Calidrid conservation: unrequited needs

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While factors influencing shorebird migration, stopover and overwintering ecology are topical, potential linkages between individual morphometrics, foraging preferences and prey communities have too often been overlooked. We argue that morphological variations between individuals are likely to produce differential foraging efficiencies and, given that there could be a latitudinal gradient in foraging opportunities, afford a new mechanism to account for patterns in the overwintering distribution of shorebirds. Concomitantly, there appear opportunities for work at stopover sites to test hypotheses on the proposed mechanism as well as implications for monitoring and conservation.

INTRODUCTION

Here, drawing on our experience with the Western Sandpiper *Calidris mauri* Research Network (Nebel & Lank and Butler *et al*., this volume), we reflect on the course of shorebird research and the potential for currently operating paradigms to engender effective conservation.

Habitat managers need to know why certain birds are in a given place at a given time and also how to maintain the underlying ecological processes that support the food base for those particular birds (Durell 2000, Butler *et al*. 2001). Although behaviour-based hypotheses (Dierschke 1998, Ydenberg *et al*. 2002, Lank *et al*. in review) appear compelling in explaining the former need, experimental testing is logistically difficult and they do not address the latter need. Also, the complex and apparently opportunistic and highly plastic nature of food choice in shorebirds may have tended to discount requirements for fine-scale consideration of predator–prey processes in favour of management efforts to maintain invertebrate populations in general (Skagen & Oman 1966). In the following work, we argue that major advances in both shorebird conservation and biology are stalled until there is a deeper understanding of calidrid–prey interactions over the expansive overwintering range. By doing so, we respond to the call for synergistic, multi-disciplinary approaches (Nebel & Lank, this volume) and use bricks of existing knowledge to construct a series of testable hypotheses to account for the overwintering distribution and stopover ecology of Western Sandpipers.

CALIDRID FORAGING ECOLOGY

Calidrid shorebirds forage in wetlands and soft-bottom aquatic habitats between breeding grounds in sub-polar latitudes and extensive overwintering ranges along tropical to temperate coastlines (Hayman *et al*. 1991). Correspondingly, natural diets tend to be diverse, encompassing a variety of, variously, suspended, epibenthic and infaunal invertebrate taxa reflective of local feeding conditions (Holmes 1966, Baker & Baker 1973, Senner *et al*. 1989, Skagen & Oman 1996).

The remarkable foraging plasticity of calidrids is subject to much comment (Zweers & Vanden Berge 1997) yet basic appreciation of the underlying functional morphology of feeding and relationship to diet remains lacking (Rubega 2002). The foraging modes utilized by calidrids have been most commonly categorized as surface feeding, such as the archetypal pecking mode (Zweers *et al*. 1994), that targets epifauna (Sutherland *et al*. 2000), and deep feeding, such as probing (Zweers 1985, Zweers & Berkhoudt 1991, Zweers *et al*. 1997), that targets infauna (Sutherland *et al*. 2000). Also, calidrids have been shown to use a surface tension transport mechanism to feed on prey suspended in water (Rubega 1997). However, commonalities notwithstanding, calidrid bills exhibit subtle morphological variations in size, shape and internal structure both between species and between sexes within species that can affect feeding performance (Burton 1974, Summers *et al*. 1990, Rubega 1996, Durell 2000). Thus, while bill morphology can be seen as a functional compromise to plasticity in feeding behaviour (Gerritsen & van Heezik 1985, Zweers & Gerritsen 1997, Rubega 2002), individuals have unique distinctions suited to particular specialization(s) within a wider more opportunistic foraging repertoire (Recher 1966, Skagen & Oman 1996). Further, a gradient of feeding preferences may exist within a species, such that although both sexes of Western Sandpiper can feed on marine epifauna and infauna (Couch 1966, Senner *et al*. 1989, Sutherland *et al*. 2000) long-billed females appear better adapted to deep feeding and short-billed males might be better surface feeders. Such may be inferred from disproportionate use of deep foraging in Peru, near the southern extreme of the overwintering range (Ashmole 1970) where females predominate (Nebel *et al*. 2002) and the

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relatively greater use of surface feeding by males, compared to females, in Mexico in the northern part of the range where males predominate (G. Fernández, unpubl. data). Additional evidence stems from observations that males dedicate a larger proportion of their foraging effort to surface feeding than females while streaming through the Fraser River delta during northward migration (K. Mathot & R.W. Elner, unpubl. data).

OVERWINTERING ECOLOGY: LATITUDINAL GRADIENTS IN MORPHOMETRICS AND PREY

The Western Sandpiper (Nebel *et al.* 2002) and at least three other calidridine sandpipers (Myers 1981) exhibit latitudinal segregation between the sexes over the overwintering range. While data are incomplete, and it is, therefore, unknown how common this trait is within the subfamily, the literature suggests that other calidridines may exhibit at least partial segregation over parts of their overwintering range (e.g. Dunlin: Shepherd *et al.* 2001). Further, as only one species, Sanderling, has been shown to not exhibit this trait (Myers 1981) insights on the gender-based requirements of Western Sandpipers during migration stopover and overwintering may be relevant to a larger suite of species. Further, for Western Sandpipers, there is a morphometric gradient, or cline, within each sex over the overwintering range, with a tendency for longer-billed and larger birds within both sexes to establish further south and, conversely, shorter-billed, smaller birds further north (O'Hara 2002). We infer that individual Western Sandpipers with similar (subtle, minor yet functionally important) morphometric configurations will share distinctive and characteristic advantages in one or more feeding modes that translate into a preference for prey regimes characteristic of a particular overwintering latitude. Thus, we contend that the morphometric cline is structured by an underlying latitudinal gradient in the prey base, with, at the extremes, birds in the southerly part of the overwintering range deep feeding and northerly birds surface feeding because of selective advantages for their, respective, preferred feeding mode. We hypothesize that the likely mechanism involves individual adaptations to a latitudinal gradient in, not prey community composition and food abundance patterns *per se,* but rather, the relative availability of epi- versus in-faunal food over the overwintering range, N.W. United States to Peru (Wilson 1994). The increasing abundance (R.W. Elner, personal observations) and diversity (Vermeij 1978, Abele 1982) of epifaunal feeding crabs from temperate through subtropical to tropical intertidal zones could account for either differential displacement of shorebirds by habitat alteration (Botto *et al.* 2000) and/or reduction in surface food available to shorebirds with decreasing latitude. While we are aware of no work that relates to biogeographical patterns in abundance of infaunal food, the species richness of marine invertebrates increases dramatically towards the equator (Vermeij 1978) and so might opportunities for infaunal feeding.

Western Sandpipers have been reported to exhibit morphometric variation across their breeding range (Senner *et al.* 1981) and we expect that further work will show a morphometric cline, mirroring the morphometric cline over the overwintering range but with the sexes overlapping, over the breeding grounds, as determined for some other calidrids (e.g. Dunlin: Senner *et al.* 1981; Semipalmated Sandpiper: Gratto-Trevor 1992; Little Stint: Tulp *et al.* 2002). Distin-

guishing the most probable evolutionary forces responsible for either the sexual size dimorphism or the variation within sexes is difficult (Summers *et al.* 1990). However, whether the situation is a consequence of selective pressures related to breeding or a response to the overwintering situation, we infer that the morphological variations have functional significance and are adapted to the overwintering range given a reliance on simple archetypal pecking (Zweers & Vanden Berge 1997) to forage on a superabundance of insects and spiders on the breeding grounds (Wilson 1994). Further, given that final morphometrics are set by the time a juvenile departs the breeding grounds (Nebel *et al.* 2003), we suggest that the overwintering distribution is established by local experience. We can presume that a juvenile will move southward until settling at an overwintering latitude providing the optimal prey template to match its individual morphometrically pre-set foraging proficiencies. The tendency of Western Sandpipers to exhibit overwintering site fidelity, as shown by return rates of 50% or higher (Rice 1995, Fernández *et al.* 2001, O'Hara 2002), is evidence that the selective advantage of the successful juvenile experience establishes the individual's overwintering preference as an adult. However, it should be noted that fidelity to a specific site is not a fixed phenomenon as demonstrated by recent studies indicating lower fidelity at some locations and the possibility of juvenile dispersal (Fernández *et. al.* 2003).

STOPOVER ECOLOGY: ENIGMAS AND OPPORTUNITIES

Western Sandpipers stream through major stopover sites during northward migration, males followed by females (Butler *et al.* 1987) in a sequence reflecting their north to south overwintering distribution; essentially a "film-strip" of the entire range of behavioural, morphological and functional variation of the species projected through a narrow temporal and spatial lens. Enigmatically, exclosure experiments designed to measure invertebrate prey removal by these millions of migrating shorebirds have yielded ambiguous results (Sewell 1996). While the "feeding footprint" could have been obscured by extremely patchy prey distributions (Sewell & Elner 2001) as well as failure to consider the full size spectrum of available food (Sutherland *et al.* 2000), difficulties may have been compounded by not considering the preferred predation mode(s) of the birds present during the experimental period. Given the tendency for calidrids to segregate spatially and temporally on overwintering grounds and stopover sites, respectively, we would predict the depletion of invertebrate prey from the surface fraction of sediment cores to coincide with the presence of largely epifaunal-feeding, short-billed, male sandpipers. In contrast, infaunal depletion would appear more likely when, longer-billed, females are predominant. Quantification of invertebrates without consideration of vertical distribution could dilute the predation "signal" and reduce the power of the experiment to detect significant declines in prey densities. We recommend that experimental designs distinguish epi- and infaunal components of sediment cores in order to address possible differential prey depletion related to the morphometrics, gender and foraging mode(s) of the shorebirds present.

Paradoxically, intensive short-term studies at a single stopover site may afford a powerful new tool to understanding and/or predicting the overwintering distribution and

health of the species over the whole latitudinal range. We reason that variation in sandpiper life histories are driven not by morphometrics *per se* but, rather, the subtle influences of morphometrics on the relative foraging proficiency of individuals within an arsenal of potential foraging modes. Major stopover sites can be presumed to afford an abundance of epifaunal and infaunal prey resources (Butler *et al.* 2001) to accommodate the needs of all sandpipers challenged to make a timely arrival on the breeding grounds in good condition (Clark & Butler 1999). Thus, foraging behaviours and small scale habitat use patterns of individual Western Sandpipers on northward migration within a stopover site can be supposed to reflect true individual preferences, as would be displayed over the overwintering area by that individual, rather than "plasticity". The variation would otherwise be observable only by studies over the extensive overwintering range. Similarly, as the "film" of Western Sandpipers streaming northward through a stopover site is observed, the relative abundance of any given morph can be presumed to relate to its absolute abundance at a predictable latitude in the overwintering distribution. Thus, any "gaps" or depressions in relative abundance in the "film" sequence may indicate real low abundance at a particular overwintering area. Interannual comparisons of the "films" might provide a novel means to not only assess population status throughout the entire overwintering range but also, by tracking relative abundance trends for a given morph, evaluating conservation actions at a particular latitude. In addition, presuming a morphometric cline over the breeding grounds, there is the possibility of predicting breeding location and overwintering latitude as well as assessing relative breeding success from sampling adult and juvenile sandpipers on southward migration.

While there is substantial evidence for foraging plasticity on the species level, to what degree individual plasticity exists is uncertain. We suggest that the plasticity of the individual will be less than that exhibited by the population. Studies at different stopover habitats within the Georgia Basin/Puget Sound indicate that, based on site averages, the fattening rates achieved by Western Sandpipers do not correlate with foraging mode (D.A. Seaman & T.D. Williams, unpubl. data). These findings argue against the existence of a globally superior foraging mode for this species. Further, birds at sites with similar mean foraging modes expressed a wide range of fattening rates, which indicates that ecological site characteristics influence the resulting fattening and, thus, cannot be ignored. These studies show that the Western Sandpiper, on the species level, can achieve fat deposition on both epifauna and infauna. However, these data do not allow us to predict the outcome of a single individual of a particular bill length foraging at two different sites with different prey regimes (i.e. whether the bird would shift foraging modes between sites and the resulting fat deposition rates).

NEW CONSERVATION NEEDS

The Western Sandpiper is one of the most abundant shorebirds migrating along the Pacific Flyway (Morrison *et al.* 1998, Page *et al.* 1999) and serves as a focal species for local conservation strategies. Coastal mudflats and wetlands forming the major stopover sites are under constant threat of development and are, generally, in an ongoing state of decline (Dahl 1990). Currently, the major lever for shorebird

conservation is protection of sites within the Western Hemisphere Shorebird Reserve Network (Bildstein *et al.* 1991). Admission criteria for the network are based on the numbers of shorebirds using the site and, as such, sites of regional and hemispheric importance are defined as those being used by at least 20,000 and 500,000 individuals, respectively (Bildstein *et al.* 1991). Page *et al.* (1999) determined that targeting sites for conservation based on the percentage of the population rather than the absolute number of individuals supported will protect an overall greater proportion of the population. However, we suggest that, should differential foraging mode requirements exist, both strategies require reappraisal as neither will necessarily maintain population diversity if particular prey regimes represent an advantage in fattening ability for particular morphs. To be more certain, stopover habitat conservation strategies should target the underlying ecological factors that maintain predator–prey diversity and afford a complete mosaic of stopover opportunities in addition to total area protected. The concern is that if the complete spectrum of individual-based needs is ignored then conservation measures may only protect segments of the population. If unprotected segments are reduced, discontinuities in the latitudinal overwintering pattern may be expected with consequential changes in the breeding distribution, impacts at the population level and reduced capacity of the species to accommodate emerging global issues, such as climate change (global warming).

CONCLUSION

To provide efficacious conservation advice, researchers should take multi-scale and multi-disciplinary approaches to address all plausible ecological factors that may drive fattening during stopover and correlatively migration success. We contend that conservation measures need to protect the entire spectrum of shorebird food types at stopover sites or else risk alienating, and potentially losing, segments of the morphometric diversity (overwintering and breeding subpopulations) of the species. New hypotheses (Table 1) invoking latitudinal gradients in prey availability, spatial and vertical distribution patterns, and intraspecific differences in predatory abilities related to morphometric heterogeneity for Western Sandpipers seem at least complementary considerations to shorebird predator-based models deemed responsible for driving migration (Butler *et al.,* this volume) and, possibly, overwintering (Page & Whitacre 1975, Cresswell & Whitfield 1994) patterns. While there is correlational evidence for the migration behaviour of a sandpiper being influenced, if not shaped by, risk of predation (Ydenberg *et al.* 2002, Lank *et al.* in review, Butler *et al.,* this volume), the underlying mechanism relates to the threat's effect on foraging success, that is, where a Western Sandpiper feeds and how long it remains there. Ultimately, an individual's success in migration is linked to its ability to fatten and advance through successive stopover sites, and any influence that predation may have on this ability must be deemed important. However, a bird's ability to fatten at a stopover site will necessarily be affected not only by predation risk but also by food availability. Because there is no predictable relationship between predation risk and food availability, they need to be addressed together as separate factors driving the same issue, fattening rate. There is compelling evidence that where and how a bird feeds is influenced by both prey distribution and bill morphology and these factors, therefore, also deserve attention.

Table 1. Testable companion hypotheses and some derivatives invoked in this paper to account for patterns in the overwintering distribution and stopover ecology of Western Sandpipers.

Concerning Western Sandpiper Foraging:

Hypothesis I: Inter- and intrasexual variation in morphology, especially bill morphometrics, for Western Sandpipers is functionally related to feeding mode specialization on overwintering and stopover habitats.

- Derivative I (a): Short billed morphs will tend to utilize a surface feeding mode relatively more frequently than longer billed morphs.
- Derivative I (b): Long billed morphs will tend to utilize a deep feeding mode relatively more frequently than shorter billed morphs.
- Derivative I (c): The foraging plasticity and efficiency of individuals is less than the plasticity observable over the whole population.
- Derivative I (d): Individuals on stopover sites will prefer the same feeding mode as on their overwintering grounds.

Concerning Prey Distribution:

Hypothesis II: There is a latitudinal gradient in the relative availability of epi- versus infaunal food for Western Sandpipers over the overwintering range.

- Derivative II (a): Epifaunal food is relatively more available than infaunal food in the northern part of the overwintering range.
- Derivative II (b): Infaunal food is relatively more available in the southern part of the overwintering range.
- Derivative II (c): Increasing crab abundance, north to south, over the overwintering range differentially affects habitat suitability for male versus female Western Sandpipers.
- Derivative II (d): Increasing crab predation pressure, north to south, over the overwintering range reduces the availability of epifaunal food in the southern part of the overwintering range.

Concerning Overwintering Ecology:

Hypothesis III: Over the overwintering range, the latitudinal gradient in prey availability (Hypothesis I) matches latitudinal clines in sex ratio and morphometrics for Western Sandpipers.

- Derivative III (a): A juvenile will move south from the breeding grounds until settling at an overwintering latitude with the optimal prey availability to match its individual feeding mode preference.
- Derivative III (b): An adult will return to the same overwintering latitude it used as a juvenile.

Concerning Stopover Sites:

Hypothesis IV: Morphometrics of Western Sandpipers at a stopover site can be used to predict their overwintering latitude.

Hypothesis V: Morphometrics of Western Sandpipers at a stopover site can be used to predict their breeding area.

While our hypotheses are not mutually exclusive from other hypotheses on shorebird overwintering (Myers 1981, Cristol *et al.* 1999, Nebel *et al.* 2002) we trust that the possibility of prey-related differentials driving distribution patterns will resonate with other researchers. We support testing on all current hypotheses of factors affecting distribution and behaviour over the overwintering grounds and advocate universal protocols, including collection of full morphometric data (culmen, tarsus, wing chord) and foraging mode (peck/probe) observations, as routine for future shorebird field studies as a means to such testing.

In conclusion, we tender the Western Sandpiper as a metaphor for all calidrids and present a case for improved understanding of the prey base of these shorebirds and the functional morphology of feeding responsible for their apparent plasticity and foraging mode preferences. We suggest that such understanding is necessary to complement current behavioural-based approaches and better address conservation needs. Success in these endeavors will necessitate stronger, even more diverse multidisciplinary teams to tap expertise on biogeography and ecology of invertebrate prey as well as new field methodology to capture the foraging dynamics of individual birds of known morphometrics.

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