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Implications of Frequent Habitat Switches in Foraging Bar-tailed Godwits

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Temporal variation in avian foraging behavior spans a range of scales, from annual (Hejl and Verner 1990, Petit et al. 1990, Szaro et al. 1990), between-season (Ford et al. 1990, Lundquist and Manuwal 1990), and within-season (Hejl and Verner 1990, Miles 1990, Sakai and Noon 1990) to a matter of a few hours (Holmes et al. 1978). Among nonbreeding shorebirds, temporal variation in foraging behavior frequently manifests itself via habitat selection (Myers 1984). Switches between foraging habitats by shorebirds may involve movements between littoral and upland sites (Goss-Custard 1969, Prater 1972, Page et al. 1979) or between littoral habitats (Connors et al. 1981). Most of the foraging-habitat switches documented for nonbreeding shorebirds are linked to changes in habitat availability and foraging profitability across a tidal cycle (Connors et al. 1981, Myers 1984). In this paper, I present data on a population of staging shorebirds that exhibited repeated, alternating habitat shifts within single tidal cycles.

Bar-tailed Godwits (Limosa lapponica baueri) stage each fall along the Bering Sea coast of southwestern Alaska (Gabrielson and Lincoln 1959, Gill and Handel 1981, 1990). I studied foraging godwits that switched between an intertidal flat and upland dwarf shrub tundra. My objective was to document the temporal pattern of habitat switching to determine if it was consistent with the tidally induced switching reported for shorebirds elsewhere.

Study area and methods.—I studied juvenile godwits

at Duchikthluk Bay on the south side of Nunivak Island, Alaska (59°49′N, 166°09′W). Duchikthluk Bay is a 32-km² shallow lagoon fed by the Duchikmiut River and five unnamed streams, and open to the Bering Sea through a 450-m wide channel. Duchikthluk Bay is bordered on the east and west by tidally influenced graminoid meadows, and on the north and south by low uplands covered with sedge, lichen-sedge, and dwarf shrub meadows.

Several assistants and I observed godwits along the south shore of Duchikthluk Bay near Kingaktakamiut, a Yup'ik Eskimo summer fishing camp. We used a permanent fish camp tent frame for observations of both intertidal and upland foraging habitats. Several dozen godwits foraged on a 117-ha intertidal sand and mudflat 100 m northwest of the observation site, and on a 0.1-ha patch of dwarf shrub tundra immediately south of the observation site that was rich in crowberries (Empetrum nigrum).

Godwits were observed on the berry patch during receding tides by one to four observers on 11 days between 7 and 30 September 1991. The proximity of the observers to the birds (<50 m), the low stature of the vegetation (<3 cm), and the distinctive foraging behavior of fruit-eating godwits facilitated quantitative observations. As godwits arrived on the patch, each observer selected a focal individual. To avoid double-sampling the same individual during a given foraging bout, observers selected focal individuals on opposite sides of the flock. Individuals were not randomly selected, however, nor were foraging bouts independent (i.e. the same individual might have been sampled during different visits to the patch).

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These limitations preclude drawing statistical inferences from the foraging data. We determined the length of stay at the patch (i.e. foraging-bout length) and the number of crowberries eaten by each focal bird; each observer recorded data for only a single bird per visit.

On four days I measured foraging-bout lengths on the intertidal flats, defined as the interval between a godwit's arrival on the intertidal flat and its next departure for the berry patch. I was unable to determine prey items of godwits foraging on intertidal flats.

Results.—We observed juvenile Bar-tailed Godwits during and immediately after receding tides. No adult godwits were detected. On six dates, observations spanned the entire interval over which godwits were present during a receding tide; godwits were present on the flats from 101 to 240 min ($\bar{x} = 175 \pm$ SE of 20.3 min, $n = 6$).

Within a single receding tide, foraging godwits switched repeatedly from the intertidal flats to the berry patch. Because birds were not individually marked, we could not directly ascertain the number of trips between the two habitats by a particular bird. The lengths of foraging bouts in the two habitats, however, allow for an approximation of switching frequency. Foraging bouts in the berry patch were brief, averaging 1.7 ± 0.07 min ($n = 132$); intertidal foraging bouts averaged 12.5 ± 2.07 min ($n = 22$). Because travel between the habitats was direct and travel time was minimal (<30 s one way), individual godwits averaged about four trips per hour between the intertidal flats and the berry patch during a receding tide.

Godwits rarely departed from the intertidal flats en masse to visit the berry patch. Instead, flock members recruited incrementally over a few tens of seconds, as first one or a few birds took off, followed quickly by several others. Upon arriving at the berry patch, godwits began foraging immediately. Berries consumed per foraging bout ranged from 2 to 64, and averaged 21.6 ± 0.86 ($n = 132$). Berries consumed per min ranged from 1.5 to 33.2, and averaged 13.9 ± 0.47 ($n = 132$). Based on mean rates of berry consumption, length of visits to the berry patch, length of foraging bouts on the flats, duration of foraging during a single falling tide, and a maximum round-trip between the flats and the patch of 60 s, individual godwits consumed, on average, about 272 berries while foraging during each falling tide at Kingaktakamiut. The average mass of a juvenile Bar-tailed Godwit and a ripe crowberry in western Alaska is 364 g and 0.14 g, respectively (R. E. Gill, Jr. pers. comm.); thus, juvenile Bar-tailed Godwits consumed approximately 10% of their body mass in berries during each falling tide at Kingaktakamiut.

Discussion.—Previous studies of habitat switching in nonbreeding shorebirds have revealed that a bird's decision to switch habitats is based at least in part on tide-related changes in foraging efficiency (Connors et al. 1981). At Kingaktakamiut, juvenile Bar-tailed Godwits foraged on the intertidal flats only at the lower tide levels, and the habitat shifts that resulted in their first arrival at and final departure from the flats clearly were mediated by tidal effects. When the intertidal foraging substrate was covered by water, godwits did not forage there. These observations are consistent with observations elsewhere along the Bering Sea coast of western Alaska, where staging godwits feed on intertidal flats during receding tides, but roost and/or forage on graminoid and dwarf shrub meadows at high tide (Gill and Handel 1990, McCaffery unpubl. data).

The pattern of repeated habitat shifts within a single falling tide, however, does not conform to a pattern of tidal regulation. Given the frequency of habitat switches (i.e. nearly four times per hour), it seems that godwits made decisions regarding foraging habitat at a time scale rarely quantified in other foraging studies and that the currency of profitability used in most avian foraging studies (i.e. caloric intake rate) may be inappropriate for understanding this system.

Changes in foraging profitability, as measured by caloric intake rate, probably did not account for the rapid alternation between habitats. Within a single tidal cycle, berries represented a virtually stable resource. Because these berries occupied a terrestrial habitat, their absolute profitability remained constant over time, unaffected by changes in tidal level. The relative profitability of the berries might have changed with variation in foraging profitability on the mudflats, but over the time intervals involved, that seems unlikely, particularly because godwits returned to the flats repeatedly following visits to the berry patch. Although a foraging shorebird may deplete invertebrate resources locally via either predation or disturbance (Goss-Custard 1970), it need not switch habitats to find a site with uncropped or undisturbed resources. If local resource depletion accounted for the godwits' decision to move, then they should have moved elsewhere on the flats rather than to the berry patch. In addition, a resource-depletion hypothesis fails to explain why visits to the patch were so brief, certainly too brief to allow for local replenishment of a depleted invertebrate resource on the flats.

Habitat switching by godwits at Duchikthluk Bay may indicate selection for a nutritionally diverse diet. By switching repeatedly between intertidal flats and shrub meadows, godwits obtained both intertidal invertebrates and crowberries—food sources presumably high in protein and carbohydrates, respectively (Levey and Karasov 1989). Such a mix may be advantageous for juvenile godwits that simultaneously are completing growth and preparing for an arduous overwater migration to their wintering

grounds in the southwest Pacific. A mixed diet also may be important for staging godwits, particularly juveniles, that are making the transition from a relatively soft diet on the tundra breeding grounds to a postbreeding diet often dominated by hard-shelled intertidal invertebrates (Piersma et al. 1993).

The potential advantages of a mixed diet, however, do not explain the frequency and timing of habitat switching that I observed. Presumably, the nutritional and physiological advantages described above could be achieved by switching habitats between (vs. within) stages of the tidal cycle. In other words, given that access to intertidal invertebrates was time-limited due to tidal changes, why did godwits repeatedly abandon this habitat during its period of availability to forage in a habitat where the resource (fruit) was available regardless of the tidal stage?

The answer to this question is beyond the scope of my study and may be discovered only through an analysis of gut function, the "black box" (Levey and Duke 1992) of avian foraging studies. The digestive efficiency of birds is compromised when they switch between diet types (e.g. fruits and invertebrates) over a several-day period (Levey and Karasov 1989); such costs also may be borne by godwits that process very different types of food simultaneously. Presumably, the nutritional benefits accrued by godwits having intertidal invertebrates and fruit in their gastrointestinal tracts at the same time outweigh these costs. Such a foraging strategy could yield at least three types of benefits.

First, a mixed diet may help prevent the accumulation of toxins and other compounds that reduce the availability of proteins and the activity of digestive enzymes (White and Stiles 1990, Izhaki 1992), or it may provide secondary compounds that enhance nutrient assimilation (Bairlein 1991). The benefits of such chemical activity may be maximized when both types of food are in the digestive tract simultaneously. Second, the physical presence of hard and soft prey in the gut may facilitate passage through the gut and/or nutrient assimilation. For example, at other estuaries in western Alaska, staging godwits consume large numbers of the mollusc *Macoma* sp. (R. E. Gill, Jr. pers. comm.). Perhaps the presence of fruit parts eases the passage of sharp shell fragments through the birds' intestines. Perhaps hard-shelled molluscs in the gizzard serve as grit and facilitate nutrient uptake by macerating berries and/or grinding seeds prior to their passage through the pylorus. Although Whimbrels (*Numenius phaeopus*) and Bristle-thighed Curlews (*N. tahitiensis*) pass crowberry seeds intact when feeding on berries and terrestrial insects in western Alaska (McCaffery 1996), the condition of seeds excreted by Bar-tailed Godwits with intertidal invertebrates in their guts has not been determined. Third, godwits may be attempting to keep their guts nearly full at all times to maximize the rate of nutrient accumulation. Because fruits pass through avian

digestive tracts very quickly (Levey and Duke 1992), a godwit whose gut is nearly filled with energy-rich berries can return to the flats from the berry patch and begin feeding immediately on protein-rich invertebrates, with very low costs in time and energy.

The pattern of rapid habitat switches within a single falling tide at Duchikthluk Bay has not been documented in Bar-tailed Godwits staging elsewhere along the Bering Sea coast of western Alaska (McCaffery unpubl. data), where mudflats are up to several km wide, and dwarf shrub meadows rich in berries may be several km from the coast. The cost of repeated trips between these habitats probably is prohibitive. The proximity of the two habitats at Duchikthluk Bay provides a unique opportunity for godwits, an option that seldom may be available to godwits staging elsewhere in the eastern Bering Sea.

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Frequency of Extrapair Young Increases in Second Broods of Eastern Phoebes

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Extrapair fertilizations (EPFs) are most common in passerines that breed synchronously (Stutchbury and Morton 1995). Many bird species that breed at temperate latitudes produce multiple broods in a single season. Owing to renesting attempts and variation in the time to raise first broods, many (if not all) of these species are more synchronous in their first breeding attempt than in subsequent attempts. Therefore, in multibrooded, socially monogamous species that engage in EPFs, the frequency of EPFs should decrease in subsequent breeding attempts, a result confirmed by Gowaty and Bridges (1991) and Stutchbury et al. (1994).

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