Foraging Proficiency During the Nonbreeding Season of a Specialized Forager: Are Juvenile American Oystercatchers "Bumble-Beaks" Compared to Adults?

FORAGING PROFICIENCY DURING THE NONBREEDING SEASON OF A SPECIALIZED FORAGER: ARE JUVENILE AMERICAN OYSTERCATCHERS "BUMBLE-BEAKS"[1] COMPARED TO ADULTS?

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Abstract. In many species, immature individuals are less proficient at foraging than are adults, and this difference may be especially critical during winter when survival can be at its minimum. We investigated the foraging proficiency of adult and immature American Oystercatchers (*Haematopus palliatus*) during the nonbreeding season. Oystercatchers forage on prey that must be handled with specialized skills, so age-related differences in foraging behavior may be expected. We found that adults spent more time searching than did immatures, a trend toward immatures taking longer to handle prey than did adults, and immatures more often handling prey unsuccessfully than did adults. Feeding rates and diet composition did not differ by age class. We posit that the immature birds traded off longer handling times with shorter searching times and that ultimately the abundant prey in the region may contribute to the ability of immature birds to feed at rates similar to those of adults.

Key words: American Oystercatcher, diet, foraging proficiency, Haematopus palliatus, *handling time, searching time, South Carolina.*

Habilidad de Forrajeo durante la Estación No Reproductiva de un Forrajeador Especializado: ¿Son los Juveniles de *Haematopus palliatus* unos "Picos-Torpes" Comparados con los Adultos?

Resumen. En muchas especies, los individuos inmaduros son menos hábiles en forrajear que los adultos, y esta diferencia puede ser particularmente crítica durante el invierno cuando la supervivencia puede estar en su nivel más bajo. Investigamos la habilidad de forrajeo de individuos adultos e inmaduros de *Haematopus palliatus* durante la estación no reproductiva. *H. palliatus* forrajea sobre presas que deben ser manipuladas con habilidades especializadas, por lo que pueden esperarse diferencias relacionadas con la edad en el comportamiento de forrajeo. Encontramos que (i) los adultos gastan más tiempo buscando que los inmaduros, (ii) una tendencia de los inmaduros a pasar más tiempo manipulando las presas que los adultos, y (iii) los inmaduros manipulan sin éxito las presas más frecuentemente que los adultos. Las tasas de alimentación y la composición de la dieta no difirieron por clases de edad. Planteamos que las aves inmaduras compensan los mayores tiempos de manipulación con los menores tiempos de búsqueda y que en última instancia la abundancia de presas en la región puede contribuir a la habilidad de las aves inmaduras a alimentarse a tasas similares a las de los adultos.

INTRODUCTION

Foraging proficiency can be defined as skills affecting the rate of energy intake (Weathers and Sullivan 1989). In many birds, foraging proficiency improves during the first years of an individual's life (Orians 1969, Groves 1978, Puttick 1979, Richardson and Verbeek 1987). Age-related differences in foraging proficiency can result from age-specific differences in behavior or physiology. For example, adults and juveniles may differ in their selection of, or status while on, foraging sites (Goss-Custard 1980, Cresswell 1994, Durell 2003), and so the composition of the age classes' diets may differ also (Goss-Custard and Durell 1983). Adults also may have more developed beaks as well as skeletal-muscular and neurological systems, contributing to their competence at searching and handling (Cadman 1980, Marchetti and Price 1989, Durell 2000).

Age-related differences in foraging proficiency may be especially strong in longer-lived species with specialized foraging habits, and ultimately this difference may affect juveniles' survival rates. Oystercatchers (*Haematopus* spp.), for example, specialize on bivalves which require considerable

skill in handling. Goss-Custard and Durell (1987a, c) found that throughout the nonbreeding season juvenile Eurasian Oystercatchers (*H. ostralegus*) ingested less biomass per unit time than did adults and attributed this to differences in searching time, handling time, and intraspecific dominance between age classes. Surprisingly, there has been little comparative research on the American Oystercatcher (*H. palliatus*), despite its being a species of high conservation concern. We examined age-related foraging proficiency during the nonbreeding season in the core of the species winter range. We compared feeding rates, searching time, and handling time of adult and juvenile American Oystercatchers and sought to determine if foraging proficiency improved through the nonbreeding season. We compared the age classes' diet composition and activity budgets, the prevalence of aggression, and the frequency with which food was involved in aggression. Survival through the bird's first winter may be enhanced if an individual can allocate time and energy efficiently among competing demands such as predator avoidance, food intake, and inter- and intraspecific social dynamics (Wunderle 1991, Cresswell 1994, Daunt et al. 2007). Therefore an assessment of foraging proficiency in relation to age may also elucidate mechanisms operating at the population level.

MATERIALS AND METHODS

The American Oystercatcher feeds on intertidal shellfish. Our study took place during the nonbreeding season of 2007–2008 in Copahee Sound, South Carolina (32° 52′ N, 79° 45′ W). This 5.25-km^2 bay includes intertidal shellfish beds and shallow channels; it is located just south of Cape Romain National Wildlife Refuge. This area supports approximately one-fifth of the oystercatcher population wintering on the Atlantic and Gulf coasts of the U.S. (Sanders et al. 2004, Brown et al. 2005) and 50% of the immature oystercatchers in South Carolina during the nonbreeding season (Sanders et al. 2004).

We recorded behavioral data from eight observation points spaced ~200 m apart on shellfish reefs. CEH recorded data from a randomly selected observation point during daylight and either the falling (*n* = 16) or the rising (*n* = 13) stage (each ~4 hours) of the low tide on 10 days in October, 10 days in November, and 9 days in December. A second observer recorded aggressive interactions on 36 days from 7 October 2007 through 27 January 2008. On the 18 days when both observers recorded aggressive interactions simultaneously, they were located at separate observation points.

We quantified foraging proficiency, diet composition, and the rate of aggressive interactions for immature and adult oystercatchers with observations of focal animals (Altmann 1974). We classified an oystercatcher as an adult if its bill was entirely orange or as an immature if >50% of its bill was dark (Prater et al. 1977, Peters and Otis 2005). Individuals with bills with some dark but <50% dark were not included to avoid misclassification. We conducted one focal observation of a randomly selected immature oystercatcher and one focal observation of the nearest foraging adult within the same 30-min period to control for confounding variables such as tide, weather, time of day, and quality of the shellfish bed. Most individuals were not uniquely marked, so an individual may have been observed multiple times.

During a focal observation (duration 3–12 min), we recorded the times spent searching and handling and the type and size of each prey item. Following Cadman (1980) and Tuckwell and Nol (1997a), we defined searching time as the interval from the completed consumption of a prey item until the oystercatcher stabbed another prey item. We defined handling time as the interval between the first stab into an item and the moment when the oystercatcher finished consuming the item. We included data on searching and handling in the analysis only when an individual oystercatcher successfully located and consumed at least three prey items (Cadman 1980, Tuckwell and Nol 1997a). We used a stopwatch and voice recorder to record searching and handling times to ±1 sec. If the oystercatcher became inactive, preened, or was vigilant for more than 5 consecutive sec while locating a prey item, we did not record the searching time for the prey item but continued the observation (Cadman 1980). Observations were terminated if the focal individual moved out of view.

When we were able to observe an oystercatcher continuously for at least 5 consecutive min during a focal observation, we calculated the oystercatcher's feeding rate (i.e., the number of prey items consumed during the 5 min) and the number of prey items the oystercatcher handled unsuccessfully (i.e., handled but abandoned before consuming any flesh) (Cadman 1980, Durell et al. 1996, Goss-Custard et al. 1996, Meire 1996). Items kleptoparasitized from other oystercatchers were included in feeding rates when they were consumed by the focal oystercatcher.

We categorized each prey item that was not obstructed from view by the oystercatcher's body or by the shellfish bed as an eastern oyster (*Crassostrea virginica*), ribbed mussel (*Geukensia demissa*), or unknown, identifying it by the shape of the shell and flesh color and consistency. We categorized the size of consumed oysters by comparing the length of the flesh to the length of the focal oystercatcher's bill. We did not calculate the sizes of other types of prey because they were rare in the diet (see Results). When oystercatchers extracted oysters from their shells in multiple pieces, we categorized the size of each piece as <¼ of the length of the bill, between ¼ and 1 bill length, or >1 bill length (Tuckwell and Nol 1997a).

To determine if the prevalence of aggression differed by age class, we recorded aggressive interactions, categorizing the age classes by the same criteria used during focal observations. For each instance of intraspecific aggression, we recorded the age class of the aggressor and non-aggressor and whether or not a prey item was involved. We used similar criteria to record interspecific interactions, which we included in aggression rates.

At low tide, we recorded the activity budgets of adult and immature oystercatchers on foraging grounds by scan-sampling techniques (Altmann 1974). At 30-min intervals before and after low tide, we counted the number of oystercatchers of each age class within a 120-m radius of the observation point and categorized their behavior as foraging or not foraging. We chose a plot of this size because, at this distance, few oystercatchers were obstructed from view by exposed oyster beds, which at low tide can hinder viewing from a greater distance. Scans were analyzed only when ≥1 adult and ≥1 immature oystercatcher were in the scan plot. We classified all oystercatchers with dark shading on their bills as immature instead of limiting the category of immatures to individuals with ≥50% dark bills because it was difficult to quickly determine the extent of the dark area during scan samples. Oystercatchers with all-orange bills were classified as adults.

STATISTICAL ANALYSES

We used Pearson's χ^2 to determine if diet composition (defined as number of items consumed) or size class of oysters consumed (defined as proportion of oysters from each size class) by the two age classes differed. To avoid pseudoreplication, we included in these analyses only the prey type of the first unobstructed item and the size class of the first oyster consumed by each oystercatcher. We used Pearson's χ^2 to determine if the likelihood of being involved in at least one aggressive interaction during 5 min of foraging differed by age class, if the likelihood of prey being involved in aggressive interactions differed by age class, and if the likelihood of handling at least one item unsuccessfully during 5 min of foraging differed by age class. We used a two-tailed Wilcoxon two-sample test to determine if the proportion of time devoted to foraging during scan samples differed by age class.

We used mixed models (SAS version 9.1; SAS Institute, Inc., Cary, NC) to determine if mean searching time, mean handling time, or feeding rate of adult oystercatchers differed from those of immature oystercatchers or if these values varied with date. To increase the precision of the measurements while avoiding pseudoreplication, we averaged the first three searching times and handling times for each oystercatcher (Hejl et al. 1990, Tuckwell and Nol 1997a). Age class of the observed individual was included as a fixed factor, date was included as a covariate, age class × date was included as an interaction term, and a unique identification code for each set of paired focal observations was included as a random term. We used a backward selection approach until only variables with a P-value of ≤0.10 remained in each model. Mean searching and handling times were log transformed and feeding rates were square-root transformed. We present raw data, however, to ease interpretation and allow for comparisons with previous studies.

Means and regression coefficients are presented as ±1 SE unless noted otherwise. We consider P-values ≤0.05 to be significant but present actual P-values.

RESULTS

The composition of the diet of adult and immature oystercatchers did not differ ($\chi^2_2 = 1.2$, $P = 0.55$; $n = 65$ prey items each). Eastern oysters constituted 95.4% of items consumed, ribbed mussels 3.8%, and unidentifiable items 0.8%. There was no size difference ($\chi^2_2 = 0.2$, $P = 0.93$) between oysters consumed by adult ($n = 55$ oysters) or immature oystercatchers ($n = 55$ oysters). For immature birds, we classified 15.5% of consumed oysters as class 1, 77.7% as class 2, and 6.8% as class 3. For adults, we classified 15.5% of consumed oysters as class 1, 79.3% as class 2, and 5.2% as class 3.

The mean (±SD) count of oystercatchers within view of the observer during scans was 44.7 ± 29.4 (range 1–166). The mean percentage of immature oystercatchers foraging during scan samples did not differ significantly ($Z = 1.0$, $P = 0.16$) from that of adults. During the 37 scans when ≥1 immature oystercatcher and ≥1 adult oystercatcher were in the scan plots, 80.8% of the oystercatchers were foraging and 19.2% were not foraging. Of the 5-min observation periods, immature oystercatchers handled at least one item unsuccessfully during 60.4%, whereas adults handled at least one item unsuccessfully during 35.4% ($\chi^2_1 = 6.1$, $P = 0.01$, $n = 96$ periods). Oystercatchers of both age classes handled at least one item unsuccessfully more frequently during October than during December (Kruskal–Wallis $\chi^2 > 4.1$, $P ≤ 0.04$ for analysis of each age class; Fig. 1).
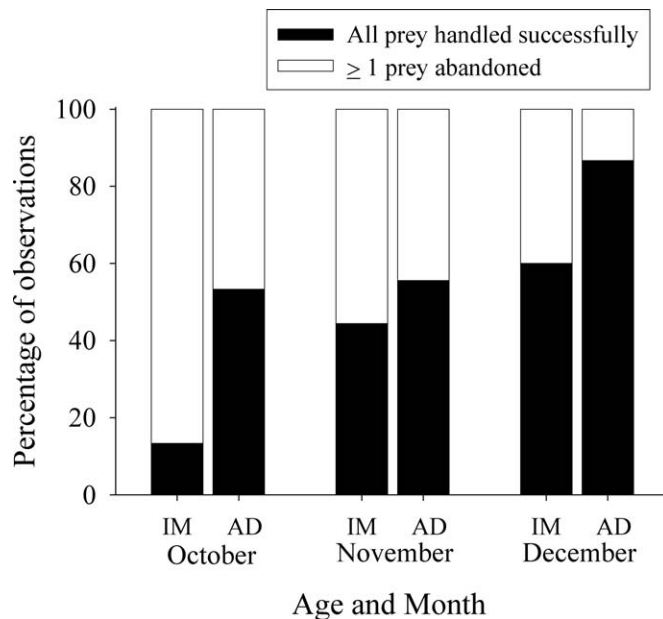

FIGURE 1.   Success of prey handling during 5-min observations of foraging immature (IM) and adult (AD) American Oystercatchers in Copahee Sound, Cape Romain region, South Carolina, October–December 2007.
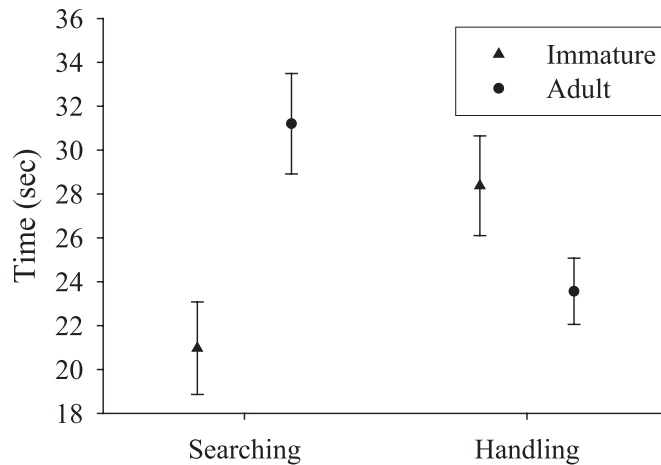
FIGURE 2.   Mean (±1 SE) searching and handling times of immature and adult American Oystercatchers foraging in Copahee Sound, Cape Romain region, South Carolina, October–December 2007.

We recorded searching time from 42 adult–immature pairings, handling time from 46 pairings, and feeding rate from 49 pairings. The mean searching time of adult oystercatchers was significantly greater than that of immature oystercatchers ($F_{1,41}$ = 17.2, P < 0.01; Fig. 2), and the mean handling time of immatures tended to be longer than that of adults ($F_{1,45}$ = 3.9, P = 0.06, Fig. 2). The mean feeding rate of immature oystercatchers, 5.1 ± 0.3 items per 5 min, did not differ from that of adults (4.9 ± 0.3 items per 5 min; $F_{1,48}$ = 0.1, P = 0.77). In none of the models did mean searching or handling time or feeding rate vary with date (all P > 0.34) or with the interaction term (age class × date; all P > 0.71).

Rates of aggressive interactions during paired focal observations that lasted 5 continuous min did not differ by age class (χ^2_1 = 2.2, P = 0.14, n = 96 5-min observations), and we recorded no aggressive interactions during 91.7% of the observations. Prey was involved in significantly more (χ^2_1 = 7.5, P = 0.02, n = 89 instances of aggression) of the aggressive interactions initiated by immature oystercatchers (61.2%, n = 49 instances) than during interactions initiated by adults (37.5%, n = 40 instances). We noted Willets (*Tringa semipalmata*) attempting to kleptoparasitize both adult (n = 17) and immature (n = 14) oystercatchers.

DISCUSSION

For immature oystercatchers, handling times were longer, searching times were shorter, and intake rates were equivalent in comparison to those of adults. Immature birds' shorter search times have been attributed to immatures' reduced selectivity of prey (Goss-Custard and Durell 1983, Weathers and Sullivan 1989). During our study the type and size of prey oystercatchers chose did not differ by age class, so a difference in selectivity could not have contributed to the difference in search times we observed. However, attributes such as the spatial orientation of prey on the reef, distance of gape between the valves of oysters, or shell thickness also may influence oystercatchers' search strategy (Ens and Alting 1996). A difference between age classes in time allocated to behaviors other than foraging during the searching period also may result in differences in search time. For example, juvenile Eurasian Oystercatchers interrupted foraging by glancing upward (i.e., vigilance; Barbosa 1995) less frequently than did older birds (Goss-Custard et al. 1998). In our study area, predation by raptors poses a threat to oystercatchers, and vigilance is elevated when avian predators are in the area (Peters and Otis 2005). Therefore, differences in the frequency of vigilance or in selectivity for prey on an attribute other than size or type may have contributed to the difference between age classes we observed in searching.

Differences between age classes in handling skills may be particularly common in species in which foraging skills are specialized (Hockey et al. 1989, Wunderle 1991, Heise and Moore 2003). We found a trend for immature birds' handling times to be longer than those of adults, and the difference was similar in magnitude to that reported by Cadman (1980) for wintering oystercatchers in Virginia. We found that immature birds also mishandled items during more observation periods than did adults. During trials of captive Eurasian Oystercatchers, Wanink and Zwarts (1996) found that handling time could be reduced as foraging experience increased and that a particular skill, such as efficiency of flesh cutting, could affect handling time. Immature oystercatchers also may be less proficient at identifying vulnerable prey or may open empty shells more frequently. If immature birds' longer handling times did result from prey selection, then such a scenario would be consistent with a less efficient search strategy as posited above. The relative homogeneity of the diet also may allow immature birds to specialize on a single prey, which may improve learning and reduce handling time (Tinker et al. 2008). Immature birds in their second or third year also may handle items more efficiently than do hatch-year birds, although we were not able to discern age at this level of detail.

For both age classes, the proportion of 5-min observations during which the focal oystercatcher handled at least one prey item unsuccessfully decreased through the study period. In immature birds, the improvement in success rates may be due to an improvement in foraging skill, which may benefit from a single-item diet that does not require a wide repertoire of skills (Cunningham and Hughes 1984, Tinker et al. 2008). The lower success rates of adults in October may, however, be related to the influx of migrants that arrive after the breeding season. Two-thirds of the oystercatchers that winter in South Carolina originate from more northern states (Sanders et al. 2008) where oysters may not be the predominant prey. Therefore, nonresidents may have to hone their handling skills with respect to oysters.

Although we observed differences in searching and handling times between adult and immature oystercatchers,

the two age classes' feeding rates did not differ. In contrast, adult Eurasian Oystercatchers feeding on mussels consumed ~1.6× as much biomass as did juveniles (Goss-Custard and Durell 1987a, b, c). In our study the exact mechanism that allowed immature birds to achieve intake rates similar to those of adults is unclear. Our data suggest that immatures may have compensated for longer handling times by reducing searching time. We posit that in this region the relatively high availability of a single species of prey, of appropriate size (i.e., small to mid-sized oysters; Luckenbach et al. 2005), simplifies searching behavior, particularly for immature birds, and is consistent with the narrow diversity we observed in the diet (Schoener 1971, Thompson and Colgan 1990, Tinker et al. 2008) and with immatures' relatively consistent level of foraging proficiency by month (Tuckwell and Nol 1997a). Although immature oystercatchers may increase their food intake via kleptoparasitism (Tuckwell and Nol 1997b, Goss-Custard et al. 1998), during our study kleptoparasitism was rare. Additional research that compares the foraging proficiency of adult and immature birds in other portions of the winter range where diet diversity and food availability differ from those at Cape Romain would be beneficial. Comparative data on adults' and immatures' survival rates and foraging proficiency would be valuable because foraging proficiency can affect survival, particularly of immature birds (Weathers and Sullivan 1989, Donnelly and Sullivan 1998, Wheelwright and Templeton 2003). These efforts would be enhanced by continued efforts to band chicks and adults throughout the region.

ACKNOWLEDGMENTS

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