

EVOLUTION OF FORAGING STRATEGIES IN SHOREBIRDS: AN ECOMORPHOLOGICAL APPROACH

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ABSTRACT.—We studied the relationships between bill and hindlimb morphology and foraging behavior in 17 species of shorebirds within a phylogenetic framework. The results show that the evolutionary change in bill length is related to the evolutionary change in foraging strategies from visual hunting to tactile hunting. We also found evolutionary relationships between an increase in bill length and both plunging and sweeping foraging movements, and a decrease in bill length and “routing” behavior. No relationships were found between hindlimb morphology and movement pattern (continuous hunting species vs. pause-travel species). Examining the evolutionary rate of change in bill and hindlimb structures shows that the family Scolopacidae and the subfamily Recurvirostrinae evolved more rapidly than the species of Charadriinae. Results from our ecomorphological and evolutionary analysis support the hypothesis by Zweers and co-workers on the evolution of feeding mechanisms in shorebirds. Received 5 January 1998, accepted 14 December 1998.

RELATIONSHIPS BETWEEN MORPHOLOGY and foraging ecology are well known in birds (e.g. Newton 1967, Hespenheide 1973, Lederer 1975, Eckhardt 1979, Grant 1986, Carrascal et al. 1990). In shorebirds, the importance of bill morphology with regard to prey handling (Swennen et al. 1983), diet (Strauch and Abele 1979, Lifjeld 1984), and microhabitat selection (Baker 1979, Gerritsen and van Heezik 1985) also has been recognized. The relationship between bill morphology and foraging strategies in shorebirds provides a useful example for the explanation of morphological relationships within a phylogenetic framework. Zweers (1991a), Zweers and Gerritsen (1997), and Zweers and Vanden Berge (1997) used deductive reasoning to construct a hypothesis about the evolution of foraging strategies in several aquatic birds, including shorebirds. However, their methods were mainly a reconstruction of evolutionary characters, in contrast to methods that are used to detect adaptations (see Lauder 1990, Baum and Larson 1991) in which the change in form and function should be congruent along the phylogeny (Brooks and McLennan 1991, Larson and Losos 1996).

In this study, we analyze the ecomorphological patterns relating skeletal morphology

(feeding and locomotion) and foraging behavior in 17 species of shorebirds. Our main goal is to demonstrate the coevolution of morphological and ecological traits, thereby demonstrating the adaptive value of morphological traits (Brooks and McLennan 1991, Larson and Losos 1996). We also test hypotheses of Zweers and co-workers on the evolution of feeding mechanisms.

METHODS

We studied foraging behavior (Appendix 1) and skeletal morphology of the bill and hindlimb (Appendix 2) of 17 species of shorebirds. The study was conducted at the Ebro Delta Natural Park in northeastern Spain (40°43'N, 01°00'E), which is one of the most important areas for shorebirds in the Mediterranean (Grimmet and Jones 1989, Barbosa 1997a). Observations were made between November and April in 1990–1991 and 1991–1992. The area consists of 32,000 ha, 15,000 ha of which are rice fields, 9,500 ha are market gardens, and 7,500 ha are natural wetlands; 16,000 ha are potentially suitable for shorebirds (Barbosa 1996).

We used the focal-observation method (Altmann 1974) to study foraging behavior. Focal birds were randomly chosen during regular surveys, and their behaviors were recorded onto a tape recorder during a 2-min period on average (range 1 to 3.5 min). Foraging behavior was classified as pecking (penetration of substrate by less than one-quarter of bill length), probing (penetration of substrate by more than one-quarter of bill length), routing (manipulation of seaweed or stones by “bulldozing” or turning

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and then capturing prey by pecks), plunging (head and neck enter water [Hamilton 1975]), sweeping (side to side movements of bill introduced in water), walking, and stopping. Although not all of the foraging behaviors were used by all species, they were representative of all the behavioral mechanisms exhibited by the shorebirds. Time spent using each behavior during the sample period was recorded excluding handling time. Foraging behavior is known to vary within species between locations owing to differences in prey abundance, prey size, and substrate differences. At the behavioral level of this study (i.e. the description of general foraging behavior of a species), changes in foraging behavior due to differences in prey abundance would affect the less behaviorally stereotyped species as sandpipers and allies but not plovers. Previous work on Dunlins (*Calidris alpina*) showed that foraging techniques were not related to different habitats that varied in resource abundance, nor did they differ between years (Barbosa 1996, 1997b).

To reduce problems of pseudoreplication, we tried to sample individuals only once. Because birds were not marked, we sampled no more birds in a flock than would have prevented us from being sure they were different individuals. For example, in a flock of about 100 individuals, we sampled 5 to 10 birds each from the upper, lower, left, and right sides of the flock. Each bird sampled was at least at 20 m from the previous bird sampled. Both the size of the study area (16,000 ha) and the number of shorebirds (20,000 to 30,000 individuals) made it virtually certain that different individuals were sampled with this method.

Morphological data were obtained from 350 prepared skeletons (see Acknowledgments). Variables measured were bill length, bill depth, bill width, maximum femur length, maximum tibiotarsus length, maximum tarsometatarsus length, pelvis length, and antitrochanteric width (see Fig. 1). All measurements were made with digital calipers (± 0.01 mm). We selected these variables in relation to their specific biological functions assessed through previous studies in such a way that any relative difference in character morphology could be correlated with foraging data that we thought should be related based on functional properties (Barbosa and Moreno 1995). Morphological variables were grouped into functional units (feeding apparatus and hindlimb). Information on the number of mechanoreceptors in the bill was taken from Hoerschelmann (1972) and from museum specimens for *Himantopus himantopus* and *Recurvirostra avosetta*. We corrected the number of mechanoreceptors by the length of the bill where mechanoreceptors were present so that the data were comparable with those of Hoerschelmann (1972). We did not use any variable related to rynchokinesis because it is a mechanism related to handle burrowing prey (Zusi 1985, Zweers and Gerritsen 1997),

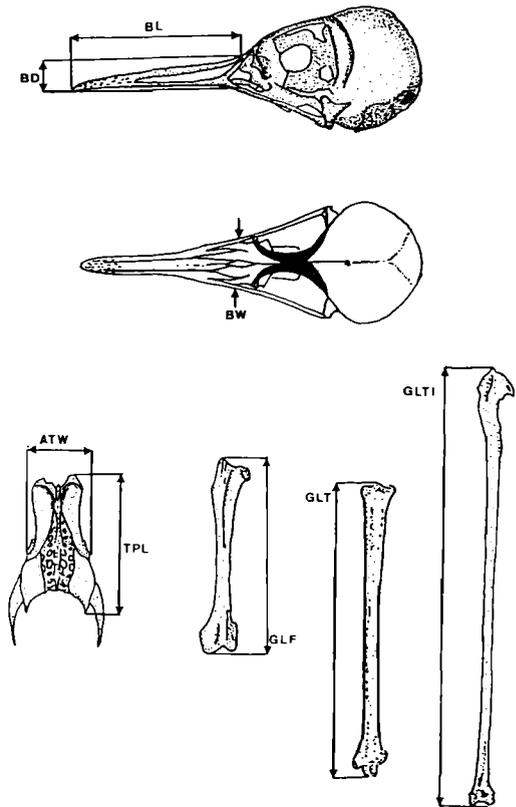


FIG. 1. Measurements of morphological variables. BL = bill length; BW = bill width; BD = bill depth; GLF = maximum femur length; GLTI = maximum tibiotarsus length; GLT = maximum tarsometatarsus length; TPL = pelvis length; ATW = antitrochanteric width.

whereas our behavioral data were related to foraging behavior during searching exclusive of handling times (see Methods).

Behavioral and morphological data were analyzed using principal components analysis (PCA). A PCA was performed to characterize foraging strategy, and two PCAs were performed on morphological variables, one on the feeding system and one on the hindlimb. PCAs were based on correlation matrices to overcome the problem of character scaling (Freeman and Jackson 1990). Prior to analyses, the original data were normalized by arcsin transformation or log transformation, as appropriate. Results presented for analyses are correlations (loadings) of transformed variables with orthogonally rotated multivariate factors (varimax rotations of the principal components). Morphological variables were divided by the cube root of body mass to obtain size-corrected lengths. Mass data were not available for

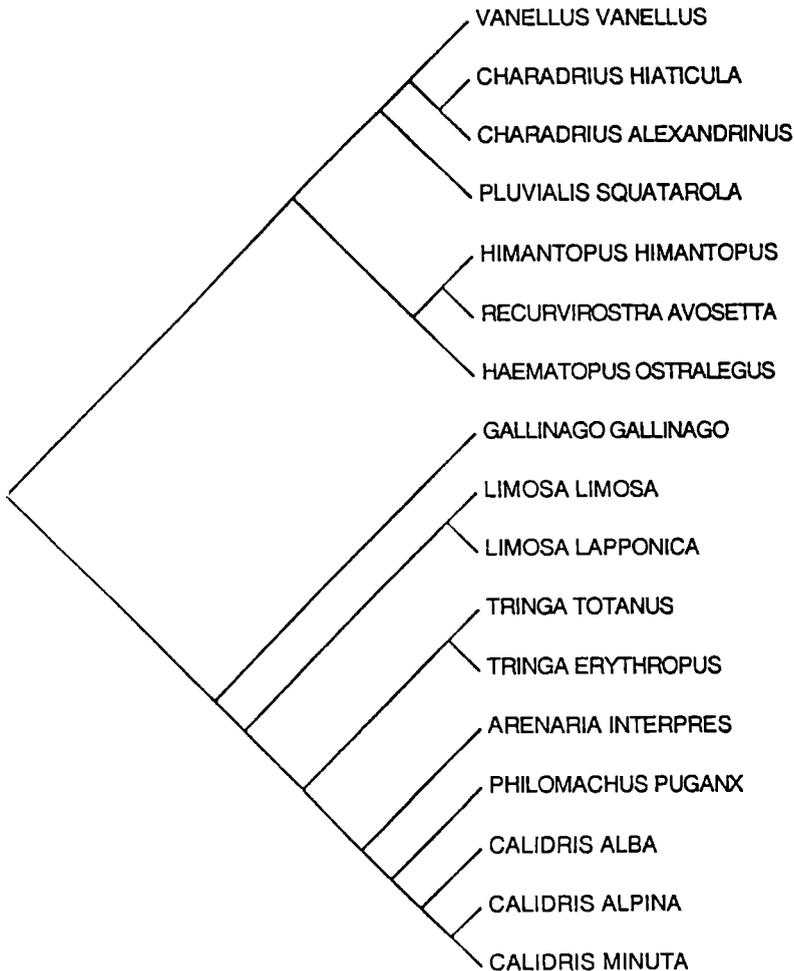


FIG. 2. Hypothesized phylogenetic relationships for waders used in the evolutionary analyses (based on Strauch 1978, Sibley and Ahlquist 1990).

most of the skeletons in museum collections. Hence, body-mass data were obtained from Cramp (1983).

The relationship between foraging behavior and morphology was studied using analysis of independent contrasts (Felsenstein 1985). These contrasts are calculated as the value of a trait at one tip (or node) of a phylogeny subtracted from the value of its sister tip or node. Thus, each species or node is compared with its closest included relative. If characters have evolved in a Brownian fashion, the contrasts are statistically independent (see Harvey and Pagel 1991, Martins and Garland 1991, Garland et al. 1992). Therefore, phenotypic data for the tip species of any monophyletic group can be transformed into $n - 1$ independent contrasts.

Felsenstein's method requires complete knowledge of phylogenetic relationships among species and branch lengths (in units of expected variance of char-

acter change). We used phylogenetic information (Fig. 2) from Sibley and Ahlquist (1990), which differs from AOU (1998) in placing avocets in a subfamily of the Charadriidae rather than in their own family. Phylogenetic relationships of species not analyzed by these authors have been inferred from Strauch (1978). Two phylogenies of the Charadriiformes have recently been published (Björklund 1994, Chu 1995) based on data from Strauch (1978). Although some differences arise in both phylogenies from those of Strauch (1978) and Sibley and Ahlquist (1990), they do not affect the species used in our study.

Because phenotypic evolution is not necessarily so perfectly gradual, adequate standardization of contrasts by branch lengths must be tested empirically. Following Garland et al. (1992), we regressed the absolute values of contrasts against their standard de-

TABLE 1. Results of principal components analysis on foraging behavior of shorebirds.

	PC1E	PC2E	PC3E	PC4E	PC5E
% Pecking	0.78**	0.07	-0.32	-0.08	-0.04
% Probing	-0.94**	0.07	-0.19	-0.10	-0.02
% Walking	0.39	0.75**	0.23	0.03	0.06
% Stopping	0.48	-0.79**	0.11	-0.01	0.01
% Routing	0.00	0.03	-0.01	0.00	0.99**
% Sweeping	0.01	0.03	-0.02	0.99**	0.00
% Plunging	-0.02	0.07	0.93**	-0.02	-0.02
Eigenvalue	1.91	1.29	1.03	1.01	0.97
% Variance explained	27.4	18.5	14.8	14.5	13.6

** P < 0.01.

viations. No significant trends were found, indicating that standardization was adequate. Because the direction of subtraction in each contrast is arbitrary, regression through the origin was used (Garland et al. 1992).

Evolutionary rates of change have been analyzed following the methodology developed by Garland (1992) based on phylogenetically independent contrasts. The absolute value of contrasts provides an independent index of the minimum amount of phenotypic evolution that has occurred as one hypothetical ancestor diverged to yield two daughter species scaled by the square root of time (Garland 1992). Scores from the PCAs were used to obtain independent contrasts and to analyze the evolutionary rate of change. The "evolutionary gradualist model" has been used in the analyses. Statistical tests are indicated when used. Probabilities smaller than 5% are termed significant. Differences in evolutionary rates of change were analyzed graphically owing to the low number of clades (subfamilies) within the species studied.

RESULTS

Foraging behavior.—The first five factors in the PCA analysis of behavioral variables accounted for 88% of the variance (Table 1). The first factor (PC1E) was positively related with the percentage of time pecking and negatively with the percentage of time probing. PC1E defined a behavioral gradient related to searching technique that ranged from visual hunting (i.e. species spending most of their time pecking) to tactile hunting (i.e. species spending most of their time probing; Fig. 3A). The second factor (PC2E) was negatively related with the percentage of time stopping and positively related with the percentage of time walking. This factor also defined a behavioral gradient related to movement patterns during searching that ranged from continuous searching to pause-travel foraging (Fig. 3A). These two factors defined two groups of species that were separated by foraging strategies: (1) pause-travel (or stop-run-

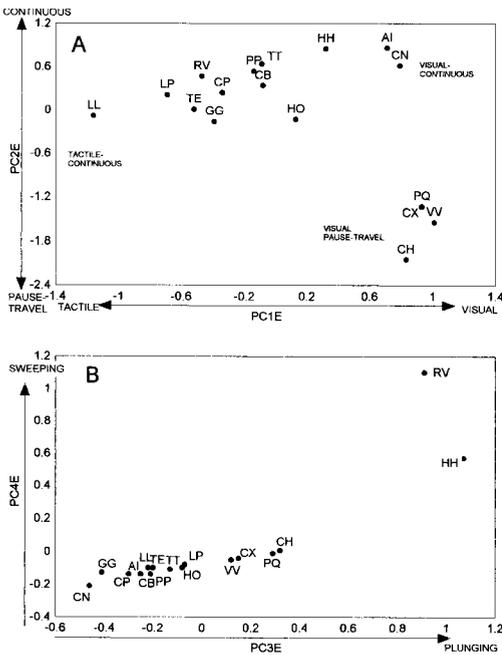


FIG. 3. Ordination of wader species within the plane spanned by behavioral factors from (A) the first and second PCA factors and (B) the third and fourth PCA factors. AI = *Arenaria interpres*; CB = *Calidris alba*; CH = *Charadrius hiaticula*; CN = *Calidris minuta*; CP = *Calidris alpina*; CX = *Charadrius alexandrinus*; GG = *Gallinago gallinago*; HH = *Himantopus himantopus*; HO = *Haematopus ostralegus*; LL = *Limosa limosa*; LP = *Limosa lapponica*; PP = *Philomachus pugnax*; PQ = *Pluvialis squatarola*; RV = *Recurvirostra avo-setta*; TE = *Tringa erythropus*; TT = *Tringa totanus*; VV = *Vanellus vanellus*.

stop) species that mainly forage by scanning the area in front of them and pecking at the substrate surface when they detect a prey item (*Vanellus vanellus*, *Charadrius hiaticula*, *Charadrius alexandrinus*, *Pluvialis squatarola*); and (2) continuously feeding species that either probe as they walk (*Limosa limosa*, *Limosa lapponica*, *Tringa erythropus*, *Recurvirostra avosetta*) or peck at items that they see on the substrate surface (*Arenaria interpres*, *Calidris minuta*). Several species occupied an intermediate position along the gradient, such as *Gallinago gallinago*, *Tringa totanus*, *Philomachus pugnax*, *Calidris alpina*, *Calidris alba*, *Himantopus himantopus*, and *Haematopus ostralegus*.

The other factors obtained from the PCA were related to specialized behaviors in resource use and were mainly restricted to one species each. The third factor (PC3E) was positively related to the percentage of time plunging, and the fourth factor (PC4E) was positively related with foraging by sweeping. These two factors clearly segregate *Himantopus himantopus* and *Recurvirostra avosetta* from the other species (Fig. 3B). The fifth factor (PC5E) was related to the routing behavior displayed by *Arenaria interpres*.

Morphology.—The PCAs performed on bill morphology resulted in a factor that was related to an increase in bill width and depth (PC1MB) and a second factor that was related to an increase in bill length (PC2MB; Table 2). Figure 4A shows the location of species in the plane spanned by the two factors. A group of short-billed species composed of *Charadrius hiaticula*, *Charadrius alexandrinus*, *Vanellus vanellus*, *Pluvialis squatarola*, and *Arenaria interpres* was clearly segregated from the other species along the second factor. The first factor showed a continuous gradient across species, from *Tringa erythropus* and *Himantopus himantopus* with the narrowest and more flattened bills, to *Calidris minuta*, *Haematopus ostralegus*, and *Gallinago gallinago* with the widest and deepest bills.

Results of PCAs performed on hindlimb variables (Table 2) showed a first morphological factor (PC1MH) related to an increase in relative length of the tibiotarsus and tarsometatarsus. The second factor (PC2MH) was related to an increase in the relative length of the femur and total pelvis length. The third factor (PC3MH) was related to an increase in relative

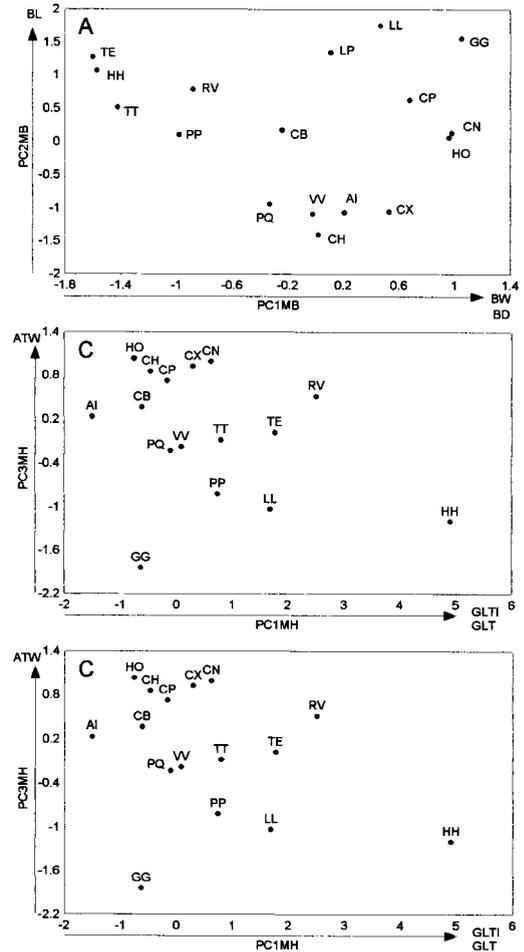


FIG. 4. Ordination of species within the plane spanned by morphological factors from the PCA. (A) Bill factors, PC1MB vs. PC2MB; (B) hindlimb factors PC1MH vs. PC2MH; (C) hindlimb factors PC1MH vs. PC3MH. Morphological variables as in Figure 1; species code as in Figure 2.

antitrochanteric width. Figure 4B shows a gradient in species location within the plane spanned by the two first morphological factors. This gradient ranges from *Himantopus himantopus*, with the longest tibiotarsus and tarsometatarsus and the shortest femur and pelvis, to *Haematopus ostralegus*, with the shortest distal segments and the longest femur and pelvis. A gradient also existed from *Gallinago gallinago*, with the narrowest pelvis, to *Haematopus ostralegus*, with the widest pelvis (Fig. 4C).

Ecomorphological and evolutionary analyses.—Bill length (factor PC2MB) was the only mor-

TABLE 2. Results of principal components analysis performed on bill and hindlimb variables of shorebirds after removing size effects.

Variable	PC1MB	PC2MB	PC1MH	PC2MH	PC3MH
Bill					
Bill length	0.13	0.98**			
Bill depth	0.82**	0.19			
Bill width	0.86**	0.04			
Eigenvalue	1.63	0.82			
% Variance explained	54.4	27.6			
Hindlimb					
Femur length			-0.02	0.67*	-0.36
Tibiotarsus length			0.97**	0.06	-0.06
Tarsometatarsus length			0.97**	0.03	-0.13
Total pelvis length			0.09	0.86**	0.11
Antitrochanteric width			-0.14	-0.06	0.93**
Eigenvalue			2.11	1.23	0.86
% Variance explained			42.2	24.6	17.2

* $P < 0.05$; ** $P < 0.01$.

phological variable that was significantly correlated with foraging behavior. Bill length was correlated on the one hand with the behavioral factor that defined visual and tactile foraging strategies (PC1E; $r = -0.67$, $P = 0.003$) and on the other hand with factors that defined sweeping (PC4E; $r = 0.48$, $P = 0.05$) and routing (PC5E; $r = -0.57$, $P = 0.016$) behavior. No morphological hindlimb factors were related to any behavioral factor ($P > 0.05$). The number of mechanoreceptors was highly correlated to the behavioral factor defining visual and tactile foraging strategies (PC1E; $r = -0.60$, $P = 0.010$).

Evolutionary correlations showed a positive and significant relationship between an increase in bill length with an increase in hindlimb length ($r = 0.84$, $P = 0.00001$). Results of analyses of evolutionary rate of change of bill length showed a rate of change slightly higher in the Scolopacidae than in the Charadriidae (Fig. 5A). Charadriids showed a high value in the contrast that segregated the subfamilies Charadriinae and Recurvirostrinae. However, the evolutionary rate of change in bill width and bill depth did not show any difference between the Scolopacidae and the Charadriidae (Fig. 5B).

Barbosa (1993) analyzed evolutionary rates of change in the hindlimb in a larger number of species than that considered here. Our results are consistent with those previous results. Considering the distal segments of the hindlimb (tibiotarsus and tarsometatarsus), there were no differences between the families Scol-

opacidae and Charadriidae (Fig. 6A). However, the contrasts of species in the subfamily Recurvirostrinae showed the fastest change in the lengthening of the tibiotarsus and tarsometatarsus, the Charadriinae showed the slowest rate of change in these distal segments, and the Tringinae showed an intermediate position. No clear differences existed in the evolutionary rate of change in femur and pelvis length, although again, the rate of change in the Recurvirostrinae and the Tringinae was higher than that in the Charadriidae (Fig. 6B). We found no differences among clades in the change in antitrochanteric width (Fig. 6C).

Results of evolutionary rate of change in behavior (from visual to tactile hunting) showed a slightly higher rate in the Scolopacidae than in the Charadriidae, and within these, the Recurvirostrinae showed the highest rate of change (Fig. 7A). Evolutionary changes in mode of locomotion (continuous vs. pause-travel) showed that the Charadriidae had a higher rate than the Scolopacidae, and again, the subfamily Recurvirostrinae changed at the highest rate (Fig. 7B).

DISCUSSION

Several studies of shorebirds have pointed out that morphology and foraging behavior are related (Strauch and Abele 1979, Swennen et al. 1983, Lijfeld 1984). Whether this relationship is adaptive can be assessed only if the evolution of morphological traits has occurred in parallel with that of behavioral traits (Brooks and

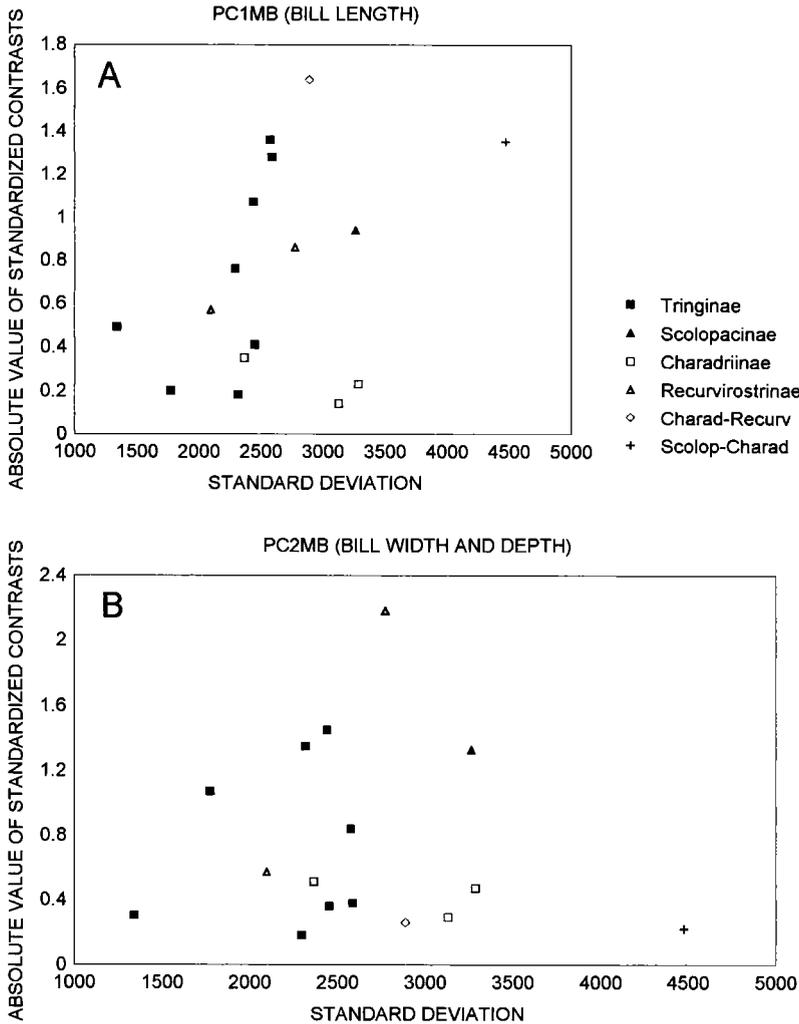


FIG. 5. Evolutionary rate of change in bill morphology. (A) Bill length (PC1MB); (B) bill width and depth (PC2MB). Filled triangles = Scolopacinae; filled squares = Tringinae; open squares = Charadriinae; open triangles = Recurvirostrinae; open rhombus = basal node between Charadriinae and Recurvirostrinae; cross = basal node between Scolopacidae and Charadriidae.

McLennan 1991), and this can be achieved only within a phylogenetic framework (Losos and Miles 1994). Our results show that at least within the species studied, an ecomorphological pattern relates bill shape and feeding technique: longer bills are adaptively coupled to the use of a tactile foraging strategy, whereas shorter bills are related to a visual strategy.

The functional requirements of a tactile foraging strategy are (1) high penetration capacity, and (2) high inspection capacity (Zweers 1991a, Zweers and Gerritsen 1997, Zweers and Vanden Berge 1997). Maximizing penetration

requires a bill shape that minimizes penetration costs through the lengthening, narrowing, and flattening of the bill. Zweers (1991a) and Zweers and Gerritsen (1997) pointed out the general morphological requirements for probing: (1) the bill should be long and narrow, but not very slender; and (2) the penetrating portion should be flattened either vertically or horizontally. Our results show that the only modification that has coevolved with a tactile foraging strategy is the lengthening of the bill, whereas any change in bill width and depth does not seem to be coupled with becoming a

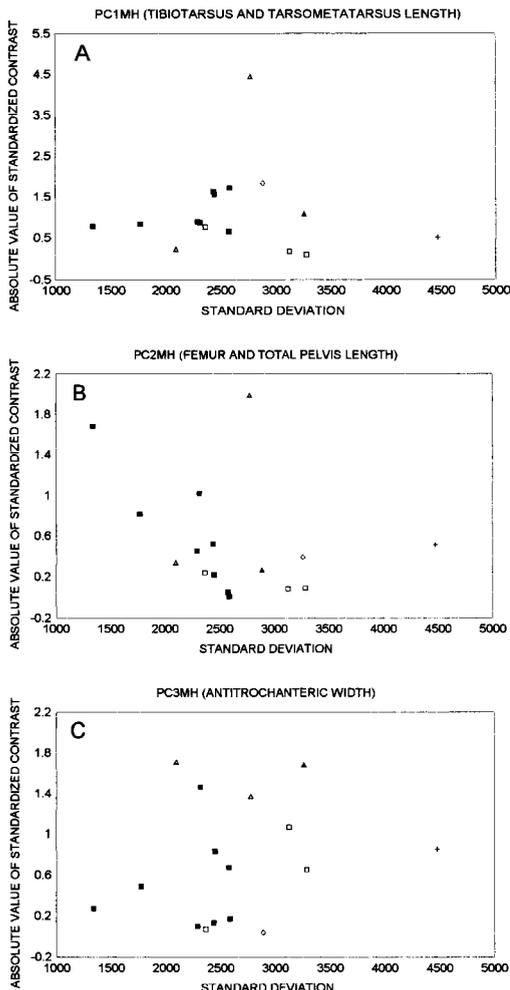


FIG. 6. Evolutionary rate of change in hindlimb morphology. (A) Tibiotarsus and tarsometatarsus length (PC1MH); (B) femur length and total pelvis length (PC2MH); (C) antitrochanteric width (PC3MH). Symbols as in Figure 5.

prober. However, this disagreement could have resulted because our measurements of bill width and depth were taken proximal to the penetrating portion of the bill (see Fig. 1).

A remote touch system is thought to be required for a tactile foraging strategy (Gerritsen et al. 1983, Gerritsen and Meijboom 1986). Piersma et al. (1995) experimentally showed the use of a remote-touch mechanism for prey capture in Red Knots (*Calidris canutus*). Our results show a link between the evolution of a foraging strategy from pecking to probing and an increase in the number of mechanoreceptors in

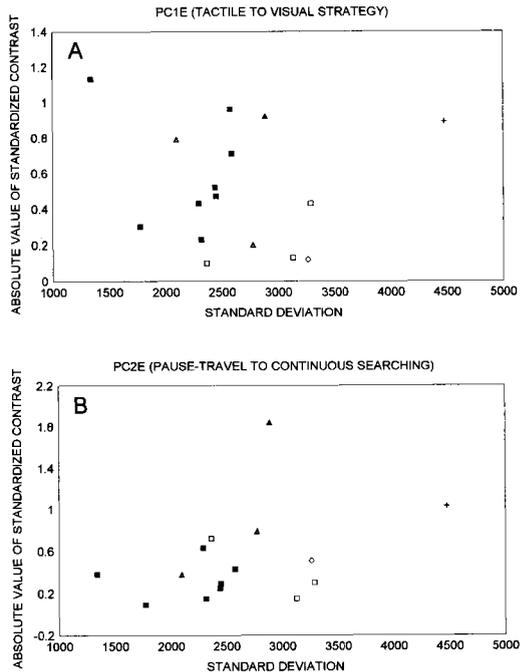


FIG. 7. Evolutionary rate of change of foraging behavior. (A) Tactile and visual strategy (PC1E); (B) pause-travel and continuous searching strategy (PC2E). Symbols as in Figure 5.

the bill tip, which suggests that these specialized structures are an evolutionary adaptation for tactile foraging. An evolutionary pathway from pecking to probing has been proposed by Zweers (1991a), Zweers et al. (1995), Zweers and Gerritsen (1997), and Zweers and Vanden Berge (1997) using deductive methodology. This hypothesis considers pecking to be the "historical initial condition" for avian feeding mechanisms (Zweers 1991b; Zweers et al. 1994, 1997). Basically, in coastal habitats that have a rich food supply during low tide, a pause-travel strategy with superficial probe-hunting mechanisms was favored. This strategy initiated lengthening of the legs, likely to increase the amount of area searched (Barbosa 1994, Barbosa and Moreno 1999), and as a compensation, a lengthening of the bill. Afterward, by accidental deeper penetrations, increased food supplies in the substrate were discovered, and penetration became rewarding, which led to longer bills. From this, two bifurcations occurred; first, direct touch-hunting with lengthened slender beaks led to inspection of the water column, so that head sweeping became re-

warding. Second, remote touching developed, which decreased penetration costs and supported a tactile foraging strategy.

Although the hypothesis of Zweers and co-workers was not developed from a strict phylogenetic framework, our results confirm the evolutionary scenario that they defined. The co-evolution between bill morphology (bill lengthening and increasing mechanoreceptors) and foraging behavior, the parallel change in the lengthening of the bills and legs, and the results shown by the evolutionary rate of change in morphology and behavior in each clade considered (higher rate in the Scolopacidae [which are tactile feeders] and the Recurvirostrinae [which are visual or direct-touch species that mainly forage in deep water] than in the Charadriinae [which mainly forage on dry surfaces]), support Zweers' hypothesis.

In ecomorphological studies, a problem arises if the ecological or behavioral data provided are not representative of the ecology or behavior of the species in question. This problem could be due to restricted geographic sampling or to restricted seasonal sampling. In shorebirds, species in the genera *Calidris* and *Tringa* could be very sensitive to behavioral sampling procedures because these birds vary considerably in the use of pecking and probing depending on the factors noted above (Baker and Baker 1973). On the other hand, to determine the adaptive character of a trait, it is necessary to take into account the possible selective pressure acting on the trait (Larson and Losos 1996); therefore, sampling must be made when the pressure is most likely to be highest. Selective pressures are not necessarily present during the entire annual cycle. In our study, despite the restricted geographic sampling, we found no differences in foraging behavior compared with other geographic areas (see Bengtson and Svensson 1968, Burton 1974, Szekely and Bamberger 1992, Boettcher et al. 1994, Moreira 1994). With respect to seasonal sampling, Baker and Baker (1973) pointed out that shorebird populations are regulated through competitive processes that occur on the wintering grounds. Therefore, it seems that winter is the time when selective pressures are high for shorebirds, which coincides with our sampling period. Moreover, Burger (1984) stated that shorebirds spend 60% or more of the year on the wintering grounds, which are mainly coast-

al areas such as those we sampled. In conclusion, we believe that our behavioral data are representative of the foraging behaviors of the species in question and that evolutionary conclusions we have obtained are correct. Moreover, the confirmation of the hypothesis on the evolution of foraging strategies in shorebirds (Zweers 1991a, Zweers et al. 1995, Zweers and Gerritsen 1997, Zweers and Vanden Berge 1997) indicates that this is the case.

Relative to movement patterns, shorebirds show a gradient from continuous-hunting species to pause-travel species (Fig. 2A; see McLaughlin [1989] for discussion of foraging-modes classification). Results of our evolutionary analysis did not show a relationship between changes in hindlimb morphology and differences in foraging behavior. In shorebirds, hindlimb morphology (skeletal and muscular) is correlated with variables that describe locomotion relative to frequency and length of stride (Barbosa and Moreno 1999). Although Eckhard (1979) found differences in morphology between similar categories of insectivorous birds, it seems that relationships between morphology and foraging mode (movement pattern) are not very tight (Garland and Losos 1994). Continuous-hunting species must maintain locomotion over a long time period; therefore, such species must have great endurance. Fry (1947) and Bennett (1985, 1989) pointed out that endurance is explained by the maximum rate of aerobic metabolism and not by the structure of the muscular-skeletal system. Walton (1993) has shown in hyliid frogs, the relationship between the increase in rate of aerobic metabolism and endurance has been maintained over evolutionary time. This relationship also may hold for shorebirds, but experimental work such as respirometry studies must be performed to explore this possibility.

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APPENDIX 1. Use of various foraging behaviors by shorebirds (mean % use \pm SE). "Other" refers to activities not related specifically to foraging (e.g. preening, scanning, and fighting).

Species	Pecking	Probing	Walking	Stopping	Sweeping	Plunging	Routing	Others
<i>Vanellus vanellus</i> (36)	18.2 \pm 2.11	0.0 \pm 0.00	26.3 \pm 1.97	53.1 \pm 3.24	0.0 \pm 0.00	0.0 \pm 0.00	0.0 \pm 0.00	1.6 \pm 0.71
<i>Charadrius alexandrinus</i> (31)	15.0 \pm 1.82	0.0 \pm 0.00	29.2 \pm 2.96	46.7 \pm 3.34	0.0 \pm 0.00	0.0 \pm 0.00	0.0 \pm 0.00	9.0 \pm 2.88
<i>Charadrius hiaticula</i> (7)	7.5 \pm 1.43	0.0 \pm 0.00	20.5 \pm 4.03	66.7 \pm 3.65	0.0 \pm 0.00	0.0 \pm 0.00	0.0 \pm 0.00	5.2 \pm 2.24
<i>Pluvialis squatarola</i> (35)	10.7 \pm 1.45	0.0 \pm 0.00	34.4 \pm 2.89	52.4 \pm 3.22	0.0 \pm 0.00	0.0 \pm 0.00	0.0 \pm 0.00	2.2 \pm 0.76
<i>Haematopus ostralegus</i> (8)	20.3 \pm 6.40	12.1 \pm 4.90	37.6 \pm 3.39	12.8 \pm 5.81	0.0 \pm 0.00	0.0 \pm 0.00	0.0 \pm 0.00	17.2 \pm 5.43
<i>Himantopus himantopus</i> (25)	5.9 \pm 1.63	5.9 \pm 1.90	65.6 \pm 4.92	2.1 \pm 1.25	3.6 \pm 2.09	4.3 \pm 3.07	0.0 \pm 0.00	7.4 \pm 1.54
<i>Recurvirostra avosetta</i> (51)	2.0 \pm 0.99	31.2 \pm 3.68	49.0 \pm 2.63	0.1 \pm 0.04	1.7 \pm 0.90	4.5 \pm 1.49	0.0 \pm 0.00	10.6 \pm 2.12
<i>Gallinago gallinago</i> (7)	18.0 \pm 12.3	36.9 \pm 15.60	20.4 \pm 7.20	0.0 \pm 0.00	0.0 \pm 0.00	0.0 \pm 0.00	0.0 \pm 0.00	16.2 \pm 9.48
<i>Limosa limosa</i> (63)	2.2 \pm 1.18	67.4 \pm 2.75	25.4 \pm 2.09	0.0 \pm 0.00	0.0 \pm 0.00	0.0 \pm 0.00	0.0 \pm 0.00	4.8 \pm 1.13
<i>Limosa lapponica</i> (10)	2.6 \pm 1.88	48.0 \pm 7.88	38.2 \pm 6.98	1.8 \pm 1.76	0.0 \pm 0.00	0.0 \pm 0.00	0.0 \pm 0.00	9.1 \pm 2.23
<i>Tringa totanus</i> (29)	10.3 \pm 2.20	31.6 \pm 5.75	50.5 \pm 4.96	0.3 \pm 0.28	0.0 \pm 0.00	0.0 \pm 0.00	0.0 \pm 0.00	5.8 \pm 1.24
<i>Tringa erythropus</i> (10)	9.6 \pm 5.91	43.4 \pm 11.20	33.1 \pm 10.52	1.2 \pm 0.81	0.0 \pm 0.00	0.0 \pm 0.00	0.0 \pm 0.00	8.3 \pm 2.90
<i>Arenaria interpres</i> (11)	23.1 \pm 4.03	7.2 \pm 3.74	57.1 \pm 5.84	0.3 \pm 0.21	0.0 \pm 0.00	0.0 \pm 0.00	0.7 \pm 0.38	10.8 \pm 3.71
<i>Philomachus pugnax</i> (28)	14.4 \pm 3.12	35.3 \pm 4.20	44.0 \pm 2.86	0.0 \pm 0.00	0.0 \pm 0.00	0.0 \pm 0.00	0.0 \pm 0.00	6.1 \pm 2.62
<i>Calidris alba</i> (28)	18.0 \pm 4.12	37.4 \pm 5.84	41.1 \pm 2.84	2.0 \pm 0.97	0.0 \pm 0.00	0.0 \pm 0.00	0.0 \pm 0.00	1.5 \pm 0.62
<i>Calidris minuta</i> (45)	39.0 \pm 3.74	10.9 \pm 3.02	45.5 \pm 3.24	1.0 \pm 0.52	0.0 \pm 0.00	0.0 \pm 0.00	0.0 \pm 0.00	1.4 \pm 0.35
<i>Calidris alpina</i> (116)	15.6 \pm 2.06	43.8 \pm 2.85	34.4 \pm 1.82	0.7 \pm 0.33	0.0 \pm 0.00	0.0 \pm 0.00	0.0 \pm 0.00	5.5 \pm 1.19

APPENDIX 2. Skeletal measurements of shorebirds. Values are $\bar{x} \pm SE$ in mm, with n in parentheses.

Species	Bill length	Bill width	Bill depth	Femur length	Tibiotarsus length	Tarsometatarsus length	Pelvis length	Antitrochanteric width
<i>Vanellus vanellus</i>	32.9 ± 2.11 (40)	8.1 ± 0.59 (43)	6.6 ± 0.50 (16)	36.9 ± 0.19 (39)	70.3 ± 0.31 (39)	48.6 ± 0.32 (38)	41.4 ± 0.24 (34)	25.3 ± 0.25 (17)
<i>Charadrius alexandrinus</i>	23.3 ± 0.79 (9)	5.4 ± 0.29 (9)	3.8 ± 0.19 (7)	20.8 ± 0.18 (8)	41.9 ± 0.29 (9)	28.1 ± 0.28 (9)	25.4 ± 0.22 (7)	16.1 ± 0.22 (5)
<i>Charadrius hiaticula</i>	19.9 ± 1.25 (19)	5.6 ± 0.39 (19)	4.7 ± 0.25 (11)	23.0 ± 0.24 (20)	43.2 ± 0.37 (20)	26.2 ± 0.18 (21)	27.3 ± 0.28 (20)	18.2 ± 0.18 (9)
<i>Pluvialis squatarola</i>	35.2 ± 1.67 (21)	8.3 ± 0.62 (20)	6.6 ± 0.55 (17)	36.9 ± 0.26 (20)	70.3 ± 0.38 (21)	47.4 ± 0.38 (21)	45.8 ± 0.40 (22)	25.2 ± 0.34 (11)
<i>Haematopus ostralegus</i>	75.7 ± 5.54 (13)	13.2 ± 0.87 (17)	9.0 ± 0.87 (17)	47.0 ± 0.41 (18)	84.2 ± 0.67 (19)	51.6 ± 0.60 (19)	65.0 ± 1.61 (18)	35.0 ± 0.34 (10)
<i>Himantopus himantopus</i>	80.8 ± 8.10 (5)	10.2 ± 0.41 (6)	4.9 ± 0.20 (3)	34.8 ± 0.55 (8)	131.5 ± 3.61 (8)	119.2 ± 2.97 (8)	40.8 ± 0.40 (4)	20.8 ± 0.30 (4)
<i>Recurvirostra amoissetta</i>	71.0 ± 4.21 (6)	7.7 ± 0.39 (8)	4.3 ± 0.12 (5)	37.0 ± 0.38 (6)	106.9 ± 2.44 (5)	82.4 ± 1.97 (5)	49.6 ± 1.71 (4)	27.6 ± 0.63 (4)
<i>Gallinago gallinago</i>	74.4 ± 2.62 (24)	7.3 ± 0.41 (25)	7.0 ± 0.32 (14)	31.6 ± 0.16 (24)	53.7 ± 0.37 (24)	33.2 ± 0.26 (25)	34.7 ± 0.22 (23)	17.1 ± 0.14 (21)
<i>Limosa limosa</i>	109.2 ± 5.39 (8)	9.6 ± 0.53 (7)	9.2 ± 0.29 (4)	42.9 ± 0.68 (7)	98.7 ± 1.49 (7)	79.3 ± 1.80 (7)	49.4 ± 0.82 (4)	24.7 ± 0.92 (2)
<i>Limosa lapponica</i>	92.6 ± 11.6 (12)	9.5 ± 0.65 (15)	8.3 ± 0.71 (14)	39.2 ± 0.53 (20)	76.8 ± 1.05 (19)	54.6 ± 0.79 (20)	51.4 ± 0.62 (17)	26.5 ± 0.47 (6)
<i>Tringa totanus</i>	49.4 ± 2.96 (23)	6.4 ± 0.59 (23)	4.7 ± 0.32 (16)	31.1 ± 0.27 (24)	64.9 ± 0.62 (23)	48.2 ± 0.54 (24)	37.7 ± 0.29 (22)	21.1 ± 0.24 (12)
<i>Tringa erythropus</i>	66.2 ± 3.30 (6)	6.8 ± 0.52 (9)	4.8 ± 1.32 (6)	33.3 ± 0.31 (5)	78.4 ± 1.25 (6)	59.5 ± 1.23 (7)	39.9 ± 0.83 (8)	21.6 ± 0.23 (6)
<i>Arenaria interpres</i>	26.5 ± 2.19 (17)	6.6 ± 0.23 (18)	5.6 ± 0.43 (15)	28.9 ± 0.53 (19)	46.3 ± 0.23 (19)	26.0 ± 0.11 (18)	34.0 ± 0.16 (19)	20.9 ± 0.17 (10)
<i>Phlimachus pugnax</i>	42.1 ± 3.15 (12)	6.4 ± 0.87 (12)	5.6 ± 0.75 (10)	33.4 ± 1.13 (14)	69.1 ± 1.95 (14)	47.7 ± 1.38 (14)	41.3 ± 1.46 (10)	20.1 ± 1.22 (6)
<i>Calidris alba</i>	31.8 ± 0.89 (7)	5.2 ± 0.36 (7)	4.8 ± 0.48 (2)	22.6 ± 0.41 (9)	41.3 ± 0.48 (8)	25.3 ± 0.28 (8)	26.8 ± 0.31 (8)	17.0 ± 0.28 (3)
<i>Calidris minuta</i>	26.2 ± 3.23 (4)	4.2 ± 0.15 (4)	3.8 ± 0.45 (2)	17.7 ± 0.51 (5)	36.5 ± 0.59 (5)	21.7 ± 0.49 (6)	20.2 ± 0.86 (4)	13.1 ± 0.80 (3)
<i>Calidris alpina</i>	38.4 ± 2.77 (38)	5.2 ± 0.56 (42)	5.0 ± 0.30 (26)	21.4 ± 0.11 (46)	41.5 ± 0.25 (42)	25.4 ± 0.28 (45)	24.5 ± 0.14 (41)	16.7 ± 0.11 (36)