# DIETS, ENERGY INTAKE, AND KLEPTOPARASITISM OF NONBREEDING LONG-BILLED CURLEWS IN A NORTHERN CALIFORNIA ESTUARY

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ABSTRACT.—We documented differences in diet composition of territorial Long-billed Curlews (*Numenius americanus*) feeding in different locations within the Elk River Estuary, Humboldt Bay, California. We used direct observations to measure diet because curlews often handled prey for long periods (up to 4 min), which enabled us to identify prey and to estimate size. Curlews ate mainly five benthic organisms: yellow shore crabs (*Hemigrapsus oregonensis*), bivalves (various species), marine worms (polychaetes), ghost shrimp (*Callianassa* spp.), and a burrow-dwelling fish (arrow goby, *Clevelandia ios*). During summer, curlews on eight territories ate different proportions of bivalves, shrimp, and worms, but similar proportions of crabs, fish, and unknown prey. The proportion of prey types captured changed slightly during fall and winter. More shrimp and fish were eaten during summer than during fall and winter; more worms were eaten during winter than during summer. Despite differences in diet across some territories and seasons, energy intake rates (kcal/h) were not significantly different, but were highly variable within territories and seasons. Curlews lost worms and shrimp to gulls and other shorebirds more than expected, but lost bivalves and crabs less than expected based on capture frequency. We suggest that possible reasons for interterritorial variation in diet are temporal and spatial variation in prey availability, phenotypic differences of curlews, competition or interference, and risk of kleptoparasitism. *Received 21 Aug. 2000, accepted 14 June 2001.*

Dietary studies provide insight into ecological relationships between birds and their prey, habitat, community structure, and population dynamics. Individuals within a population may use multiple foraging strategies to capture different prey species, or may specialize by consistently using a particular feeding technique or prey species (Goss-Custard and Sutherland 1984, Price 1987, Van Buskirk and Smith 1989, Whitfield 1990). The study of diet often is considered in the context of optimal foraging theory, but what is optimal for one individual may not necessarily be optimal for another (Partridge and Green 1985). The use of alternative strategies by some individuals suggests selective pressures may not be the same for all individuals within a population (Maynard Smith 1982) due to variable food supplies, phenotypic differences, and frequency-dependent pay-offs such as competition (Partridge and Green 1985).

The Long-billed Curlew (*Numenius americanus*) is an ideal species for the study of variation in diet using direct observations because it captures large, easily observed prey that are handled for long periods before swallowing (Stenzel et al. 1976). During the nonbreeding season, curlews often defend feeding territories in intertidal habitats (Colwell 2001), allowing repeated observations of curlews in specific locations. The focus of this study was to quantify the variation in diet composition and intake rates of territorial curlews feeding in different locations in an estuary. We tested whether curlews occupying different territories consumed different proportions of prey and if such differences resulted in different energy intake rates. We also examined seasonal changes in diet and energy intake rate for a subset of territories.

## METHODS

*Study area.*—We studied curlews along the lower 2 km of the Elk River Estuary (40° 46′ N, 124° 11′ W), which empties into Humboldt Bay, California (Fig. 1). The Elk River Estuary has a mixed semidiurnal tide pattern, with two unequal highs and lows occurring daily. At its southern extent, the estuary consisted of a 1-km long, steep-banked river channel bordered by salt marsh (containing *Spartina densiflora* and *Salicornia virginica*) and dune habitat (dominated by *Ammophila arenaria*). To the north, the estuary widened
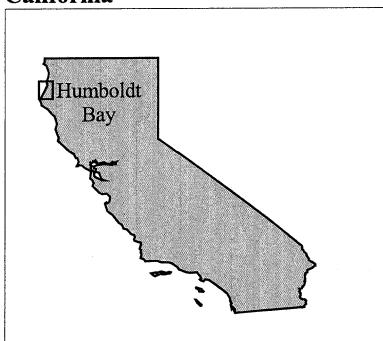
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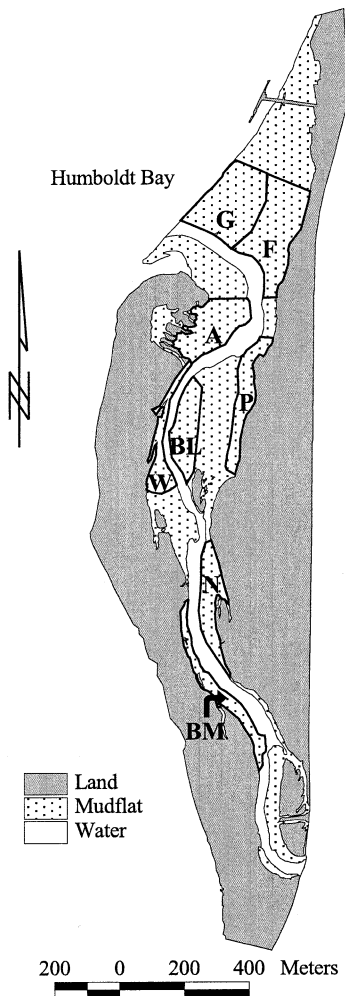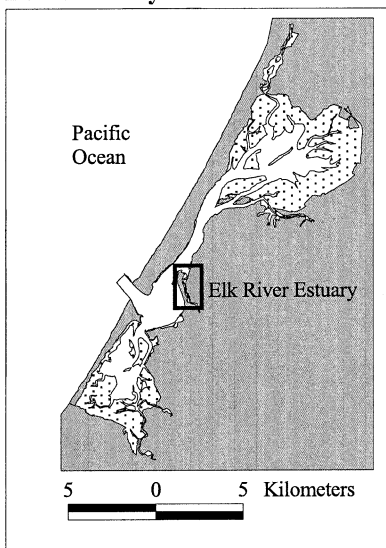[4] Corresponding author; E-mail: leemanl@edaw.com

FIG. 1. Elk River Estuary, Humboldt County, California. Outlined areas containing letters refer to well-defined territories of Long-billed Curlews.

to include high- and low-elevation intertidal flats, dissected to varying degrees by channels. Immediately northeast of the river's confluence with the bay was a 11.9-ha broad, gently sloping mudflat, sparsely vegetated by eelgrass (*Zostera marina*). Estuary sediments varied from gravel and sand to finer clay particles.

*Curlew observations.*—We repeatedly observed unmarked territorial curlews occupying specific locations. Therefore, we treated the data as comparisons between territories rather than individuals. Although we did not capture and mark individuals, we were able to identify some individuals based on distinct morphology (e.g., overall size, bill length), plumage characteristics that existed for intervals that were short (e.g., molt patterns lasting weeks) or long (e.g., distinct markings present over the course of this study), and consistent use and defense of specific areas. During 2-h focal observation sessions (see below), observers

mapped curlew locations at 2-min intervals, resulting in 3–19 independent maps of each curlew's movements to verify consistency of area used.

We used focal sampling (Altmann 1974) to collect diet information during 96 sessions for a total of 170.4 h. Focal observation sessions bracketed the predicted diurnal low tide. Using a 20–60× spotting scope, we watched curlews from elevated locations, which allowed nearly constant visual contact at distances of 15–300 m. If curlews moved out of sight, observers either changed observation points to relocate focal curlews or terminated the observations. We recorded the identity and estimated sizes of prey, using bill length as a reference (Zwarts and Esselink 1989, Ens et al. 1990). We also recorded attempts by other species to steal prey from focal curlews.

Prior to fieldwork, we familiarized ourselves with potential prey of curlews by sampling the benthos. Us-

ing collected prey, observers estimated prey type and size at approximately 75 m using models of female and male curlew bills. Curlews often handled prey for periods (5 s–4 min) that enabled easy identification and size estimation. With the exception of bivalves and unknown prey, curlews frequently (73%) captured conspicuous, large (≥2 cm) prey items. From 14–27 June 1998, we practiced observational methods in the field; we did not use data from these dates in the diet composition or intake rates analyses, but included them in the kleptoparasitism analyses.

We categorized observations into three seasons: summer (28 June to 22 September 1998), fall (6 October to 17 December 1998), and winter (12 January to 12 March 1999), corresponding with changes in tidal and weather patterns. Curlews arrived at Humboldt Bay during mid-June from their inland breeding grounds and stayed until mid-March (Colwell and Mathis 2001). During summer, the lowest of two low tides occurred during daylight and typical weather was cool and dry, with fog (Barnhart et al. 1992). During fall, diurnal low tides were relatively high with the lowest low tides occurring after dark (Dodd and Colwell 1996). In addition to changes in tides, intermittent rainstorms moved through the area in October, beginning the wet, mild winter (Barnhart et al. 1992).

Numbers of curlews in the estuary varied between 18 and 20 during summer and between 5 and 7 during winter. During summer, we repeatedly observed curlews on eight territories ($n = 3$–9 focal observation sessions per territory). During fall and winter, curlews were consistently present on three of eight territories occupied during summer; other individuals abandoned territories in early fall (Colwell and Mathis 2001). We observed these three territories through fall ($n = 4$–5 focal observation sessions per territory) and winter ($n = 4$–5). We included only those observations ≥1 h in duration in analyses of diet composition and intake rates.

*Energy calculations.*—We developed regression models to estimate dry weights of prey from observed lengths and used published energy values of prey based on dry weight to estimate the caloric value of each captured prey item. We retained all exoskeletons in dry weight calculations because curlews consumed prey whole and shells contain some organic compounds that may be digestible (Cameron et al. 1979). For details see Leeman (2000). For each focal observation session, we summed the caloric value of all prey ingested and calculated intake rate as kcal/h.

*Data analyses.*—We calculated the proportion of each prey type based on the total number of prey items eaten during the 2-h focal observation session. Because of small sample sizes, we used nonparametric analysis of variance to compare proportions of each prey type among territories during summer. Because proportions were not independent, we used Bonferroni adjusted *P*-values to account for multiple tests (Afifi and Clark 1996). We tested whether proportions of each prey type were equal among territories during summer. Because the proportion of each prey captured

by curlews on the three territories that were consistently occupied during fall and winter did not differ among territories within each season, we pooled the three territories to test for seasonal differences in diet composition. For energy intake rates, we used nonparamatric ANOVA to examine differences among territories during summer. Because intake rates did not vary among the three territories observed during three seasons, again, we pooled territories to examine if intake rates varied among seasons.

We analyzed the frequency of prey kleptoparasitism using all prey captured by curlews. We tested the null hypothesis that the observed proportion of kleptoparasitism attempts for each prey type occurred in proportion to capture frequency, using chi-square analysis and methods described by Neu et al. (1974). We also compared the number of kleptoparasitism attempts among territories and seasons using chi-square analyses. We used SAS ver. 6.12 (SAS Institute, Cary, North Carolina) and an alpha level of 0.05 for all analyses.

## RESULTS

*Summer diets.*—Curlews captured five main prey types: yellow shore crabs (*Hemigrapsus oregonensis*, ≤4 cm), bivalves (various species, ≤3 cm), marine worms (polychaetes, 0.5–45 cm), shrimp (*Callianassa* spp., 2–15 cm), and a burrow-dwelling fish (arrow goby, *Clevelandia ios*, ≤6 cm). During summer, based on prey number captured, diet consisted of 31% crabs (range 1–49%), 26% bivalves (1–97%), 15% worms (1–20%), 10% fish (1–16%), 4% shrimp (1–16%), and 14% unknown prey (0–25%; Fig. 2). Diet composition varied among some territories in proportions of bivalves, shrimp, and worms, but proportions of crab, fish and unknown prey were similar. The proportion of bivalves eaten differed significantly ($H = 21.3$, df $= 7$, $P = 0.015$). On territory G, a curlew consumed more bivalves, averaging 259 bivalves/h (97% of diet), than curlews at locations BM and N. Curlews at other locations averaged 0–26 bivalves/h (1–45% of diet). Shrimp was consumed in different proportions among territories ($H = 19.6$, df $= 7$, $P = 0.03$). A curlew on territory BM ate significantly more shrimp than the curlew on territory N. Differences in the proportions of crabs consumed among territories were not significant ($H = 17.5$, df $= 7$, $P = 0.07$). In addition, curlews on all territories ate similar proportions of fish ($H = 11.4$, df $= 7$, $P = 0.62$). The curlew on territory N consumed significantly more worms than the curlew on territory BM ($H = 18.3$,
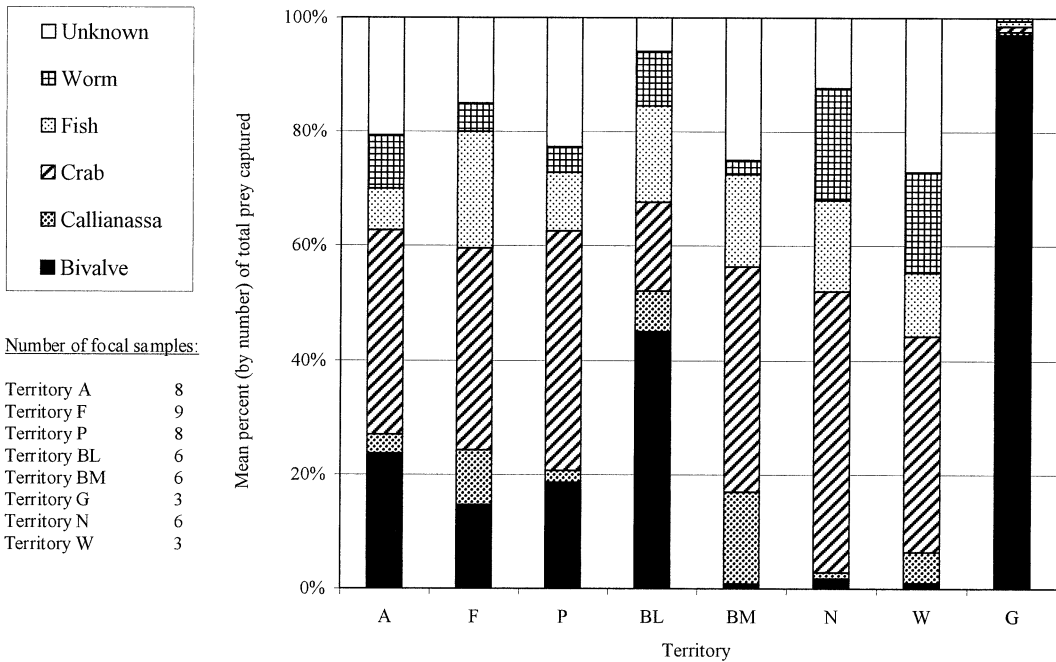
FIG. 2. Mean percent (by number) of each prey type in the diet of Long-billed Curlews during summer (28 June to 22 September, 1998) at the Elk River Estuary, California.

df = 7, $P$ = 0.05). The proportion of unknown prey in the overall diets did not differ significantly among territories ($H$ = 14.8, df = 7, $P$ = 0.19).

*Seasonal changes in diet.*—Diets changed seasonally for all prey types except bivalves ($H$ = 7.4, df = 2, $P$ = 0.13) and crabs ($H$ = 5.0, df = 2, $P$ = 0.42; Fig. 3). During summer, diet included more fish ($H$ = 17.5, df = 2, $P$ = 0.002) and shrimp ($H$ = 19.8, df = 2, $P$ = 0.002) than during fall and winter. During winter, worm consumption was higher than during summer ($H$ = 14.3, df = 2, $P$ = 0.004). Unknown items occurred in the diet more during summer than during fall and winter ($H$ = 11.5, df = 2, $P$ = 0.016), possibly reflecting observer experience.

*Kleptoparasitism.*—We observed 80 instances of attempted kleptoparasitism during 4805 prey captures. Kleptoparasites successfully stole prey from curlews 57 times (75% of known outcomes; four attempts had unknown outcomes). Gulls (*Larus occidentalis, L. californicus, L. glaucescens, L. delawarensis*) most commonly (90%, 72 attempts, 56 successes) attempted to steal prey. Other species observed kleptoparasitizing curlews in-

cluded Willets (*Catoptrophorus semipalmatus*; six attempts, one success), a Marbled Godwit (*Limosa fedoa*; one unsuccessful attempt), and a Whimbrel (*Numenius phaeopus*; one unsuccessful attempt).

Worms were the most commonly stolen prey item, accounting for 59% of all attempts. The observed number of kleptoparasitism attempts differed significantly from the expected number of attempts based on capture rate of each prey type ($\chi^2$ = 285.9, df = 4, $P$ < 0.0001) with all territories and seasons combined. Attempts to steal bivalves and crabs were fewer than expected, whereas attempts to steal shrimp and worms were greater than expected. The number of kleptoparasitism attempts differed among territories ($\chi^2$ = 45.1, df = 6, $P$ < 0.0001), with the observed number of attempts greater than expected for territory A and less than expected for territory G. The curlew on territory A had the highest rate of kleptoparasitism (3.9% of 739 captures) with 12 of 28 attempts occurring on one day. The curlew on territory W was kleptoparasitized at a similar rate (3.8% of 78 captures), but was observed for less time, and only during summer. Although the curlew on
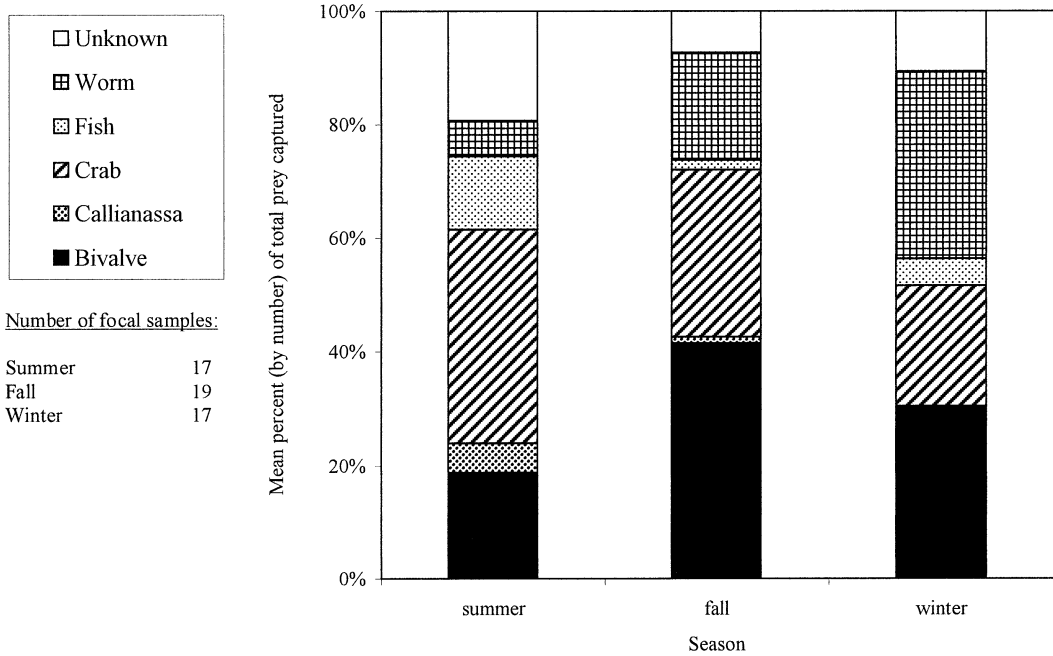
FIG. 3.   Seasonal variation in diet composition of Long-billed Curlews (territories A, F, and P pooled) at the Elk River Estuary, California, 1998–1999.

territory N ate the greatest proportion of worms, its rate of kleptoparasitism was among the lowest (0.4% of 236 captures). Since the proportion of worms captured was not significantly different among territories A, F, and P during any season, the data were pooled and examined for seasonal differences in number of worms kleptoparasitized. No significant difference was found among seasons for kleptoparasitism of worms based on capture rates ($\chi^2 = 0.5$, df = 2, $P = 0.78$).

*Energy intake.*—During summer, mean energy intake rates were 25.8 ($\pm$15.5 SD) kcal/ h. Intake rates did not differ significantly among territories ($H = 7.2$, df = 7, $P = 0.41$; Table 1). During fall and winter, mean intake rates were 26.9 ($\pm$16.5 SD) and 16.2 ($\pm$9.2 SD) kcal/h, respectively. Intake rates did not differ significantly with respect to season ($H = 3.5$, df = 2, $P = 0.18$).

## DISCUSSION

The results of this study are similar to those of Stenzel et al. (1976), who reported that Long-billed Curlews in Bolinas Lagoon in central California ate mostly crabs (*Hemigrapsus oregonensis*; 55–63% of direct observations, 59% of prey in pellets). However, at Bolinas curlews ate more shrimp (20–24% of direct observations and 34% of prey in pellets) than in this study (1–16%). At Bolinas, curlews also ate mud shrimp (*Upogebia pugettensis*; 7–15% of direct observations, 6% of prey in pellets), which are not found in the Elk River Estuary. Stenzel et al. (1976) did not observe curlews eating worms or bivalves, but occasionally they did see curlews eat small fish in submerged areas. In pellets ($n = 30$), they found remains from one nereid worm, several talitrid amphipods, one gastropod (*Littorina scutulata*), six small bivalves (*Gemma gemma*), insects (adult and pupae), and seeds.

Although we analyzed the data by territory, the curlews occupying each territory most likely were the same individuals throughout the study. We based this assertion on two pieces of evidence: the curlew on territory P had a unique plumage feature and was observed using the same area for two consecutive years, and all focal curlews consistently defended specific areas and had repeated border disputes with neighbors in precise locations within their territories, suggesting recognition of

TABLE 1. Territory and seasonal variation in energy intake rates of Long-billed Curlews feeding in the Elk River Estuary, California. Variation in intake rates within territories A, F, and P was greater than variation among these territories.

| Territory | Season | Mean Kcal/h ± SD | Range | $n$[a] | Hours of observation |
|---|---|---|---|---|---|
| A | Summer | 21.7 ± 13.2 | 7.3–45.4 | 7 | 14.0 |
| A | Fall | 24.9 ± 15.5 | 7.7–41.4 | 4 | 7.7 |
| A | Winter | 13.7 ± 6.2 | 8.2–22.9 | 5 | 8.5 |
| F | Summer | 28.6 ± 16.2 | 9.8–52.0 | 5 | 10.0 |
| F | Fall | 32.3 ± 23.4 | 9.0–65.0 | 5 | 9.9 |
| F | Winter | 15.3 ± 12.4 | 4.8–35.7 | 5 | 7.9 |
| P | Summer | 28.0 ± 22.9 | 5.9–56.6 | 8 | 15.6 |
| P | Fall | 23.1 ± 10.0 | 13.4–36.0 | 5 | 8.0 |
| P | Winter | 20.4 ± 8.7 | 9.8–30.3 | 4 | 7.9 |
| BL | Summer | 23.0 ± 14.1 | 9.8–43.8 | 5 | 9.3 |
| BM | Summer | 24.1 ± 14.0 | 6.0–41.6 | 6 | 12.0 |
| G | Summer | 37.1 ± 6.4 | 31.5–44.1 | 3 | 5.2 |
| N | Summer | 29.8 ± 13.1 | 17.2–53.5 | 6 | 12.0 |
| W | Summer | 8.3 ± 2.6 | 6.5–10.1 | 2 | 4.0 |
| Total | Summer | 25.8 ± 15.5 | 5.9–56.6 | 42 | 82.1 |
|  | Fall | 26.9 ± 16.5 | 7.7–65.0 | 14 | 25.6 |
|  | Winter | 16.2 ± 9.2 | 4.8–35.7 | 14 | 24.3 |

[a] Number of focal samples for energy intake analyses.

boundary locations and/or neighbors by individuals. Curlews feeding at different locations within the Elk River Estuary consumed different prey but achieved similar energy intake rates.

The risk of kleptoparasitism differed among prey types; larger prey (shrimp and worms) were stolen more often than smaller prey (bivalves and crabs). The number of kleptoparasitism attempts differed among territories, with most attempts occurring on territory A. The curlew resident in this location may have been more susceptible to kleptoparasitism because of its proximity to a gull roost. There was no apparent difference in the frequency of kleptoparasitism attempts on worms between seasons, although the proportion of worms in the diet changed between summer and winter.

Individual specializations in diet or behavior are not uncommon within species and are well documented for Eurasian Oystercatchers (*Haematopus ostralegus*; Goss-Custard and Sutherland 1984) and Ruddy Turnstones (*Arenaria interpres*; Whitfield 1990). Three non-exclusive mechanisms have been proposed to explain alternative strategies (Partridge and Green 1985). First, food resources may be distributed in patches throughout the environment where different strategies are most ap-

propriate. Second, differences in individual phenotypes may affect which resource is most appropriate to use. Third, the behavior of an individual may depend upon the behavior of other individuals, even when individuals are identical in phenotype, resulting in a frequency-dependent, mixed strategy. We suspect that the interterritorial variation in diet of curlews is due to a combination of all three mechanisms: temporal and spatial variation in prey availability, phenotypic differences, and the behavior of conspecifics and kleptoparasites.

Benthic invertebrates are markedly patchy in distribution, which may partially explain why different proportions of prey were captured in different locations; this patchiness is linked to differences in salinity, sediment characteristics, inundation time, and biotic interactions (Raffaelli and Hawkins 1996). However, in the absence of data on prey abundance and distribution within the estuary, we cannot determine if curlews were selecting prey or if they were consuming prey in proportion to availability in their territories.

In addition to possible differences in spatial availability, temporary availability of prey varied, due to the different elevation and thus, exposure length among territories. Some species of shorebirds feeding on tidal flats can predict how long their foraging area will be

exposed and can adjust their intake rates according to foraging time (Swennen et al. 1989). If an individual has a short amount of time to feed, it will choose to feed on reliable prey items, which are not patchily distributed (Sutherland 1996). If more time is available for feeding, the bird can afford to spend more time searching for prey items that may be more profitable, but encountered infrequently. Indeed, specialization can increase feeding efficiency (Partridge and Green 1985). Given that territory G was located in an area subject to earlier inundation and later exposure than other territories in this study, specialization to increase feeding efficiency may partially explain why the curlew on this territory ate bivalves almost exclusively.

In addition to habitat effects, morphological differences (e.g., bill length) and age of curlews may influence prey choice (Townshend 1981, Partridge and Green 1985). Longer-billed individuals are able to probe deeper into the substrate and are better equipped to capture deeper burrowing organisms. Young individuals may lack feeding experience, or may be more vulnerable to predation, which may alter their feeding behavior (Partridge and Green 1985).

An individual's behavior also may be regulated by the behavior of others. Competition may force less successful individuals to feed on less preferred foods (Partridge and Green 1985). Other frequency-dependent behaviors, such as interference, also may influence the profitability of prey choice (Goss-Custard 1980). Goss-Custard et al. (1999) showed that vigilance to reduce the chances of losing prey to kleptoparasites increased among Eurasian Oystercatchers as bird density increased. It follows that the proximity of potential kleptoparasites could influence prey choice, since various prey have different risks of being stolen.

*Conclusion.*—Dietary choices must balance the trade-offs of searching and handling time, and nutritional and energy value, with other variables, such as experience level, kleptoparasitism risk, and social constraints (Partridge and Green 1985, Zwarts et al. 1996). Although curlews appeared to have similar energy intake rates, the variation of individual curlew diet measured here may be in response to different distribution and availability of prey among areas within the estuary, or reflect individual constraints and choices, and attempts to minimize prey loss to kleptoparasites. Because of their conspicuous foraging behavior, Long-billed Curlews are an ideal species to use for future studies.

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