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PATTERNS OF HABITAT USE FOR PIED AND SOOTY OYSTERCATCHERS NESTING AT THE FURNEAUX ISLANDS, AUSTRALIA[1]

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Abstract. We studied patterns of habitat use at the levels of general habitats (islands and substrates), feeding territories, and nest sites for two species of oystercatchers nesting sympatrically at the Furneaux Islands, Australia. Sooty Oystercatchers (*Haematopus fuliginosus*) nested only on small islands while Pied Oystercatchers (*H. longirostris*) nested on Flinders Island, a large island as well as small islands. Sooty Oystercatchers nested more commonly at rocky shores while Pied Oystercatchers nested more commonly at sandy shores. This was in part related to their selection of islands since small islands were rockier than Flinders Island and to their selection of foraging habitats relative to nesting areas. Pied Oystercatchers only placed nests on beaches where intertidal mudflats were available for foraging territories; these beaches were generally sandy. Sooty Oystercatchers used either muddy and rocky substrates (the primary available substrates) for foraging and their choice of feeding territories played little role in their selection of nesting substrates. At the light colored beaches of the Furneaux Islands, Sooty Oystercatchers (uniformly black) placed eggs in low visibility nest sites next to and under vegetation, while Pied Oystercatchers, with their countershaded color pattern, chose higher visibility nest sites on open beach. We suggest that at this study site Sooty Oystercatchers were less cryptic than Pied Oystercatchers and compensated by choosing vegetative characteristics at nest sites that hid the presence of their nests from diurnal, visually hunting predators. Gulls were the most likely predators to influence choice of vegetative characteristics at nest sites.

Key words: Oystercatcher; nest site; feeding territory; island; color pattern; predation; visibility.

INTRODUCTION

The oystercatchers form a monogeneric family of shorebird (Haematopodidae) whose species nest along the coastlines of the world. Black species of oystercatchers generally nest at small islands where beaches are rocky and dark in color while pied species of oystercatchers usually nest at mainland or island locations on sand beaches that are light in color (Bent 1929, Heppleston 1972, Baker 1974a, Hartwick 1974, Hockey 1982, Hockey and Underhill 1984, Lane 1987, Lauro and Burger 1989, Nol 1989, Lauro and Nol 1993). Most species of oystercatchers place nests on the ground above the high tide line in high visibility locations (Heppleston 1972, Hartwick 1974, Hockey and Underhill 1984, Lauro and Burger 1989, Lauro and Nol 1993). At several regions around the world (Baja California, southern South America, New Zealand and Australia) black and pied species of oystercatchers occur sympatrically (Hayman et al. 1986), usually where there is a mixture of rocky and sandy shoreline. Thus, the differences in habitat use for pied and black species of oystercatcher may result in ecological segregation, facilitating coexistence.

Important factors that may influence patterns of habitat use for the oystercatchers include: species differences in foraging ecology and response to potential predators given species color pattern. Black species appear to be better adapted to capturing prey on rocky shores (Bent 1929; Baker 1974a, 1974b; Hartwick 1976; Frank 1982; Hockey and Branch 1984; Hockey and Underhill 1984; Lindberg et al. 1987; Lauro and Nol 1995) while pied species of oystercatchers appear to be better adapted for capturing prey on soft substrates such as intertidal mudflat (Bent 1929; Heppleston 1972; Dare and Mercer 1973; Swennen et al. 1983; Hulscher 1985; Baker 1974a, 1974b; Goss Custard et al. 1992; Lauro and Nol

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1995). Therefore, species may select nesting sites that allow efficient access to territories with suitable feeding substrates and prey.

Jehl (1985) noted that American Black Oystercatchers (*Haematopus bachmani*) and American Oystercatchers (*Haematopus palliatus*; a pied species) nesting in sympatry appeared cryptic when nesting at dark rocky shores and light sandy beaches respectively. A pied oystercatcher may be more cryptic than a black oystercatcher at a light colored beach because of the visual effect created by the countershaded color pattern (Thayer 1909, Endler 1978). Incident sunlight illuminating the dorsal side of a uniformly dark bird creates a shadow on the belly making its three dimensional shape readily apparent. By contrast, the white belly of a pied bird creates an optical illusion that obliterates the effect of shadow, making individuals appear cryptic with respect to open habitats. Therefore, it may be the case that oystercatchers select nesting habitats that maintain crypsis with respect to color pattern.

The purpose of this study is to examine patterns of habitat use for Pied (*Haematopus longirostris*) and Sooty (*H. fuliginosus*) Oystercatchers (a uniformly dark species) nesting at the Furneaux Islands, Tasmania, Australia. We examine habitat use at three scales: general habitats (e.g., island choice), territories (e.g., nesting or feeding) and nest sites as it is believed that birds select habitats in this respective order (Burger 1985a, Klopfer and Ganzhorn 1985, Sherry and Holmes 1985). We present basic information on reproductive biology and discuss how factors like the location of preferred prey and potential predators may have influenced the habitat selection for these sympatric oystercatchers during the breeding season.

STUDY AREA AND METHODS

STUDY AREA AND GENERAL HABITAT USE

Habitat use data were collected in the austral spring and summer of 1988/1989 and 1989/1990, at the Furneaux Island Group, the Bass Strait, Tasmania, Australia (40°00′S, 148°00′E). Data were collected for Pied and Sooty Oystercatcher nests found on Flinders Island, the large island of the group (137,430 ha, Edgecombe 1986), and for eight small offshore islands (all less than 200 ha; Fig. 1).

The shorelines of the Furneaux Islands consisted of rocky and sandy beaches. On Flinders Island, sandy beaches predominated on the eastern and southwest coast, while rocky beaches predominated on the north, and northwest coasts; offshore islands were mainly rocky (Edgecombe 1986).

The general habitat of each nest was classified as all rocky, all sandy, or mixed beach (predominately sand with large boulders interspersed). To examine how the two species selected nesting substrates with respect to available substrates, the proportions of the distances of available rocky, sandy, and mixed beaches at Flinders Island, Big Green Island (a main study area, Figs. 1, 2), and all small islands were compared to the proportions of nests found on these same substrates at these same locations, for each season.

FORAGING TERRITORY USE

At the Furneaux Islands, Pied and Sooty Oystercatchers generally defended feeding territories in front of their nest sites. On Big Green Island (Fig. 2) in the 1989/1990 season we examined the characteristics of these feeding territories. Using aerial photographs we demarcated nest locations for measurement and comparison of the total length, rock length, and mud length extending from the high to the low tide line for: (1) each nest, (2) a random site within 100 m radius of each nest (i.e., a random site at a territory), and (3) 50 random points along the perimeter of the island. The coordinates of random sites were chosen from a random numbers table.

NEST SITE USE

For each species we visually estimated seven physical and vegetative characters at nest and random sites (Burger 1985a). A random site was selected within a 100 m radius of each nest. Nest sites and random sites for a species were compared to examine how habitats were selected. Nest site characters were compared to examine species differences in habitat use. Random sites for each species were compared to determine whether habitat characteristics were generally different at locations where Pied and Sooty Oystercatchers were breeding.

In the 1988/1989 season on Big Green Island the tone of all nest sites and random locations around nest sites was measured to examine whether the two species matched their color pattern to the color of the nesting area. All substrates and species of vegetation within a 1 m and 5 m

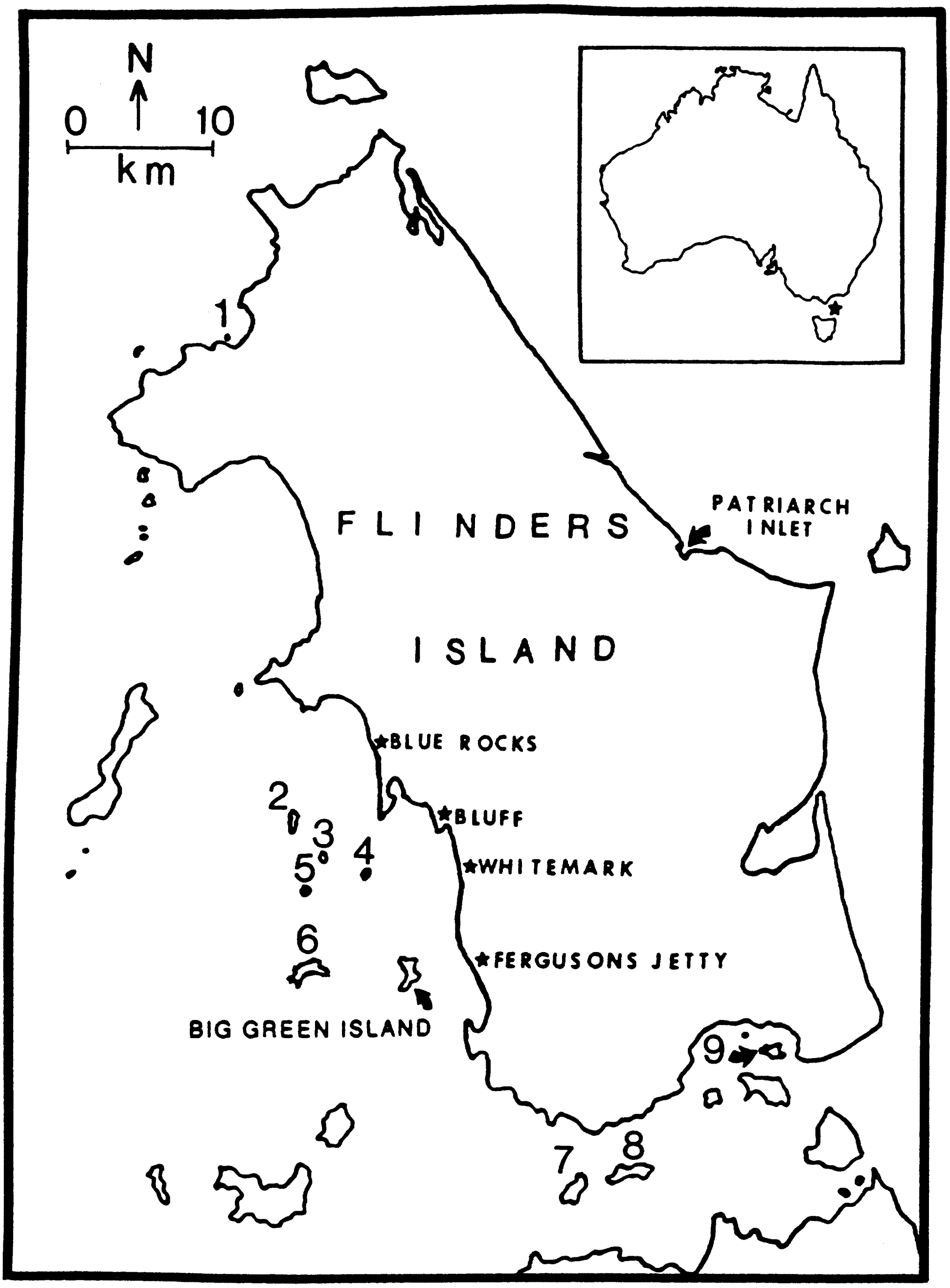

FIGURE 1. A map of the Furneaux Islands, Australia. The eight small islands surveyed were: Big Green Island, an unnamed island (1), Chalky (2), Mile (3), Isabella (4), Little Chalky (5), Kangaroo (6), Little Anderson (7), Tin Kettle (8) and Little Green (9).

radius of nest and random sites were ranked on a tonal scale of 1–10 (1-white and 10-black). A color index at a site was calculated for 1 and 5 m circles by multiplying the proportion of area covered by substrates and species of vegetation by their color ranking and then summing them.

Several habitat characters were used to assess nest site visibility. The percent of each substrate

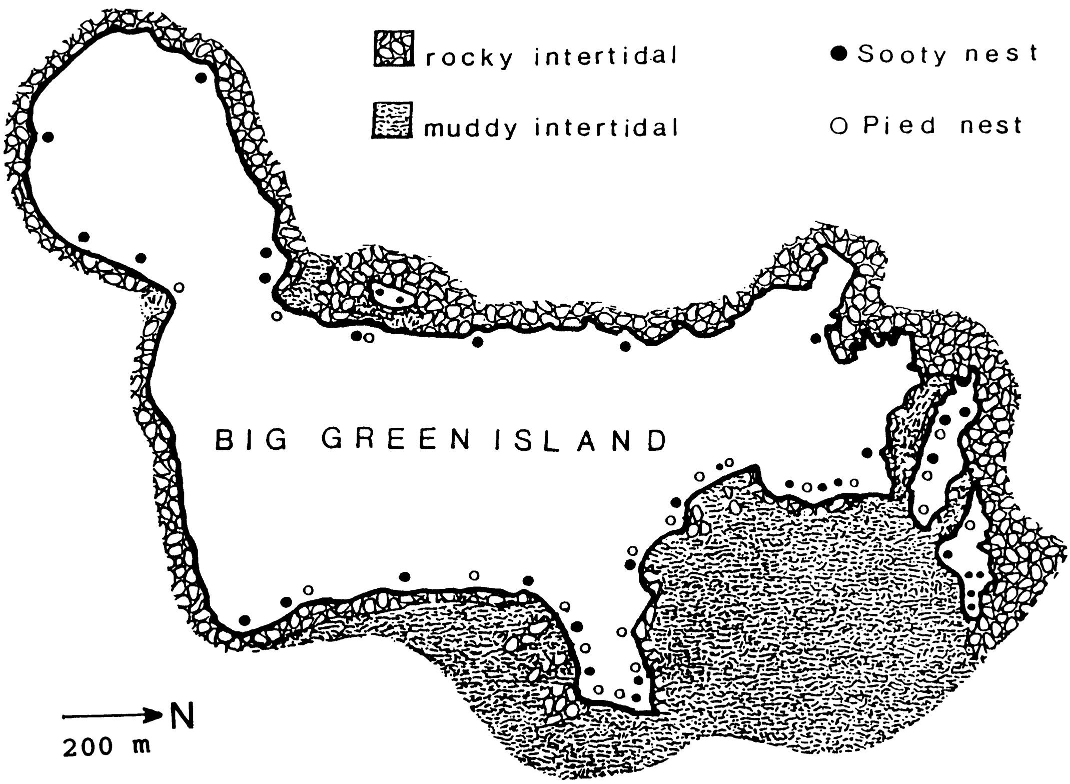

FIGURE 2. A map of nest sites for Sooty and Pied Oystercatchers on Big Green Island in the 1989/1990 season.

and the percent of each species of vegetation were measured within a 1 and 5 m radius of the sites. The categories of substrates were rock, sand, wrack (dead sea weed washed onto the shore) and other. The angle of view (AOV) from nest sites was estimated as the degrees of a circle visible to a bird sitting on a nest. Nest cover was estimated as the percentage of vegetation covering a 0.25 m radius of a circle at a height of 50 cm above the ground at the site where eggs were placed or where a random point was selected. Vegetation distance (Veg. Dst.) was the distance to the nearest piece of live vegetation from the nest or random site. Vegetation height (Veg. Ht.) was the height of the nearest species of live vegetation.

Since nests were either under vegetation or out in the open the species values for percent cover and vegetation height were extremes over the range of characteristics with distributions containing many zero values. Therefore, chi-square analyses were used for tests of significance rather than the Mann Whitney *U*-tests which were used for all other comparisons.

We examined whether the distance of nests to those of potential competitors, both conspecific and congeneric, influenced the choice of nest site visibility. This was done in the 1989/1990 field season by examining the correlations between angle of view and nearest neighbor distances for nests on Big Green Island (Burger 1977).

Finally, given the potentially high correlation between habitat variables we performed a principal components analysis using the variables percent substrate and vegetation at 1 and 5 m, vegetation distance, vegetation over nest, and angle of view using the 1988/1989 data to determine if there were: (1) species differences in some combination of these data, and (2) to determine whether successful or unsuccessful nests differed in their scores on principal components 1 or principal components 2 (i.e., Schieck and Hannon 1993). For the 1990 data we also added the variable ‘locale visibility’, which was a measure of the long distance visibility to determine if this variable added significantly to the variation explained by the principal components. For locale visibility, open beaches, intermediate beaches, and coves were coded as 1, 2 and 3 respectively.

REPRODUCTIVE BIOLOGY

Information on the reproductive biology for Pied and Sooty Oystercatcher pairs was recorded on Big Green Island in both seasons. Clutch sizes were recorded for first nests and renests. A pair that hatched at least one egg (including renests) was considered as successfully hatching. A pair that fledged at least one chick was categorized as successfully fledging. Where possible we recorded reasons for egg and chick loss including tidal flooding, severe weather and predation.

POTENTIAL PREDATORS

Throughout the first field season (25 September 1988–31 January 1989), censuses were conducted on Flinders Island and Big Green Island to document the presence of potential predators of Pied and Sooty Oystercatchers during daylight hours. We recorded every half-hour over a period of several hours, the number of visible, potential predators on nesting beaches. On Flinders Island, observations were conducted at four sandy beaches: Blue Rocks, the Bluff, Ferguson's Jetty and the Patriarch Inlet (Fig. 1). On Big Green Island observations were conducted at two mixed (rocky and sandy) beaches on the eastern shore and at three rocky beaches on the western shore (Figs. 1, 2). In addition to censusing potential predators at half hour intervals the frequency of all potential predators that were seen less regularly (i.e., raptors and ravens) was recorded throughout the observation periods.

RESULTS

GENERAL HABITAT CHOICE

Only Pied Oystercatchers nested on Flinders Island, the largest island of the Furneaux group, whereas both species nested on the smaller surrounding islands (Table 1, Fig. 1). The frequency of nests for the two species on rocky, sandy, and mixed habitat (primarily sand with large boulders interspersed) was significantly different (1988/1989: $\chi^2 = 39.49$, df = 2, $P < 0.001$; 1989/1990: $\chi^2 = 29.89$, df = 2, $P < 0.001$) with Pied Oystercatchers nesting more commonly at sandier locations and Sooty Oystercatchers nesting more commonly at rockier locations.

On Flinders Island, Pied Oystercatchers nested at sandy beaches only and not at rocky or mixed beaches although these habitats were available (Table 1). On small islands the proportions of their nests on mixed beach and rock beach (all sand beaches were rare) were greater and less (respectively) than that which would be expected given the habitats available (1988/1989: $\chi^2 = 29.00$, df = 1, $P < 0.001$; Table 1). In addition, the number of breeding pairs per km for Pied Oystercatchers on Flinders Island was low at 0.5 pairs per km compared to that on Big Green Island where the number of breeding pairs per km at sandy, mixed beach, rock beach and overall was: 4.8, 8.8, 1.4 and 3.1 per km (respectively, Table 1, Fig. 2).

Sooty Oystercatchers did not nest at sandy beaches but did nest at rock and mixed beaches (Table 1). The proportion of nests on rock beach and mixed beach was not significantly different than that which would be expected given the habitats available (1989/1990: $\chi^2 = 0.44$, df = 1, $P > 0.05$; Table 1). In addition, the number of breeding pairs per km at rock beach, mixed beach and overall was 4.6, 7.5 and 4.9 pairs respectively (Fig. 2).

The availability of substrates in the intertidal region (Figs. 2, 3) influenced the choice of nesting locations by Pied Oystercatchers at Big Green Island. The frequency of Pied Oystercatcher nests with respect to beach/intertidal habitats was significantly different than that which would be expected based on the habitats that were available (Fig. 3; $\chi^2 = 17.58$, df = 3, $P < 0.005$). The proportion of Pied Oystercatcher nests on mixed beach/mixed intertidal and rock beach/rock intertidal was greater and in near equal proportion (respectively) to that which was available (Fig. 3). Oystercatchers did not nest at locations where rock was the only substrate present on the beach and in the intertidal region (Fig. 3).

At Big Green Island, Sooty Oystercatchers nested at most combinations of beach/intertidal habitats and the frequency of nests with respect to beach/intertidal habitat was not significantly different than that which would be expected based on the habitats that were available (Figs. 2, 3; $\chi^2 = 3.40$, df = 3, $P > 0.05$). They did not nest at two small sand beach/mud intertidal locations. However, since these locations made up a small

TABLE 1. A comparison of the proportion of available substrates to the proportion of nests on each substrate by year.[a]

	Total	Rock (%)	Sand (%)	Mixed (%)
Flinders Island				
All beaches (km)	225.6	67.7 (30)	110.5 (70)	0.0 (0)
Beaches surveyed (km)	40.9	10.2 (25)	30.7 (75)	0.0 (0)
Pied nests (1988/89)	16	0 (0)	16 (100)	0 (0)
Pied nests (1989/90)	18	0 (0)	16 (100)	0 (0)
Big Green Island				
Beaches (km)	7.1	5.3 (74)	0.2 (3)	1.6 (23)
Pied nests (1988/89)	14	4 (29)	1 (7)	8 (64)
Pied nests (1989/90)	22	8 (36)	1 (5)	3 (59)
Sooty nests (1988/89)	28	19 (68)	0 (0)	9 (32)
Sooty nests (1989/90)	36	24 (67)	0 (0)	12 (33)
All small islands[a]				
Beaches (km)	30.8	25.0 (81)	0.0 (0)[b]	5.8 (19)
Pied nests (1988/89)	14	4 (31)	0 (0)	9 (69)
Sooty nests (1988/89)	44	34 (77)	0 (0)	10 (23)

[a] Eight small islands including Big Green Island (BGI) were surveyed in 1988/1989; only Big Green Island and Flinders Islands were surveyed in 1989/1990.
[b] On surveys of small islands it was observed that most beaches labelled sand on maps were mixed beaches. Therefore, for this comparison beaches labelled sand on maps were assumed to be mixed. See methods for further details.

proportion of the island's coastline it was not possible to statistically assess whether they avoided this habitat at this location.

FORAGING TERRITORY USE

At Big Green Island, Pied Oystercatchers selected locations that had significantly longer expanses of mud for foraging territories in front of nest sites compared to random sites along the perimeter of the island (Figs. 2, 4; Mann-Whitney U-test: $Z = 2.53$, $P = 0.0114$). When nest sites and random sites at territories were compared no differences were found for length of mud ($Z = 1.67$, $P = 0.0945$) or for length of rock ($Z = -1.11$, $P = 0.2769$). Pied Oystercatchers, compared to Sooty Oystercatchers, selected nest sites with more mud ($Z = 3.43$, $P = 0.0006$) and less rock in the intertidal zone ($Z = -2.32$, $P = 0.0206$); random site comparisons for species were not significantly different for rock ($Z = -0.28$, $P = 0.7821$) but were different for mud ($Z = 2.45$, $P = 0.0144$).

Sooty Oystercatchers nested around the perimeter of Big Green Island irrespective of the length of rock or mud substrate in the intertidal region. When nest sites and random sites around the perimeter of the island were compared, no significant differences were found for rock length (Fig. 4; $Z = 0.69$, $P = 0.4885$) or mud length ($Z = 0.08$, $P = 0.9302$). When nest sites and random sites at territories were compared, no significant differences were found for rock length ($Z = 0.23$, $P = 0.8124$) or mud length ($Z = 0.63$, $P = 0.5270$).

Intertidal mudflats extended out further at low tide than did rocky intertidal habitats (Figs. 2, 4). Therefore, since Pied Oystercatchers chose muddier sites, the total length of transects in front of their nests was significantly longer than random locations around the perimeter of the island (Fig. 4; $Z = 2.00$, $P = 0.0456$), while no differences were found for the same comparison for Sooty Oystercatchers ($Z = 1.28$, $P = 0.2018$). In addition, the length of substrate at Pied Oystercatcher nest sites and at random sites at territories was greater than that for Sooty Oystercatchers (nest: $Z = 2.43$, $P = 0.0156$; random: $Z = 2.38$, $P = 0.0175$; Fig. 4).

NEST SITE USE

Habitat color. The rocky and sandy habitats at the Furneaux Islands were light colored and ranked as a light grey on a scale of 10 (1-white, 10-black; Table 2). Therefore, neither Pied nor Sooty Oystercatchers had the opportunity to match plumage color to nest site color. Neither species selected nest sites that were darker or lighter than random locations and no species differences with respect to the color of nesting substrate were found (Table 2).

Visibility. Both species selected nest sites that were more open than surrounding habitat. Nest sites had more substrate (rock, sand, or wrack)

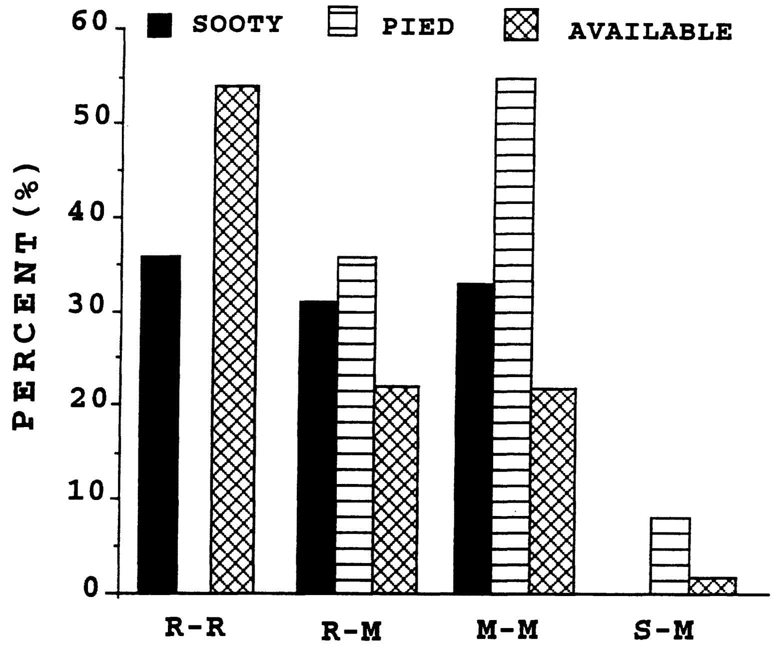

FIGURE 3. A comparison of the percentage of nests for Sooty Oystercatchers and for Pied Oystercatchers at different beach/intertidal habitats (rock/rock: R-R; rock/mud: R-M; mixed/mud: M-M; sand/mud: S-M) relative to the percentage that was available on Big Green Island in 1989/1990. Since mixed beaches with rocky intertidal areas were rare they were grouped into the category rock beach/rock intertidal. All other combinations of beach/intertidal substrates not mentioned on the table (e.g., rock beach/mud intertidal) did not occur at Big Green Island.

than vegetation as compared to random sites. Differences were significant for Pied Oystercatchers within a 5 m radius of nests and for Sooty Oystercatchers within a 1 and 5 m radius of nests (Table 2).

Within open areas, Sooty Oystercatchers usually placed nests next to and under a clump of vegetation while Pied Oystercatchers usually placed nests in the open. Pied Oystercatcher nest sites had a significantly higher angle of view and lower percent cover than random locations. Sooty Oystercatchers selected sites where distances to the closest piece of vegetation were significantly closer than random locations (Table 2). In addition, Sooty Oystercatcher nest sites had a significantly lower angle of view, higher percent nest cover, and shorter vegetation distance than Pied Oystercatcher nests while the comparisons for the random characters for the two species were not significantly different (Table 2).

In the 1989 and 1990 seasons, PC1 and PC2 together explained 70% and 66% of the variation in the data respectively (Table 3). The loadings were similar in direction in 1989 and 1990, despite the inclusion of an additional variable in 1990. In both years, positive values of PC1 appeared to represent greater proportions of substrate, less vegetation around nest, little to no vegetation over the nest and a low value for angle of view whereas negative values represent more enclosed sites with more vegetation near nests, less substrate, and more vegetation over the nest. PC2 had a particularly high negative loading on the variable of locale visibility, which suggests that PC2 also measured the tendency to nest in coves (locale visibility = 3), without the long distance visibility of beaches (locale visibility = 1).

When we compared the average values of PC1 and PC2 for the two species, they were, as expected, significantly different in both years (Table 4). Sooty Oystercatchers had significantly lower values for PC1 and PC2 than did Pied Oystercatchers. This confirms the univariate results that Pied Oystercatchers nest in the open, with less vegetation or no vegetation over their nests, while Sooty Oystercatchers have both reduced local and long distance visibility.

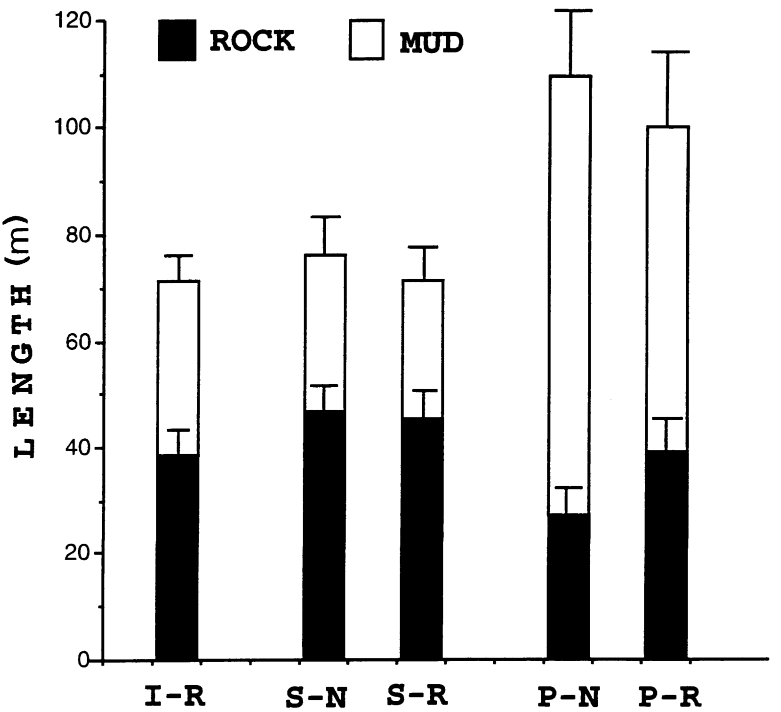

FIGURE 4. A comparison on Big Green Island in 1989/1990 of the average length (m) of rock and mud between the high tide line and the low tide line at: random sites along the island perimeter (I-R, $n = 50$); Sooty Oystercatcher nest sites (S-N, $n = 33$) and random sites at nesting territories (S-R, $n = 33$); Pied Oystercatcher nest sites (P-N, $n = 17$) and random sites at nesting territories (P-R, $n = 17$). Error brackets are ± one standard error.

Finally, when conspecifics were near, both species chose sites with lower angles of view, perhaps reducing the potential for intraspecific conflict. Nearest conspecific neighbor distances and angle of view were positively and significantly correlated for Pied ($r = 0.69$, $P = 0.0023$) and Sooty Oystercatchers ($r = 0.73$, $P = 0.0001$) while weaker positive and nonsignificant correlations were found for congeneric neighbor distances for Sooty ($r = 0.33$, $P = 0.1301$) and Pied ($r = 0.46$; $P = 0.0619$) Oystercatchers.

NESTING SUBSTRATES

Species differences with respect to rocky and sandy substrates were found at nest sites and random sites and were related to their general habitat preferences. Sooty Oystercatchers, who nested more commonly at rocky shores, had more rock within a 5 m radius of nests compared to random sites (Table 2). By contrast, Pied Oystercatchers, who nested more commonly at sandy beaches, had significantly greater percentages of sand within a 1 and 5 m radius of nests as compared to random sites (Table 2).

Both species placed nests on a soft substrate that cushioned eggs. Sooty Oystercatchers commonly placed nests on wrack apparently because it was the primary soft substrate available at rocky habitat. Therefore, Sooty Oystercatchers selected sites with more wrack than random sites (Table 2). Twenty four (63%) Sooty nests were placed on a base of wrack, eight (20%) were on dead vegetation, three (9%) were on rock, two were (5%) on sand and one was (3%) on pigface (*Disphyma australe*). Twelve (42%) Pied Oystercatcher nests were placed on a base of sand, ten (33%) were on wrack, four (13%) on dead vegetation, one (4%) was on rock, one (4%) was on shells and one (4%) was on pigface. The frequency of Sooty Oystercatcher nests on a base of wrack and sand was significantly higher and lower respectively than for Pied Oystercatchers (wrack: $\chi^2 = 5.953$, df $= 1$, $P < 0.025$; sand: $\chi^2 = 15.30$, df $= 1$, $P < 0.005$).

REPRODUCTIVE BIOLOGY

Clutch size. At Big Green Island the modal clutch size for first nests for each species was two eggs.

TABLE 2. Comparisons of habitat characteristics of Sooty ($n = 38$) and Pied Oystercatcher ($n = 29$) nests and random sites within 100 m of nests, in 1988/1989.

	Sooty Oystercatcher		Pied Oystercatcher		Comparisons[a]			
	Nest	Random	Nest	Random	Nest–Random		Sooty–Pied	
	$\bar{x}$ (S.E.)	$\bar{x}$ (S.E.)	$\bar{x}$ (S.E.)	$\bar{x}$ (S.E.)	Sooty	Pied	Nest	Ran-dom
1 m Circle:								
Color Index[b]	3.1 (0.20)	3.2 (0.25)	2.9 (0.26)	2.8 (0.44)	ns	ns	ns	ns
% Vegetation	32.6 (3.13)	55.7 (6.83)	24.4 (4.78)	48.1 (8.06)	*	ns	ns	ns
% Substrate	67.4 (3.11)	44.3 (6.81)	75.6 (4.78)	51.9 (8.06)	*	ns	ns	ns
% Rock	32.3 (4.50)	27.8 (6.33)	9.8 (3.91)	9.3 (5.11)	ns	ns	***	*
% Sand	9.1 (2.94)	9.9 (3.51)	38.1 (5.88)	25.1 (7.14)	ns	*	***	ns
% Wrack	18.8 (3.63)	1.5 (0.93)	21.6 (5.16)	12.6 (5.36)	***	ns	ns	ns
% Other	6.7 (1.60)	5.1 (2.23)	6.1 (2.29)	4.9 (2.07)	ns	**	ns	ns
5 m Circle:								
Color Index[b]	2.8 (0.13)	3.1 (0.23)	2.8 (0.23)	2.5 (0.82)	ns	ns	ns	*
% Vegetation	35.8 (2.73)	59.7 (6.63)	27.7 (4.91)	57.0 (7.30)	**	**	ns	ns
% Substrate	64.2 (2.73)	40.3 (6.63)	72.3 (5.06)	42.9 (7.25)	**	**	ns	ns
% Rock	38.2 (3.85)	27.4 (5.95)	15.6 (5.01)	6.7 (3.02)	*	ns	***	**
% Sand	9.7 (2.64)	5.9 (1.96)	41.8 (6.47)	26.2 (6.72)	ns	***	***	*
% Wrack	8.8 (1.73)	4.5 (2.77)	11.6 (3.24)	8.6 (3.57)	***	ns	ns	ns
% Other	7.4 (2.57)	2.5 (0.97)	3.3 (1.83)	1.4 (1.38)	**	**	ns	ns
AOV (°)	87.0 (11.47)	144.9 (26.00)	219.2 (13.38)	140.0 (25.79)	ns	*	***	ns
% Nest Cover[c]	25.5 (6.22)	20.8 (6.54)	0.1 (0.07)	13.0 (6.16)	ns	*	***	ns
Veg. Dst. (cm)[c]	25.9 (15.24)	103.9 (33.19)	140.6 (42.0)	99.1 (36.7)	*	ns	*	ns
Veg. Ht. (cm)	84.6 (14.92)	46.5 (12.13)	45.4 (11.8)	62.4 (11.4)	ns	ns	ns	ns

[a] Mann-Whitney, NS = $P > 0.05$; * = $P < 0.05$; ** = $P < 0.01$; *** = $P < 0.001$.
[b] Data were for Sooty Oystercatcher nests ($n = 30$) and Pied Oystercatchers nests ($n = 18$) located on Big Green Island in the second field season.
[c] Chi-square contingency table analyses were conducted on categories.

For Pied Oystercatchers, the mean clutch size for first nests in the first and second field seasons was 1.7 (± 0.21, $n = 10$) and 1.9 (± 0.06, $n = 15$) while the range in each year was 1–3 eggs per clutch. No renests were documented in the first season but in the second season three were documented with clutch sizes of 1, 2 and 2 eggs per clutch. Pied Oystercatchers usually only raised one chick but in the first season one pair fledged two chicks and in the second season two pairs each fledged two chicks.

For Sooty Oystercatchers at Big Green Island the mean clutch size for first nests in the first and second field seasons was 1.7 (± 0.09, $n = 26$) and 2.0 (± 0.03, $n = 30$; respectively). The range for clutch size in both years was 1–2 eggs per clutch; no three egg clutches were observed in either season and in the second season only one clutch had one egg. In each field season one renest was documented and the clutch size in 1988/1989 was one egg while the clutch size in 1989/1990 was two eggs. Sooty Oystercatchers were never observed to raise more than one chick.

Clutch and brood loss. At Big Green Island,

TABLE 3. Loadings of habitat variables on first and second principal components (PC1 and PC2) in 1988/1989 and 1989/1990.

	1989		1990	
	PCA1	PCA2	PCA1	PCA2
Substrate 1m	0.44	0.37	0.50	0.06
Vegetation 1m	−0.44	−0.37	−0.49	−0.05
Substrate 5m	0.39	−0.57	0.39	−0.35
Vegetation 5m	−0.39	0.57	−0.35	0.40
Distance to veg.	0.33	0.19	0.29	0.18
Veg. over nest (%)	−0.32	−0.10	−0.35	−0.16
Angle of view	0.30	0.18	0.18	0.57
Locale visibility	—	—	−0.01	−0.58

TABLE 4. Principal component scores for PC1 and PC2 for Pied and Sooty Oystercatchers for 1989 and 1990.

Year	Variable	Sooty	Pied	*t*	*P*
1989	PC1	−0.36 (0.379)	0.60 (0.300)	2.00	0.052
	PC2	−0.36 (0.191)	0.60 (0.295)	2.88	0.006
1990	PC1	−0.37 (0.378)	0.61 (0.301)	2.02	0.048
	PC2	−0.44 (0.200)	0.74 (0.337)	3.22	0.002

in the 1988/1989 season, seven of fourteen first clutches (50%) for Pied Oystercatchers were lost (Table 5). No nest was known to be flooded by high tides but one nest on the south coast was lost because high winds eroded the base of the nest. One clutch of eggs was destroyed when a local sheep farmer threw gear onto a nest by mistake. No apparent reason was found for the loss of the remaining clutches, but they were presumed to be depredated (see section below on potential predators). Of the seven clutches to hatch chicks, four (57%) fledged at least one chick, while three (43%) fledged no chick. No apparent reason for chick loss was observed but gull predation was suspected.

In the 1989/1990 season, eight of twenty-two first clutches (36%) for Pied Oystercatchers were lost (Table 5). The causes for clutch loss were as follows: two were trampled by sheep, two were flooded, one was abandoned due to interspecific competition and three were unknown but presumed depredated. The Pied nest was abandoned just before hatching because of a continual attack on adults by a pair of Sooty Oystercatchers nesting twenty meters away. For the three pairs that were observed to renest, one clutch was flooded, one was lost for unknown reasons and presumed depredated, while one clutch hatched but fledged no chick. Of the 14 clutches (including renests) that hatched, 10 (71%) fledged at least one chick, while four (29%) did not fledge a chick and were presumed depredated.

For Sooty Oystercatchers, in the first and second season, 10 of 28 (36%) and 16 of 36 (44%; respectively) first clutches were lost (Table 5). In the first season, the one pair that renested hatched one chick which did not fledge. In the second season the one pair that renested hatched no chicks. No nests were known to be damaged due to tidal flooding or wind damage. In the first and second seasons, for the 18 and 20 pairs that hatched at least one chick, 11 (61%) and six (30%; respectively) complete broods were lost (including renests). We were unable to document any direct causes for egg or chick losses but predation was suspected.

Success. There were no overall differences in hatching or fledging success between species in either season or for the two seasons combined (Table 5). Pied Oystercatcher hatching or fledging success with respect to habitat type was not significantly different in either field season (Table 5). Sooty Oystercatcher hatching success with respect to habitat type was also not significantly different in either field season (Table 5). However, in the second season, Sooty Oystercatchers

TABLE 5. Pied and Sooty Oystercatcher hatching (H) and fledging (F) success at Big Green Island. The total number of nests by species, year and habitat is followed by the number (percent) hatching and fledging.

	Mixed (sand and rock)			Rock			Sand			Overall		
	n	H (%)	F (%)	*n*	H (%)	F (%)	*n*	H (%)	F (%)	*n*	H (%)	F (%)
1988/1989[a]												
Sooty	9	5 (56)	3 (33)	19	13 (68)	4 (21)	—	—	—	28	18 (64)	7 (25)
Pied	8	4 (50)	2 (25)	5	3 (60)	2 (40)	1	0 (0)	0 (0)	14	7 (50)	4 (29)
1989/1990[a]												
Sooty	12	4 (33)	1 (8)[b]	24	16 (67)	13 (54)[b]	—	—	—	36	20 (56)	14 (39)
Pied	14	8 (57)	5 (36)	7	6 (86)	5 (71)	1	0 (0)	0 (0)	22	14 (64)	10 (45)

[a] When data were combined for the two seasons no differences occurred between species for hatching (df = 1, $\chi^2 = 0.10$, $P > 0.05$) or fledging (df = 1, $\chi^2 = 0.37$, $P > 0.05$) success.
[b] Significant differences occurred between mixed and rock habitats for Sooty Oystercatchers in 1989/1990 (df = 1, $\chi^2 = 7.07$, $P < 0.01$).

TABLE 6. Comparison of PC1 and PC2 scores ($\bar{x}$, SE) for hatched and unsuccessful nests of Sooty and Pied Oystercatchers by year. No comparisons were significantly different.

Year	Species	Variable	Hatched	Did not hatch
1988/1989	Sooty	PC1	−0.24 (0.745)	−0.08 (0.525)
		PC2	−0.18 (0.326)	−0.13 (0.388)
		n	11	12
	Pied	PC1	0.10 (0.481)	0.68 (0.859)
		PC2	0.37 (0.458)	0.09 (0.262)
		n	8	4
1989/1990	Sooty	PC1	−0.21 (0.379)	−1.81 (1.637)
		PC2	−0.50 (0.218)	0.10 (0.301)
		n	27	3
	Pied	PC1	0.96 (0.335)	0.05 (0.533)
		PC2	0.63 (0.505)	0.91 (0.393)
		n	11	7

had lower fledging success on mixed habitat than rocky habitat (Table 5); no differences were found in the first season (Table 5).

There were no significant differences in the PC1 and PC2 scores for nests that ultimately hatched and those that did not (Table 6). Thus, the degree to which the nest was visible (principally) did not appear to explain differential reproductive success for either species.

POTENTIAL PREDATORS

The average number of half-hour censuses per day on the sandy beaches of Flinders Island was 5.1 (±0.68, n = 19). On Big Green Island the average number of censuses per day on mixed beaches and rocky beaches was 4.9 (±0.36, n = 26) and 5.1 (±0.52, n = 25) respectively. The only potential predators observed during these daytime censuses were birds; no mammals or reptiles were recorded. Six species of potential avian predators were seen including: Pacific Gulls (*Larus pacificus*), Silver Gulls (*Larus novaehollandiae*), Ravens (*Corvus tasmanicus*), Harriers (*Circus aeruginosus*), Brown Falcons (*Falco berigora*), and Sea Eagles (*Haliaeetus leucogaster*). The first three species mentioned would more likely be predators of eggs and chicks while the three remaining species would more likely be predators of juveniles and possibly adults (Pizzey 1980, Lane 1987).

Both species of gull were observed commonly during behavioral observations while the remaining bird species were seen rarely (Table 7). Silver Gulls were observed more frequently on sandy beaches on Flinders Island than on rocky beaches or on mixed beaches at Big Green Island (Table 7). There were no differences in the frequency of Silver Gulls between the mixed and rocky beaches of Big Green Island (Table 7). Pacific Gulls were seen more frequently on the rocky shores of Big Green Island than on the sandy shores of Flinders Island or on the mixed beaches of Big Green Island (Table 7). When the frequency data for Silver Gulls on rocky and mixed habitat on Big Green Island were combined and compared to the frequency of Silver Gulls on Flinders Island, there were more Silver Gulls on Flinders Island than on Big Green Island (Mann-Whitney U-test: Z = 3.003, P = 0.0027; Table 7). There were no differences in the frequency of Pacific Gulls on rocky and mixed habitat (combined) on Big Green Island compared to the frequency of Pacific Gulls on Flinders Island (Z = −0.245, P = 0.8062; Table 7). When the frequencies for all potential avian predators were combined for observation periods it was found that there were more individuals found on Flinders Island than on Big Green Island (Z = 2.356, P = 0.0056; Table 7). This was due primarily to the greater numbers of Silver Gulls found on the beaches of Flinders Island as compared to Big Green Island.

We did not statistically compare the frequencies of Ravens, Brown Falcons, Sea Eagles, and Harriers occurring either between habitats or between locations since individuals for these species were all observed rarely. None of these species were seen more than eight times during observation periods.

A Pacific Gull on one occasion was observed to go after Sooty Oystercatcher eggs while on another occasion a Pacific Gull was observed to

TABLE 7. A comparison of the mean (standard error) number of potential predators observed in 1988/1989 at Flinders Island and Big Green Island for different beach substrate.

	Flinders Island		Big Green Island			
	Sand (n = 19 days)		Mixed (n = 26 days)		Rock (n = 25 days)	
Species	$\bar{x}$	SE	$\bar{x}$	SE	$\bar{x}$	SE
White Breasted Sea Eagle	0.02	0.018	0.00	0.000	0.00	0.000
Swamp Harrier	0.01	0.009	0.00	0.000	0.01	0.000
Brown Falcon	0.00	0.000	0.01	0.005	0.01	0.010
Silver Gull	5.92	1.354[a,b]	2.15	0.472[a]	1.95	0.589[b]
Pacific Gull	1.45	0.327[c]	0.81	0.201[d]	2.24	0.349[c,d]
Raven	0.01	0.009	0.02	0.019	0.00	0.000
Total	7.41	1.546	2.99	0.603	4.21	0.898

Significance values for Mann Whitney tests: a, $Z = 2.54$, $P < 0.01$; b, $Z = 2.76$, $P < 0.01$; c, $Z = -1.96$, $P < 0.05$; d, $Z = 4.19$, $P < 0.001$.

go after Sooty Oystercatcher chicks. In both situations, attacks were unsuccessful. One Sooty Oystercatcher egg, which was probably abandoned, was found to be eaten by a rat.

DISCUSSION

Pied and Sooty Oystercatchers exhibited differences in habitat use at the levels of general habitats (islands, substrates), territories and nest sites, ecologically segregating and presumably facilitating their coexistence at the Furneaux Islands, Australia. Sooty Oystercatchers nested on small islands only, and although nesting and feeding territories appeared to be available on Flinders Island (a large island), they did not nest there. Pied Oystercatchers nested on all sized islands. In addition, the number of breeding pairs per km was higher for both species at Big Green Island, a small island, than for Pied Oystercatchers at Flinders Island.

Coastal birds commonly nest at higher densities on small islands as compared to larger bodies of land (e.g., large islands or mainland sites) and two important factors that may contribute to this pattern are reduced predation risk and lower human disturbance at smaller islands as compared to larger islands (Buckley and Buckley 1980, Williamson 1981, Blondel 1985, Nilsson et al. 1985, George 1987, Erwin et al. 1995). Censuses conducted for this study did show that gulls, known predators of oystercatcher eggs and chicks (Harris 1967, Heppleston 1972, Hartwick 1974, Hockey 1983, Safriel 1985, Nol 1989), were more common at the shoreline of Flinders than at the shoreline of Big Green Island. In addition, human disturbance would have been higher on Flinders as it was inhabited by people while the small islands were not. However, we only surveyed one large island in this region and a survey on other large islands in the Bass Strait (e.g., Cape Barren and King) would be valuable.

At the Furneaux Islands, Sooty Oystercatchers nested more commonly at rocky shores while Pied Oystercatchers nested more commonly at sandy shores. Black and pied species of oystercatchers may select nest sites at rocky and sandy habitats (respectively) since these habitats are commonly dark and light in color (respectively) hence aiding in maintenance of nest site crypsis relative to color pattern (Jehl 1985). However, at the Furneaux Islands, Sooty Oystercatchers nested at rocky habitat even though they were light and not significantly different in color from sand beaches.

One factor at the Furneaux Islands that was related to rock versus sand nesting was island choice. Sooty Oystercatchers nested only at small islands that were mainly rocky while Pied Oystercatchers nested on Flinders Island, a large island which was mainly sandy, as well as small islands. Another factor involved was the location of nesting areas relative to preferred feeding substrates. Pied Oystercatcher nesting areas were restricted to locations that had intertidal mudflat for feeding. At intertidal mudflats, Pied Oystercatchers fed primarily on soft bodied prey and they were not observed to capture prey off rocks at any location (Lauro and Nol 1995). The location of suitable foraging substrates did not appear to limit where Sooty Oystercatchers nested; they selected sites that had mud or rock at adjacent intertidal areas. This pattern was related to the fact that Sooty Oystercatchers captured high proportions of hard-shelled prey at intertidal mudflats and at rocky shores (Lauro and Nol 1995).

An important difference in nest site use for the two species was that Sooty Oystercatchers selected lower visibility sites compared to Pied Oystercatchers. There are several possible explanations for this pattern which may not be mutually exclusive. Sooty Oystercatchers may have nested in lower visibility locations because they were seeking sites which provided shade. Dark and light colored birds experience different heat loads which may affect behavior (Walsberg et al. 1978). Therefore, the uniform black plumage of Sooty Oystercatchers may have caused higher head loads than the countershaded plumage of Pied Oystercatchers. Yet, both species are dark from above and may therefore experience similar dorsal heat loads. In addition, thermoregulatory stress for the two species was rarely witnessed during two field seasons of behavioral observations. The Bass Strait Islands experience a temperate climate with high winds and daily sea breezes (Edgecombe 1986) that cool incubating birds. Wind negates heat load differences associated with different color patterns of birds (Walsberg et al. 1978).

Sooty Oystercatchers may have nested in lower visibility sites to avoid interspecific conflict with Pied Oystercatchers. If this was the case, it would be expected that when Sooty Oystercatchers nested close to Pied Oystercatchers the visibility about their nest sites would be lower than when they nested at greater distances from Pied Oystercatchers. For certain species of gulls, the closer the congeneric or conspecific neighbor, the lower the visibility at the nest site and when vegetation about nests was experimentally removed interspecific and intraspecific interaction increased (Burger 1977). However, for this study there was no significant correlation between nearest neighbor distance and angle of view for congenerics although there was a significant positive correlation for conspecifics.

A more tenable explanation for species differences in choice of nest site visibility is that species selected vegetative characteristics that minimized predation risk with respect to color pattern. Numerous studies have shown that breeding birds select vegetative characteristics at nest sites, such as visibility, to reduce potential risks of predation (Burger 1977, 1985a, 1985b; Yahner and Cypher 1987; Burger and Gochfeld 1988; Watts 1990; Holway 1991; Pingjuin and Martin 1991; Martin 1988, 1992; Kelly 1993; Lima 1993; Norment 1993; Schieck and Hannon 1993). Although predation on adults presumably would be low, our data on reproductive success suggest predation on chicks and eggs was probably occurring. Thus, at the Furneaux Islands, where the rocky and sandy beaches were generally light in color, Sooty Oystercatchers may compensate for their uniformly dark and presumably non-cryptic color pattern by selecting low visibility nest sites. In contrast, Pied Oystercatchers with a countershaded and presumably more cryptic color pattern nested in higher visibility nest sites. This pattern of nest site use would be especially important in avoiding predators that hunt visually during the day, such as gulls. Silver Gulls and Pacific Gulls rested, fed and nested within and about oystercatcher territories. Pacific Gulls were observed to attack oystercatcher eggs and chicks.

Other evidence suggested that predation was influencing patterns of nest site use for both species. Both species selected areas about nest sites that were more open and that were closer to the waters edge than randomly selected sites (Lauro and Nol 1993, Lauro 1994). Open sites around nests provide adults with the opportunity to detect predators before eggs or chicks can be discovered (Burger 1977, Burger and Gochfeld 1988). Hartwick (1974) showed that American Black Oystercatchers nested at open sites, close to the waters edge, even though nests were commonly flooded at these locations. He suggested that nesting pairs selected these sites because at higher elevated sites, in denser vegetation at distances further from the waters edge, eggs and chicks were more susceptible to predation by nesting gulls.

Interspecific competition (past or present day) may have had subtle influences on species choice of nesting habitats. For example, the fact that Sooty Oystercatchers were not observed to nest on sand beaches and Pied Oystercatchers were not observed to nest at rock intertidal/rock beach suggests competitive exclusion. However, presently it seems unlikely that Pied Oystercatchers excluded Sooty Oystercatchers from any habitat since they were smaller and appeared to be competitively inferior. At mixed beaches, where both species nested side by side (Fig. 2), Sooty Oystercatchers regularly chased Pied Oystercatchers from desired foraging areas, and in one case a Sooty Oystercatcher pair excluded a Pied Oystercatcher pair from nesting; Pied Oystercatchers rarely chased Sooty Oystercatchers at these sites.

It also seems unlikely that Sooty Oystercatchers excluded Pied Oystercatchers from rock beach/rock intertidal locations for nesting. On Flinders Island, where no Sooty Oystercatchers nested, Pied Oystercatchers did not nest at rock beach/rock intertidal areas although these habitats were available. Removal experiments would help to clarify the question of whether present-day interspecific competition influences species patterns of habitat use.

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