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NESTING DENSITY AND COMMUNAL BREEDING IN AMERICAN OYSTERCATCHERS[1]

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Key words: Communal breeding; polygyny; American Oystercatchers; Haematopus palliatus.

American Oystercatchers (Haematopus palliatus) are typically monogamous shorebirds. The two sexes exhibit highly synchronized behavior during the period when females are susceptible to extra-pair copulations; they have stable, highly complementary pair bonds over many years; they have low divorce rates (about 2.5%, Nol, pers. observ.); and the care of both parents appears to be required for successful reproduction (Nol 1985).

One case of communal breeding involving two pairs attending and defending one communal nest has been reported for American Oystercatchers nesting along the Texas coast (Chapman 1982). Little is known regarding the ecological conditions in this study. Unlike most birds that breed communally (Fry 1972, Brown 1974, Brown 1987), some populations of American Oystercatchers are migratory and breed in a seasonal environment. Here, we document several cases of communal breeding in American Oystercatchers and the

ecological conditions that appear to influence the occurrence of this unusual social system.

STUDY AREAS AND METHODS

We compared two breeding populations of oystercatchers. In Virginia, American Oystercatchers bred on Wallops and Assawoman Islands and were studied from 1978 to 1983. We include in the study, those breeding around the Chincoteague Channel (37°55′N, 75°23′W) from 1981 to 1983. In Virginia, pairs nested on sand habitat at the ocean side of the barrier island between the dunes and the high tide line, and in the salt marsh on elevated sandy dredge soil. Each year the number of nesting pairs was recorded. At the end of the study, aerial photographs (dated from 1982) were used to determine the area of nesting habitat available within the study site. Available habitat was defined as any habitat that had been used by nesting oystercatchers during the study period. We calculated the nest densities as the number of pairs on a given area. Clutch sizes ranged from two to four eggs ($\bar{x} = 2.24$ eggs for 294 nests, Nol et al. 1984).

In New York, we studied a population in the salt marshes around South Oyster Bay (40°38′N, 73°28′W) and Great South Bay (40°36′N, 73°20′W), Long Island, from 1983–1985 and 1987–1988. Oystercatchers bred in this region until the turn of the century, when hunting pressure presumably drove them southward (Bent

TABLE 1. Density of nests (pairs per hectare) in Virginia.

Location	Year	No. nests	Density (pairs/ha)
Virginia	1978	23	0.66
	1979	33	0.95
	1980	26	0.75
	1981	40	0.96
	1982	41	1.00
	1983	36	0.87

TABLE 2. Frequency of pairs and communal associations among sand-nesting birds in New York.

Year	No. of pairs	No. of communal associations (%)	Density (pairs/ha)
1983	16	1 (5.9)	4.86
1984	4	2 (4.1)	11.06
1985	34	4 (10.5)	9.29
1987	55	2 (3.5)	12.83
1988	53	4 (7.0)	13.05

1929). They returned to the area in 1957 and their numbers have increased, particularly in the 1970s and 1980s (Zarudsky 1985). This increase was attributed to both reduced hunting pressure and to the creation of sandy dredge spoil deposits used as nesting grounds by the birds.

In New York, birds nested on sand, grass (*Spartina patens*) and detrital wrack (Lauro and Burger 1989). We determined the total area of available sand with a measuring wheel. Available sand habitat was defined as in Virginia. All sand areas in the study area were included to calculate densities. In both study areas, oystercatchers fed predominantly off the territory (Nol 1989; Lauro, pers. observ.), so birds were defending nest sites.

Clutches containing four or fewer eggs were attributed to monogamous pairs, while those containing five or six eggs were attributed to the two females attending the nest. The two females (distinguished from males by brighter orange, and longer bills [Nol 1985]) were present throughout the breeding season, from before laying to when chicks fledged. Fledging success was not recorded because chicks often moved into the marsh, making them difficult to follow. The eggs in nests containing more than four eggs were of two distinct background colors. No distinction was made between first and second clutches. Although the modal clutch size was three eggs, two-egg clutches were not uncommon and it is possible that some four-egg clutches were also due to communal associations. However, in Virginia as we once observed a new egg in a nest every other day, for eight days, for a total of four eggs, it was assumed that some females could lay four-egg clutches, although this has never been reported for American Oystercatchers. Egg dumping and nest parasitism may also account for some four-egg clutches. Thus, the latter were never attributed to communal nesting, even though this may have resulted in an underestimate of its occurrence.

RESULTS

We examined an average of 33 pairs per year in Virginia and 41 pairs per year in New York. Nesting densities in Virginia were consistent over the six years of the study and quite low (Table 1). No communal nests were ever found at the Virginia study site, regardless of the number of nests examined in any year. In New York, however, nesting densities were an order of magnitude higher than in Virginia and from 4.1% (in 1984) to 10.5% (in 1985) of nests were communal, with one male and two females present. One communal nest

was even found in 1983 although only a small number of nests was examined (Table 1). Thus, at higher nesting densities there were more communal nests, across study sites (Spearman's $r = 0.87$, $P < 0.005$). In New York no significant correlation existed ($r = 0.51$, $P = 0.38$).

Communal nests in New York were always associated with one of six locations. All of these were on sandy substrates. By contrast, 21.3% of monogamous pairs nested on grass or wrack substrates (55 of 260 nests, $G = 6.01$, $P < 0.02$). Pairs nesting on sand had significantly greater hatching success than those nesting on grass or wrack. Over the entire study period, only 2.4% of monogamous nests on sand failed due to flooding, whereas 27% of those on grass and wrack were flooded out ($G = 23.2$, $P < 0.0001$). This difference was probably due to the higher elevation of the sand nests, which made them less susceptible to flooding (Lauro and Burger 1989). Thus, it appears that nest sites on sand were superior to those on grass or wrack, at least for hatching success.

The proportion of communal nests hatching at least one egg was similar to that of monogamous nests. Hatching data on ten of the former were available: nine of these hatched at least one egg (as compared to 173 out of 229 monogamous nests [$G = 1.315$, ns]. However, per capita hatching success appears to be lower at communal nests. In all, eight eggs (in 4 of 13 communal nests) were found cracked or left unattended after the other eggs had hatched. Cracked eggs in nests of monogamous pairs were rare (2 in 229 nests in New York study area).

In at least two communal nests at the same location, but in different years (1985 and 1987), the second clutch of eggs was begun four days after the first clutch was complete. Only eggs from the first clutch hatched in both years (and possibly in a third year, 1984). In another nest at a different location, four of six eggs appeared to hatch, all at about the same time, as four chicks all about three to four days old were observed together. Therefore, the laying periods of the two females can sometimes overlap.

DISCUSSION

Communal nesting in the American Oystercatcher appeared to be a direct consequence of the high nesting densities in the New York study area. The habitat saturation model for the evolution of cooperative breeding (Emlen 1982) predicts that territories are occupied in descending order of quality (Brown 1987). Communal associations should occur when there is a short-

age of high quality territories, and only in superior habitats. These conditions appeared to be met in our study, at least insofar as sand sites with communal nests were those with higher hatching success. Although we do not know the lifetime reproductive success of the communal breeders, nor their relatedness to assess other models of communal breeding (e.g., Stacey and Ligon 1987), we can tentatively assess the costs and benefits.

Female oystercatchers, although not as territorially aggressive as males, participate actively in territorial defense (Nol 1985). A third bird may have been tolerated because three birds were more effective in keeping the superior territories. When model oystercatchers were placed in the territories of communal trios all birds participated in piping displays (Lauro, unpubl. data). Increased territorial defense has been suggested as an explanation for communal nesting in three other shorebirds (European Oystercatchers, *Haematopus ostralegus*, review in Cramp and Simmons 1983; Southern Lapwings, *Vanellus chilensis*, Walters and Walters 1980; American Avocets, *Recurvirostra americana*, Giroux 1985), where nesting densities have been unusually high. These species are all in the family, Charadriidae (Sibley et al. 1988), which implies some phylogenetic tendency toward cooperative breeding (Russell 1989).

The costs to communal nesters (and in particular to the female that lays the second clutch of eggs) include reduced hatching success either due to ineffective incubation or early cessation of incubation (although this did not appear to be the case in the Texas communal nest, Chapman 1982). Reduced fledging success can also result if the age difference between the chicks in the two broods is too great, because the larger chicks will obtain most of the food (e.g., Safriel 1981, Groves 1984).

Chicks may also benefit from attendance by three adults. Fledging success of monogamous pairings in American Oystercatchers is very low, and egg and chick losses are due to flooding of nest sites, and predation in both study areas (Lauro and Burger 1989, Nol 1989). Food for the young is usually collected away from the nesting territory in both study sites (Lauro, pers. observ., Nol 1989) so chicks are sometimes left in the care of only one adult some time. If the chicks are all of the same age, as they appeared to be in at least one of the cases of communal breeding seen here, three adults feeding and protecting the young, might be advantageous. This additional protection is unlikely to be the proximate cause of communal nesting in this species, or this social system would be more common.

We are probably observing polygynous trios, as mate guarding in this species is so well-developed (Nol 1985) that copulation of one of the females by another territorial male seems unlikely, and unmated birds were never observed. Polygynous associations may be a result of a skewed sex ratio (Mayr 1939). Male oystercatchers expend more energy defending territories than their mates (Nol 1985) and may experience greater mortality at higher densities as the frequency of territorial encounters increases (Briggs 1984, Safriel et al. 1984). In Black-legged Kittiwakes, *Rissa tridactyla*, male mortality increased at a rate faster than female mortality as the density of breeding pairs increased over a 16-year period (Coulson and Wooler 1976). This was attributed to density-dependent stress on the males in occupying and defending nests. In European oystercatchers, increased mortality during the breeding season was attributed to the stress of territorial defense (Safriel et al. 1984). The Texas case of communal breeding in American Oystercatchers involved four, rather than three adults (Chapman 1982), so polygyny is not necessarily associated with communal breeding in this species. Migratory species nesting in the temperate zone are less likely to be communal nesters because breeding densities are generally lower, and there is less natal philopatry (Brown 1987). However, oystercatchers possess some characteristics of obligate communal nesters. They have delayed breeding and low adult mortality (Safriel et al. 1984, Nol 1985, Brown 1987, Smith 1990) and they are social in the non-breeding season (Cramp and Simmons 1983). Habitat loss along the east coast of North America appears to have artificially increased the densities of oystercatchers nesting in the salt marshes (Lauro and Burger 1989), and this factor, along with the characteristics listed above, and a phylogenetic affinity (Russell 1989, van Rhijn 1990), likely account for their crossing the "communal breeding" threshold. In addition, the short migration of this species (probably no more than 500 km) facilitates the maintenance of kin units, if these are involved in the facultative communal breeding seen here.

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SCARCITY OF HAEMATOZOA IN BIRDS BREEDING ON THE ARCTIC TUNDRA OF NORTH AMERICA[1]

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Key words: Haematozoa; tundra; arctic; parasites; longspur; ptarmigan; redpoll; plumage color.

Despite widespread interest in documenting the blood parasites of birds (e.g. Loye and Zuk 1990), there is little information available on the haematozoa of species occurring in arctic regions. Laird (1961) reported that none of the 149 individuals of 23 bird species he sampled on Prince of Wales Island (72–74°N, 96–103°W) during one summer harbored haematozoa, but no other intensive surveys have been done of North American arctic-nesting birds. In a review of haematozoan prevalence in North American birds, Greiner et al. (1975) indicate that less than 3% of birds sampled from the "arctic barrens" (their region 6) were parasitized, but they provide no further information on the sample of birds involved in this analysis.

In this paper, we report on the haematozoa found in 276 breeding birds of 10 species sampled in the course of field studies of their behavior and ecology at four very different arctic sites. While some of these species have been sampled for haematozoa before, our samples allow us to compare haematozoa prevalence between habitat types, both within and between sites. We also discuss the implications of our findings for recent comparative analyses of parasite prevalence in relation to plumage brightness in birds (see Møller 1990).