Characteristics and Functions of the Lining of Piping Plover Nests in the Great Lakes Region

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ABSTRACT.-- Great Lakes Piping Plovers nest on gravel beaches and line their nests with primarily light-colored fragments smaller than 0.5 cm. Through constructing artificial piping plover nests with different types of linings in the field and in the laboratory, I explored three possible functions of the nest lining. Linings may serve to reduce the amount of water retained in the nests after rain. Protection from sand deposition is not a function of the nest lining under normal wind conditions. Light-colored fragments remain cooler than unlined sand scrapes or scrapes lined with dark fragments. From simulations, I found that when adults are not incubating, the temperature in the nests increases significantly. Therefore, human disturbances which interrupt incubation may be detrimental to hatching success.

INTRODUCTION.-- The Great Lakes sand dunes are a globally rare ecosystem which supports many habitat-specific species (Nature 1994). The population of Piping Plovers (*Charadrius melodus*) that nest on the Great Lakes shores was designated as federally endangered under the Endangered Species Act in January of 1986 (50 Federal Register 50726-34). One of the steps recommended by the recovery team for the Great Lakes and North Great Plains Piping Plovers to aid population recovery is "to assess characteristics of breeding habitats" (USFWS 1994). Piping plovers generally nest on wide, sparsely vegetated gravel beaches, away from the water, and often near large objects such as stones, logs, or clumps of grass (Cairns 1982, Faanes 1983, Haig 1992, Russell 1983). Piping Plovers are more likely to select territories which are covered with significantly more gravel than found in adjacent nonterritories (Prindiville 1986, Whyte 1985). Prindiville (1986) suggested that the combination of unvegetated beach and a high concentration of evenly distributed stones creates a homogeneous substrate which may provide camouflage for incubating birds. In the Great Plains, Piping Plovers which nested on gravel beaches had significantly higher nesting success than those nesting on salt-encrusted alkali mud flats. Successful territories contained significantly more gravel than nonsuccessful territories and the stones were more evenly distributed in successful territories (Prindiville, 1986).

Stone fragments are an integral part of Piping Plover nests, which are shallow scrapes in the sand usually lined with primarily small light-colored fragments of stones or shells from the surrounding gravel (Haig 1992). Often directly after copulation, the male and female will stand to the side of the scrape and toss pieces of stones or shells into the nest with their beaks. The lining is usually completed within one day, though the stone-tossing behavior continues sporadically as adults continue to add fragments throughout laying and incubation (Haig, 1992). Nests typically contain four buff-colored, speckled eggs which are incubated by both adults for approximately twenty-eight days. Ambient temperatures may be near freezing at night in the spring during early incubation; and they exceed 35°C towards the end of incubation (Haig, 1992).

The nest lining has not been characterized in detail, nor has its function been addressed. According to Collias (1984), the primary and most general function of a nest is to insure warmth and safety for the developing eggs and young. Piping Plover nests do not protect the precocial chicks, but their design may protect the eggs from biotic and abiotic factors. The objectives of this study are to document the specific characteristics of the nest lining and the explore three possible purposes of lining the nest: drainage, protection against sand deposition, and temperature regulation. I propose that Piping Plovers prefer fragments that are light colored and smaller than 0.5 cm. Light-colored fragments may absorb less heat from the sun keeping the eggs at a lower temperature. Therefore, eggs would remain cooler than if they were in contact with the sand. Fragments may also cool the eggs by allowing more air to circulate under them. Eggs may be protected from prolonged exposure to moisture in wet sand by increased drainage through the nest fragments. Nests which are not used frequently become blown over with sand (Haig 1992). The fragments may also aid in preventing eggs from being covered as a result of sand deposition; or they may prevent the nest from becoming too deep or misshapen during incubation.

METHODS.-- *Nest Sites--* In the Great Lakes region this year, 21 Piping Plovers pairs established nests at the following sites: Cross Village South, Cross Village Central #1, Cross Village Central #2, Sturgeon Bay South, Sturgeon Bay Central, Sturgeon Bay North, Waugoshance Point East, Waugoshance Point West, Temperance Island, Pointe aux Chenes, Grand Marais Superior Beach, Grand Marais East Beach, Grand Marais Lonesome Point, Vermilion, High Island, Beaver Island, Thorne Swift Nature Preserve, North Manitou Island West, North Manitou Island East, and Platte River Mouth (Figure 1). Plovers do not use their nests after the chicks hatch; therefore the nests were available for study with minimal disturbance to the birds during July and August. Several nests were destroyed by severe weather before experiments could be conducted, creating different sample sizes for the various experiments. Each nest was surrounded by 50 ft of wire fencing to exclude predators and all experiments were conducted inside these enclosures.

Nest Fragment Characteristics-- To determine whether plovers prefer specific types of fragments, I compared the nest lining to substrate samples from around the nest (n=17). The area surrounding the nest was divided into four quadrants and a transect was randomly selected in each quadrant to collect samples at 1 m, 5 m, and 10 m away from the nest. I used a sieve 20 cm in diameter to collect all material larger than 2 mm. Fragments were then separated into stones and shells. I categorized stones into four size classes (<0.5 cm, 0.5 cm - 1.0 cm, 1.0 cm - 4.0 cm, >4.0 cm) and three color classes (light, medium, dark). Shells were separated into two size classes (<0.5 cm, 0.5 cm - 1.0 cm). Chi square tests were used to determine whether the relative abundance of size and color classes differed between the nest lining and surrounding substrate. Only the smallest two size classes were analyzed based on the assumption that plovers are incapable of tossing fragments larger than 1 cm. The distribution of shells was not analyzed due to limited abundance.

Drainage-- With dimensions identical to that of the plover nest, I constructed three artificial nests: an unlined sand scrape, a scrape lined with black fragments smaller than 1 cm, and a scrape lined with light-colored fragments smaller than 1 cm at each site (n=7). I placed four Japanese Quail eggs (*Coturnix coturnix*) in each nest. Rain was simulated by passing 1 L of Lake Michigan water through holes in the bottom of a coffee can held a uniform height above each nest. After fifteen minutes, the eggs were removed and the underlying substrate was collected in two soil tins to the depth of 0.5 cm. The tins were then dried in a drying oven for 24 hours at 65°C. I used the weights of the tins before and after drying to determine the percent soil moisture which was analyzed by nest type using a MANOVA (Wilkinson 1989).

Protection against sand deposition-- Three nests: an unlined sand scrape, a scrape lined with randomly selected fragments smaller than 1 cm, and a scrape lined with light-colored fragments smaller than 1 cm, were constructed 1 m apart at each site (n=15). Scrapes were 9.0 cm in diameter and positioned in a line perpendicular to the prevailing wind direction. Each nest contained four Japanese Quail eggs and I placed a hardware cloth cover over each scrape to prevent depredation of the eggs. After four days, I assessed the damage by measuring the area of the nest still intact. Percent cobble and percent gravel in the 3 x 3 m square up wind from the nests were estimated, and the linings were collected and weighed. Rocks larger than 1.0 cm were considered cobble; rocks smaller than 1.0 cm were considered gravel. The data could not be analyzed due to lack of disturbance by the wind at most sites.

Temperature Regulation-- Three scrapes were constructed at each site (n=8) as described for the drainage experiment. Four Japanese Quail eggs were be placed in each artificial nest and in the plover nest. A thermocouple attached to a StowAway miniature data logger was placed between an egg and the substrate in each nest, and a square of cotton was placed over the nest to simulate an incubating adult. Temperature was recorded every 48 seconds for 24 hours. During the last 45 minutes of the recording, I removed the cotton to simulate the temperature change when an adult is not incubating. This length of time was chosen based on the longest adult absence observed during incubation, 30 minutes and 41 seconds (Doolittle, pers comm). The maximum, minimum, and final temperatures were analyzed by nest type using a MANOVA (Wilkinson 1989).

To eliminate extraneous variation in temperature experienced in the field due to wind and other factors, I constructed three artificial nests: an unlined scrape, a scrape lined with black fragments smaller than 1.0 cm, and a lined scrape reconstructed from a plover nest collected from each site, in a plastic washtub filled with sand (n=16). The scrapes were 9.0 cm in diameter and equidistant from the center of the washtub. I placed four Japanese Quail eggs in each nest and thermocouples were placed under the eggs closest to the outer edge of the washtub. A heat lamp was suspended 38 cm above the sand and the washtub was rotated at 0.17 rpm to insure that all nests received equal heat. A pad of cotton 12.4 cm x 14.0 cm was placed over each nest for the first hour of heating, recording temperature every 3 seconds. I then removed the cotton for the remaining 30 minutes to simulate non-incubated nests. The rate of change of temperature during the simulated incubation and non-incubation periods was analyzed by nest type using a MANOVA (Wilkinson 1989).

RESULTS.-- *Nest Characteristics--* The average nest lining contained 1289 fragments, approximately 3.2 times the average number of fragments found in equal areas in the surrounding substrate. On average, linings contained 51.5% small light-colored fragments, 33.5% small medium-colored fragments, 9.9% small dark-colored fragments, 3.0% large light-colored fragments, 1.9% large medium-colored fragments, and 0.2% large dark-colored fragments (Figure 2). "Small" fragments are classified in the 0.2 cm - 0.49 cm size category; "large" fragments belong to the 0.5 cm - 1.0 cm size class. Plover nests had an average diameter of 11.96 cm and an average depth of 0.86 cm. The average diameter of nests was found to be larger than the values (6 cm and 9-10 cm) reported by the Recovery Plan (1994) and Haig (1992). The average depth was smaller than the values (2 cm and 1-2 cm) reported by the same sources. These discrepancies are probably due to weather damage to the nests during the time after the chicks hatched and before the measurements were taken.

To determine whether the proportions of the fragments in the nest lining were due to the abundances of the fragments in the surrounding area, the nest lining was compared to substrate samples surrounding the nest. The distribution of fragments varied significantly between plover nests and the surrounding substrate at all sites (Table 1), though the direction of preference varied among sites. Fifteen nests contained greater concentrations of medium-colored fragments smaller than 0.5 cm and eleven nests contained greater concentrations of light-colored fragments smaller than 0.5 cm. Dark-colored fragments smaller than 0.5 cm were preferred at two sites. Plovers selected fragments in the 0.2 - 0.5 cm category at all 17 sites, and fragments in the 0.5 - 1.0 cm size category were selected at 11 sites. Light-colored fragments in the larger size class were selected more often than medium or dark-colored fragments in that size class. The distance from the nest at which the samples were taken was insignificant to the distribution of the substrate. Low concentrations of shell fragments prevented comparison of their distribution.

Drainage-- Scrapes lined with dark-colored fragments held significantly less water than unlined scrapes (p=0.004), plover nests (p=0.08), and scrapes lined with light-colored fragments (p=0.127) (Figure 3). The degrees of drainage from the plover nests and the light-colored scrapes were very similar (p=.81).

Protection against sand deposition -- Only two of the fifteen sets of nests were covered by sand (Table 2), both occurring at the same site, Cross Village Central #2. All three nest types sustained damage, though the scrapes containing the randomly selected fragments retained a greater area intact than the scrapes lined with light-colored fragments or the unlined sand scrape. Linings from these four nests weighed the least, and the percent cobble and percent gravel up wind from the nests was low.

Temperature Regulation: -- The maximum and minimum temperatures in the nest linings over a 24 hour period did not differ significantly between nest types (Figure 4). There was also no significant difference between the nest types in rate of temperature increase during the 45 minute period when the cotton was not on the nests or in the temperature at the end of the simulated non-incubation period. This probably occurred due to the greater variability in ambient temperature between sites and because of the large number of extraneous variables, such as wind, experienced in the field. In all trials, during the 45 minutes the cotton was not on the eggs, the temperature in the linings dramatically increased, exceeding the maximum temperature experienced during incubation. The maximum temperature during incubation usually occurred during midday, and though the periods of adult absence all occurred during early morning or late afternoon, the temperature in the linings surpassed midday temperatures.

Under extreme heat conditions simulated by the heat lamp, the temperature in scrapes lined with light-colored fragments increased significantly slower than the temperature in scrapes lined with dark-colored fragments (p=0.010) and unlined scrapes (p=0.109). This trend was greatly amplified during the non-incubating period. The removal of the cotton caused a dramatic increase in the rate of change of temperature in all lining types compared to the rate of change while the cotton was on the nests (Figure 5). The differences in the slopes of the temperature curve during incubation and non-incubation were highly significant (p=0.00001) regardless of the type of nest lining. At the end of the non-incubation period, the scrape lined with light-colored fragments was significantly cooler than the scrape lined with dark-fragments (p=0.00005) or the unlined sand scrape (p=0.078).

DISCUSSION -- The distinct discrepancy between nest linings and stone fragments in the surrounding substrates indicate that plovers preferentially select medium and light-colored stone fragments smaller than 0.5 cm. I observed a large degree of variation between sites in which the types of stone fragments were most abundant in the area around the nest, even though the types of fragments in the nest lining were similar in proportions at each site. This strong preference indicates that using lighter colored fragments to line the nest probably has some adaptive advantages.

The presence of nest lining reduces the amount of moisture to which eggs are exposed over at least a 15 minute period after a rain storm. Sand particles have a greater surface area than stone fragments, and therefore more water remains adhered to the sand. Since dark colors absorb more heat, increasing evaporation, dark-colored linings retain less water than light-colored linings. If exposure to water is detrimental to hatching success, it would be more advantageous for plovers to select dark fragments. In Red-capped Dotterel nests, the amount of lining is directly proportional to the dampness of the site (Hobbs 1972), indicating that exposure to water may affect some avian eggs. This may not be influential to Piping Plovers, according to Cairns (1982) who reported three water soaked Piping Plover clutches hatched successfully. The amount of moisture which actually enters a nest during rain is unknown since adult incubation behavior in the rain has not been documented.

Under normal wind conditions, the presence or type of nest lining is not critical to protect the nest against sand deposition. The data suggest that damage caused by sand deposition is more specific to the topography of each site or the amount of lining in the nest. The hardware cloth covers may have provided some protection from the wind, reducing the damage. Adults would probably remain on the nest during severe winds, and therefore sand deposition in the nest is most likely not a threat to hatching success. Cases of adults digging out eggs buried by sand have been observed (Cairns 1982).

Temperature data recorded in the field suggest that under mild heat, nest linings do not regulate egg temperature. Under severe heat, the temperature in light-colored linings increased at a significantly slower rate than the temperature in unlined scrapes and scrapes lined with dark fragments. This suggests that the light-colored lining serves as a cooling mechanism. The high temperatures experienced in June before the chicks hatch could be detrimental to the developing eggs. On hot days, incubating adults leave the nest more frequently or stand over the eggs to shade them (Haig 1992). Therefore, the lining is exposed to more direct and indirect sunlight in warm temperatures, making the color of the lining critical to temperature regulation. The dramatic increase in temperature change during the non-incubation period both in the field and in the laboratory suggest that the presence of the adult on the nest is critical to regulation of egg temperature. When adults are absent, eggs are exposed to significantly higher temperatures, which could reduce hatching success.

There may be alternative functions of the primarily light-colored nest lining. The fragments may aid in concealing the eggs from predators. Cairns (1977) found that nests on mixed sand and gravel substrates were less conspicuous than those on sand alone, though nests on alkali mud flats were more conspicuous because of the light-colored lining (Prindiville 1986). Light-colored linings are more conspicuous in the rain against wet sand (Cairns 1982). The lining may also aid adults in turning the eggs. Stone fragments may be a more suitable substrate than sand on which to rotate eggs during incubation.

The conservation of the Great Lakes Piping Plover is critical to survival of the populations and to the species as a whole. Haig and Oring (1985) stated that loss of breeding activity in the Great Lakes not only decreases species' productivity, but creates a gap between the prairie and Atlantic breeding areas. Human disturbances, such as off-road vehicles, foot traffic, and unleashed dogs, in Piping Plover territories often curtail reproductive success (USFWS 1994). This study has shown that interruption of incubation behavior may significantly increase the temperature of the eggs, which could lead to reduced hatching success. The presence of humans in Piping Plover territories should be limited to avoid disrupting incubation and consequently exposing the eggs to elevated temperatures.

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Table 1. Stone fragment size and color preference in the lining of Piping Plover nests in the Great Lakes Region. The lining of the Piping Plover nests in the Great Lakes region contained significantly difference distributions of fragments compared to the substrate at 1, 5, and 10 m away from the nest. The preference of size and color of fragments varied among sites.

Site	1 m	5 m	10 m	$\sum X^2$
CVS	M1	D1, M1	M1, M2	185.50
CVC#1	L1, M1	L1, M1	L1, M1	330.35
CVC#2	M1	M1	D2, M1, M2	185.05
SBS	L1, M1	L1	L1, M1	87.78
SBC	L1, M1	L1, M1	D2, L1, M2	45.54
SBN	L1, M1	M1	M1	67.43
WPE	L1, M1	L1, M1	L1, M1	119.73
WPW	M1	M1	L1, M1	181.65
TI	M1	L2, M1, M2	M1	195.05
GMSB	L1, M1	L1, M1	L1, M1, M2	161.88
GMEB	L1, L2, M1	M1	L1, M1, M2	315.80
GMLP	L1, L2, M1	L1, L2, M1	L1, L2, M1	158.49
VER	L1, L2, M1	L1, L2, M1	L1, L2, M1	149.41
HI	L1, L2, M2	L1, L2, M2	L1, L2, M2	270.33
NME	L2, M1, M2	L1, M1	L1, L2, M2	50.44
NMW	D1, D2, M1	D1, D2, L2, M1	D1, D2, M1	25.26
PR	L1, M1	L1, M1	L1, M1	149.95

D= dark-colored fragment
L= light-colored fragment
M= medium-colored fragment

1= size class 0.2-0.49 cm
2= size class 0.5-1.0 cm

TABLE 2. Percent of simulated Piping Plover nests intact after four days exposure to wind

Site	Random Fragments	Light-colored Fragments	Unlined Sand	Percent Cobble Up Wind	Percent Gravel Up Wind	Weight of Random Lining (g)	Weight of Light-Colored Lining (g)
CVC#1	1.00	1.00	1.00	0.60	0.20	52.25	25.80
CVC#2	0.73	0.70	0.54	--	--	28.20	18.10
CVS	1.00	1.00	1.00	0.05	0.20		67.30
WPE	1.00	1.00	1.00	0.80	0.05	77.20	62.80
WPW	1.00	1.00	1.00	0.30	0.70	50.30	61.60
SBS	1.00	1.00	1.00	0.20	0.20	59.30	40.70
TI	1.00	1.00	1.00	0.20	0.70	--	--
SBC	1.00	1.00	1.00	0.05	0.00	63.30	61.70
SBN	1.00	1.00	1.00	0.80	0.15	102.90	59.00
CVC#2	0.70	0.50	0.25	0.05	0.50	28.55	21.40
WPE	1.00	1.00	1.00	0.70	0.10	41.10	37.40
WPW	1.00	1.00	1.00	0.45	0.50	124.25	85.70
SBS	1.00	1.00	1.00	0.025	0.02	75.15	34.05
CVS	1.00	1.00	1.00	0.20	0.20	79.60	51.40
SBC	1.00	1.00	1.00	0.80	0.10	111.00	63.30

A=Platte River Mouth
B=North Manitou Island West
C=North Manitou Island East
D=Thorne Swift Nature Perserve
E=Beaver Island
F=High Island
G=Cross Village South

H=Cross Village Central #1
I=Cross Village Central #2
J=Sturgeon Bay South
K=Sturgeon Bay Central
L=Sturgeon Bay North
M=Waugoshance Point East
N=Waugoshance Point West

O=Temperance Island
P=Pointe aux Chenes
Q=Grand Marais Superior Beach
R=Grand Marais East Beach
S=Grand Marais Lonesome Point
T=Vermilion

FIGURE 1. Nest sites of Piping Plovers in the Great Lakes Region in 1995.

From: Department of the Interior
US Geographical Survey, 1976

FIGURE 2. Characteristics of the stone fragments lining Piping Plover nests in the Great Lakes region

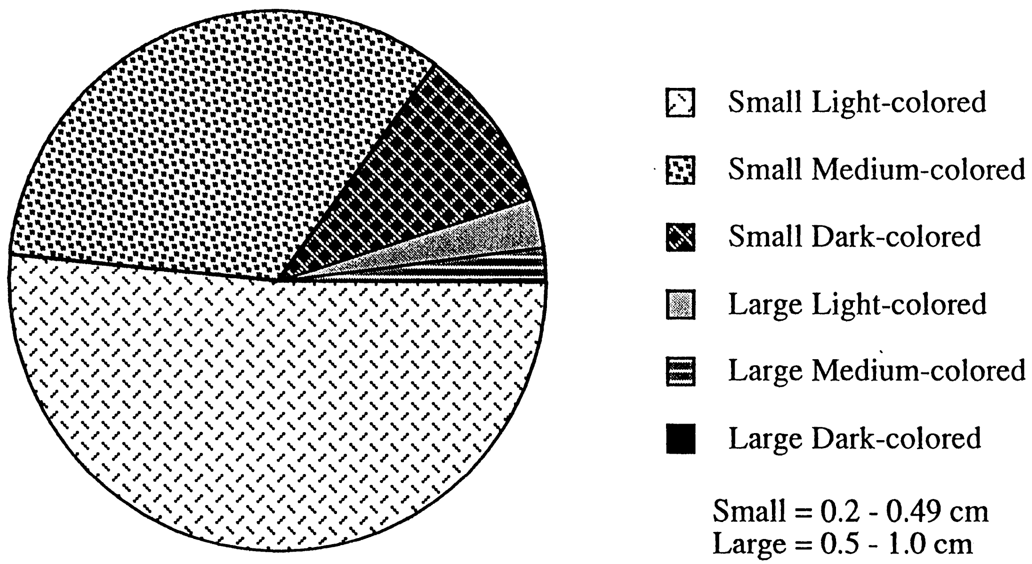

FIGURE 3. Percent water retention in the linings of Great Lakes Piping Plover nests fifteen minutes after rain simulation

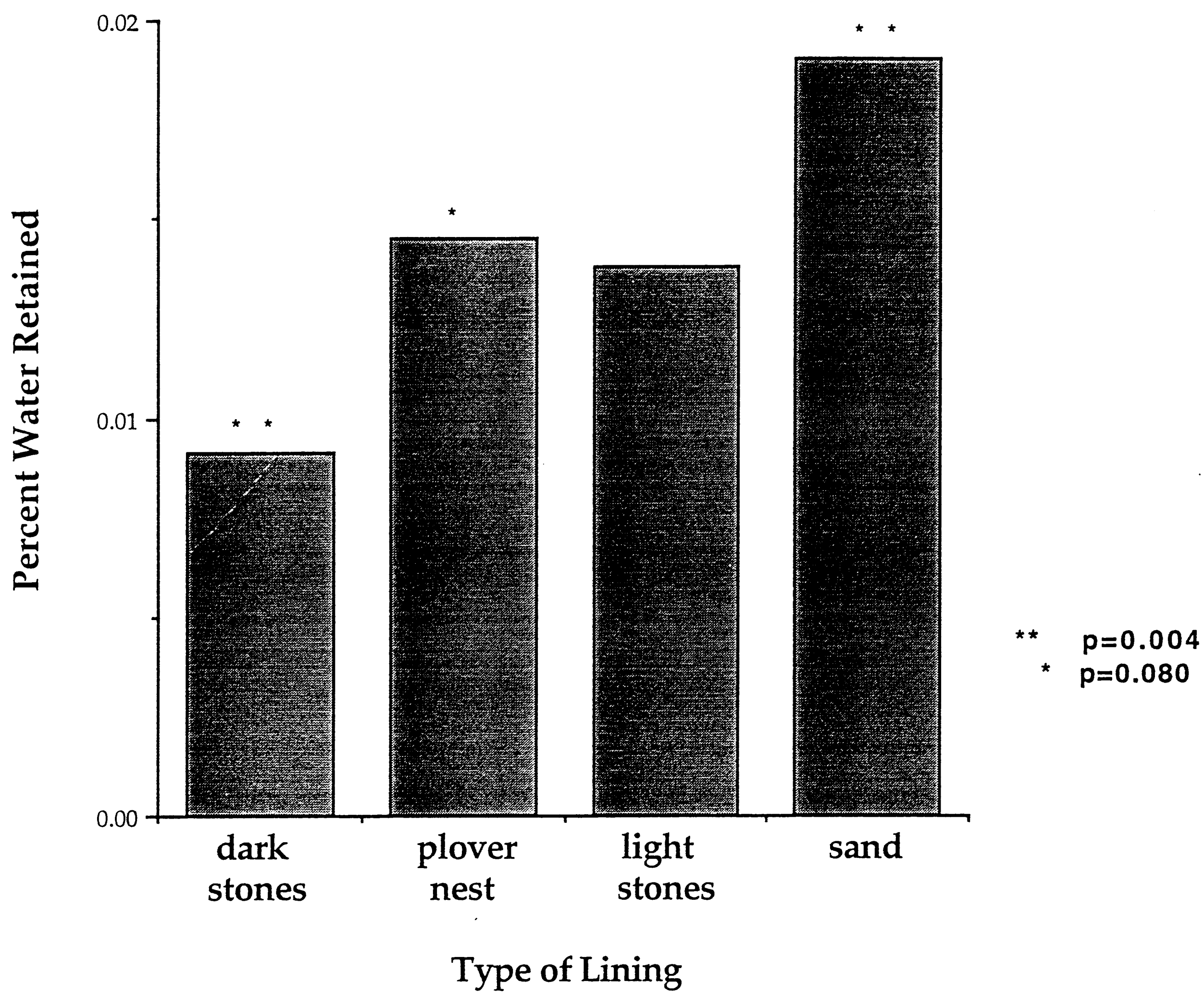

FIGURE 4. Temperature fluctuations in Great Lakes Piping Plover nests during simulations of 24 hours of incubation and 45 minutes of adult absence

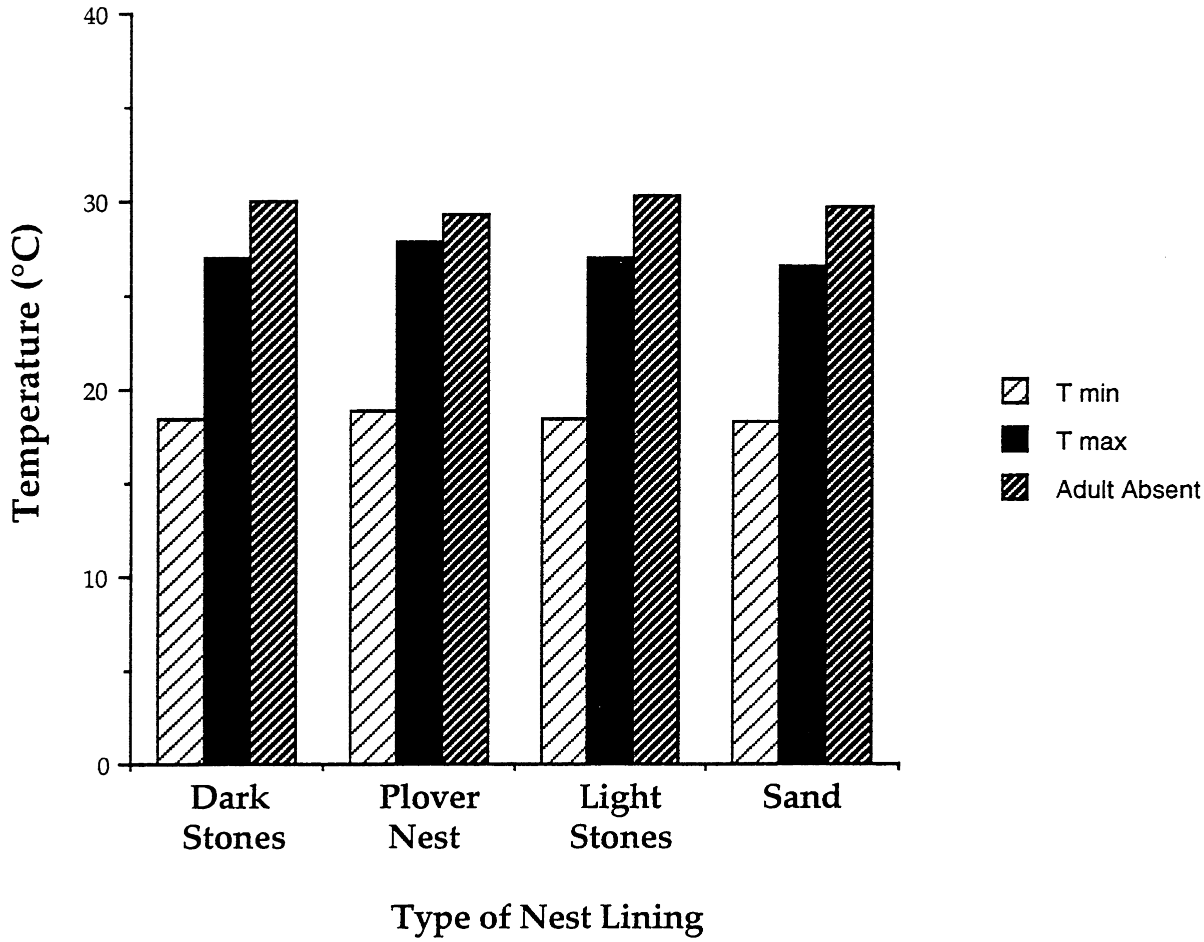

FIGURE 5. **Temperature in the lining of reconstructed Great Lakes Piping Plover nests during simulations of incubation and adult absence under severe heat**