FEEDING BEHAVIOR, PREY SELECTION, AND BILL SIZE OF PIED AND SOOTY OYSTERCATCHERS IN AUSTRALIA

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ABSTRACT.—We studied the relationships between feeding behavior, prey selection and bill size for sympatric Pied (Haematopus longirostris) and Sooty (H. fuliginosus) Oystercatchers feeding at Australian intertidal mudflats. Foraging Sooty Oystercatchers used a rapid pecking behavior for a greater proportion of time and used a slow pecking behavior for a lesser proportion of time as compared to Pied Oystercatchers. Within each species males used a rapid pecking behavior for more time and used a slow pecking behavior for less time than females. As rapid pecking was used mainly for the capture of crabs, snails and bivalves while slow pecking was used mainly for the capture of polychaete worms, the diet of Sooty Oystercatchers contained significantly more hard-shelled prey and less softbodied prey than Pied Oystercatchers. For each species, males took more hard-shelled prey and fewer worms than females. Thus, species and sexual differences in foraging behavior and prey selection segregated the foraging roles of Pied and Sooty Oystercatchers, potentially reducing competition, facilitating their coexistence. A general pattern for oystercatchers is that longer bill length is associated with higher percentages of soft-prey in the diet for different species, and for sexes within species. A comparison of bill lengths indicated that in Tasmania Sooty Oystercatchers had longer bills than Pied Oystercatchers and within each species, females had longer bills than males. Thus, our results for species are counter to general expectations while results for sexes are consistent with general patterns. Received 28 July 1994, accepted 20 May 1995.

The Oystercatchers are a cosmopolitan family of shorebird (Charadriiformes: Haematopodidae) whose species exhibit a general pattern with regard to foraging habitat, prey selection and bill size. Uniformly black species forage more commonly on hard substrates at rocky coastal habitat and have higher percentages of hard-shelled prey than soft-bodied prey in their diet (Bent 1929, Baker 1974, Hartwick 1974, Considine 1979, Hockey and Underhill 1984, Lane 1987, Lauro 1994) compared to pied species (dark upper torso with a white belly) who forage primarily on soft substrates at estuaries (Bent 1929; Heppleston 1972; Baker 1974; Goss-Custard and Durell 1983, 1987; Nol 1984; 1985; Lane 1987; Lauro 1994). Black species generally have shorter bills and larger bodies when compared to pied species (Baker 1974, 1975; Nol 1984).

Within all species of oystercatchers, females on average have longer bills than males (Heppleston 1970; Baker 1974, 1975; Hockey 1981;

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Swennen et al. 1983; Hulscher 1985; Jehl and Murray 1986; Hulscher and Ens 1992; Durell et al. 1993; Marchant and Higgins 1993; Lauro 1994). This sexual dimorphism has been correlated with differences in foraging ecology with females capturing higher percentages of soft-bodied than hard-bodied prey as compared to males (Heppleston 1970, Dare 1977, Swennen et al. 1983, Hockey and Underhill 1984, Hulscher 1985, Hulscher and Ens 1992, Durell et al. 1993, Lauro 1994).

Thus, for oystercatchers it may be the case that shorter bill length is better adapted for capturing hard prey, especially off rock, while longer bill length may be better adapted to capturing soft-bodied prey submerged in mud, especially soft-bodied prey (Baker 1974, Nol 1984, Lauro 1994). In addition, species and sexual differences in the foraging ecology, correlated with bill length, may act to ecologically segregate Black and Pied oystercatchers where they occur in sympatry.

This study compares the foraging behavior and prey selection of Pied (*H. longirostris*) and Sooty (*H. fuliginosus*) Oystercatchers in Tasmania, Australia. At the Furneaux Islands, where this study takes place, Pied Oystercatchers fed only on intertidal mudflat while Sooty Oystercatchers fed at rocky shores as well as intertidal mudflats (Lauro 1994). We compare foraging ecology for the two species at overlapping feeding territories on intertidal mudflat adjacent to nesting areas. In addition, we compare bill sizes for species and for sexes within species using museum specimens and information presented in Marchant and Higgins (1993). Our objective is to determine what mechanisms, if any, existed to subdivide the foraging roles of the two sympatric species during the breeding season. We discuss the extent to which bill length and species specific behavior predict foraging behavior and prey selection.

STUDY AREA AND METHODS

We conducted field studies in the austral spring and summer of 1989/1990 on Big Green Island ($40^{\circ}11'S$, $147^{\circ}59'E$) at the Furneaux Islands, Tasmania, Australia. Big Green Island is 3 km west of the village of Whitemark on Flinders Island (the main island of the Furneaux Group) and is 122 ha in area. Pied and Sooty Oystercatchers were territorial and excluded conspecifics from nesting areas along the beach and at feeding sites adjacent to nesting locations. Therefore, it was possible to identify pairs by breeding location. The identity of feeding individuals was confirmed by watching birds return to nest sites, change positions with incubating mates or by association with chicks. In addition, the feeding territories for the two species were overlapping, and although interspecific competition was observed, one species did not exclude the other (Lauro, pers. obs.).

Oystercatchers can be sexed based on bill and body size (Considine 1979, Hockey 1981, Hayman et al. 1986). For this study individuals of breeding pairs were sexed by comparing them together during observations and by position during copulation. Female oystercatchers of both species were larger, had browner backs, and longer bills than males (Considine 1979).

Ten-minute observations of feeding individuals in nesting pairs were made over the breeding season from observation blinds, using a 10×20 telescope. No distinction was made for the stage of the breeding season. Observations were recorded on a laptop computer using a BASIC program that chronologically recorded all feeding behaviors and prey captured. From these data calculations were made for the proportion of times using different feeding behaviors, pecks per minute, and handling times for different prey types. In addition, we tallied the number of different prey groups captured during the 10-min observation periods.

Prey captured by oystercatchers was identified by observation in the field and classified into the following groups (since it was not always possible to identify to species): snails, mussels, other bivalves, polychaete worms, crabs, and surface items. Surface items were prey that were picked off the surface and could not be identified because they were too small to see.

The range of 10-min observation periods was 1–5 and we used weighted means for each individual for the analysis of proportion data. The distributions of the proportion data were not normal and contained many zeros. In this situation no statistical test is exact (Sokal and Rohlf 1995). The data were analyzed using two different methods: (1) non-parametric tests, and (2) analysis of variance (ANOVA). The results from the two methods were similar. We use ANOVA's for statistical tests because they are robust when assumptions of normality are not met (Sokal and Rohlf 1995) and because, in some cases, of the value of interpreting the interaction term between species and sex. Distribution of the data for bill dimensions was normal or near normal justifying ANOVA, and transformation of data (e.g., log-transformation) did not change the significance levels of ANOVA's. Analyses reported hence are for untransformed data.

Intertidal mudflats were sampled to compare relative proportions of prey groups available to the proportion of prey groups captured by oystercatchers. Every 20 m along the 1.7 km stretch of beach where birds nested, a 0.25 m \times 0.25 m quadrat was randomly placed on a transect from the high to low tide line. Data collected for rocky sections of the beach were not included in the analysis since birds rarely used these habitats for feeding. The distance at which the quadrat was placed along the transect was determined using a random numbers table. Quadrats were selectively sampled for known prey of oystercatchers. This included invertebrates recorded as prey (turbellarians, amphipods and isopods) from another study of the foraging ecology of Sooty Oystercatcher (Considine 1979), since these would be likely prey of Sooty Oystercatchers at the Furneaux Islands. Prey were identified using guides to Australian coastal invertebrates (MacPherson and Gabriel 1962, Phillips et al. 1984).

Within each quadrat potential prey items were recorded to a depth of 90 mm (estimated maximum depth that an oystercatcher bill can reach). For each quadrat a summation was made for prey located at the surface and for prey located below the surface. The total number of different prey items below the surface was estimated based on the number of different species found in a mud sample core and the volume of an entire quadrat. The size of the cylindrical core was 120 mm in diameter and 90 mm deep. For each quadrat, invertebrates were categorized into the same prey groups used by oystercatchers.

Manly's alpha indices (Manly 1974) for preference were used to compare the relative proportion of prey in the diet of the species and sexes to that which was available on intertidal mudflats.

We measured bills of museum specimens from the Royal Ontario Museum (ROM) and the American Museum of Natural History (AMNH). Our measurements included: (1) length from the bill tip to the base of the head on the dorsal side where feathers start to grow (i.e., exposed culmen), and (2) width and depth measured at the center of nasal opening at the base of the bill. The distribution of data for bill characters was normal or near normal justifying the use of analysis of variance (ANOVA) for data interpretation. In addition, we evaluate data presented in Marchant and Higgins (1993) for bill dimensions for Pied and Sooty Oystercatchers. Since we did not have the raw data for information presented in Marchant and Higgins (1993) we do one-way ANOVA's for unplanned comparisons and Tukey Kramer multiple comparison tests (Sokal and Rohlf 1995).

RESULTS

Two distinct behaviors were used by both species while feeding on the intertidal mudflat: slow pecking and rapid pecking. Slow-pecking birds moved with a regular pace over the mudflat when feeding while rapid-pecking birds would concentrate their efforts in a small area and then move to a new spot. A slow-pecking bird would move across the mudflat apparently searching visually for sites to test for the presence of worms. Birds would appear to see a likely spot, touch their bill to the surface (a peck) and, on detection, probe into the mud for capture. The probing action for worms was often very quick and birds did not always place their bills deep into the mud. Therefore, it was difficult to differentiate a peck from a probe so we recorded only pecks and not the final probe that resulted in prey capture.

Birds that used the rapid pecking behavior appeared to depend less on visual cues and more on tactile cues. Remaining fairly stationary birds moved their bills up and down on the surface to cover as much area as possible to detect prey covered by weed or a film of mud. The rapid pecking behavior was generally associated with the capture of hardshelled prey such as crabs and snails (that were hammered open) and with the capture of small, usually unidentifiable surface items.

Sooty Oystercatchers used the rapid pecking behavior for a significantly greater proportion of time and used the slow pecking behavior for a significantly lesser proportion of time than did Pied Oystercatchers (Table 1). When slow pecking, Sooty Oystercatchers had a lower peck rate than Pied Oystercatchers, probably because they spent more time walking in search of sites to use the rapid pecking behavior and less time actually foraging (Table 1). Peck rates were not compared during the rapid pecking behavior because the pecks occurred too quickly to record accurately. No differences in prey handling times occurred between species (Table 1).

The diet of Sooty Oystercatchers was broader than that of Pied Oystercatchers and included all prey groups (Table 2; Fig. 1). Sooty Oystercatchers had a higher percentage of hard-shelled prey in their diet than Pied Oystercatchers (Table 2; Fig 1) because they commonly fed on crabs and snails. Pied Oystercatchers were never observed to eat these prey and fed mainly on worms (Table 2; Fig 1). Consequently, Sooty Oystercatchers had significantly fewer worms in their diet as compared to Pied Oystercatchers (Table 2; Fig. 1).

A Comparison of Feeding Behavior between Species and Sexes ^a				
Behavior	Sooty Oystercatchers		Pied Oystercatchers	
	$\begin{array}{c} \text{Male} \\ \bar{x} \pm \text{SE} \end{array}$	Female $\bar{x} \pm SE$	$\begin{array}{c} \text{Male} \\ \bar{x} \ \pm \ \text{SE} \end{array}$	Female $\vec{x} \pm SE$
Slow peck time ^a				
(% of total)	0.47 ± 0.098	0.60 ± 0.109	0.71 ± 0.125	0.93 ± 0.044
Rapid peck ^a (% of				
total)	0.53 ± 0.098	0.40 ± 0.109	0.29 ± 0.125	0.07 ± 0.044
Pecks/min. in				
slow-peck ^b	6.52 ± 1.938	10.47 ± 2.170	10.83 ± 2.353	19.15 ± 4.943
Handling time—				
worms (sec)	1.6 ± 0.18	1.9 ± 0.40	1.9 ± 0.30	2.6 ± 0.74
Handling time—				
crabs (sec)	11.4 ± 3.15	6.8 ± 2.87	_	—
N	12	12	10	11

TABLE 1

^a Species, $F_{1,41} = 8.83$, P < 0.01; sex, $F_{1,41} = 3.42$, P < 0.05; species × sex $F_{1,41} = 0.23$, P > 0.05 (NS). ^b Species, $F_{1,41} = 10.31$, P < 0.001; sex, $F_{1,41} = 5.78$, P < 0.02; species × sex $F_{1,41} = 0.23$, P > 0.05 (NS).

Within each species males used the rapid pecking behavior more often and the slow pecking behavior less often than females (Table 1). Males of both species had a lower peck rate when using the slow peck behavior (Table 1) and captured significantly fewer worms compared to females (Table 2). Sooty Oystercatcher males had a greater proportion of crabs in their diet than females (Table 2, Fig. 1). Neither species showed a difference in prey handling times between sexes (Table 1).

When the proportion of prey captured was compared to the proportion

Proportio	n of Different Pr	TABLE 2 EY TYPES CAPTURE	ed for Each Speci	es and Sex
Survey	Sooty Oystercatcher		Pied Oystercatcher	
Food item	$Male \\ \bar{x} \pm SE$	Female $\vec{x} \pm SE$	$Male \\ \bar{x} \pm SE$	Female $\bar{x} \pm SE$
Snails	0.08 ± 0.052	0.01 ± 0.003		
Mussels	0.03 ± 0.028	0.01 ± 0.005	_	0.01 ± 0.001
Other bivalves	0.01 ± 0.005	0.00 ± 0.003	0.09 ± 0.093	_
Worms ^a	0.32 ± 0.084	0.76 ± 0.074	0.69 ± 0.155	0.93 ± 0.027
Crabs ^b	0.29 ± 0.074	0.07 ± 0.036		
Surface items ^c	0.26 ± 0.071	0.15 ± 0.059	0.22 ± 0.142	0.06 ± 0.027
Ν	12	11	9	11

^a Species, $F_{1,41} = 14.4$, P < 0.0005; sex, $F_{1,41} = 14.7$, P < 0.0005; species × sex, $F_{1,41} = 1.78$, P > 0.05 (NS). ^b Sex, t = 2.51, P = 0.02.

^c Species, $F_{1,41} = 5.39$, P < 0.05; sex, $F_{1,41} = 1.36$, P > 0.05 (NS); species × sex, $F_{1,41} = 0.62$, P > 0.05 (NS).

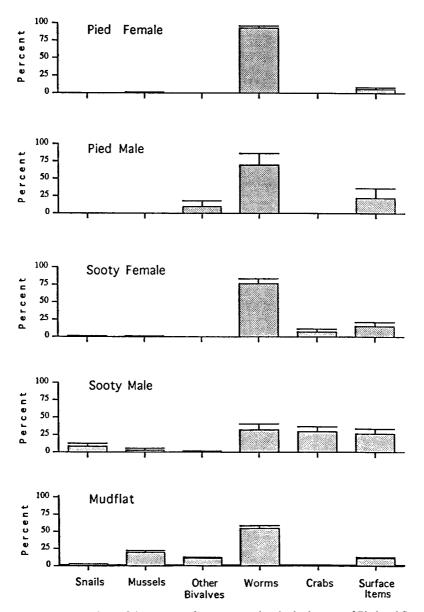


FIG. 1. A comparison of the percent of prey types taken by both sexes of Pied and Sooty Oystercatchers and of that recorded on the intertidal mudflat.

Prey type	Sooty Oystercatcher		Pied Oystercatcher	
	Female	Male	Female	Male
Snails	0.03	0.08	0.00	0.00
Mussels	0.01	0.00	0.02	0.00
Other bivalves	0.00	0.07	0.00	0.20
Worms	0.15	0.02	0.73	0.31
Crabs	0.72	0.83	0.00	0.00
Surface items	0.09	0.00	0.24	0.49

TABLE 3
PREFERENCES FOR PREY TYPES RELATIVE TO THAT AVAILABLE ON INTERTIDAL MUDFLAT
Using Manly's Alpha Index (Manly 1974) ^a

^a A preference for a prey type occurs when a value is above $\frac{1}{6}$ or 0.17 (which equals 1/m where m is the number of prey groups). When a value of 0.17 occurs no preference is shown and values below 0.17 indicate the avoidance of a prey type.

of prey available on the intertidal mudflat, male and female Sooty Oystercatchers showed a preference for crabs (Table 3, Fig. 1). Pied Oystercatchers of both sexes were found to have a preference for worms and surface items but only Pied Oystercatcher males showed a preference for bivalves other than mussels (Table 3, Fig. 1).

Along the mainland coast, Pied Oystercatcher bill length appears to be longer than that of Sooty Oystercatchers (Table 4). However, data for museums specimens (ROM and AMNH) and information presented in Marchant and Higgins (1993) suggest that in Tasmania, Sooty Oystercatcher bill length is longer than Pied Oystercatcher bill length (Table 4). A one-way ANOVA for the four species/sex classes showed a significant difference for bill length ($F_{3,27} = 20.51$, P < 0.0001). If a Pied male is assigned a mean bill length of 1, then the relative mean bill lengths of Sooty male, Pied female, and Sooty female would be 1.09, 1.10 and 1.25 respectively. When a Tukey-Kramer multiple comparison test was conducted it was found that: bill length for Pied Oystercatcher males was significantly shorter than that for Sooty Oystercatcher males (P < 0.05); bill length for Sooty Oystercatcher males was not significantly different than that for Pied Ovstercatcher females (P > 0.05); bill length for Pied Oystercatcher females was significantly shorter than that for Sooty Oystercatcher females (P < 0.05, Table 1).

For all data sets examined females within each species had longer bills than males (Table 4). No species or sexual differences were found for bill depth or width for data collected around the coastline (Table 4) or for the Tasmanian data (one-way ANOVA's, bill depth: $F_{3,27} = 1.37$, P > 0.05; bill width: $F_{3,27} = 0.01 P > 0.05$).

Variable	Sooty Oystercatcher		Pied Oystercatcher	
	$\begin{array}{c} \text{Male} \\ \vec{x} \ \pm \ \text{SE} \end{array}$	Female $\bar{x} \pm SE$	$\begin{array}{c} \text{Male} \\ \bar{x} \pm \text{SE} \end{array}$	Female $\bar{x} \pm SE$
Tasmania ^{a,b}		· · · · · ·		2
Length	73.4 ± 1.16	83.6 ± 2.85	67.0 ± 3.83	73.9 ± 1.14
Depth	17.4 ± 0.48	17.6 ± 1.05	15.7 ± 0.78	16.1 ± 0.93
Width	15.6 ± 0.30	15.3 ± 0.53		
Ν	7	8	8	8
All locations ^{c,d}				
Length	71.5 ± 1.09	81.6 ± 2.21	74.5 ± 0.72	83.9 ± 1.14
Depth	16.9 ± 0.39	17.0 ± 0.89	17.0 ± 0.35	18.0 ± 0.47
Width	15.5 ± 0.21	14.6 ± 0.56	14.4 ± 0.38	15.2 ± 0.27
Ν	11	12	22	17

TABLE 4
A COMPARISON OF BILL DIMENSIONS (MM) BY SPECIES AND SEX

^a Data for Sooty Oystercatchers come from the AMNH and the ROM. Data for Pied Oystercatchers come from Marchant and Higgins (1993).

^b Bill lengths were significantly different for sexes within each species: Sooty, $F_{1,14} = 10.40$, P < 0.01 (this study); Pied, *t*-test, P < 0.01 (Marchant and Higgins 1993). See text for discussion of species differences.

^c Data for both species comes from the AMNH and the ROM. The breakdown of the number of specimens for different states are as follows. Sooty male: Western Australia (1), New South Wales (2), Tasmania (8); Sooty female: Western Australia (2); New South Wales (1), Victoria (1), Tasmania (8); Pied male: Western Australia (4), Northern Territory (4), Queensland (3), Victoria (3), Tasmania (1), unknown (7); Pied female: Western Australia (5), Northern Territory (1), Queensland (4), New South Wales (2), unknown (5).

^d Species, $F_{1.58} = 5.39$, P < 0.05; sex, $F_{1.58} = 13.45$, P < 0.0001; species × sex $F_{1.58} = 0.80$, P > 0.05 (NS).

DISCUSSION

This study documents a mechanism that segregates sympatric Pied and Sooty Oystercatchers foraging on mudflats adjacent to nesting areas at the Furneaux Islands, Australia. Our results showed that patterns of prey selection were generally consistent with that for other pied and black species of oystercatchers (Bent 1929, Heppleston 1972, Baker 1974, Hartwick 1974, Considine 1979, Hockey and Underhill 1984, Goss-Custard and Durell 1983, Nol 1984, Hayman et al. 1986, Hulscher and Ens 1992, Durell et al. 1993, Marchant and Higgins 1993) in that Sooty Oystercatchers captured higher proportions of hard prey and lesser proportions of soft prey when compared to Pied Oystercatchers. In addition, within each species males captured higher proportions of hard prey and lesser proportions of soft prey then females. However, our results suggest that bill length alone does not explain species differences in foraging behavior.

If bill size data which we present can be correctly applied to the birds we observed foraging, the results from our study contradict others regarding the relationship between foraging ecology and bill size for oystercatchers. If bill length alone predicted foraging behavior it would be expected that Sooty Oystercatcher females, who had the longest bills, would capture more soft prey than hard prey when compared to Pied Oystercatcher females. Studies for other oystercatcher species have consistently shown that individuals with longer bills capture higher proportions of soft-bodied prey submerged in mud (Heppleston 1970, Swennen et al. 1983, Hockey and Underhill 1984, Hulscher 1985, Hulscher and Ens 1992, Durell et al. 1993). However, in our study Pied Oystercatcher females had a higher percentage of worms in their diet than Sooty Oystercatchers females.

Method of foraging (rapid or slow pecking) was invariably correlated with the type of prey captured (hard or soft-bodied) but was not always correlated with bill length. For those aspects of foraging behavior where we found significant differences, species differences were always stronger than the sex differences irrespective of bill length: males and females within a species were always more similar to each other in foraging behavior than the males or females of the two species were to each other. For example, time spent slow pecking for male and female Sooty Oystercatchers was more similar than the time spent slow pecking for males of each species. Thus, these results suggest that at the Furneaux Islands, species specific behavior was important in segregating the foraging roles of Pied and Sooty Oystercatchers.

Other evidence to suggest the importance of species specific differences in behavior to ecological segregation was that at foraging areas adjacent to nesting sites Sooty Oystercatchers fed at rocky shores as well as intertidal mudflats while Pied Oystercatchers utilized only intertidal mudflat for feeding (Lauro 1994). When nesting at rocky shores Sooty Oystercatchers fed primarily on the large intertidal limpet Cellana solida which they pried and hammered off rocks. Non-breeding Pied and Sooty Oystercatchers generally fed together in large groups (several hundred individuals) at intertidal mudflats adjacent to the western shore of Flinders Island (the main island of the Furneaux Group) and rarely fed at the available rocky coastline (Lauro, unpubl. data). Thus, Sooty Oystercatchers showed a dimorphism in feeding habitat choice and prey selection while Pied Oystercatchers showed no such dimorphism. A diet dimorphism related to habitat choice has also been documented during the breeding season for the European Oystercatcher (Haematopus ostralegus) (Safriel 1985)

Bill length is likely a better predictor for behavior and prey selection for sexes within species than between species. African Black Oystercatchers (H. moquini) at rocky shores have diet separation based on sexual dimorphism in bill size as males pried a greater proportion of limpets and whelks off rocks while females took more polychaete worms and small

unshelled prey (Hockey and Underhill 1984). Diet separation between the sexes in European Oystercatchers is similar, with females eating a higher percentage of soft-bodied prey (mainly worms) than males and employing different foraging techniques (Dare 1977, Swennen et al. 1983, Hulscher 1985, Hulscher and Ens 1992, Durell et al. 1993). In this species the difference was hypothesized to be due to similar differences in bill length and/or shape.

Three evolutionary hypotheses may explain sexual dimorphisms in bill morphology for birds in general (Shine 1989, Hedrick and Temeles 1989) and for oystercatchers specifically: (1) reduction of competition between males and females for limited resources (usually food), (2) partitioning of reproductive roles, or (3) sexual selection. These hypotheses explain in some combination the differences in foraging behavior and prey selection in our study. Consistent partitioning throughout the breeding season, both before and after the presence of chicks (Lauro, pers. obs.), and a lack of overt competition between the species in the non-breeding season (Nol, unpubl. data) lends some support to the hypothesis that the dimorphism functions to partition reproductive roles. Sexual selection is also likely to be important in explaining bill differences between oystercatcher sexes (Durell et al. 1993). The bills of ovstercatchers are bright red and are used in ritualized breeding displays known as Piping (Hayman et al. 1986). Importantly, there is overlap in bill size for the sexes, yet within breeding pairs, males invariably have shorter bills than females, suggesting that there may be selection by sexes based upon bill length (Baker 1975, pers. obs.). The process of mutual sexual selection is likely involved (Jones and Hunter 1993). However, testing for this by either manipulation of bill coloration or bill length will be difficult in the oystercatchers because their long term pair bonds (Nol 1985) may preclude the opportunity to effectively quantify mate choice. Finally, bill shape in ovstercatchers is somewhat plastic (Heppleston 1970, 1972; Swennen et al. 1983; Hulscher 1985) and future studies will be needed to determine the extent to which behavior and environment control the sexual dimorphism, as well species differences, in bill morphology.

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LITERATURE CITED

BAKER, A. J. 1974. Ecological and behavioral evidence for the systematic status of New Zealand Oystercatchers (Charadriiformes: Haematopodidae). Life Sciences Contr., Royal Ontario Museum, 96.

—. 1975. Morphological variation, hybridization and systematics of New Zealand oystercatchers (Charadriiformes: Haematopodidae). J. Zool (Lond.) 175:357–390.

- BENT, A. 1929. Life histories of North American Shorebirds, Part II. Smithsonian Institute, United States National Museum, Bulletin 146.
- CONSIDINE, M. T. 1979. The feeding behaviour of the Sooty Oystercatcher (*Haematopus fuliginosus*) on rocky shores in Victoria. B.Sc. thesis, Monash Univ., Victoria, Australia.
- DARE, P. J. 1977. Seasonal changes in body weight of Oystercatchers Haematopus ostralegus. Ibis 119:494–506.
- DURELL, S. E. A. LE V. DIT, J. D. GOSS-CUSTARD, AND R. W. G. CLADOW. 1993. Sex-related differences in diet and feeding method in the oystercatcher *Haematopus ostralegus*. J. Anim. Ecol. 62:205–215.
- GOSS-CUSTARD, J. D. AND S. E. A. LE V. DIT DURELL. 1983. Individual and age differences in the feeding ecology of oystercatchers, *Haematopus ostralegus*, wintering on the Exe estuary, Devon. Ibis 125:155–171.
- . 1987. Age-related effects in oystercatchers, *Haematopus ostralegus*, feeding on mussels, *Mytilus edulis*. I. foraging efficiency and interference. J. Anim. Ecol. 56:521– 536.
- HARTWICK, E. B. 1974. Breeding ecology of the Black Oystercatcher (*Haematopus bachmani* Audubon). Syesis 7:83–92.
- HAYMAN, P., J. MARCHANT, AND T. PRATER. 1986. Shorebirds—An identification guide. Houghton Mifflin Company, Boston, Massachusetts.
- HEDRICK, A. AND E. TEMELES. 1989. The evolution of sexual dimorphism in animals: hypotheses and tests. Trends Ecol. Evol. 4:136–138.
- HEPPLESTON, P. B. 1970. Anatomical observations on the bill of the Oystercatcher (*Haematopus ostralegus*) in relation to feeding behaviour. J. Zool. (London) 161:519–524.
- ------. 1972. The comparative breeding ecology of Oystercatchers (*Haematopus ostralegus* L.) in inland and coastal habitats. J. Anim. Ecol. 41:23-51.
- HOCKEY, P. A. R. 1981. Morphometrics and sexing of the African Black Oystercatcher. Ostrich 52:244–247.

AND L. G. UNDERHILL. 1984. Diet of the African Black Oystercatcher on rocky shores: spatial, temporal and sex related variation. S. Afr. J. Zool. 19:1–11.

HULSCHER, J. B. 1985. Growth and abrasion of the oystercatcher bill in relation to dietary switches. Neth. J. Zool. 35:124-154.

AND B. J. ENS. 1992. Is the bill of male oystercatchers a better tool for attacking mussels than the bill of the females? Neth. J. Zool. 42:85–100.

- JEHL, J. R. AND B. G. MURRAY. 1986. The evolution of normal and reverse sexual size dimorphism in shorebirds and other birds. Curr. Ornith. 3:1–86.
- JONES, I. L. AND F. M. HUNTER. 1993. Mutual sexual selection in a monogamous seabird. Nature 362:238-239.
- LANE, B. A. 1987. Shorebirds of Australia. Nelson Publishers, Melbourne, Australia.
- LAURO, B. 1994. Patterns of habitat use for Pied (*Haematopus longirostris*) and Sooty (*Haematopus fuliginosus*) Oystercatchers at the Furneaux Islands, Australia: the role of potential predators and food supply. Ph.D. diss., Queen's University, Kingston, Ontario, Canada.

- MARCHANT, S. AND P. J. HIGGINS. 1993. Handbook of Australian, New Zealand and Antarctic Birds, Raptors to Lapwings. Vol. 2. Oxford Univ. Press, Melbourne, Australia.
- MACPHERSON, J. H. AND C. J. GABRIEL. 1962. Marine Molluscs of Victoria. Melbourne University Press, Victoria, Australia.
- MANLY, B. 1974. A model for certain types of selection experiments. Biometrics 30:281–294.
- NoL, E. 1984. Reproductive strategies in the Oystercatchers (Aves: Haematopodidae). Ph.D. diss., Univ. of Toronto, Toronto, Canada.

----. 1985. Sex roles in the American Oystercatcher. Behaviour. 95:232–260.

- PHILLIPS, D. A. B., C. P. HANDRECK, P. E. BOCK, R. BURN, B. J. SMITH, AND D. A. STAPLES. 1984. Coastal invertebrates of Victoria. Marine Research Group of Victoria in Association with the Museum of Victoria, Melbourne, Victoria.
- SAFRIEL, U. 1985. 'Diet dimorphism' within an oystercatcher population—adaptive significance and effects on recent distribution dynamics. Ibis 127:287–305.
- SHINE, R. 1989. Ecological causes for the evolution of sexual dimorphism: a review of the evidence. Quart. Rev. Biol. 64:419–461.
- SOKAL, R. AND F. ROHLF. 1995. Biometry. 2nd edition. W. H. Freeman and Company, New York, New York.
- SWENNEN, C., L. L. M. BRUIJN, P. DUIVEN, M. F. LEOPOLD, AND E. C. L. MARTEIJN. 1983. Differences in bill form of the Oystercatcher *Haematopus ostralegus*; a dynamic adaptation to specific foraging techniques. Neth. J. Sea. Res. 17:57–83.

GRADUATE AND POST-GRADUATE RESEARCH GRANTS

The Biological Research Station of the Edmund Niles Huyck Preserve offers grants (max. = \$2500) to support biological research which utilizes the resources of the Preserve. Among the research areas supported are basic and applied ecology, animal behavior, systematics, evolution, and conservation. The 2000-acre Preserve is located on the Helderberg Plateau, 30 miles southwest of Albany. Habitats include northeast hardwood-hemlock forests, conifer plantations, old fields, permanent and intermittent streams, 10 and 100 acre lakes and several waterfalls. Facilities include a wet and dry lab, library, and houses/cabins for researchers. Deadline = February 1, 1996. Application material may be obtained from Dr. Richard L. Wyman, Executive Director, E.N. Huyck Preserve and Biological Research Station, P.O. Box 189, Rensselaerville, New York 12147.