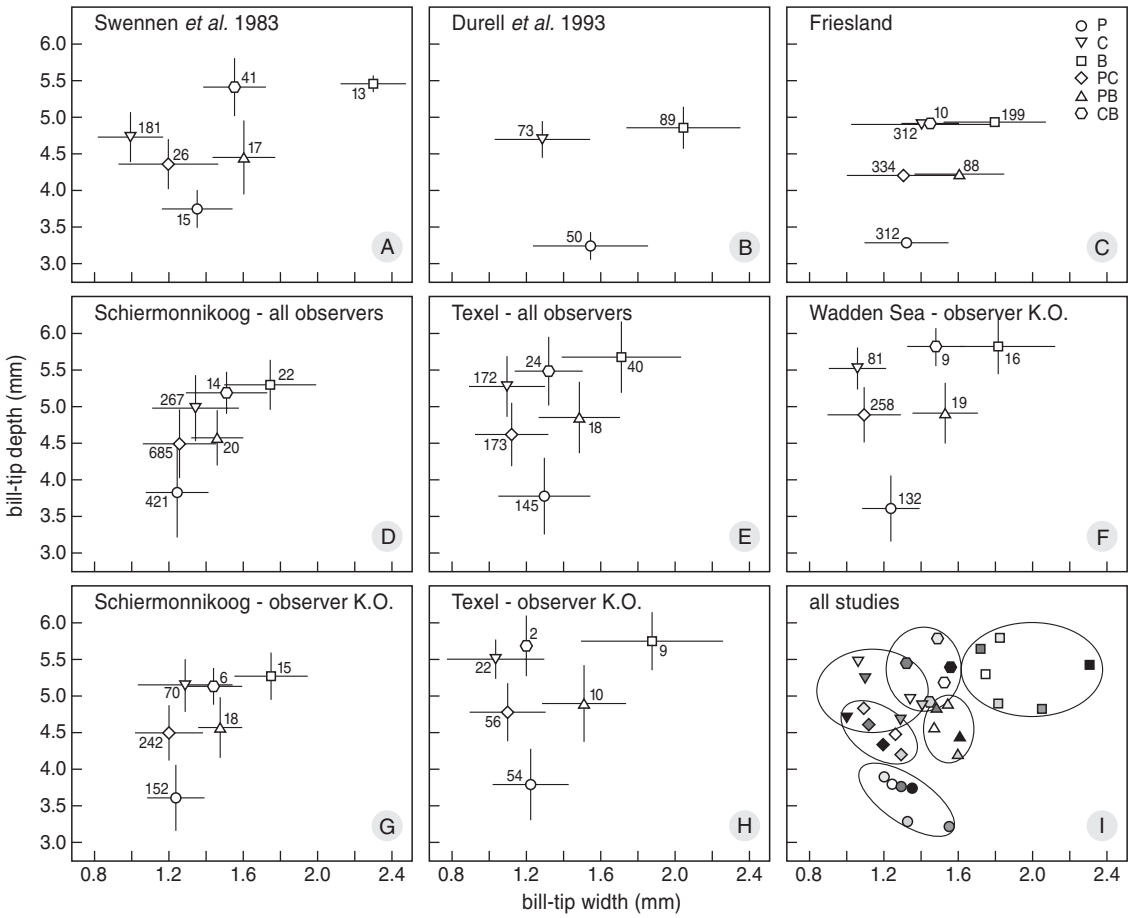

Figure 3. Across-studies comparison in the width and depth of the bill tip (Fig. 1) of the three main (P = pointed, C = chisel, B = blunt) and intermediate bill-shape types (PC = pointed-chisel, PB = pointed-blunt, CB = chisel-blunt). Numbers in the graph refer to sample sizes; error bars represent one SD. In (B) the intermediate bill types are not shown as these were rare (<5%) and their values were not reported in Durell *et al.* (1993). In (C) the bill-tip depth of C-, B- and CB-bills were only available as an aggregated mean, and are thus assumed to be the same (with some jittering for graphical reasons, similar for the bill-tip depth of PB- and PC-bills); consequently, standard deviations of bill tip heights were not available. In (I) mean values of (A)–(F) are plotted in one panel, using different shading for each study; ellipses are drawn by hand for graphical reasons only.

other studies. When comparing the dimensions of blunt bills across studies, substantial variation exists among studies in bill-tip width and depth (fixed effect study, width: $F_{5,374} = 17.8$, $P < 0.001$, $R^2 = 0.19$; depth: $F_{4,375} = 52.6$, $P < 0.001$, $R^2 = 0.54$). Similarly, substantial variation exists among studies in bill-tip width and depth of chisel bills (fixed effect study, width: $F_{5,1081} = 75.1$, $P < 0.001$, $R^2 = 0.26$; depth: $F_{4,1082} = 69.8$, $P < 0.001$, $R^2 = 0.17$) and of pointed bills (fixed effect study, width: $F_{5,1070} = 25.8$, $P < 0.001$, $R^2 = 0.11$; depth: $F_{4,1071} = 15.0$, $P < 0.001$, $R^2 = 0.06$).

Potentially, these differences between studies may have been caused by systematic observer effects. However, when comparing measurements by the same observer (KO) across the Wadden Sea, Schiermonikoog and Texel datasets, there were still substantial differences in bill dimensions of the same bill type among these datasets (especially between Schiermonnikoog and the other datasets; Fig. 3F-H). More specifically, measurements by KO of bill-tip depth varied substantially among studies for pointed, chisel and blunt bills (fixed effect study, all $P < 0.001$, $R^2 = 0.09$–0.33). Furthermore, measurements by KO of the bill-tip width varied significantly among studies for chisel bills (fixed effect study, $P < 0.001$, $R^2 = 0.23$), but not statistically significant for pointed and blunt bills. Alternatively, KO may have unconsciously adjusted his classification criteria between catching sites, such that he was biased

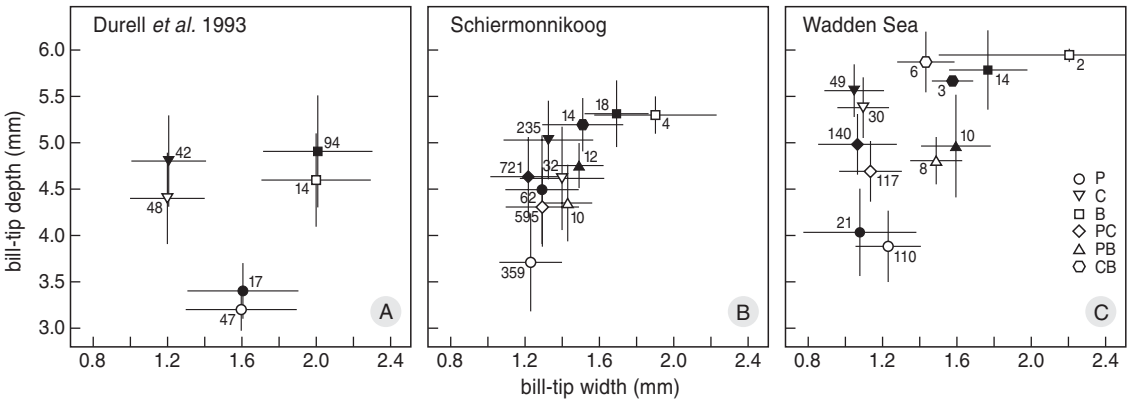

Figure 4. Sex differences in the dimensions of the bill-tip width and depth of the three main (P = pointed, C = chisel, B = blunt) and intermediates types of bill shapes (PC = pointed-chisel, PB = pointed-blunt, CB = chisel-blunt). Males are depicted by black symbols and females by white symbols. Numbers in the graph refer to sample sizes; error bars represent one SD. In (A) intermediate bills are absent as these were rare (< 5%) and their values were not reported in Durell *et al.* 1993; x-values were slightly jittered for graphical reasons. In (B) females with a CB-bill were absent in the sample caught.

towards classification into the rare bill shape. However, the annual frequency of a given bill-shape type in each of the three studies in which KO was involved was not correlated to how strong bill dimensions in that study deviated from the other studies (deviation bill-tip width: $r = 0.0$, $n = 18$, $P = 0.95$; deviation bill-tip depth: $r = 0.1$, $n = 18$, $P = 0.71$). These results strongly suggest that the bill dimensions of specific bill-shape types differed genuinely between studies and are unlikely to be methodological artefacts.

Bill-differences between the sexes

As expected, females were more likely to have pointed bills than males, while males were most likely to have chisel or blunt bills (Fig. 4). More important for the question at hand here: when comparing males and females with the same bill-shape types, males generally had substantially higher bill-tip depths than females (Fig. 4; on average 0.30 ± 0.03 mm, 7% or 0.5 SD higher). Durell *et al.* (1993) reported that this sex-difference in bill dimensions reached statistical significance for chisel bills, but not for pointed and blunt bills in their dataset (Fig. 4A). In the two new datasets of known sex, the bill-tip depth of birds with the same bill-shape type differed between sexes (fixed effect of sex while accounting for differences among bill types: Schiermonnikoog: $F_{1,1421} = 77.3$, $P < 0.001$; sex×type $F_{4,1417} = 8.29$, $P < 0.001$; Wadden sea: $F_{1,503} = 27.1$, $P < 0.001$; sex×type $F_{5,498} = 2.38$, $P = 0.094$). For the Schiermonnikoog dataset, this overall difference between the sexes was mainly the result of sex-differences in bill-tip depth among birds with pointed, chisel and pointed-chisel bills (Fig. 4B; post-hoc Student's *t*-test, all $P < 0.01$). For the Wadden sea dataset this difference between the sexes was mainly the result of sex-differences in bill-tip width among birds with chisel and pointed-chisel bills (Fig. 4C; post-hoc Student's *t*-test, both $P < 0.01$). The bill-shape types for which we did not find a statistically significant sex-difference in the post-hoc tests were also the bill-shape types for which sample sizes were lowest ($n < 25$ in either sex; Fig. 4).

Since males had higher bill-tip depths than females with the same bill-shape type, we investigated whether the higher – and thus probably more robust – bill tips of males were less likely to be damaged. Averaged over all bill types males were not less likely to have damaged bill-tips (Fig. 5; GLM fixed effect sex: $\chi^2_1 = 1.51$, $P = 0.22$) and there was no difference between the Schiermonnikoog and Wadden Sea dataset (GLM fixed effect study and sex×study both N.S.). Notwithstanding, there was substantial variation among bill-shape types in the amount of bill-tip damage (Fig. 5; GLM fixed effect type: $\chi^2_5 = 40.7$, $P < 0.001$). Most interestingly, the interaction sex×type was close to significance (GLM $\chi^2_5 = 9.7$, $P = 0.082$), suggesting that among specific bill-shape types the sexes did differ in the occurrence of bill-tip damage. In fact, females were indeed more likely to have damaged bills among birds with chisel bills, while in all other bill types the opposite was true (Fig. 5; sex differences only reached statistical significance for pointed and chisel bills in post-hoc tests).

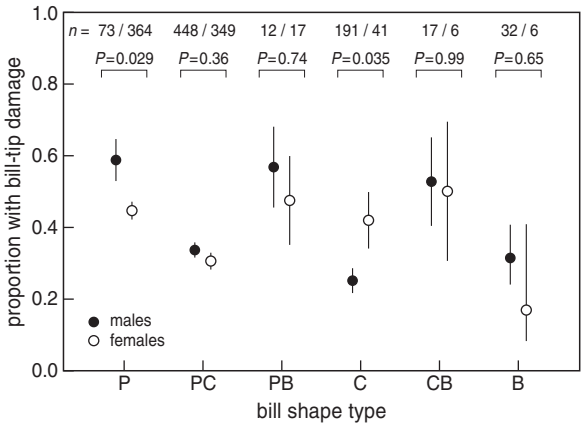

Figure 5. Occurrence of bill-tip damage in relation to bill-shape type for males and females in the Wadden Sea and Schiermonnikoog dataset combined (P = pointed, C = chisel, B = blunt, PC = pointed-chisel, PB = pointed-blunt, CB = chisel-blunt). Error bars are based on asymmetrical SE around the means; *P*-values are based on post-hoc Fisher's exact tests.

Bill-shape type and diet choice relationships among studies

Notwithstanding differences among studies in the description of diet choice and in the seasons and habitats under study (see Methods and Table 2), some general patterns were apparent in our literature review. Pointed bills were typically associated with eating deep-buried soft-bodied prey (worms, insects) and soft-shelled bivalves; hard-shelled bivalves only made up a small proportion of their diet (Table 2). Exactly which species and how much of each species are eaten by birds with pointed bills may depend on the availability of each species in a specific area and season. For example, the main bivalve species eaten by birds with pointed bills in the winter in the Exe estuary was Peppery Furrow Shell, while the main bivalve prey during breeding on Schiermonnikoog was the Baltic Tellin (Durell *et al.* 1993, Hulscher & Ens 1991).

The diet of birds with pointed-chisel and/or pointed-blunt bills was also quite comparable across three out of five studies (Table 2) and typically consisting of fewer worms and more soft-shelled bivalves than in the diet of birds with pointed bills. An interesting exception is the study of Swennen (1990), that reported that overwintering birds in the Banc d'Arguin estuary in Mauritania all had pointed-chisel bills and were feeding predominantly on Giant Bloody Cockles *Anadara senilis* (a prey species absent over most of Eurasian Oystercatchers' range). Interestingly, these Giant Bloody Cockles – probably the largest and toughest prey item known to be eaten by Eurasian Oystercatchers – are always opened using the stabbing technique, but this apparently does not result in a completely chisel-shaped bill.

The diet of birds with chisel or blunt bills was much less consistent across studies. Both Durell *et al.* (1993) and Hulscher (1985) reported that such birds predominantly fed on Mussels and Cockles in winter. However, Hulscher & Ens (1991) reported that Mussels actually were quite rare (10%) in the diet of birds with chisel or blunt bills during the breeding season on Schiermonnikoog. Surprisingly, on Schiermonnikoog the diet of birds with chisel or blunt bills consisted mostly of worms and soft-shelled bivalves, a diet typically associated with pointier bill types in other studies (Table 2).

Within studies there were clearer bill shape – diet relationships. In Durell *et al.* (1993) there was little overlap in diet among birds with pointed and chisel/blunt bills, and when comparing across the gradient of bill shapes suggested by White & Gittins (1964) (pointed→intermediate→blunt) there is a clear gradient from specializing on worms via specializing on soft-shelled bivalves to specializing on hard-shelled bivalves (Table 2). A similar gradient can be observed in Hulscher & Ens (1991) across this pointed→intermediate→blunt axis, however this specialization gradient is more subtle and concerns only minor differences in diet specialization (somewhat less worms and more bivalves, Table 2). Finally, in Ens *et al.* (1996) the same axis is associated with increasing proportions of Mussels and decreasing proportions of Cockles, suggesting that opening Mussels results in a blunter bill than opening Cockles. However, the data from Ens *et al.* (1996) should be interpreted with care, as they did not provide any quantitative data on soft-bodied prey species. Potentially soft-bodied prey were also more common among birds with pointed bills, as experiments have shown that it is quite unlikely that birds feeding solely on Mussels and Cockles would have a pointed bill (Table 2; Swennen *et al.* 1983, Hulscher 1985).

Bill-shape type and diet choice relationships between the sexes

Further analyses of the data from Hulscher & Ens (1991) – who ignored sex differences – complemented with more years of data, suggested that the relationship between bill shape and diet also differed between the sexes (Fig. 6). Females typically had more Ragworms and Soft-shell Clams in their diet than males with similar bill-shape types. Moreover, males typically had more Baltic Tellin and Mussels in their diet than females with similar bill-shape types.

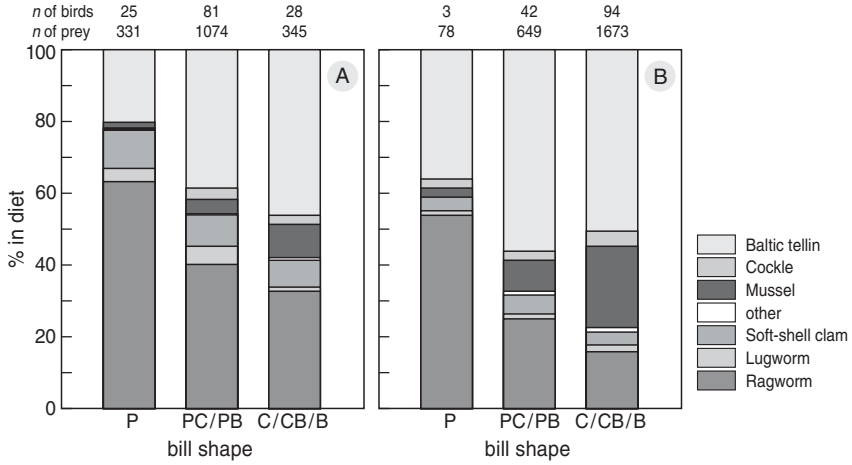

Figure 6. Diet of (A) female and (B) male Oystercatchers with different bill-shape types. Data from Schiermonnikoog 1986–1993.

DISCUSSION

Differences in bill morphology among studies and between the sexes

The bill-tip shapes and dimensions in all six datasets discussed in this paper were categorized and measured using the same methodology (as in Swennen *et al.* 1983). It is generally thought that these six bill-shape types sufficiently describe most of the biological variation of interests in Eurasian Oystercatchers' bill morphology (Sutherland *et al.* 1996, Hulscher 1996). However, the results from our study suggest that discrete bill types may only exist in the eye of the human observer (Fig. 2). Moreover, we found that the bill-tip dimensions of a specific type of bill shape varied across studies and between the sexes (Figs. 3 and 4). These differences were unlikely to be caused by observer effects, as the same patterns were also evident in the measurements of one observer that participated in multiple studies.

Potentially, differences between studies in quantitative dimensions of the same bill type simply reflect different rates of abrasion of the same feeding technique in different areas or periods. The rates and specific location of abrasion is influenced by a variety of factors that could differ among studies due to the fact that studies differed in geographical location and the season or year in which was sampled (Table 1). Such factors could include the behaviour of prey (e.g. gaping width of shells, burrowing depth), prey morphology (e.g. hardness of shells, strength of the adductor muscle) as well as the toughness of the sediment in which they feed (mudflats, sandy flats, agricultural land). Nonetheless, these factors cannot easily be used to explain the sex differences in bill dimensions we observed within studies (Fig. 4).

The critical question now is whether the current categorization into distinct bill shapes captures the biological variation of interest or whether the additional micro-morphological differentiation described in this study has a further functional meaning. Do birds with the same bill-shape type, but different quantitative bill dimensions have a different (mixture of) feeding specialization or diet choice? Do they differ in the benefits (e.g. foraging efficiency) and costs (e.g. bill damage) of their feeding specialization? And, do they differ in their costs of switching between feeding specializations? Since all previous studies have used bill shape categorizations to describe bill dimensions these questions cannot be fully answered yet. Nonetheless, our results suggest that the higher bill tip of males (Fig. 3) is indeed associated with diet differences (more shellfish; Fig. 6), but not always with lower costs (bill damage; Fig. 5) when comparing males and females with the same bill-shape type.

The usefulness of bill-shape types as a proxy

Bill shape–diet relationships of free-living birds were only partly consistent across studies (Table 2). Within studies there were much clearer bill shape–diet relationships, with the proportion of shellfish increasing and worms decreasing in the diet when comparing a bill shape gradient from pointed to chisel/blunt bills. Nonetheless, in one winter study this within-study

gradient reflected large differences in diet, while in one summer study differences were rather subtle (Table 2). Food availability varies in space and an Oystercatcher's diet is known to differ between summer (more worms) and winter (more bivalves). However, this does not explain why bill shape–diet relationships differ between seasons or sites. It thus remains unclear why bill shape–diet relationships vary across studies.

The idea of using bill-shape types as a proxy for diet choice (Verhulst *et al.* 2004) is based on the clear-cut results from diet manipulation experiments on captive birds and knowledge about the mechanism (abrasion) causing the different bill shapes (Swennen *et al.* 1983, Hulscher 1985). However, in the wild the interpretation of bill shape as a proxy for diet choice in Oystercatchers seems to be different for each study. In addition, the observation that females and males have different bill shape–diet relationships (Fig. 6) suggests that it might be problematic to use bill-shape types as a proxy for diet choice in studies that ignore sex differences. Consequently, using results on bill shape–diet relationships from studies conducted in other areas and/or seasons to justify the use of bill-shape types as a proxy for diet can be problematic. When using bill-shape types as a proxy for diet in a specific area or season, it seems important to validate bill shape–diet relationships for at least a subset of the data for each sex, even though such a validation is contradictory to the idea of a proxy as a quick measure to infer the value of a variable of interest that is more difficult to measure. In addition, as the bill-tip is continually growing (0.4 mm/day; Hulscher 1985) and abrading it is important to measure both bill morphology and diet choice of the same individual within an as short a time span as possible. Finally, more agreement across studies is required in how an individual's diet is quantified.

Are quantitative bill dimensions a better proxy?

We propose that when studying bill morphology it is more fruitful to focus on quantitative bill dimensions than on a visual categorization of bill shapes. First, because in contrast to the existence of distinct feeding techniques, there is no evidence that bill-shape types are distinct entities (Fig. 2), and thus the categorization omits potentially useful information about bill morphology (Figs. 3 and 4). Second, because quantitative measurements of bill dimensions are more likely to be repeatable between observers and studies than the visual categorization of bill shapes. Third, because bill-tip width and depth seem a logical choice of biological relevant traits as they are directly affected by the amount of lateral, dorsal and frontal abrasion resulting from the various feeding specializations. Probably bill length and bill depth (Fig. 1) are useful additional quantitative measures to include in such a proxy. Same-sex birds with the same bill-shape type can differ substantially in bill length (see Fig. 3.7 in Sutherland *et al.* 1996), which could directly affect how deep they can probe for food and thereby which diet is available to them. Furthermore, short bills with a high bill depth are thought to be most suitable for specializing on hard-shelled bivalves, as they probably can exert most force when hammering the shell and prizing the valves apart (Hulscher & Ens 1992).

Possibly, a visual classification may capture aspects of the bill shape that are not captured by the bill-tip width and depth (Fig. 1). In fact, Swennen *et al.* (1983) argued that the overlap found in ranges of bill-tip measurements between bill shapes was largely due to the fact that the classification by eye is done at the very end of the tip, whereas measurements were done at 3 mm from the tip. The 3 mm from the tip was chosen for practical reasons as the jaws of most callipers are 3 mm thick, which facilitates easy measurement. Furthermore, measuring the bill-tip width and depth closer to the bill tip can be problematic due to bill-tip damage. However, we see no reason why measuring bill-tip width and depth at 3 mm from the tip should give less reliable impression of bill shapes. Lateral and dorsal abrasion occurs well up to 3 mm from the tip, and frontal abrasion also affects where exactly on the bill the bill-tip depth is measured. In fact, Durell *et al.* (1993) already showed that bill-tip width and depth at 3 mm from the tip are a good predictor of prey-handling technique. Nonetheless, an important verification would be to compare whether more of the variation in diet choice can be explained by a combination of quantitative bill measurements than by bill shape alone (for which the required data is regrettably still lacking). Thus, although we think that there are many reasons to prefer quantitative measurements over visual bill-shape qualification, it still remains to be formally tested whether quantitative bill dimensions are a better proxy for feeding specialization than bill-shape types are.

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SAMENVATTING

De Scholekster *Haematopus ostralegus ostralegus* is een klassiek voorbeeld van een voedselspecialist. Het eten van verschillende prooien, zoals wormen en schelpdieren, veroorzaakt slijtage op verschillende plekken op de snavelpunt, en daarmee variatie in snavelvormen. De snavelvorm van de Scholekster is dan ook gebruikt als een indicator ('proxy') voor voedselspecialisatie, omdat het een snelle en makkelijke manier is om het menu van deze mariene toppredator te bepalen. Echter, een aantal aspecten met betrekking tot de bruikbaarheid van de snavelvorm als indicator voor voedselkeuze zijn tot nu toe onderbelicht. Zo wordt de snavelvorm van Scholeksters doorgaans visueel geclassificeerd in discrete typen, terwijl er sprake zou zijn van een geleidelijke overgang tussen de types. Ook is het onduidelijk in hoeverre classificaties van de snavelvorm vergelijkbaar zijn tussen de verschillende studies en tussen de seksen, en hoe universeel de snavelvorm–voedselrelaties zijn. In het onderhavige artikel wordt op basis van vier nieuwe en twee gepubliceerde datasets de bruikbaarheid van de snavelvorm als indicator voor de voedselkeuze van Scholeksters onderzocht. Metingen aan de snavelvorm leverden geen aanwijzingen op voor het bestaan van discrete types van de snavelvorm. Verder bleken de maten van dezelfde types snavelvorm tussen de studies te verschillen. Gesteld wordt dat dit verschil geen gevolg is van verschillen in methodologie, maar mogelijk een gevolg is van een additionele subtiele voedselspecialisatie bij vogels met een zelfde type snavelvorm. Verder bleek de snavelpunt van mannetjes doorgaans 7% hoger te zijn dan die van vrouwtjes met een zelfde type snavelvorm. Een hogere, en waarschijnlijk sterkere, snavelpunt bij mannetjes kan verklaren waarom mannetjes meer schelpdieren eten en minder last van snavelbreuk hebben dan vrouwtjes met een zelfde type snavelvorm. Op grond van een literatuurstudie laten we ten slotte zien dat gepubliceerde snavelvorm–voedselrelaties tussen verschillende studies en tussen de seksen verschillen. We concluderen dat de interpretatie van snavelvormtype als indicator voor voedselkeuze bij Scholeksters sterk kan verschillen tussen studies. Daarnaast stellen we voor dat een combinatie van verscheidene kwantitatieve maten van de snavelvorm een betere indicator van voedselspecialisatie is dan snavelvormtypes.

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