POPULATION ECOLOGY OF THE LONG-BILLED CURLEW (NUMENIUS AMERICANUS) IN WESTERN IDAHO

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ABSTRACT.—In western Idaho, a breeding population of Long-billed Curlews (*Numenius americanus*) remained relatively stable over a 7-yr period. Productivity was monitored closely from 1977 through 1979. Clutch mortality rates did not differ significantly among years, and mean clutch survival for a 32-day nesting period (4 days egg laying and 28 days incubation) was 40% for all 3 yr combined. Females laid just one clutch (usually of 4 eggs) each season, and mean clutch size was significantly smaller in 1979 than in 1977 and 1978. Estimated fledging success ranged from 0.40 in 1977 to 0.17 in 1978 and was consistently greater for females that nested early each season. Mean annual adult survival was estimated at 85% based on resightings of color-marked individuals. Limited data for subadult survival precluded complete demographic analysis. Nevertheless, given the estimates of productivity and adult survival pooled for 3 yr, survival of subadults from fledging until first breeding as 3-year-olds needed to be only 58% to maintain the stable population size observed through 1983. *Received 10 June 1985, accepted 7 April 1986.*

THE population ecology of shorebirds (Charadrii) is not well known, probably because many species are wary, breed in remote areas, or both. Most thoroughly studied are species that nest at temperate latitudes such as the Eurasian Oystercatcher (*Haematopus ostralegus*; Goss-Custard et al. 1982, Safriel et al. 1984), Common Ringed Plover (*Charadrius hiaticula*; Laven 1940, Bub 1962, Pienkowski 1984a), and Common Redshank (*Tringa totanus*; Grosskopf 1959, 1964; Yates 1982). Many aspects of breeding biology are known for other shorebirds, especially in Europe and Scandinavia (see Cramp and Simmons 1982, Evans and Pienkowski 1984). But even among calidridine sandpipers (Scolopacidae), a subfamily with diverse social adaptations and mating systems (Pitelka et al. 1974, Myers 1981), detailed demographic parameters have been reported only for the Dunlin (*Calidris alpina*; Soikkeli 1967, 1970a, b) and Temminck's Stint (*C. temminckii*; Hildén 1978). Tringine sandpipers exhibit a wider range of body sizes and tend to breed at lower latitudes than do calidridines (Johnsgard 1981). Hence, they should be more accessible for study, and also more accessible for comparative demographic analyses. Long-term reproductive performance and population dynamics, however, are known for only a few smaller species such as the Spotted Sandpiper (*Actitis macularia*; Oring et al. 1983), Common Sandpiper (*A. hypoleucos*; Hol-

land et al. 1982), and Common Redshank (Yates 1982). Larger species tend to be better studied during the nonbreeding season, and survival estimates based on annual returns to wintering grounds exist for Bar-tailed Godwits (*Limosa lapponica*) and Eurasian Curlews (*Numenius arquata*) (Evans and Pienkowski 1984).

We studied breeding density, clutch size, nesting mortality, reproductive success, and adult survival in a population of Long-billed Curlews (*Numenius americanus*). These demographic data are integrated by life-table analyses, and the longer-term reproductive performance of the population is evaluated.

STUDY AREA AND METHODS

Study area.—The study area was an upland strip of shortgrass rangeland (~21,600 ha) in western Idaho (Redmond and Jenni 1982). We concentrated on a portion of the area (~1,600 ha) that supported high breeding densities of Long-billed Curlews. This smaller plot was grazed intensively by large bands of sheep from late March through early May each year; other portions of the study area were grazed by cattle from November to June.

Methods.—The nesting cycle was divided into prelaying, laying, incubation, and prefledging periods. A standard clutch of 4 eggs was laid in 4–7 days, and incubation began after the last egg was laid. Time from laying to hatching of the last egg was considered the incubation period; it ranged from 28 to 30 days ($\bar{x}$ = 28.4 days).

Population densities were estimated each year by a modified Finnish line-transect method (Redmond et al. 1981), and nests were located during egg laying or incubation according to methods described by Redmond (1986). When found, each nest was marked with a numbered wooden stake (2.5 × 5 × 40 cm) placed 10 m upslope from the nest cup. To deter mammalian predators from following our scent trails, paradichlorobenzene (PDB) crystals were sprinkled at a 1-m radius around each nest cup. On subsequent visits, a nest was always approached directly from the marking stake; when departing, a line of PDB crystals was spread across this path. Because the crystals were small and very volatile, they evaporated quickly and probably had only a short-term effect. Whereas the efficacy of this method for discouraging mammalian predators has never been tested, Lehner et al. (1976) showed that similar chemicals deterred coyotes (Canis latrans) and dogs (Canis familiaris) from food rewards. Similarly, Knight (1983) found PDB and napthalene to be useful in repelling skunks from specific areas.

Nests found during incubation usually were checked every 2–5 days until the eggs first starred or pipped, and then every day until hatching was completed. Nests located during egg laying were not checked for the first 2–3 weeks of incubation. Clutch size was estimated by the maximum number of eggs found in a given nest.

The diversity of potential predators on and around the study area made it difficult to interpret every act of predation and to identify responsible species. Mammalian carnivores that hunted regularly over portions of the study area included coyotes, feral dogs, feral cats (Felis domesticus), badgers (Taxidea taxus), and long-tailed weasels (Mustela frenata). Red foxes (Vulpes fulva), striped skunks (Mephitis mephitis), and raccoons (Procyon lotor) occurred on adjacent agricultural lands but were never seen hunting in upland habitat.

Nest loss was attributed to a badger if the nest cup was damaged and buried under several centimeters of soil. Large, crushed shell fragments often lay beneath this soil or in the immediate vicinity of the destroyed nest. Canids were presumed to be responsible for an empty, undamaged nest cup whenever the previous visit had revealed an intact clutch. In several cases also attributed to canids, the nest cup was damaged but not buried, and large shell fragments lay nearby.

Avian predators usually did not destroy entire clutches; instead, they opened and consumed portions of 1 or 2 eggs. Partially destroyed clutches were abandoned by adult Long-billed Curlews, and remaining eggs were subsequently consumed. Black-billed Magpies (Pica pica) were the most abundant avian egg predator. Common Ravens (Corvus corax) and several gull species (California Gulls, Larus cali-

fornicus; Ring-billed Gulls, L. delawarensis; and Franklin's Gulls, L. pipixcan) occasionally passed over the study area during April and May. Only ravens were mobbed by adult curlews.

Grazing livestock also destroyed curlew nests. Characteristically, one or more eggs disappeared from a nest coincident with the presence of sheep or cattle in the vicinity. Sometimes a crushed egg remained in the cup or an egg was dislodged a short distance.

Gopher snakes (Pituophis melanoleucus) were the only reptiles capable of preying on curlew eggs or chicks. These snakes were encountered regularly during late spring, but individuals were always relatively small and probably unable to swallow a curlew egg whole. The existence of individual gopher snakes large enough to ingest whole curlew eggs was documented in Nebraska (Tremaine 1975), but we doubt that such predation was frequent on this study area.

Daily mortality rates were calculated for all clutches, for individual eggs within successful nests, and for chicks before fledging according to Mayfield's (1975) method as modified by Willis (1981). When the day of nest destruction was not known, it was assumed to have occurred at 40% of the interval since the last visit (Johnson 1979). Variance estimates of these mortality rates follow Johnson (1979), and rates were compared by G-tests of independence (Willis 1981). Capture and marking techniques were described by Redmond and Jenni (1982), and Redmond (1984) provided details about radio-tracking methods.

Resightings of natally philopatric curlews (individuals color-banded as chicks in the study area and resighted there in later years) were made opportunistically along survey routes from 1979 through 1981. By themselves, these resightings represent minimum survival rates for subadults. Because of a significant male bias in natal philopatry (Redmond and Jenni 1982), however, subadult survival for males was estimated as one half the number of color-marked chicks known to fledge and later resighted. Estimates of annual adult survival utilize resighting data from 1978 through 1981 and are based on the maximum-likelihood method of Cormack (1964). To obtain resightings of color-marked adults, their previous nesting territories and adjacent territories were searched regularly during the prelaying and incubation periods.

RESULTS

Breeding density.—Because of high variances, there were no significant differences among annual density estimates of territorial male Long-billed Curlews on the 1,600-ha study plot (Fig. 1). Thus, for the duration of the study, we assumed that the breeding population was relatively stable in size, even though a gradual
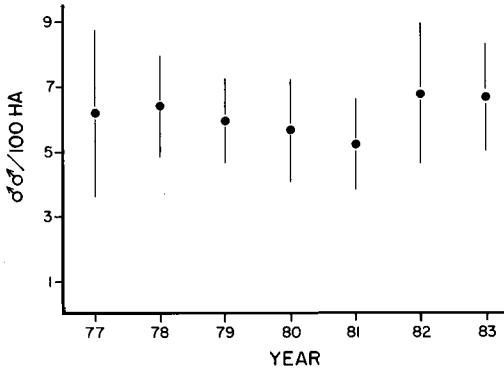
Fig. 1.   Annual density estimates (mean ± SD) of male Long-billed Curlews attempting to breed on the study site from 1977 to 1983. Estimates are based on Finnish line-transect method of Järvinen and Väisänen (1975) as modified by Redmond et al. (1981). Actual data are available in Redmond (1984).

TABLE 1.   Clutch size of Long-billed Curlews in western Idaho.

Year	Frequency of clutch size[a]			Mean ± SE[b]
	3	4	5	
1977	1	24	0	3.96 ± 0.039
1978	1	36	1	4.00 ± 0.037
1979	8	32	0	3.80 ± 0.063
1977–1979	10	92	1	3.91 ± 0.000

[a] Clutch size could not be determined for 16 additional nests because they were either destroyed during laying or found during hatching.

[b] ANOVA among years: $F = 4.56$, 2,100 df, $P = 0.01$.

decline in males attempting to breed probably occurred between 1978 and 1981 (see Discussion).

Clutch size.—Female Long-billed Curlews commonly laid a single clutch of 4 eggs in 1977 and 1978 (Table 1). In 1979, however, the frequency of 3-egg clutches increased dramatically, and mean clutch size was significantly less than in the previous 2 yr (GT-2 multiple comparison test, $P < 0.05$). There was no evidence of renesting by any color-banded or radio-marked female in any year.

Egg and clutch mortality.—Mean clutch mortality rate for all years was 0.029 nests lost per day (Table 2). Daily clutch mortality rates were remarkably constant in 1977 and 1978, and increased insignificantly in 1979 ($G = 0.02$, 2 df, $P = 0.90$).

Mammalian carnivores were the most important predators of Long-billed Curlew eggs and clutches (Table 2). The relative intensity of predation by canids and badgers differed significantly among years ($G = 6.10$, 2 df, $P < 0.05$). During 1977 badgers were particularly destructive of curlew eggs in an area of high Townsend ground squirrel (*Spermophilus townsendii*) density, where 67% of all nests were found. During 1978 and 1979, when only 15% of all nests were found in this area, canids were the dominant egg predator (Table 2).

It is difficult to identify any specific canid as the most important egg predator. Dogs (unat-

tended, abandoned, or wild) were the most frequently seen. Coyotes were seen infrequently, and red foxes were sighted occasionally in agricultural fringe areas within 3–5 km of curlew nesting habitat.

Other causes of clutch loss were grazing livestock, other birds, and investigator disturbance (Table 2). When large bands of sheep passed through an area, chance seemed to play a role in the actual destruction of Long-billed Curlew nests. On two occasions in 1977, bands of more than 500 ewes and lambs trampled past the same two neighboring nests en route to a water trough. Neither clutch was damaged, but both times one of the wooden marking stakes was snapped off and crushed. Soon after each incident, the adult curlews returned and resumed incubation. Similar, but less dramatic, interactions resulted in several broken eggs and 4 nest desertions in 1978 and 1979.

Adult Long-billed Curlews could readily defend their nests against magpies and other avian egg predators. We therefore suspect that these birds probably gained access to curlew clutches only as a result of nest desertion or abnormal inattendance by the adults. Two unusual cases of egg damage and nest abandonment were attributed to birds (1 each in 1977 and 1979) and may have been caused by other Long-billed Curlews. All eggs in both clutches were pecked, but their contents were not eaten. The holes, approximately 15–30 mm in diameter, were considerably smaller than those made by magpies. Both of these nests were within 40 m of other active curlew nests.

Individual egg losses or hatching failures were recorded each year in nests that produced one or more chicks (Table 3). This mortality

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TABLE 2. Losses of Long-billed Curlew clutches.

	1977	1978	1979	Total	Percent
Clutches	30	40	49	119	
Losses to:					
Canids	3	8	10	21	17.7
Badgers	7	3	3	13	10.9
Birds	2	2	4	8	6.7
Livestock	0	3	2	5	4.2
Trapping	0	0	2[a]	2	1.7
Unknown	0	0	1	1	0.8
Total	12	16	22	50	42.0
Nest-days	449	592	705	1,749	
Mortality/day	0.0277	0.0280	0.0294[a]	0.0285	
SE	0.00761	0.00666	0.00625	0.00391	

[a] Two clutches were abandoned because of trapping efforts in 1979; mortality rate assumes these would have hatched successfully.

was a result of addled eggs ($n = 7$), parental abandonment of late, asynchronously hatching eggs ($n = 5$), and grazing livestock ($n = 6$). Patterns of single egg losses or hatching failures in otherwise successful nests did not differ significantly among years ($G_{adj} = 6.00$, 4 df, $P = 0.20$).

Hatching success.—Probabilities of clutch survival for a 32-day nesting period were remarkably constant each year (Table 4). Egg survival in successfully hatching nests showed more variability among years (Table 4), probably because of the absence of livestock damage in 1977; nevertheless, these differences were not significant ($G = 4.47$, 2 df, $P > 0.80$).

Chick mortality.—Each year individual chicks that had not survived more than a few hours were found in or near a nest cup ($n = 3$ of 79 color-marked chicks in 1977, 1 of 69 in 1978,

and 2 of 62 in 1979). The 3 nonviable hatchlings in 1977 were from 3 different 4-egg clutches, and each weighed 20–25% less than their siblings. All had poorly healed umbilical regions and incomplete yolk sac retention, with small pieces of dried shell or membranes adhering to the yolk sac. There was nothing peculiar about the appearance of nonviable hatchlings in 1978 or 1979, and they may have perished from inadequate brooding.

Long-billed Curlew chicks have cryptic plumage and behavior, which makes them very difficult to locate after they leave the nest. Consequently, we relied heavily on the fates of radio-marked individuals to determine chick mortality rates. The average age when chicks were radio-marked decreased each year from 15.8 (1977), to 14.0 (1978), to 6.0 days (1979). We found no mortality of radio-marked chicks

TABLE 3. Egg losses and hatching failures from successful Long-billed Curlew nests.

	1977	1978	1979	1977–1979
Eggs in successful nests	68	95	91	254
Number of eggs				
Addled	1	3	3	7
Abandoned	3	1	1	5
Damaged[a]	0	4	2	6
Egg-days	1,258	1,702	1,743	4,703
Loss rate[a]/day ± SE ($\times 10^3$)	0.00	2.42	1.18	1.31
	±0.000	±1.174	±0.811	±0.521
Percentage surviving 32 days[b]	100.0	92.5	96.3	95.9
Percentage addled or abandoned	5.88	4.40	4.49	4.84

[a] Caused by grazing livestock only. It is assumed the 4 other eggs damaged in 1979 because of trapping efforts would have hatched.

[b] Four days for egg laying and 28 days for incubation.

TABLE 4.   Estimates of hatching and fledging success per breeding adult.

Year	Nesting class[a]	Hatching success		Fledging success[c]	Mean clutch size	No. of young fledged/adult
		Clutches	Eggs[b]			
1977	Early	0.408	0.972	0.565	4.00	0.45
	Late	0.408	0.906	0.437	3.91	0.32
	All	0.408	0.941	0.495	3.96	0.38
1978	Early	0.403	0.878	0.293	4.00	0.21
	Late	0.403	0.890	0.100[d]	4.00	0.07
	All	0.403	0.884	0.229[e]	4.00	0.16
1979	Early	0.385	0.856	0.485	3.77	0.30
	Late	0.385	0.978	0.216	3.86	0.16
	All	0.385	0.920	0.318	3.80	0.21
1977–1979	Early	0.397	0.896	0.436	3.92	0.30
	Late	0.397	0.927	0.262[e]	3.92	0.19
	All	0.397	0.913	0.350[e]	3.91	0.25

[a] Early clutches were completed before the median date of clutch completion each year; late clutches were completed on or after the median date.

[b] Hatchability of eggs in successful clutches (i.e. those in which at least 1 egg hatched).

[c] Based on chick survival estimates from age 6 days to fledging (Table 7) times 75% in 1977 and 1978 and 65% in 1979, except as noted below (see text).

[d] Fraction of color-marked, late-hatching nestlings that were resighted postfledging in 1978 (2/20).

[e] Based on adjusted chick loss ($n = 1.87$ rather than 8) among late-nesting females in 1978; see Table 6 and text.

in the 0–5-day-old age class during 1977 or 1978, but our sample sizes were only 3 and 4 for each year. In 1979, when our sample was much larger, mortality in this very young age class was 57% (12/21). Six conspicuously feeble chicks perished within a few hours of hatching. Two others died on their fourth and fifth day, respectively. Neither gained weight nor showed signs of feeding; we inferred that both starved. One chick died mysteriously on its second day, and the radio signal from another disappeared when the chick was 5 days old. Finally, 2 siblings may have succumbed to heat stress on their fourth day. They hatched late in the season (18 June) within 100 m of a well-traveled road. The female parent disappeared just after hatching, leaving the male to provide all parental care. The family crossed the road on 20 June and entered a sparse, crested wheatgrass (*Agropyron cristatum*) planting where grasshoppers were abundant and shade was scarce. Excessive traffic along this road on 21–22 June (both clear, hot days) may have interfered with the male's ability to provide needed shade to the chicks.

Predation on radio-marked chicks varied dramatically among years (Table 5). In 1977, 75% (9/12) of these chicks survived through

fledging. One chick was eaten by a long-tailed weasel, and the fates of 2 others were unknown. In 1978, only 2 of 13 radio-marked chicks (15%) survived to fledge, and both were killed soon thereafter. Raptors were responsible for at least 73% (8/11) of all prefledging losses in 1978, and no mortality was attributed to mammalian carnivores. The fate of 1 individual was unknown, however, and it may have been captured by a mammal and carried underground. In 1979, predation was again light,

TABLE 5.   Mortality of radio-marked Long-billed Curlew chicks aged 0–45 days.

	1977	1978	1979	Total	Percent
Chicks	12	13	26	51	
Losses to:					
Raptors	0	8	1	9	17.7
Mammals	1	0	2	3	5.9
Aspergillosis	0	2	0	2	3.9
Other factors[a]	0	0	12	12	23.5
Unknown[b]	2	1	2	5	9.8
Total	3	11	17	31	60.8

[a] See text for fates of these 12 chicks aged 0–5 days in 1979.

[b] Radio signals were lost, and chicks almost certainly were depredated.

TABLE 6. Survival of radio-marked Long-billed Curlew chicks from age 6 days to fledging.

Year	Nesting class[a]	No. of chicks	No. lost	Chick-days	Mortality rate/day ± SE	P[b]	Days to fledge[c]	Percent survival
1977	Early	5	1	116	0.009 ± 0.0086		32.0	75.3
	Late	7	2	123	0.017 ± 0.0114	0.60	32.0	58.3
	All	12	3	239	0.013 ± 0.0072		32.0	66.0
1978	Early	5	3	130	0.024 ± 0.0132		39.5	39.1
	Late	8	8	42	0.211 ± 0.0606	0.001	40.0	0.01
	All	13	11	172	0.066 ± 0.0187		39.8	6.5
1979	Early	6	1	120	0.009 ± 0.0083		34.3	74.6
	Late	8	4	122	0.034 ± 0.0161	0.15	32.0	33.2
	All	14	5	242	0.021 ± 0.0091		33.2	48.9
1977–1979	Early	16	5	366	0.014 ± 0.0061		35.3	60.8
	Late	23	14	287	0.051 ± 0.0127	0.01	34.7	16.4
	All	39	19	653	0.030 ± 0.0066		35.0	34.4

[a] Early clutches were completed before the median date each year; late clutches were completed on or after median dates.

[b] Probability that daily mortality rates do not differ between early and late clutches; obtained by G-tests (Willis 1981).

[c] Means for each period in each year.

with just 4% (1/26) of the sample being lost to raptors and 8% (2/26) to mammals.

The only other known cause of mortality to radio-marked chicks was aspergillosis, a pulmonary mycotic infection from which 15% (2/13) perished in 1978 (necropsies and diagnoses by Dr. B. W. O'Gara, Montana Cooperative Wildlife Research Unit). Aspergillosis has been reported for a wide range of free-living, avian species, particularly waterfowl and gamebirds (O'Meara and Witter 1971), but never for Long-billed Curlews.

Fledging success.—Survival of very young chicks (aged 0–5 days) probably depends more on their learning to feed effectively and receiving occasional thermoregulatory assistance from parents than on avoiding predation. In 1977 and 1978 few chicks were monitored for this period, and no mortality was detected. From the larger sample in 1979, we estimated 14.1% of chicks lost per day (12 lost over 85 chick-days) or 40.2% survival to age 6 days. These figures were almost certainly biased by stress to very young chicks associated with their carrying a radio transmitter and being disturbed daily. Such stress might have increased mortality as much as 50–100%, which would result in survival values of 60–80% from hatching to age 6 days. Our estimates of fledging success (Table 4) were based on 75% of chicks surviving to 6 days in 1977 and 1978, and 65% in 1979.

The estimate for 1979 was lower because smaller eggs were laid that year (Redmond 1986), and in other Charadriiformes there is an inverse relationship between egg size and chick mortality (Lundberg and Väisänen 1979).

The variable intensity of predation on radio-marked chicks aged 6 days to fledging suggests variation among years in either predation pressure or effectiveness of parental care, or both. Because late-hatching chicks tend to receive reduced parental care as a result of early departure by females (Redmond 1984), we compared daily mortality rates from age 6 days to fledging between chicks that hatched early (before median date) and late (on or after the median) each year. In 1977 and 1979 these rates did not differ significantly, but in 1978 late-hatching chicks experienced significantly greater mortality than those that hatched early (Table 6).

Resightings of color-marked juveniles that were marked as nestlings provide a minimum estimate of fledging success. The fractions resighted in 1977 (16/56) and 1979 (1/47) were much lower than the estimates of survival from age 6 days to fledging for radio-marked chicks (Table 6). In 1978, however, we resighted as juveniles 17% (5/30) of the color-marked chicks that hatched early and 10% (2/20) of those that hatched late. This 10% minimum survival of late-hatching chicks was considerably greater than the 0.01% estimated from the sample of

TABLE 7. Resightings of natally philopatric Long-billed Curlews.[a]

Sex	Hatch year	No. resighted	Year resighted			
			1978	1979	1980	1981
Males	1977	5				
	1978	4				
	1979	0				
Females	1977	1				
	1978	0				
	1979	1				

[a] Each horizontal line represents the resighting of one Long-billed Curlew that was color-marked as a chick; a dashed line indicates nonbreeding status for that year.

radio-marked chicks. To adjust for the possibility that in 1978 mortality was greater among radio-marked chicks than among color-marked chicks (see Discussion), we assigned a 10% fledging success rate to the late-nesting class (Table 4). Based on this adjustment, estimated fledging success in 1978 was 23% for all females.

Because female Long-billed Curlews are monogamous and lay just one clutch each season, the number of young fledged per breeding adult equals half the number fledged per nest. Estimates of young fledged per female varied considerably among years (Table 4). More importantly, early-nesting pairs consistently fledged more young than did late-nesting pairs (from 0.13 to 0.14 more; see Table 4).

Juvenile and adult mortality.—Only 2 radio-marked chicks were known to perish after fledging. Both were taken by raptors in 1978 within a week of fledging. All other radio-marked chicks that were monitored past fledging (8 each in 1977 and 1979) survived.

There was no evidence of nonhuman predation on adult Long-billed Curlews at any time during this study. The fact that many clutches were lost to predators, often in twilight or complete darkness, suggests that incubating adults can effectively detect and escape mammalian carnivores. One unsucceessful attack by a Prairie Falcon (*Falco mexicanus*) was observed in early April 1979.

All adult mortality observed during this study was related to human disturbance activities. Carcasses of 9 adults were found during May and June (8 in 1977, 1 in 1979). Three were shot with small-caliber firearms, but the other 6 were too decomposed and damaged to ascertain the cause of death. We believe that they also were shot because all were found along roads accessible to the public and during late May, when many humans used the upland for recreation and when breeding adults were most vigorous in mobbing intruders (Redmond 1984).

Survivorship.—Because of a significant male bias in natal philopatry (Redmond and Jenni 1982), and the tendency for males not to return and attempt to breed until they are 3 or more years of age (Table 7), subadult survival could be estimated only for males from the 1977 and 1978 cohorts. For these years, 29 and 16 color-marked chicks were sighted postfledging. If half of these were actually males, then subsequent resightings of 21% (3/14) and 50% (4/8) for the respective cohorts provide a minimum estimate of survival for the 33-month period between fledging and the first attempt to breed. These estimates were unreliable because both resighting components (numbers returning to breed and numbers resighted postfledging) represent minimums, and therefore actual survival could be either greater or less than the estimates. Given the relatively stable population size (Fig. 1) and the results of a demographic analysis (see below), both figures probably underestimated subadult survival.

TABLE 8. Resighting data and annual survival estimates[a] for adult Long-billed Curlews of both sexes breeding during 1977–1981.

Year	No. marked	No. re-sight-ed	No. seen for last time	Estimated probability of Disap-pear-ing	Surviving ± SD
1977	9	—	1		
1978	17[b]	8	9	0.11	0.89 ± 0.10
1979	17	16	12	0.36	0.64 ± 0.10
1980	4[c]	11	6	0.36	0.84 ± 0.16
1981	6[d]	19	—	—	—

[a] Based on maximum-likelihood method of Cormack (1964).

[b] Sixteen adults captured and color-banded + 1 albino male (seen from 1978 to 1980).

[c] All 4 individuals were color-banded as chicks in 1977 and first sighted as adults in 1980.

[d] Another 6 individuals color-banded as chicks in 1978–1979 and first sighted as adults in 1981.

Fig. 2. Net reproductive rate (R_0) as a function of female fledging success and survival of subadults (S_1) from fledging to first breeding at 3 yr (2 yr for line A) and of adults thereafter (S_2). See text for details.

Estimates of annual adult survival based on resightings of color-marked individuals (Table 8) represent minimum values. We believe that survival was substantially higher than 64% in 1979 (see Discussion), and we consider average adult survival to be approximately 85% per year. For an adult just starting to breed, such a figure predicts a mean further expected life span of 6.15 yr (Brownie et al. 1978: 39). Thus, depending on age at first breeding, which appears to be 2–3 yr for females and 3–4 yr for males, the average longevity of Long-billed Curlews may be 8–10 yr.

Demographic analysis.—To evaluate the reproductive performance of this population, annual fledging success rates were compared with a range of values for a stable population that assume maximum possible (100%) and minimum observed (36%) survival from fledging until first breeding. These values were obtained by plotting net reproductive rates (R_0, calculated after Ricklefs 1973: 408) as a function of fledging success per female for different rates of subadult survival (Fig. 2). Adult mortality was assumed to be age-constant (Deevey 1947, Lack 1954), and the maximum possible number of female young fledged per female equals 2.0 (or the number of females in the largest mean clutch size, 4.0/2, assuming a primary sex ratio of 1:1). If all eggs and young survive to breed at age 2 yr, and thereafter experience 15% mor-
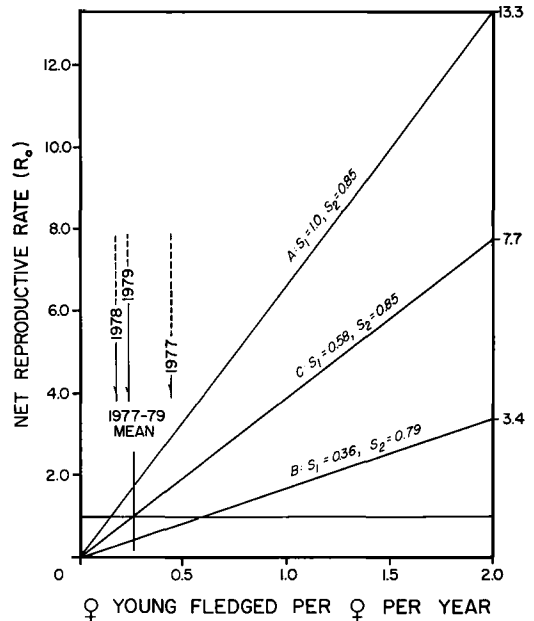
tality per year, R_0 equals 13.3 (Fig. 2: line A). At the other extreme, if all eggs and young fledge but survival from fledging to first breeding at 3 yr drops to 36%, and minimum adult survival thereafter is set at the observed mean of 79% (Table 8), then R_0 drops to 3.4 (Fig. 2: line B).

By definition, R_0 equals 1.0 in a stable population. For this population of Long-billed Curlews to be stable, with annual survival of 79% for adults (mean observed for all years) and 36% for subadults from fledging to 3 yr, females must fledge on average 0.59 female young per year (where line B crosses $R_0 = 1$). This did not occur in any year. Estimated fledging success per female in 1978 (0.17) was close to the intercept of line A with $R_0 = 1$, confirming that this was a year of poor productivity. Depending on actual values of subadult survival and age at first breeding, the 1979 estimate of average fledging success (0.21 female young/ female) was probably marginal. In 1977, and especially among early-nesting females, estimated fledging success reached or exceeded 0.38 female young. Such productivity may have been

enough to offset the relatively poor success in the following years. Mean fledging success per female pooled for all years was 0.25 female young, which, assuming a stable population size and 85% adult survival, predicts survival from fledging to first breeding at 3 yr to be 58% (Fig. 2: line C).

DISCUSSION

Breeding density.—The modified Finnish line-transect method can be used to estimate densities of territorial male Long-billed Curlews only. Females are less detectable before hatching of their eggs, and consequently their density cannot be estimated reliably (Redmond et al. 1981). Nevertheless, spot-mapping during prelaying and incubation in 1978 and 1979 confirmed that at least 85% of males acquired mates, and there was no evidence of a skewed, breeding sex ratio (Redmond et al. 1981).

The gradual decline in male density from 1978 to 1981 was likely real in spite of the large variances. During August 1981, a range fire burned 142 ha of the study plot. Transect counts during April 1982 were substantially greater, and estimated breeding density increased almost 30% from the previous year (Fig. 1). Territorial males were especially common in the burned area during the spring of 1982, probably because of reduced vegetative cover. Bicak et al. (1982) found a significant negative relationship between vegetative cover and numbers of breeding Long-billed Curlews on this study area.

Clutch size.—Significant annual variation in clutch size has never been reported among scolopacid shorebirds. At north temperate and arctic latitudes nearly all shorebirds (Charadrii) lay clutches of 4 eggs, and especially within Scolopacidae, intraspecific variation is slight (Maclean 1972). Yet in 1979, female Long-billed Curlews laid significantly more 3-egg clutches than in other years. Because clutch size was estimated by the maximum number of eggs found in a nest, it is conceivable that many of these nests in 1979 initially contained 4 eggs, but that 1 egg was lost from each nest before its being found. If this were so, one would expect single egg losses in 1979 to continue after nests were found and to be significantly greater than in other years. Single egg losses were greatest, however, in 1978 (Table 3).

We believe that clutch size actually was reduced in 1979, especially among early-nesting females, and that this was an adaptive response. Unusually dense vegetation covered most breeding territories early that season, and curlews flew considerable distances to find food (Redmond 1986). Clutch size and egg quality are associated with levels of protein reserves stored in the flight muscles of gulls (Houston et al. 1983) and other birds (Jones and Ward 1976, Fogden and Fogden 1979). If female Long-billed Curlews also rely on flight muscles for protein storage, then strenuous use of these muscles before laying might limit protein reserves and thereby affect reproductive effort. We suggest that reduced clutch size was an alternative to delayed laying and reduced egg size for some females in 1979 (see Redmond 1986). We also predict that intraspecific variation in clutch size is more likely to be detected, at least among shorebirds, during seasons of marked environmental contrast that may stress female reproductive physiology.

Reproductive success.—The hatching success of shorebirds is extremely variable among species, and even within species it tends to vary among years (see reviews by Goss-Custard 1981, Evans and Pienkowski 1984). Evidence for a general decline in hatching success with latitude (as proposed by Ricklefs 1969) is mounting for shorebirds (Pienkowski 1984a). Consistent with such a trend, the mean clutch mortality rate of Long-billed Curlews in western Idaho (0.0285/day) was significantly higher than that of Whimbrels (*Numenius phaeopus*) nesting on the Canadian subarctic tundra [0.0150/day, calculated from Skeel's (1983) data for all three habitats combined; $G = 4.34$, $P < 0.05$].

Reports of clutch losses between 20 and 50% are common for shorebirds that nest at temperate latitudes. These figures, however, are biased in many studies (exceptions are Sordahl 1980, Page et al. 1983, Pienkowski 1984a, Lank et al. 1985) and underestimate actual mortality. This is because nests were found throughout incubation, yet rates were not adjusted for unknown losses (Mayfield 1975, Johnson 1979). If this bias is ignored for Long-billed Curlews, the percentage of clutches lost each year was 40–45%, which, although still high, is more comparable to data from these other shorebirds (see Cramp and Simmons 1982).

Survival of shorebird chicks is difficult to de-

termine because of their precocial development and nidifugous habit. Estimates of fledging success are available for only a few species (Safriel 1975, Page et al. 1983, Pienkowski 1984b). Chick mortality between hatching and learning to feed is inferred to be high for many species (Holmes 1966, Soikkeli 1967, Jehl 1973, Hildén 1978, Oring et al. 1983). Among Common Ringed Plovers breeding in northeastern England, 53% of all chick mortality occurred during the first week after hatching, and it was attributable to predation and starvation (Pienkowski 1984b). Mortality of young Long-billed Curlews (age 0–5 days) was most often the result of inadequate parental care (resulting in overheating, chilling, or predation), starvation, or some physical inviability.

In 1977, 5% (3/57) of nestlings handled showed signs of incomplete yolk sac retention and adherence of eggshell fragments. All 3 chicks died within hours of hatching. There was no evidence of similar inviability from 118 nestlings handled in 1978 and 1979. Incomplete yolk sac retention and a poorly healed umbilicus are signs of either inadequate or excessive warming of eggs during incubation (Rol'nik 1968). Adherence of chick embryos to portions of the eggshell occurs under conditions of insufficient humidity (Rol'nik 1968). The drought conditions in 1977 (Redmond 1986) may have reduced humidities in Long-billed Curlew nests, which in turn may have increased egg water loss (Ar and Rahn 1980, Walsberg 1980). The response of Long-billed Curlew embryos to dehydration is not known, but yolk sac adherence to the outer membranes and eggshell proper may have been a consequence of excessive embryonic water loss.

Late-nesting pairs of Long-billed Curlews had lower reproductive success (in terms of number of young fledged per adult) than early-nesting pairs (Table 4). This was due primarily to differences in fledging success between the two groups. Fledging success was greater among chicks that hatched before the median date in all three years. In 1978 this difference was particularly dramatic because of the intense predation of radio-marked chicks by raptors late in the season. Although likely to exist, differences in clutch survival between early- and late-nesting pairs could not be evaluated because laying dates of many destroyed nests were not known. Egg survival, however, was higher

among late-hatching than early-hatching nests in 1978 and 1979. This probably reflects the decline in numbers of grazing livestock that occurred throughout May each season.

Abnormally heavy spring rainfall in 1978 produced unusually lush vegetative cover (vertical density and biomass; Redmond 1986). The tall, thick vegetation probably reduced small mammal vulnerability to raptor predation, and hindered the movements of Long-billed Curlew chicks, especially as they grew larger. If chicks then favored more open areas, they might have become more vulnerable to avian predators. We recorded no losses of radio-marked chicks to raptors before 14 June 1978, two days after most adults abandoned their broods (Redmond 1984). This emphasizes the importance of parental care to chick survival and suggests that the abnormally early departure of adults in 1978 facilitated a major shift in diet by local raptors to include Long-billed Curlew chicks. The cause of this adult departure remains unclear, but the tall, dense vegetation may have interfered with their ability to tend chicks or forage efficiently, or both.

Survivorship and demographic analysis.—An important assumption underlying estimates of adult survival is that all marked individuals alive in future years are equally likely to be resighted (Cormack 1964). Because no sex bias was detected in annual resightings of males and females (Redmond and Jenni 1982), we assumed approximately equal survival rates for both sexes. But females that were captured and subsequently lost their clutch were less likely to be resighted than females that nested successfully in their year of capture (Redmond and Jenni 1982). The same was not true of males. Resightings of females captured in 1978 were particularly low in 1979 (6/12; Redmond and Jenni 1982: table 1), but not because of poor hatching success. We suspect that females were discouraged from nesting in this area once they encountered the hostile vegetative conditions present during March and April of 1979. Thus, if female breeding dispersal rather than adult mortality produced the lower resightings in 1979, then the 64% survival estimate for that year was too low. Given the estimates of 84% and 89% for two separate years, and the likelihood that some breeding dispersal was undetected in 1979, we consider 85% to be a reasonable estimate of average annual adult

survival. Comparative data, however, suggest that even this figure might be too low for such a large shorebird (Goss-Custard 1981, Evans and Pienkowski 1984).

The life-table analysis also assumes that both clutch size and adult mortality are age-constant. The former is reasonable for a species with a relatively fixed clutch size; the latter is widely accepted (Deevey 1947, Lack 1954, Ricklefs 1973) but difficult to evaluate (see Botkin and Miller 1974). Because annual resightings estimate minimum adult survival, calculations of net reproductive rate (R_0) based on such estimates are necessarily conservative.

The critical data missing from this analysis are annual survival rates for juveniles and subadults. For this population to be stable in size with females producing an average of 0.25 female fledglings per year (the mean observed for all years), survival from fledging to first breeding 33 months later must be 58%. This requires survival of about 84% of juveniles and subadults each year. Mortality is likely to be higher than this, however, at least for juvenile birds undertaking their first migration. Yearlings were never sighted on this breeding ground, and reports of Long-billed Curlews remaining on their winter range throughout the year (McCaskie 1970, Jurek 1974) suggest that yearlings, and perhaps some 2-year-olds, may not attempt a northward migration. In this case, subadult survival approaching 95% on the wintering grounds would be sufficient to offset mortality of up to 36% of juveniles during their first migration and still provide for 58% returning to attempt breeding as 3-year-olds. These figures are indeed plausible considering that in Britain 50% of Eurasian Curlews banded as chicks survived to 1 year of age when the species was legal quarry (Bainbridge and Minton 1978). Other limited data indicate that 2-year-old Eurasian Curlews survive better than adults, perhaps at a rate well over 90% (Evans and Pienkowski 1984).

Even if 58% represents a reasonable estimate of average subadult survival for Long-billed Curlews, a further complication remains. Males were more likely to return and breed in their natal area than were females (Table 7), suggesting that females disperse before first breeding (Redmond and Jenni 1982). The relative isolation of this breeding population suggests that females may disperse long distances. This

has important ecological and management implications for Long-billed Curlews or any species with geographically isolated populations and sex differences in natal philopatry and dispersal (see Greenwood 1980). It means that adequate productivity, subadult survival, and adult survival in one population may not be sufficient to ensure its growth or stability. Clearly, the productivity of other populations that supply female recruits, as well as subadult survival of these recruits, also must be considered. In other words, the fates of geographically isolated populations may be interconnected by strong, sex-biased natal dispersal.

To conclude that this breeding population was stable, one must be relatively certain that local recruitment from marginal, surrounding areas was not responsible for the stable densities observed on the study plot. A method was devised to monitor numbers of breeding adults over about 70% of the entire study area, and no major declines were detected between 1977 and 1983 (Redmond et al. unpubl. data).

Productivity on the 1,600-ha study plot varied considerably among years. In 1977, a drought year, fledgling production was greatest and probably sufficient to offset the poor productivity associated with abnormally wet conditions the next year. But the abnormal rainfall in the spring of 1978 had an additional effect on Long-billed Curlew reproduction in 1979, mediated by the abundant, standing dead vegetation present during prelaying. Thus, the population faced unusual environmental conditions each year we monitored its productivity. If, in years with more normal rainfall and vegetative cover (see Redmond 1986), fledgling production varies between the values estimated for 1979 and 1977, and if our estimates of survival after fledging are realistic, then this population should remain stable within limits set by habitat quality and density-dependent mortality factors (Lack 1966).

The fact that population surveys in 1980 and 1981 did not reflect the poor fledgling production in 1978 is no doubt a function of the species' longevity. Populations of longer-lived organisms, because they are made up of individuals that vary widely in age, are less vulnerable to short-term fluctuations. Yet this numerical inertia makes population declines difficult to detect until they are well underway unless age structure can be determined.

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