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Beak elongation as a candidate key innovation underlying ecological transitions in shorebirds

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Adaptive radiations are often associated with phenotypic innovations that broaden ecological opportunity and bias subsequent ecological divergence. In shorebirds (Charadriiformes), variation in beak length has long been linked to resource partitioning, yet its role as a functional innovation has remained largely untested. Here, we integrate behavioural, morphological, and phylogenetic data from 29 Western Palearctic shorebird species to evaluate whether beak elongation fulfils key expectations of a candidate innovation by being repeatedly associated with ecological and functional transitions. Species with longer than expected beaks relative to body size consistently exhibit both a change in sensory organs (more sensory pits on the beak and smaller eyes) and distinct locomotor, prey capture, and food transport strategies. These integrated morphological-behavioural syndromes recur across independent lineages, suggesting convergent evolution driven by shared ecological environments. Phylogenetic analyses indicate independent origins of relative beak elongation, supporting its role as a repeated evolutionary solution. Together, our results support a functionally integrated view of adaptation, in which coordinated changes in morphology, sensory investment, and behaviour facilitate access to alternative foraging microhabitats and enable ecological transitions within shorebirds. More broadly, this study provides a testable framework for identifying candidate innovations based on replicated trait-niche associations.

KEYWORDS
adaptive radiation, convergent evolution, food acquisition behaviour, morphological-behaviour syndrome, phenotypic variation, resource partitioning

Introduction

Adaptive radiation refers to the evolutionary emergence of phenotypic diversity within a lineage as a response to divergent selection pressures (Schluter, 2000; Gavrilets and Losos, 2009). This process often depends on the availability of ecological niches, which may be accessed through the emergence of a key innovation - that is, a phenotypic modification enabling individuals to exploit previously inaccessible ecological opportunities (Stroud and

Losos, 2016). While the role of key innovations in driving adaptive radiation has been widely acknowledged, Miller et al (Miller et al., 2023). argue that the concept has gradually shifted in meaning. Specifically, they note a conflation between lineage diversification (e.g., Simões et al., 2016) and trait-dependent ecological transitions (e.g., Baguette et al., 2020). In response, they advocate for a return to a more ecologically grounded definition of key innovations. They propose two complementary approaches to operationalizing this concept, by elucidating the mechanisms through which phenotypic traits alter the interaction between organisms and their environments, and/or demonstrating that these trait changes lead to measurable shifts in the organism's ecological niche. In this study, we adopt the second of the two approaches they proposed (Miller et al., 2023), focusing on identifying phenotypic shifts that may have facilitated ecological transitions in shorebirds. More specifically, we investigate if beak elongation functions as a candidate key innovation in shorebirds, in which case it should consistently be associated with shifts in ecological performance and behaviour.

The relationship between beak morphology and ecological function is not always straightforward. Comparative analyses across birds show that similar diets can be associated with markedly different beak shapes, and conversely that similar morphologies can serve different ecological roles (Navalón et al., 2019). Moreover, the beak is involved in multiple non-trophic functions, including thermoregulation, communication, and maintenance behaviours, which may also shape its evolution (Tattersall et al., 2017; Olsen, 2017). These multiple selective pressures complicate attempts to directly link beak morphology to ecological specialization. This complexity makes birds a particularly relevant system in which to test whether specific aspects of beak morphology can be consistently associated with ecological and functional transitions when considered jointly with behaviour.

Shorebirds represent a group of approximately 215 species (Colwell, 2010), encompassing two of the three suborders within the order Charadriiformes: Scolopaci (e.g., shanks, tattlers, sandpipers, godwits, snipes, curlews) and Charadrii (e.g., plovers, avocets, oystercatchers, lapwings). A recent time-calibrated phylogeny, integrating genetic, morphological, and paleontological data, provides a robust framework for understanding the remarkable species diversity found within the Charadriiformes (Černý and Natale, 2022). Shorebirds constitute one of the most prominent avian radiations, not only in terms of species richness but also with respect to morphological, behavioural, and biogeographical variation (van Tuinen et al., 2004; Colwell, 2010). They are frequently cited as a textbook example of resource partitioning, wherein contrasting morphological traits, particularly beak and leg structures, facilitate the localization, capture, and ingestion of food items. During the non-breeding season, most shorebirds predominantly forage along land-water interfaces in freshwater, brackish, or marine environments, where they feed primarily on invertebrates, but also on small vertebrates and plant material. It is widely assumed that interspecific variation in beak length allows different shorebird species to access prey located at different sediment or water column depths, while variation in leg length permits foraging across a range of water depths. However, the functional and ecological correlates of beak-length difference have rarely been evaluated quantitatively in an explicit comparative framework.

In a previous study, we described and classified food acquisition behaviours of 26 western Palearctic shorebird species during migration and wintering periods (Baguette et al., 2024). Food acquisition can be decomposed into two main behaviours: foraging, which includes locomotion and prey capture, and feeding, which includes handling and transport of the food item toward the pharynx. Among these components, locomotion, prey capture, and prey transport constitute ecological performances in the sense of Irschick and Higham (2016), i.e., quantifiable traits that reflect how effectively an individual performs ecological tasks critical to its fitness. Locomotion, prey capture, and prey transport indeed directly determine how efficiently individuals locate, acquire, and ingest food resources. Prey handling is inherently idiosyncratic, as it strongly depends on both the ecological context (i.e., prey type) and the individual's condition (i.e., its experience). As a result, its quantification is of limited informative value unless based on extremely large datasets, which is not the case here.

Locomotion, prey capture and prey transport can be described using a limited set of stereotyped and repeatable behaviours, following Tinbergen's hierarchical model of behavioural complexity (Tinbergen, 2020). Locomotion primarily involves either stop-run-stop movements, in which individuals alternate between scanning and short bursts of movement, or continuous walking. Prey capture includes pecking (visual detection and rapid picking), probing (insertion of the beak into the substrate), or an intermediate pecking-probing strategy. Food transport is achieved through lingual transport, in which the prey remains in contact with the tongue, or through ballistic and surface-tension mechanisms, in which the prey is moved toward the pharynx via head movements and fluid-mediated processes.

Our previous work showed that these behaviours do not vary independently but form a coordinated behavioural syndrome, characterized by consistent covariation among locomotion, capture, and transport strategies (Baguette et al., 2024). For example, species exhibiting stop-run-stop locomotion typically rely on visual detection and pecking, combined with lingual transport, whereas species using continuous walking more frequently employ probing or mixed capture strategies and rely on ballistic or surface-tension transport. Importantly, these combinations are not randomly distributed across species but show a clear phylogenetic structure, with closely related taxa tending to share similar behavioural profiles. Recent work further suggests that such coordinated trait variation may contribute to ecological differentiation among co-occurring shorebird species (Hernandez–Possémé et al., 2026), reinforcing the need to consider morphology and behaviour jointly.

Crucially, these behavioural syndromes are closely associated with variation in beak length. Species exhibiting stop-run-stop locomotion, visual detection and pecking, and lingual transport typically possess relatively short beaks, whereas species relying on continuous walking, probing or mixed capture strategies, and ballistic or surface-tension transport tend to have relatively longer beaks. This pattern suggests that beak length plays a structuring role in shaping coordinated behavioural strategies.

Functionally, beak elongation is expected to facilitate access to prey located deeper within the substrate, particularly through the development of tactile foraging supported by mechanosensory structures (sensory pits) in the distal part of the beak. At the same time, increasing beak length imposes mechanical constraints on food transport, as the tongue cannot reach the distal extremity of the beak. This constraint is likely to have favoured the evolution of alternative transport mechanisms, such as ballistic and surface-tension-based transport. Together, these considerations suggest that variation in beak length may underlie a coordinated shift in detection, capture, and transport processes, making it a strong candidate trait linking morphology, behaviour, and ecological niche use, and therefore a plausible candidate key innovation underlying ecological transitions in shorebirds.

In the present study, we compiled a comprehensive set of morphological traits related to body structure (body mass, body length, and the size of musculoskeletal appendages), sensory organs (eye diameter and the number of sensory pits on the beak, used as proxies for visual and tactile foraging abilities, respectively), as well as beak and tongue lengths. In parallel, we expand our behavioural dataset by incorporating information from three additional Scolopaci species.

To develop a standardized morphological baseline, we first combined body structure traits (excluding beak length) to construct a global body size index for each of the 29 species. We then quantified allometric relationships between this index and key morphological traits involved in food acquisition, namely sensory structures, beak length, and tongue length, representing their respective roles in food detection, capture, and transport. Based on these relationships, we calculated Relative-to-Expected (RTE) values, which express species-specific deviations of each trait from its expected value given body size, i.e. correcting raw morphological measurements for allometry.

Using this framework, we first tested whether these traits follow distinct evolutionary trajectories between the two shorebird suborders by comparing RTE trait values between Charadrii and Scolopaci. Second, we examined whether variations in RTE beak length across species are accompanied by variation in investment in sensory organs (eye and sensory pits), indicating integration between morphological and functional traits involved in prey detection. Specifically, we expect that beak elongation will covary with sensory organs: the longer the RTE beak, the lower the investment in foraging by sight (smaller RTE eye diameter) and the higher the investment in foraging by sensing (higher RTE number of sensory pits on the beak). Third, we tested the hypothesis that coordinated shifts in foraging behaviours accompany beak elongation. We investigated whether, and in what manner, the three components of the food acquisition behavioural syndrome (locomotion, prey capture, and food transport from the tip of the beak to the pharynx) are associated with variation in RTE beak length. We predict that species with longer RTE beaks will exhibit coordinated changes in locomotion, prey capture, and food transport strategies, reflecting access to alternative foraging pathways. Finally, if RTE beak length represents a recurrent evolutionary solution to similar ecological constraints, we expect these associations to be replicated across independent lineages. Altogether, by testing these predictions in a phylogenetic context, we aim to evaluate whether beak elongation can be interpreted as a candidate innovation underlying ecological transitions in shorebirds.

Material and methods

Phenotypic traits: morphology and behaviour

We collected data on the food acquisition behaviour of 29 species in wintering or migration sites (Baguette et al., 2024; Hernandez–Possémé et al. in review), which represents ca. 75% of the total shorebird fauna of the western Palearctic (Cramp and Simmons, 1983, except for vagrants), and ca. 90% of the species using land-water interfaces during migration and overwintering (Cramp and Simmons, 1983, except for vagrants). The remaining species are either primarily associated with habitats other than land-water interfaces during these periods, or occur only rarely within our study area, which has so far limited the feasibility of collecting standardized behavioural data for them.

Locomotion behaviours (how individuals move around their feeding habitats), capture behaviours (how individuals catch and locate their prey) and transport behaviours (how individuals move food particles from the tip of the beak to the pharynx) were categorized based on a recent repertoire (Baguette et al., 2024). In this study, we classified these behaviours by analysing video sequences of 26 species of Western Palearctic shorebirds, during migration or wintering. Shorebird food acquisition behaviours were opportunistically videorecorded during field trips in a variety of locations in Western and Southern Europe between 2021 and 2023. Firstly, we used BORIS (Behavioural Observation Research Interactive Software, Friard and Gamba, 2016) to annotate our records on five video sequences per species lasting at least one minute that were recorded at different places and over different time periods, to cover as far as possible the potential species-specific diversity in food acquisition behaviours. We assigned video bouts to those particular behaviours that are associated to the foraging and feeding stages. We ended with a behavioural repertoire of food acquisition in our shorebird species, in which each behaviour was well characterized by reliable diagnostic criteria. In a second step, we viewed all the video sequences of every species on which we collected data. We recorded all behaviours associated with food acquisition according to our behavioural repertoire. The final product of this step is a species-specific list of behaviours for all the 26 shorebird species of our data set. We showed that three of these behaviours are made up of stereotypical, mutually exclusive components, and can be considered as performances: locomotion can be Continuous Walking (CW) or Stop-Run-Stop (SRS); capture can be Pecking (PE), Probing (PR) or a combination of both (PE-PR); transport can be Lingual (LI), Ballistic (BA) or Ballistic associated to Surface Tension (BA-ST). Each of our study species uses one or maximum two components of these three performances, which we use here as categorical variables in our analyses. Because behavioural categories were assessed at the species level,

our analyses explicitly target macroevolutionary associations among species. They are therefore not designed to capture within-species behavioural reaction norms or individual-level plasticity, but rather to identify replicated patterns of trait-behaviour covariation across lineages.

Aggregated data at the species level were used for morphological variables (beak length, body size, weight, wing length, tarsus length, length of the longest toe, tongue length) and sensory organs (diameter of the eye, number of sensory pits on the beak). Morphological data come from Cramp and Simmons (1983), except tongue lengths, which were published by Burton (1974), diameters of the eye that come from Thomas et al. (2006) and the number of sensory pits on the beak that were measured by one of us (EL) on the available specimens of the Compared Anatomy Lab of the Muséum National d'Histoire Naturelle (Paris). The values used are averages across sexes, and when values from different geographical origins were available, we used those measured in the localities closest to our behaviour observation sites. Three variables were available for a subset of species only: eye diameter (22 species), number of sensory pits (11 species) and tongue length (19 species). Two variables were transformed before analysis: weight was cubic root transformed to account for its scaling as a volume, not a length; tongue length was expressed as a proportion of the beak length, and this tongue/beak length ratio was ln-transformed so that multiplicative variation on its original scale becomes additive on the transformed scale, enabling linear modelling and interpretation of effects as proportional rather than absolute changes.

Statistical analyses

All statistical analyses were performed in R (v 4.5.3 for Windows, R Core Team, 2025), and package versions were recorded using session information and a project–specific dependency lockfile to ensure computational reproducibility (see Supplementary Material). They explicitly considered the existing phylogenetic relations among the 29 species, except for the Principal Component Analysis and the tests for suborder difference (see below). Phylogenetic distances were inferred using a pruned tree restricted to our study species (Figure 1A) from the Charadriiformes time tree of Černý & Natale (Černý and Natale, 2022). We assumed a Brownian motion evolution model, i.e., that traits evolve through a constant-rate random walk, with changes accumulating gradually and independently across lineages, producing normally distributed trait values whose covariance structure reflects shared evolutionary history. This covariance structure was incorporated in statistical analyses either directly by appropriate options of the R packages or by providing the covariance

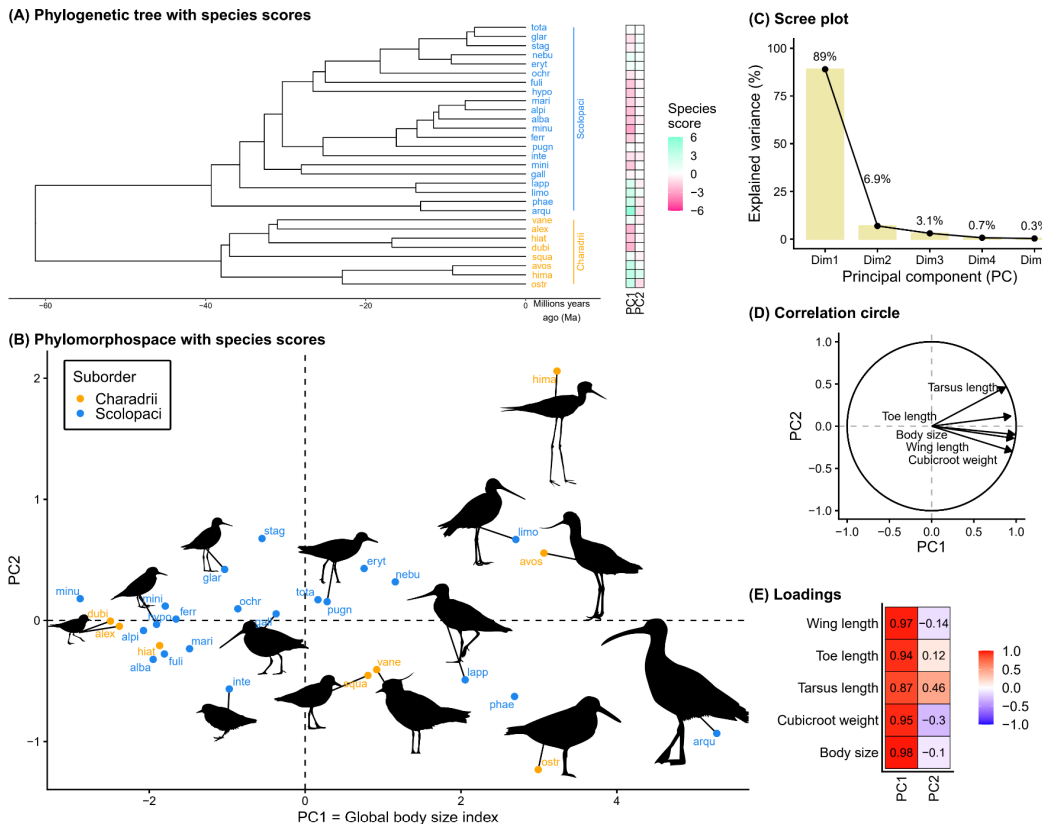

FIGURE 1
Shorebird phylomorphospace and phylogenetic global body size index. We used a phylogenetic tree of the 29 shorebirds species **(A)** to perform a Principal Component Analysis (PCA) on five morphological traits and create a phylomorphospace **(B)** using its first two principal components (PC1 and PC2). PC1 summarizes 89% of the variance, and PC2 7% **(C)**. PC1 can be interpreted as a global body size index, being highly and positively correlated with the five traits as shown on the PCA correlation circle **(D)** and loading matrix **(E)**. PC2 contrasts lighter species with longer legs with bulkier and shorter-legged species. 14 species silhouettes are represented on the phylomorphospace **(B)** at the same relative scale (bird silhouettes from phylopic.org; detailed credits in the Supplementary Material).

matrix (reconstructed from the tree using *vcv.phylo* function of the *ape* R package: Paradis and Schliep, 2019) depending on the R packages requirements.

First, we summarized the variation among the 29 species in five morphological traits (body size, wing length, tarsus length, length of the longest toe, and weight) using a Principal Component Analysis (PCA) performed with *PCA* function from *FactoMineR* R package (Lê et al., 2008) on the correlation matrix (i.e., standardized variables) to give equal weight to all body metrics. Phylogeny was not explicitly accounted for in this PCA to avoid double correction given subsequent analyses incorporated the phylogenetic covariance matrix. The first two Principal Components (PCs) were used to place the species in a phylomorphospace. As further detailed in results, PC1 summarizes a very high proportion (89%) of the morphological variation and can be interpreted as a global body size index because it is highly and positively correlated with all the five morphological traits.

Second, we used this global body size index to correct the four morphological traits of interest (eye diameter, number of sensory pits, beak length, and tongue/beak length ln-ratio) for allometry. A phylogenetic linear regression between the trait and the global body size was estimated with *phylolm* function from *phylolm* R package (Ho and Ane, 2014). For this analysis, the number of sensory pits was first ln-transform so that fitting a linear regression on ln (number of sensory pits) corresponds to fitting a negative exponential regression to the number of sensory pits, hence avoiding predicting negative values. For each of these four traits, a new Relative-To-Expected (RTE) trait variable was then created to express how much a species possesses a trait value that differs from its expected value given its body size index: RTE trait for a species was computed as the ln transformed ratio between its observed value and its predicted value from the allometric regression. The ln-transformation was performed so that multiplicative variation on the original scale becomes additive on the transformed scale, enabling linear modelling and interpretation of effects as proportional rather than absolute changes. In other words, RTE trait expresses (on a ln scale) how many times the trait for a species is bigger (or smaller) than the value to be expected given its body size index. We then tested whether species from the two suborders significantly differ for these four RTE traits using unequal variance Welch's two sample t-tests (*t_test* function of *rstatix* R package, Kassambara, 2025). Phylogeny was not explicitly accounted for in these t-tests because suborders themselves constitute high-level monophyletic groupings, and a phylogenetic correction would partition out variance attributable to deep nodes of the tree, precisely the signal we aim to test. We acknowledge as a simplifying assumption that species within each suborder cannot be considered fully independent observations, and p-values should be interpreted with this caveat in mind.

Third, we checked for specific relationships among morphological traits (RTE beak length, RTE eye diameter and RTE number of sensory pits) and with behavioural traits associated to the three main steps of food acquisition (locomotion, capture and transport) using appropriate linear models according to the nature of the response variable. For a continuous normal variable (such as RTE trait), we used phylogenetic linear regression (*phylolm* function from *phylolm* R package). For categorical variables, we use phylogenetic logistic regressions estimated with a Bayesian framework because no appropriate frequentist approach exists to fit such models with an explicit consideration of the phylogenetic covariance matrix. We used the *brm* function of *brms* R package (Bürkner, 2017) with a species random effect associated to the phylogenetic covariance matrix computed on the phylogenetic tree, and distribution of error and link function appropriate to the type of categorical variable: binomial logistic regression for a two-level categorical variable (locomotion behaviour: CW or SRS; reference is CW), cumulative logistic regression for an ordinal multilevel variable (capture behaviour: PE < PE-PR < PR; reference is PE) and multinomial logistic regression for a nominal multilevel variable (transport behaviour: LI, BA, BA-ST; reference is LI).

Linear model assumptions were assessed visually using residual diagnostics (or posterior predictive checks for Bayesian models), which indicated no major deviations. For frequentist models, we report standard inferential statistics, including the test statistic, degrees of freedom, and associated p-value. For Bayesian models, we report the posterior estimate of the slope of the predictor along with its 95% credible interval. Because the Bayesian framework does not provide a direct analogue of a p-value, we considered the effect of a predictor to be credibly supported when its 95% credible interval did not include zero, and marginally credible when 0 was near one limit of this interval.

Results

We constructed a phylomorphospace (Figure 1B) by plotting species scores along the first two axes of the Principal Component Analysis (PCA), which summarizes interspecific variation in five morphological traits across the 29 studied shorebird species. The first principal component (PC1), which accounts for 89% of the total morphological variation (Figure 1C), was interpreted as a global body size index, being positively correlated with all five traits (Figures 1D, E). Along this axis, species range from the smallest plovers and sandpipers to the largest taxa, such as the avocet, stint, godwit, and curlew, with the largest species being 3.8 times larger than the smallest (Figure 1B). The second axis (PC2) accounts for 7% of the variation and contrasts heavier and shorter-legged species with lighter and longer-legged species. The variation along this second axis was not further used in the analyses.

We used the global body size index to correct the morphological traits of interest for allometry by computing their Relative-to-Expected (RTE) counterparts, and first tested whether these traits follow distinct evolutionary trajectories between the two shorebird suborders. Eye diameter (Figure 2A) increased significantly with global body size index, and RTE eye diameter was significantly larger in Charadrii than in Scolopaci. In contrast, the number of sensory pits on the beak (Figure 2B) decreased (marginally significantly) with global body size index, and RTE number of sensory pits was significantly higher in Scolopaci than in Charadrii. Beak length (Figure 2C) scaled significantly and positively with global body size index, and species in Charadrii had significantly shorter

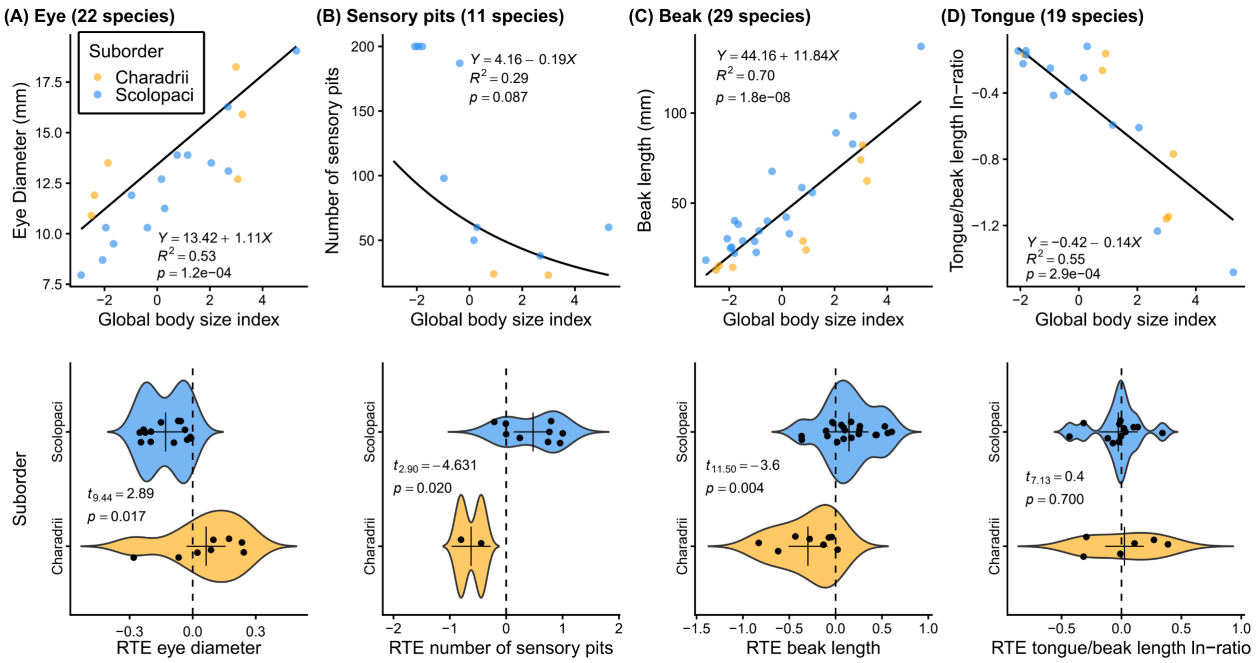

FIGURE 2
Allometric relations and difference between suborders in Relative-To-Expected (RTE) morphological traits. We used allometric relations (first line, phylogenetic linear regressions explicitly considering the covariance among species due to phylogeny) with the global body size index to correct four morphological traits for allometry by computing their RTE (Relative-to-Expected) counterparts: RTE = ln(observed/predicted). We then tested whether these RTE traits differed between the two suborders, Charadrii and Scolopaci (second line, Welch's unequal variance t-tests). The four morphological traits are the eye diameter **(A)**, the number of sensory pits on the beak **(B)**, the beak length **(C)** and the tongue length in proportion of the beak, expressed as the ln-ratio of tongue over beak length **(D)**. Sample size for each trait is indicated in panel titles.

RTE beaks than those in Scolopaci. Finally, the ratio of tongue length to beak length (Figure 2D) showed a significant negative scaling relationship with global body size index: larger species possessed proportionally shorter tongues, although not necessarily in absolute length. However, after correcting for this allometric effect, no significant difference in RTE tongue-to-beak length ln-ratio was observed between the two suborders.

We then tested the hypothesis that changes in beak length are accompanied by variation in investment in sensory organs (eye and sensory pits) indicating integration between morphological and functional traits involved in prey detection. We found that species with a longer RTE beak also presented smaller RTE eyes (Figure 3A) and larger RTE number of sensory pits (Figure 3B). Accordingly, species with larger RTE eyes should present smaller RTE number of

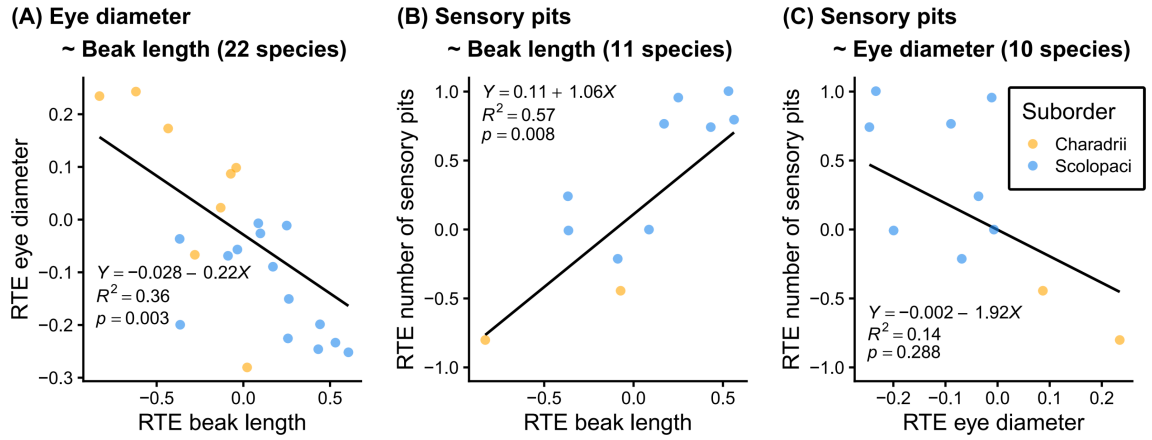

FIGURE 3
Relation between eye diameter and sensory pits. Changes in beak length are accompanied by variation in investment in sensory organs (eye and sensory pits) indicating integration between morphological and functional traits involved in prey detection. Species with a longer RTE beak also present smaller RTE eyes **(A)** and larger RTE number of sensory pits **(B)**. Species with larger RTE eyes present smaller RTE number of sensory pits but this relation is non-significant due to smaller sample size **(C)**. The three morphological variables were corrected for their allometric relation with global body size index, being expressed as their Relative-to-Expected (RTE) counterparts. Statistics refer to a phylogenetic linear regression, explicitly considering the covariance among species due to phylogeny.

sensory pits; this relation was observed (Figure 3C) but with the small sample size at our disposal (only 10 species had both a measure for eye diameter and the number of sensory pits on the beak), it appeared non significant.

RTE beak length was found to be a credible predictor of behavioural strategies employed during food acquisition. Species with longer than expected beaks were indeed more likely to exhibit: (1) Continuous Walking rather than Stop-Run-Stop locomotion (Figure 4A; marginally credible); (2) Probing rather than Pecking as a prey capture technique, with transitional species exhibiting a combination of both Probing and Pecking behaviours (Figure 4B); and (3) Ballistic rather than Lingual mechanisms for food transport, with transitional species employing both Surface tension and Ballistic strategies (Figure 4C). In addition, species with a shorter tongue relative to their beaks (RTE tongue length/beak length ln-ratio) were credibly more likely to replace Lingual transport behaviour by Ballistic only transport, the trend being not fully credible for the Ballistic + surface tension transport behaviour (Figure 4D).

Discussion

Our analyses show that relative beak elongation in shorebirds is not an isolated morphological shift, but part of an integrated functional syndrome involving sensory investment and food-acquisition behaviour. After correcting for body size and phylogenetic relations, species with longer-than-expected beaks tended to have smaller-than-expected eyes, more sensory pits on the beak, and a higher probability of using continuous walking locomotion, probing or mixed pecking-probing capture, and ballistic or surface-tension-based food transport. Conversely, species with shorter-than-expected beaks were associated with larger eyes, visually guided pecking, stop-run-stop locomotion, and lingual transport. These coordinated associations directly match our predictions that beak elongation should be accompanied by shifts in prey detection, capture, and transport. They therefore support the interpretation of beak elongation as a candidate functional innovation that may have facilitated repeated ecological transitions in shorebirds by enabling access to alternative foraging pathways.

These results gain particular significance in the ecological context in which shorebirds forage. Outside the breeding season, many species aggregate in large numbers within spatially constrained coastal and shoreline habitats, where prey biomass, accessibility and detectability can be limiting (e.g., van der Kam et al., 2004; Colwell, 2010; Lourenço et al., 2018). Under such conditions, interspecific food partitioning is commonly observed (e.g., Catry et al., 2016, Hernandez–Possémé et al., 2026), with species differing not only in diet composition but also in the behavioural and functional pathways through which resources are acquired (Catry et al., 2016; Correia et al., 2023). While optimal foraging theory has extensively documented how individuals adjust prey choice and handling to maximize energetic returns (van der Kam et al., 2004; Colwell, 2010), our results suggest that these behavioural strategies are themselves embedded within deeper, evolutionarily structured associations between morphology, sensory systems, and performance. This integrated perspective helps bridge the gap between proximate foraging decisions and the macroevolutionary patterns of ecological differentiation observed across shorebird lineages.

Sensory organs play a critical role in the successful detection of food. Shorebirds employ two primary strategies for locating prey or plant material: visual detection (hunting by sight) and tactile

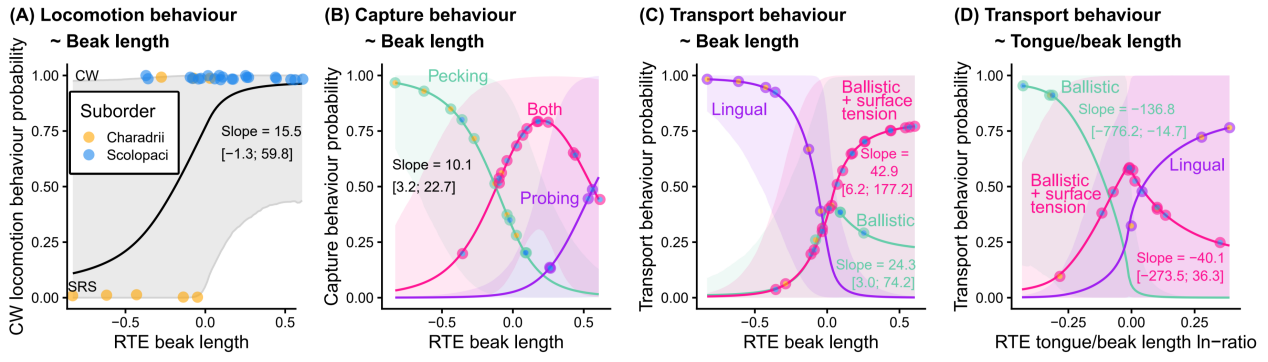

FIGURE 4
Relations between beak length and relative tongue length with food acquisition behaviours. Locomotion **(A)**, prey capture **(B)** and food transport **(C)** behaviours used by a species depended on how longer than expected its beak was given its body size index. The longer the beak, the more likely the species was to use Continuously Walking (CW) locomotion behaviour over Stop-Run-Stop (SRS) **(A)**, to complement Pecking capture behaviour with Probing (Both) and then replace Pecking by Probing **(B)**, and to replace Lingual transport behaviour by Ballistic (alone or complemented with Surface Tension) transport **(C)**. The shorter the tongue length/beak length ratio was, the more likely the species was to replace Lingual transport behaviour by Ballistic only transport, the trend being not fully credible for the Ballistic + surface tension transport behaviour **(D)**. Beak length and the tongue length/beak length ratio were corrected for their allometric relation with global body size index, being expressed as Relative-to-Expected (RTE) values. Relations are logistic regressions estimated under a Bayesian framework to allow for the explicit consideration of covariance among species due to phylogeny (see text for details). We report the posterior estimate of the slope of the predictor along with its 95% credible interval. This slope expresses how the predictor impacts the probability of using a specific behaviour: the probability of using CW over SRS for binomial locomotion behaviour **(A)**, of using both Pecking and Probing instead of Pecking alone and Probing alone instead of both for ordered multinomial capture behaviour **(B)**, the probability of using Ballistic over Lingual and Ballistic combined with Surface tension over Lingual for unordered multinomial transport behaviour **(C, D)**. Because the Bayesian framework does not provide a direct analogue of a p-value, we considered the effect of a predictor to be credibly supported when its 95% credible interval did not include zero, and marginally credible when 0 was near the end limit of this interval.

detection (hunting by touch), with some species potentially combining both approaches (e.g., van der Kam et al., 2004; Baguette et al., 2024; Barbosa and Moreno, 1999; Thomas et al., 2006; Lourenço et al., 2016; du Toit, 2021; Martin, 2017). In the present study, we use eye diameter and the number of sensory pits on the beak as proxies for a species' relative investment in visual and tactile prey detection, respectively. Across the 29 species in our dataset, eye diameter scales positively with the global body size index. Notably, six of the eight Charadrii species exhibit eye diameters that are - sometimes substantially - larger than expected based on this allometric relationship. According to the dated phylogeny by Černý and Natale (Černý and Natale, 2022), our Charadrii sample includes five species from the Charadriidae family (plovers and lapwing), which represents an early-diverging clade within the suborder, and three species from more recently diverged lineages. The six species with larger-than-expected eye diameters comprise the five Charadriidae representatives and the oystercatcher, suggesting that enlarged eye size is a retained trait within the early-diverging clade.

In contrast, the number of sensory pits on the beak shows a significant negative relationship with the global body size index. However, sensory pit data are lacking for many species, particularly within Charadrii, for which data are available for only two species: the lapwing (representing the basal clade) and the oystercatcher (a representative of the more recently diverged clade). Conclusions regarding sensory investment should therefore be interpreted cautiously given limited taxonomic coverage for sensory pits, and we treat them as preliminary proxies rather than definitive measures. Despite these data limitations, the observed differences in sensory organ morphology between Charadrii and Scolopaci are broadly consistent with their known prey capture strategies.

Most Charadrii, especially those from the basal clade, exhibit larger than expected eye diameters and rely predominantly on visual prey detection. In contrast, Scolopaci species, which locate prey by touch or through a combination of tactile and visual cues, possess more sensory pits on their beaks than expected given their body size. Furthermore, although based on a limited sample, our findings reveal that beak elongation is associated with a shift in sensory investment, with species exhibiting larger-than-expected beaks tending to have smaller-than-expected eyes and a greater number of sensory pits. This pattern is consistent with a potential trade-off between visual and tactile modes of prey detection, suggesting a tendency toward specialization along a sensory axis. However, the relationship between relative eye size and sensory pit number is not statistically supported, indicating that this pattern does not reflect a strict constraint or universal trade-off. Rather, it points to a more flexible adaptive landscape in which different species follow distinct trajectories in the allocation of sensory resources, converging on similar functional outcomes through partially independent pathways.

In our dataset, beak length exhibits a positive allometric relationship with the global body size index, indicating that larger shorebird species generally possess longer beaks. However, after correcting for this allometric effect, species belonging to the suborder Charadrii display significantly shorter than expected beak lengths compared to those in Scolopaci. This pattern is primarily driven by the five species within the family Charadriidae (plovers and lapwing), the early-diverging clade within Charadrii. In contrast, species from the more recently diverged (Haematopodidae + Recurvirostridae) clade (e.g., oystercatchers, avocets, and stints) exhibit relative beak lengths comparable to those of Scolopaci species.

The tongue plays a crucial role in the evolution of food transport mechanisms in Sauropsida, including birds (Bels et al., 2023). Among shorebirds, tongue length varies markedly, ranging from nearly equal to beak length to less than one-third of it (Burton, 1974). To account for this diversity, we expressed tongue length as a proportion of beak length and found that this ratio scales negatively with body size. These findings suggest that tongue elongation is subject to an upper constraint that prevents proportional increases in length relative to the beak, possibly due to biomechanical or physiological trade-offs. Such constraints may be linked to the evolution of specific food transport mechanisms, such as ballistic transport (Baussart et al., 2009; Harte et al., 2011; Bels et al., 2023) or surface tension-based transport (Rubega and Obst, 1993; Rubega, 1997; Prakash et al., 2008; Bels et al., 2023).

We previously identified a behavioural syndrome in shorebirds characterized by consistent associations among stereotyped behaviours of each of these performances (Baguette et al., 2024). Pecking is considered the plesiomorphic prey capture behaviour in shorebirds (Zweers, 1991; Zweers and Gerritsen, 1997), and all five Charadriidae species in our dataset exhibit a behavioural profile characterized by stop-run-stop locomotion, pecking as the primary capture strategy, and lingual transport of food particles (Baguette et al., 2024). In contrast, species from the Scolopaci suborder and from the more recently diverged Charadrii clade (Haematopodidae + Recurvirostridae) employ a mixed capture strategy combining pecking and probing, use continuous walking as their primary locomotion behaviour, and - except for one species - utilize a combination of ballistic and surface tension-based food transport strategies.

Here, we demonstrate that this behavioural syndrome aligns closely with differences in relative beak length between the basal and more derived clades. Species with shorter than expected beaks relative to body size consistently employ the behavioural combination of stop-run-stop locomotion, pecking capture, and lingual transport. Conversely, species with longer than expected beaks are more likely to exhibit probing or combined pecking-probing behaviours, continuous walking, and employ ballistic or surface tension transport mechanisms. These findings support the hypothesis that morphological divergence in beak length has co-evolved with functional behavioural adaptations that optimize food acquisition strategies within distinct ecological contexts.

In particular, the convergence of morphological and behavioural phenotypes observed between long-beaked Scolopaci and the recently diverged long-beaked Charadrii further supports the idea that beak elongation is repeatedly associated with shifts in locomotion, prey capture, and food transport, consistent with a functional role in enabling alternative food-acquisition strategies. The beak, serving as the primary grasping organ in birds and often analogized to the primate hand (Bhullar et al., 2016), plays a fundamental role in food acquisition (Xu et al., 2023). However,

studies examining the relationship between beak morphology and feeding ecology across modern birds as a whole have yielded inconclusive results (Navalón et al., 2019). Two principal factors likely account for this lack of a clear relationship: first, similar trophic resources may be exploited via markedly different beak morphologies; second, beak morphology may be shaped by selective pressures unrelated to feeding, such as communication, nest construction, preening, or thermoregulation (Olsen, 2017). These confounding factors can be mitigated by focusing analyses at lower taxonomic levels (Navalón et al., 2019), as we do here, and as previously demonstrated by Olsen, (2017), who found feeding ecology to be the primary driver of beak diversification within Anseriformes.

Much diversification within several shorebird genera has been linked to late Cenozoic climatic dynamics (Colwell, 2010; Černý and Natale, 2022), whereas the evolutionary emergence of pronounced beak elongation likely predates many of these more recent lineage splits. In this context, we propose that beak elongation represents a strong candidate innovation at the functional-ecological level: it is repeatedly associated with coordinated shifts in sensory investment and in the behavioural repertoire underlying food acquisition. This pattern is consistent with the view that certain phenotypic transitions can bias subsequent ecological divergence by enabling lineages to exploit alternative foraging microhabitats or prey-access pathways, even if they do not directly translate into detectable diversification-rate shifts. Our study therefore supports an explicitly testable framework based on replicated trait-niche associations for evaluating candidate innovations in shorebirds and beyond.

One might question whether this hypothesis is merely a "just-so" story, as criticized by Gould and Lewontin (Gould and Lewontin, 1979) for many adaptive explanations. As with most historical evolutionary hypotheses, our inference relies on comparative evidence rather than direct experimental reconstruction. Nonetheless, the repeated association between relative beak elongation and a tightly integrated food-acquisition syndrome across independent lineages is difficult to reconcile with coincidence alone and is consistent with convergent selection under similar ecological constraints. Future work combining broader taxon sampling and direct ecological measures (e.g., water depth use, prey accessibility, and fine-scale diet composition when informative) will help refine the mechanistic links between beak elongation and niche transitions.

Altogether, our findings provide empirical support for the idea that morphological innovations such as beak elongation can drive the emergence of novel behavioural repertoires, thereby opening new ecological opportunities. This functional integration between structure and behaviour highlights a broader principle in evolutionary ecology: innovations are rarely isolated events, but rather part of coordinated phenotypic transitions. While the concept of "key innovations" is often invoked post hoc, our results point to a specific sequence - elongation of the beak, followed by shifts in sensory investment and feeding mechanics - as plausible evolutionary pathway underpinning niche differentiation in shorebirds. This underscores the need to consider behavioural and sensory traits in tandem with morphology when evaluating the drivers of adaptive radiation. Furthermore, the convergence observed between unrelated long-beaked lineages suggests strong selective constraints and offers a rare example of replicated evolutionary solutions within a single avian order.

Data availability statement

The data and used R scripts in the study are included in the Supplementary Material. Further inquiries can be directed to the corresponding author.

Ethics statement

Ethical approval was not required for the study involving animals in accordance with the local legislation and institutional requirements because The study is observational - no need for ethical approval according to the French legislation.

Author contributions

MB: Methodology, Supervision, Funding acquisition, Writing – original draft, Writing – review & editing, Formal analysis, Investigation, Project administration, Conceptualization, Validation. GF: Methodology, Visualization, Investigation, Validation, Writing – review & editing, Formal analysis. EL: Investigation, Writing – review & editing, Formal analysis. VB: Investigation, Conceptualization, Supervision, Writing – review & editing, Validation. LR: Writing – review & editing, Conceptualization. NS: Visualization, Data curation, Software, Investigation, Validation, Methodology, Conceptualization, Supervision, Writing – original draft, Writing – review & editing, Formal analysis.

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Conflict of interest

The author(s) declared that this work was conducted in the absence of any commercial or financial relationships that could be construed as a potential conflict of interest.

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