



ECOSPHERE NATURALIST

On the tip of the tongue: natural history observations that transformed shorebird ecology

PETER G. BENINGER^{1,†} AND ROBERT W. ELNER²

¹Faculté des Sciences, MMS, Université de Nantes, 2, rue de la Houssinière, Nantes 44322 France

²Environment and Climate Change Canada, Pacific Wildlife Research Centre, Delta, British Columbia V4K 3N2 Canada

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Abstract. A new field of shorebird feeding ecology has been opened, stemming directly from natural history observations of previously overlooked morphological and behavioral features. We describe how the pieces of this puzzle were assembled to reveal a fascinating story of small shorebird migration, trophic level shift, and direct feeding upon mudflat superficial biofilm just prior to breeding. Many unexplored avenues of research have arisen, including a trampoline effect of resource timing, the potential trade-off between trophic imperatives and toxic co-products, and the particular utilization of this resource in small, as opposed to large, shorebirds.

Key words: biofilm; feeding; microbial mats; migrations; mudflats; shorebirds; tongue; trophic ecology.

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† **E-mail:** Peter.Beninger@univ-nantes.fr

INTRODUCTION

An important new field of shorebird ecology has been opened, stemming from field observations and from revelations of scanning electron micrographs, beginning in 1994 (Fig. 1). Conventional understanding long held that benthic invertebrates were the dominant prey of shorebirds (Skagen and Oman 1996, Sutherland et al. 2000); consequently, descriptions of mudflat food webs and conservation efforts mirrored this paradigm (see Kuwae et al. 2012, Quinn and Hamilton 2012, Mathot et al. 2018). In 1994, a package from Delta, British Columbia, arrived at a Scanning Electron Microscopy facility in Moncton, New Brunswick, containing the glutaraldehyde-cacodylate-fixed heads of four western sandpipers, *Calidris mauri* (Cabanis 1857; Fig. 1C), collected during their breeding migration at a major stopover site on Roberts Bank, in the Fraser River estuary. Accompanying was a

request to report on the morphology of the bills, whose structure was assumed to conform to the classic Darwinian theory for diet specialization and biodiversity in birds (Gill and Prum 2019).

Nothing noteworthy was observed with respect to the bills themselves. However, the exceptionally well-preserved tongues told a very different story, which continues to unfold today. On their oral-facing surfaces, the tongues were covered with long, fine bristles, giving a toothbrush appearance (Fig. 1A). When matched with field observations, the realization dawned that these small shorebirds were feeding on something other than benthic invertebrates. The tongue bristles did not seem suited for capturing large prey, but rather more appropriate for gathering paste-like food. Thus, the hitherto unthinkable hypothesis was raised that the extensive epibenthic microbial mats and transient epibenthic biofilms, produced on the Roberts Bank intertidal mudflat, were an avian food source.

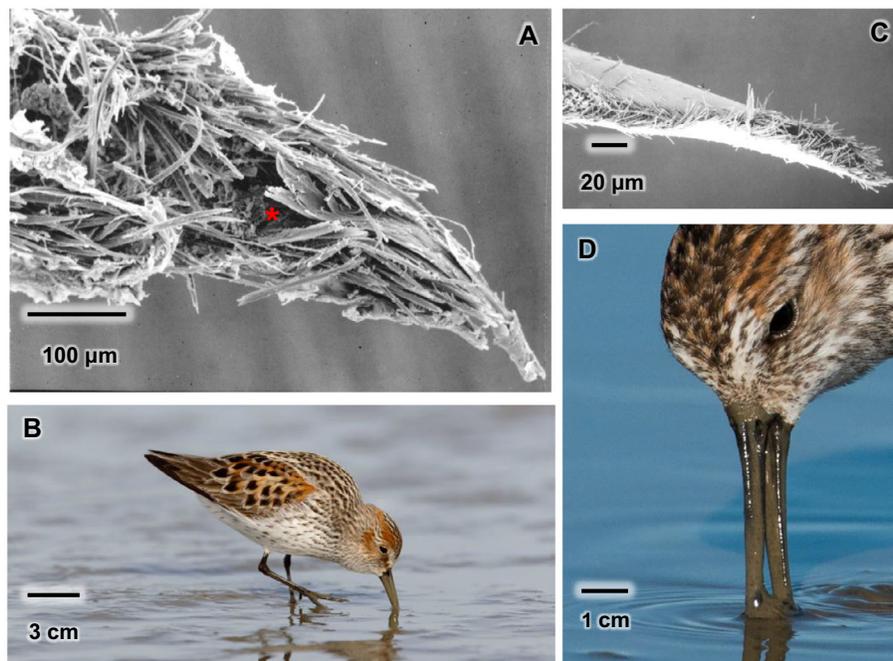


Fig. 1. Western sandpiper, *Calidris mauri*. (A) SEM micrograph of oral surface tongue-tip, showing dense array of keratinous bristles and residual dried mucus, after multiple processing rinses (*). (B) WESA feeding on the Roberts Bank mudflat, with abundant biofilm adhering to its beak. (C) General view of tongue, curled lengthwise due to processing dehydration, showing bristles along the entire length of the oral surface only. (D) Detail of WESA feeding on microphytobenthic film at Roberts Bank. Note abundant microphytobenthos in the buccal cavity and adhering to the exterior surface of the beak. (A, B) from Elner et al. (2005), with permission from Springer Nature; (C, D) with permission from Jason Puddifoot.

Mudflat microbial mats and transient epibenthic biofilms constitute an assemblage of microphytobenthos (mainly cyanobacteria and diatoms), as well as associated non-photosynthetic microbes and occasional meiofauna, all within a communally secreted mucopolysaccharide matrix (Beninger et al. 2018, Hubas et al. 2018, Moens and Beninger 2018). Microbial mats are stable over days or weeks, depending on wave conditions, whereas transient epibenthic biofilms develop and recede over the course of a single tidal cycle (Beninger and Paterson 2018). From a trophic viewpoint, a bird utilizing such food would be ingesting mainly microbes and mucus—something unheard of not only in the ornithological world, but also for any non-piscine vertebrate. Such a paradigm-shifting hypothesis was not initially received with ready assent in the research community, and the first paper did not emerge into the published literature until ten years later, and only then in a

general marine biology journal rather than an ornithology journal (Elner et al. 2005).

Both high-speed video and careful photographic field observations subsequently confirmed the real-time ingestion of large quantities of surficial mats and films, along with adhering sediment (Fig. 1C, D). Estimates based on stomach contents and stable isotopes showed that this food source was major and accounted for about 45–59% of the total diet or 50% of the daily energy budget of western sandpipers at this migratory stopover (Kuwaie et al. 2008). In addition, microbial mat and film feeding only became important at one of the last stopover sites (Roberts Bank, British Columbia, Canada), prior to breeding in Alaska, prompting the birds to descend a full trophic level overall. These observations suggested that this particular food resource is critical to reproductive success in western sandpipers (Beninger et al. 2011, Schnurr et al. 2019).

Having established that western sandpipers most definitely use epibenthic microbial mats and films as a major food source prior to breeding, the next obvious question was: Is this a quirk of nature, or do other shorebirds also feed in this manner, unbeknownst to ornithologists who had studied them for decades? To date, Elner et al. (2005) and Kuwae et al. (2012) have demonstrated that dunlin (*Calidris alpina*) and red-necked stints (*Calidris ruficollis*) actively graze microbial substrates; in addition, Kuwae et al. (2012) documented a total of 21 shorebird species with tongue spines. Similarly, the diet of another small shorebird, the semipalmated sandpiper (*Calidris pusilla*), has been shown to include substantial amounts of biofilm (Quinn and Hamilton 2012), and other epibenthic microbial mat and film grazing shorebird species are being added to the list (Mathot et al. 2018). Larger shorebirds either lack entirely or do not possess well-developed tongue spines, and are therefore assumed, variously, un- or less able to directly utilize superficial microbial substrates as a trophic resource (Kuwae et al. 2012). This raises the interesting question of why only small shorebirds are so equipped and capable.

The trophic utilization of a microbial biofilm was previously unknown in a non-piscine vertebrate, having been described only in some invertebrates and fish. Moreover, the original photomicrographs of western sandpiper tongues have opened hitherto unknown dimensions of shorebird ecology. Following the phenomenon's initial discovery, the search began to identify what dietary components of the microbial mats and films are important enough to justify switching trophic levels. Given the importance of fatty acids in bird migration (Pierce et al. 2005, Guglielmo 2010), a subsequent series of studies showed that, beyond their role as fuel, these substances, and in particular the polyunsaturated fatty acids (PUFA), are critical performance enhancers of long-distance flight (e.g., Weber 2009). A recent addition to the story showed that the arrival of western sandpipers at the Roberts Bank stopover actually coincides with the period of greatest PUFA content in the microphytobenthos (Schnurr et al. 2019), suggesting that these shorebirds are benefitting from a trampoline effect in their migration.

Whether the shorebirds are seeking PUFA and/or some other critical biofilm substance for

their final migration stages prior to breeding, the research priority is not only to identify such, but also to understand microphytobenthic spatial and temporal distribution and dynamics, in relation to shorebird demand and ultimate breeding success. However, true spatial analysis on mudflats is still very much in its infancy at present, so development of more efficient sampling and statistical techniques is an urgent research need (Beninger and Boldina 2018). Further, a coherent picture of the overall role of this food resource in shorebird physiology also necessitates analysis of associated risks and costs. For example, superficial sediment, some of which is inevitably scooped up during biofilm feeding, contains enough reducible cadmium to pose a toxic risk to western sandpipers (McCormick et al. 2014, St. Clair et al. 2014). This raises the possibility of a trade-off exploitation of mudflat microbial mats and transient epibenthic biofilms, wherein the physiological needs must be balanced against the toxic side effects.

North American shorebirds have shown the greatest population decrease of any major bird group over the past 50 yr, with approximately one-third overall reduction in numbers (Rosenberg et al. 2019). They have been put forward as integrators and indicators of overall mudflat ecology, and more generally, of global environmental change (Piersma and Lindström 2004, Mathot et al. 2018). Beyond their central roles in the mudflat food web and provision of goods and services, the data gathered since the appearance of the photograph in Fig. 1A has catapulted microbial mats and films, and the mudflats upon which they grow, into research priorities in their own right (see Beninger 2018), as well as positioning them as critical avian conservation targets (Mathot et al. 2018). This realization may have come too late to save the very species in which it was first documented, since the Roberts Bank migration stopover is slated for adjacent major port development, with unpredictable consequences for microbial mat and film production.

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