

## LONG-BILLED CURLEW DISTRIBUTIONS IN INTERTIDAL HABITATS: SCALE-DEPENDENT PATTERNS

RYAN L. MATHIS, Department of Wildlife, Humboldt State University, Arcata, California 95521 (current address: National Wild Turkey Federation, P. O. Box 1050, Arcata, California 95518)

MARK A. COLWELL, Department of Wildlife, Humboldt State University, Arcata, California 95521; mac3@humboldt.edu

LINDA W. LEEMAN, Department of Wildlife, Humboldt State University, Arcata, California 95521 (current address: EDAW, Inc., 2022 J. St., Sacramento, California 95814)

THOMAS S. LEEMAN, Department of Wildlife, Humboldt State University, Arcata, California 95521 (current address: Environmental Science Associates, 8950 Cal Center Drive, Suite 300, Sacramento, California 95826)

**ABSTRACT.** Key ecological insights come from understanding a species' distribution, especially across several spatial scales. We studied the distribution (uniform, random, or aggregated) at low tide of nonbreeding Long-billed Curlew (*Numenius americanus*) at three spatial scales: within individual territories (1–8 ha), in the Elk River estuary (~50 ha), and across tidal habitats of Humboldt Bay (62 km<sup>2</sup>), California. During six baywide surveys, 200–300 Long-billed Curlews were aggregated consistently in certain areas and were absent from others, suggesting that foraging habitats varied in quality. In the Elk River estuary, distributions were often (73%) uniform as curlews foraged at low tide, although patterns tended toward random (27%) when more curlews were present during late summer and autumn. Patterns of predominantly uniform distribution across the estuary were a consequence of territoriality. Within territories, eight Long-billed Curlews most often (75%) foraged in a manner that produced a uniform distribution; patterns tended toward random (16%) and aggregated (8%) when individuals moved over larger areas. At each spatial scale, food probably had the strongest influence on distributions, whereas predation played a relatively minor role in determining patterns.

During the nonbreeding season, shorebirds forage either alone or in flocks of varying size and density (Myers 1984, Goss-Custard 1985). Individuals form flocks in areas where the availability of food is greatest (e.g., Wolff 1969, Bryant 1979, Colwell and Landrum 1993) or owing to various antipredator benefits (Myers 1984). In a few shorebird species, dispersion patterns deviate from flocking, with individuals widely spaced in foraging habitats (Goss-Custard 1985). These hyper-dispersed patterns result mostly from territoriality (Goss-Custard 1985), with individuals defending food resources for varying durations (Colwell 2000).

The Long-billed Curlew (*Numenius americanus*) is among the most imperiled species of nearctic shorebird (Brown et al. 2001). During the nonbreeding season, curlews occupy intertidal habitats, coastal pastures, agricultural fields, and freshwater wetlands from Willapa Bay, Washington, south along the Pacific coast through Mexico (Dugger and Dugger 2002). Humboldt Bay, California, is the most northerly wintering area for large numbers of curlews (Paulson 1993). Colwell (1994) estimated that several hundred curlews use the bay, where they feed in intertidal habitats on bi-

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valves, shrimps, polychaete worms, crabs, and small fishes (Leeman et al. 2001).

At Humboldt Bay, some curlews defend low-tide territories from June through March, although territory occupancy declines in autumn (Colwell and Mathis 2001). This seasonal decline in use of intertidal habitats coincides with higher diurnal low tides (Dodd and Colwell 1996), which inundate foraging areas (Colwell and Mathis 2001), and the onset of winter rains, which increases the availability of alternative foraging habitats in pastures (Colwell and Dodd 1995, 1997, Leeman and Colwell 2005). In this study, we quantified Long-billed Curlew distributions at three spatial scales: within individual territories spanning <10 ha, in a small estuary (<100 ha), and across intertidal habitats of the entire bay (>1000 ha), corresponding to individual, local, and regional scales (Myers 1984). Understanding how curlews are distributed across intertidal habitats is critical to effective management and conservation. For example, as the largest North American shorebird, curlews foraging in areas valued for sport clamming may be most vulnerable to anthropogenic disturbance, and mitigating for this sort of habitat degradation requires knowledge of space use. Furthermore, rising sea levels associated with global warming will alter the availability of intertidal foraging habitats used by curlews (Galbraith et al. 2002), with consequences for wintering curlew populations.

### STUDY AREA

We studied curlews from 1998 to 2002 at the Elk River estuary and within Humboldt Bay (Figure 1). Humboldt Bay consists of two large basins, South Bay (1797 ha) and Arcata Bay (4103 ha), connected by a shipping channel opening to the Pacific Ocean. The bay has mixed semidiurnal tides (Barnhart et al. 1992). At mean lower low water (0.43 m), receding tides expose approximately 4492 ha of intertidal habitat (Mathis 2000) consisting of bottom sediments that range in size from silt to gravel (Danufsky and Colwell 2003). In most areas of the bay, human use of intertidal habitats at low tide during our study was minimal. The Elk River estuary covers approximately 50 ha on the east shore of the shipping channel. At the estuary's southern end, cordgrass (*Spartina foliosa*, *S. densiflora*), pickleweed (*Salicornia pacifica*), saltgrass (*Distichlis spicata*), and dunes dominated by European beach grass (*Ammophila arenaria*) border a kilometer-long steep-banked river channel. To the north, the intertidal habitat broadens to include mixed-elevation flats dissected by channels. At the river's mouth is a gently sloping tidal flat sparsely vegetated with eelgrass (*Zostera marina*) amid silt to gravel substrates.

### METHODS

#### Field Observations

To quantify baywide distributions, we coordinated multiple observers in a synchronized effort to map curlews on six occasions during fall and winter of 1998–99 and 1999–2000 (Table 1). Observers conducted surveys when

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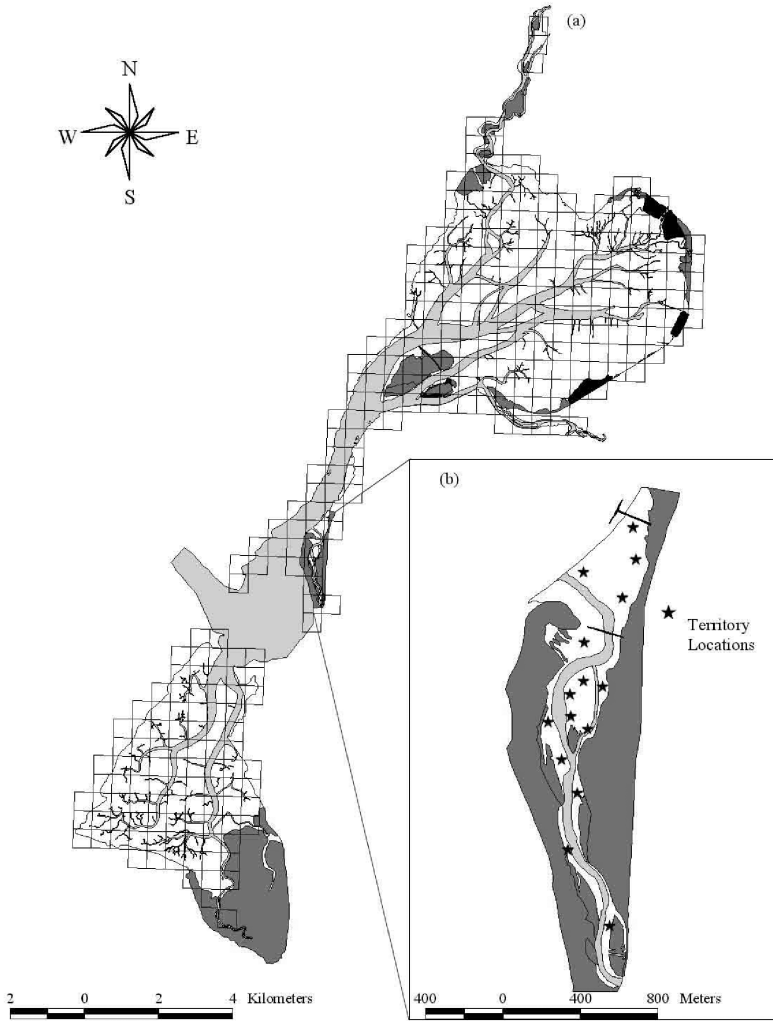


Figure 1. Humboldt Bay, California study area (a) overlaid by 500-m grid used to examine spatial variation in summed counts of Long-billed Curlews during six autumn and winter low tides. Inset (b), Elk River estuary, where stars (★) indicate approximate locations of curlew territories. Dark gray shading, salt marsh fringing the bay; lighter gray shading, main shipping channels of the bay.

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**Table 1** Long-billed Curlew Abundance and Spatial Distribution on Six Surveys of Intertidal and Pasture Habitats at Humboldt Bay

	1998–1999			1999–2000		
	4–5 Oct	30–31 Jan	27–28 Feb	23 Oct	29–30 Jan	13 Feb
Number of curlews in intertidal habitats	301	286	209	203	176	168
Curlew density (ha <sup>-1</sup> ) in intertidal habitats	0.09	0.08	0.06	0.06	0.05	0.05
Number of curlews in pastures	0	14	121	10	105	159
Total number of curlews observed	301	300	330	213	281	327
Average number of curlews per grid cell	0.91	0.87	0.63	0.62	0.53	0.51
Variance of curlews per grid cell	2.51	6.14	1.95	1.71	1.71	1.86
Dispersion index ( $J^a$ )	2.75	7.08	3.07	2.79	3.20	3.66
$t^b$	10.26	33.79	8.47	7.01	7.57	8.66
$P$	<0.001	<0.001	<0.001	<0.001	<0.001	<0.001

<sup>a</sup>Variance:mean ratio (Krebs 1989).

<sup>b</sup> $t = \frac{\text{variance} - \text{mean}}{2\sqrt{[2/n-1]}}$ , df = 329.

predicted diurnal low tides of  $\leq 0.3$  m exposed most tidal flats. We scanned tidal flats, sloughs, and adjacent pastures using binoculars and spotting scopes; we observed curlews far from shore from boats that moved slowly through the bay's channels. During surveys, we mapped curlew locations on transparencies overlaying high-resolution images (0.3-m pixel) photographed approximately 1 year prior to fieldwork (Terra-Mar 1997). For ease of data collection we overlaid images with a 50–100-m UTM-based grid; prominent landmarks (e.g., channels, wharf pilings, and peninsulas) aided mapping. We conducted surveys over 1 or 2 days, and each survey consisted of a 30- to 60-minute scan of habitats coinciding with the predicted low tide. In 2002, we quantified seasonal variation in curlew abundance at daytime high-tide roosts by surveying intertidal habitats on 28 occasions. We divided the survey interval into winter (2 January–28 February;  $N = 8$ ), spring (1 March–15 May;  $N = 10$ ), and autumn (1 August–16 October;  $N = 10$ ) intervals. See Colwell et al. (2003) for details on survey methods for roosting shorebirds.

In the Elk River estuary, we collected data on distributions of multiple curlews and on individuals within their territories. In the estuary, Colwell used a spot-mapping technique (Bibby et al. 1992) to record curlew locations on 133 low tides from 20 May 1999 to 4 April 2000. We observed curlews from the estuary's eastern edge over a 1-hour period bracketing the 1-hour interval coinciding with the predicted low tide. See Colwell and Mathis (2001) for details of survey methods.

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To quantify individual variation in space use within territories, we used a focal sampling technique (Altmann 1974) to map curlews at low tide on high-resolution images. During a 2-hour observation, we recorded curlew locations every 2 minutes, yielding 60 locations per focal sample. Observers worked in teams of two, with one person using a 20- to 60-power spotting scope maintaining constant visual contact with a curlew; a second person recorded details on diet, behavior, and location as dictated by the principal observer. In total, we conducted 65 focal observations, divided among eight territorial curlews. Although we did not capture and mark curlews to confirm that the same individuals repeatedly occupied territories, in several cases we used distinctive plumage characteristics that persisted over short (weeks) or long (years) intervals to support the notion. See Leeman et al. (2001) and Colwell et al. (2002) for details.

### Data Summary and Analyses

We digitized curlew locations into the ArcView geographic-information system (GIS; ESRI, Redlands, CA). We used two different methods to quantify dispersion owing to the relative imprecision of mapping birds across the whole of Humboldt Bay as compared with finer-scale mapping in the Elk River estuary. At the scale of Humboldt Bay, we characterized baywide distributions by entering locations as points, overlaid with a  $500 \times 500$ -m grid to reduce the number of cells with no curlews. Grid size had only a minor influence on results (Mathis 2000). For each of the six surveys (Table 1), we summed the number of curlews in each cell. Next, we calculated the mean number of curlews for 330 cells overlying intertidal habitats (Figure 1). To characterize baywide distributions, we calculated a dispersion index ( $I = s^2: \bar{x}$ ; Krebs 1989). This index equals 1 when a distribution is random, or it can be either aggregated ( $>1$ ) or even ( $<1$ ). For each survey, using a two-tailed  $t$  test (Getis and Boots 1978), we compared the significance of the distribution to a random pattern. To examine whether curlews used some areas consistently, we correlated the number of curlews in each grid cell between surveys, by means of Spearman's rank-correlation test.

To quantify dispersion within the Elk River estuary, we compared each spot-mapped distribution to a random pattern, using data from July to October, coincident with low tides  $\leq 0.3$  m ( $N = 22$ ) and when  $\geq 8$  curlews were present. We restricted analyses to these conditions because this tide level exposed nearly 100% of intertidal habitat and some curlews were more likely to be absent from territories at higher tides (Colwell and Mathis 2001). To quantify dispersion of individuals within their territories, we used the 60 locations (recorded at 2-minute intervals for 2 hours) derived from each 2-hour focal sample. We analyzed each focal sample separately ( $N = 65$ ) and summarized multiple observations for each territory.

For each focal sample and spot map, we compared curlew locations to a random spatial pattern by using the nearest-neighbor method in Animal Movement (Hooge and Eichenlaub 2000), a GIS extension. This technique compares the distance between locations to a pattern generated from random points within an area (territory or estuary). The analysis yielded an  $R$

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value as an index of dispersion. When curlews were randomly distributed, values equaled 1, whereas values greater than or less than 1 corresponded to uniform and aggregated distributions, respectively (note that this is the reverse of the dispersion index above). We used Spearman's rank correlation to compare distributions with curlew numbers or area used.

### RESULTS

#### Baywide Distributions

During six baywide surveys, most curlews were aggregated in intertidal habitats (Table 1, Figure 2). Curlews occurred in higher densities in some areas (21–39% of cells with at least one curlew) and were absent from others (61–79% of cells with no curlews). The number of curlews recorded in each cell from survey to survey was correlated positively ( $r_s = 0.35\text{--}0.69$ ,  $P < 0.001$ ), indicating that the spatial distribution was repeatable. The total number of curlews (using bay and pasture habitats) varied from 213 to 327. In intertidal habitats, 168–301 ( $\bar{x} = 224 \pm 56$ ) curlews were observed at densities of 0.05–0.09 ( $\bar{x} = 0.07 \pm 0.02$ ) birds per hectare. During winter surveys, the number of curlews using pastures ranged from 10 to 159 ( $\bar{x} = 81 \pm 66$ ). In both years, curlew numbers in intertidal habitats declined from October to February, whereas numbers in pastures increased (Table 1). We rarely observed curlews using pastures prior to the onset of winter rains. During high-tide surveys, we observed curlews roosting at a total of 58 locations around the bay, although the number of roosts varied seasonally (Figure 3).

#### Estuary Patterns

From July through October 1999, when residency of individuals on their territories in the Elk River estuary was highest (Colwell and Mathis 2001), density averaged 0.36 ( $\pm 0.09$ ) curlews per hectare, one of the highest concentrations for the bay. At the same time, distributional patterns in the estuary were mostly uniform (73%) or random (27%). Distributions were negatively correlated with abundance ( $r_s = -0.46$ ,  $N = 22$ ,  $P = 0.03$ ), indicating that a random distribution was more frequent when there were more curlews. After October, there were too few (1–9) curlews (Colwell and Mathis 2001) for spatial distributions to be analyzed.

#### Individual Curlews' Use of Space

We observed eight territorial curlews in the Elk River estuary on 65 occasions through 130 observation-hours yielding 3900 individual point locations. Distributions of these eight curlews within their territories were predominantly (75% of observations) uniform (Figure 4), although patterns were more random (16%) and aggregated (8%) as curlews foraged over larger areas ( $r_s = -0.55$ ,  $N = 65$ ,  $P < 0.001$ ). Details on these curlews' home-range sizes and distances moved during focal observations were reported by Lee-man et al. (2001) and Colwell et al. (2002).

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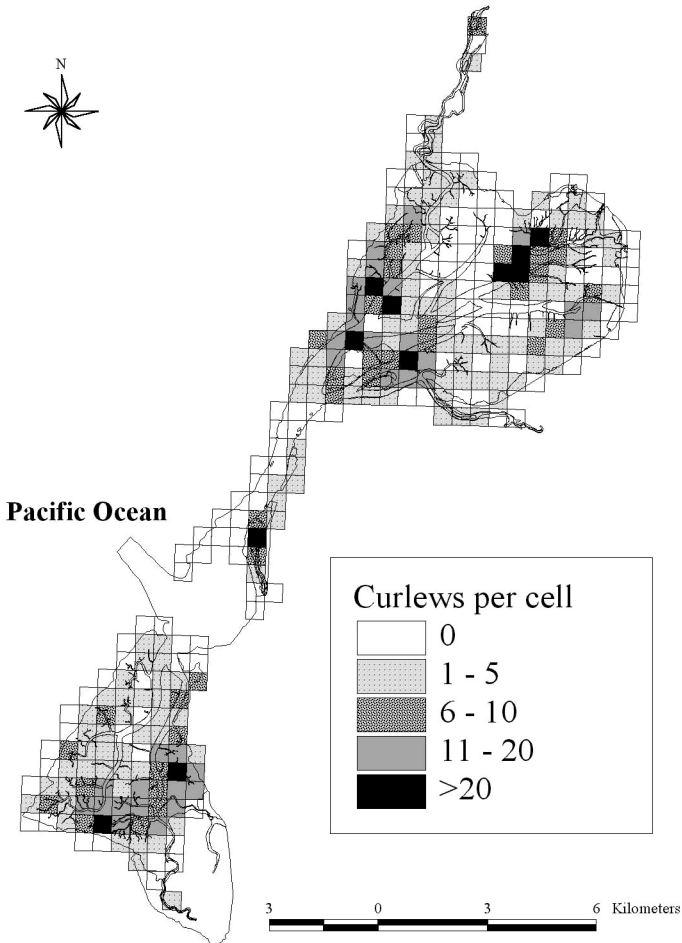


Figure 2. Spatial variation in Long-billed Curlew use of intertidal habitats of Humboldt Bay based on summed observations from six low-tide surveys (Table 1).

### DISCUSSION

Across the intertidal habitats of Humboldt Bay, the Long-billed Curlew was aggregated at low densities (0.05–0.09 birds per hectare), and these patterns were spatially correlated from survey to survey. However, these estimates mask substantial variation across habitats. Densities were an order of magnitude higher in the Elk River estuary (0.1–0.4 curlews per hectare), whereas curlews were consistently absent from some other intertidal reaches. Such patchy distributions indicate that areas of the bay vary in quality of foraging

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Figure 3. Roost locations and comparative abundances of Long-billed Curlews at diurnal high-tide roosts during winter, spring, and fall 2002.

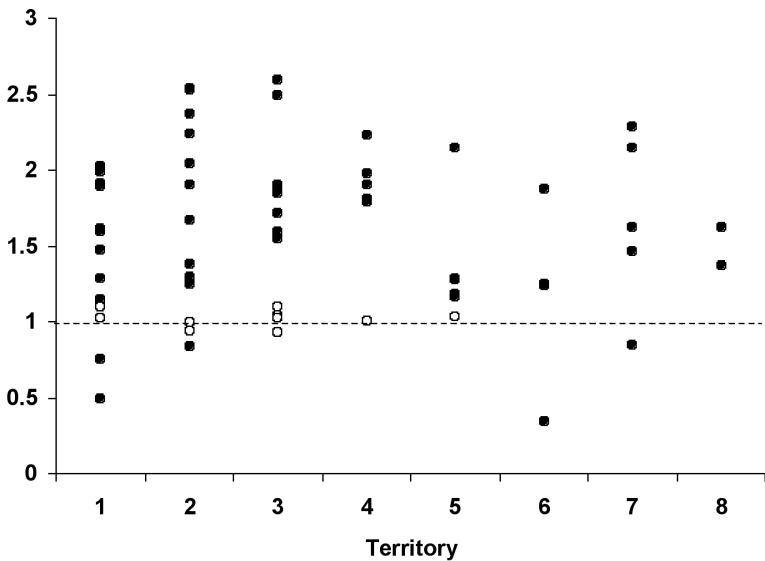


Figure 4. Spatial distributions of eight Long-billed Curlews in the Elk River estuary. Each observation represents a low-tide distribution of a focal-sampled curlew on its territory, based on 60 point locations recorded at 2-minute intervals for 2 hours. Distributions deviating from random (○) are either uniform (●; >1) or aggregated (●; <1) patterns.



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habitats, which are probably correlated with habitat features that influence prey abundance (Bryant 1979). For example, large-scale variation in the density of the Eurasian Curlew (*Numenius arquata*) is correlated with differences in the sizes of sediment particles (Yates et al. 1996) and populations of associated invertebrate prey (e.g., *Nereis diversicolor*) (Bryant 1979).

Consistent absence of curlews from some reaches of Humboldt Bay suggests that habitat quality and food availability in these areas were low. Curlews were often absent from low intertidal habitats in the center of the bay, which were exposed for shorter intervals than the high flats rimming the bay, thus affording less foraging time. Residency of curlews on low-tide feeding territories was correlated negatively with the height of low tide (Colwell and Mathis 2001). By extension, curlews were absent from the center of the bay because tides inundate these habitats sooner. Another possible explanation for the absence of curlews from these areas is that dense eelgrass beds, especially in South Bay (Barnhart et al. 1992), interfere with foraging by curlews. The patchy distribution of the Far Eastern Curlew (*N. madagascariensis*) in tidal habitats stemmed from lower densities in areas of denser sea grass (Congdon and Catterall 1994).

At the local scale, high curlew density (10–15 individuals) in the Elk River estuary was coupled with mostly (73%) uniform distributions. At this scale, a uniform distribution is widely recognized as a consequence of territoriality and the social interactions of neighbors. Individual curlews in the Elk River occurred consistently in the same locations (Colwell and Mathis 2001, Leeman et al. 2001) and were occasionally observed in territorial disputes with neighbors. On occasion (27%), curlews were distributed randomly in the estuary, and randomness tended to occur when more curlews (including occasionally nonterritorial immatures) were present during summer. These random patterns probably resulted when increased numbers of juveniles and other nonterritorial curlews (Colwell and Mathis 2001) overwhelmed the abilities of territorial birds to defend space. During the nonbreeding season, food is the resource that influences the expression of territorial behavior (Myers 1984). Goss-Custard (1985) suggested that territoriality is likely in habitats where food is moderately rich and predictable. We speculate that the uniform distributions are a consequence of the species' territorial social system at this site.

Territoriality has been reported for approximately 25% of shorebird species, but few taxa defend food resources within territories as large and for as long as curlews (Colwell 2000). Among species that defend long-term territories, similar distribution patterns have been noted and are correlated with food. For example, during the nonbreeding season, some Black-bellied Plovers (*Pluvialis squatarola*) defend territories (Turpie 1995). In South Africa, the plover is territorial where its main prey, the burrowing shrimp *Upogebia africana*, occurs in high density (Turpie 1995). These shrimp occupy permanent burrow systems. At the northern extreme of its winter range, where it feeds on polychaete worms (*Nereis diversicolor*), the Black-bellied Plover also defends territories (Turpie 1995). In the Elk River estuary (Leeman et al. 2001) and elsewhere in California (Stenzel et al. 1976), the curlew's diet consists of large prey such as burrow-dwelling shrimp similar to those eaten by territorial Black-bellied Plovers.

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Uniform distributions may arise in species with social systems other than territoriality. At low tide, Eurasian Oystercatchers (*Haematopus ostralegus*) forage on mussels (*Mytilus edulis*) and establish dominance hierarchies. Individuals of high rank benefit by having priority of access to food (Ens and Cayford 1996). As a result, individuals avoid one another, also producing a uniform dispersion pattern (Vines 1980, Moody et al. 1997), albeit on a spatial scale finer than that we found with the Long-billed Curlew. We suggest that the distribution of prey influences curlews' territoriality and their local distributional patterns.

At the scale of the individual, Long-billed Curlews were distributed mostly in a uniform (75%) pattern within their territories, although some individuals foraged in a manner that produced random (16%) or aggregated (8%) patterns. Elsewhere, we have shown that this variation is correlated with diet (Colwell et al. 2002). Curlews forage for large prey by probing into the substrate or by pecking at the surface (Leeman et al. 2001). When diets consist of more bivalves, curlews tend to be uniformly distributed, whereas diets of mostly crabs produce aggregated patterns. Relationships between individual patterns of dispersion and diet may stem from the tendency for individuals to specialize for short intervals (2 hours) on prey captured by means of either tactile (bivalves, marine worms) or visual (crabs, shrimp, fishes) cues (Leeman et al. 2001). A negative correlation between distributions and foraging area further supports the contention that diet influences distributional patterns because individuals move more widely within their territories when feeding on crabs than when feeding on bivalves (Colwell et al. 2002).

At least one other shorebird, the Eurasian Oystercatcher, has been shown to exhibit fine-scale patterns of space use within territories (Hulsman et al. 1996). Female oystercatchers feed visually on large conspicuous prey (*Nereis*) and move greater distances than males from one prey capture to the next. By contrast, males tend to use tactile cues to detect prey (*Macoma*) and move shorter distances. Although Hulsman et al. (1996) did not quantify patterns of space use by Eurasian Oystercatchers, they suggested that tactile-feeding males are more aggregated whereas visual-feeding females are uniformly distributed in territories.

Although we lack data to evaluate the contributions of food and predation to the curlew's spatial distributions critically, we offer the following observations to suggest that predation is less important than food. First, as the largest Nearctic shorebird, the Long-billed Curlew is taken rarely by only the largest avian predators, such as the Red-tailed Hawk (*Buteo jamaicensis*; Dugger and Dugger 2002, Colwell pers. obs.). Second, we rarely observed curlews forming tight flocks characteristic of evasive behavior in response to avian predation; when they did it was for short intervals coinciding with an occurrence of the Peregrine Falcon (*Falco peregrinus*). Curlews have been observed feeding in loose flocks in pastures during winter when precipitation softens soils and makes earthworms more available (Colwell and Dodd 1995, Leeman and Colwell 2005). Potential predators of curlews are equally common and readily move between pasture and tidal habitats, hence differences in flocking behavior between habitats are more likely a consequence of food. Third, if predation influenced distributions, one would predict that curlews would be less numerous or would flock to a greater extent in habitats

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offering limited visibility of approaching predators. But the curlew's highest densities and most uniform distributions occurred consistently in the Elk River estuary, where Peregrine Falcons only rarely surprised feeding curlews by approaching from fringing salt marsh and dunes near tidal flats (Colwell pers. obs.). In summary, predation may occasionally cause curlews to form transient tight flocks, but food probably exerts a stronger influence on the distribution of the Long-billed Curlew at Humboldt Bay.

### Conservation Implications

On six occasions over two years, 200–300 curlews used intertidal habitats and pastures of Humboldt Bay. This value is similar to estimates of a decade earlier (Colwell 1994) and represents ~1% of the world's population (Brown et al. 2001). According to criteria used to recognize wetlands of significance to waterbirds (e.g., Ramsar Convention), this percentage supports recognition of Humboldt Bay under the Western Hemisphere Shorebird Reserve Network. The patchy distribution of the curlew suggests that protection of high-quality foraging habitats (e.g., Elk River estuary) may be warranted, especially where areas of high human use are nearby.

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Dusky Grouse (*Dendragapus obscurus*) along trail to Mt. Audubon, Roosevelt National Forest, Colorado, 24 September 2006, during a field trip from WFO's 31st annual meeting in Boulder, Colorado.

Photo by David Krueper