Submarine Foraging Behavior of Alcids in an Artificial Environment

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We used an artificial environment at Sea World, Inc, San Diego, to study underwater foraging behavior of alcids. Larger birds dove longer and had greater wing-beat frequencies. The pigeon guillemot Cepphus columba was the only species to use both feet and wings for propulsion; all others used just wings. Aggressive interactions underwater were common. Competition among alcids in the wild may occur primarily underwater, and artificial environments may be the best means to study such interactions.

Key words: captivity, competition, diving, foraging

INTRODUCTION

The study of foraging by seabirds in their natural environments is extremely difficult as they can rarely be observed directly below the surface. Inferences concerning foraging, based on surface observations, may lead to ambiguous results. For example, Cody [1973] concluded that differences in foraging range, rather than diet or foraging depth, facilitated partitioning of food resources between species in alcid communities off the Olympic Peninsula, Washington, and off Iceland. Bedard [1976] questioned Cody's findings but did not present alternative explanations for possible partitioning of resources. We suggest that, because alcids normally capture prey below the surface of the sea [Ashmole, 1971; Bradstreet and Brown, 1985], studies of the birds' submarine foraging behavior are needed. We report here an initial study of foraging by seven alcid species kept at Sea World, Inc, San Diego, in an artificial enclosure that attempts to simulate their natural environment. We describe the underwater behavior and habitats used by foraging alcids, durations of dives in relation to body size, and observations on interspecific aggression and kleptoparasitism.

MATERIALS AND METHODS

The birds were maintained in a 1,200 m² public exhibit. The front of the exhibit was a glass window approximately 2.25 x 21 m with approximately 50% of the area below the water level of a 72,000-liter, 1.7-m-deep salt-water tank. The back of the enclosure was a 6-m artificial-rock cliff with nest-burrows built into the structure.
The alcids present in 1984 were three Atlantic Fratercula arctica, 12 horned F. corniculata, and 38 tufted puffins Lunda cirrhata, 19 common murres Uria aalge, 7 rhinoceros auklets Cerorhinca monocerata, 16 pigeon guillemots Cepphus columba, one Cassin’s auklet Pychoramphus aleuticus, one crested auklet Aethia cristatella, and one razor-billed au Alca torda. The murres and the Cassin’s auklet were salvaged from southern California beaches, the razor-billed Auk and Atlantic puffins were collected as chicks in Iceland, and the Rhinoceros auklets were from Puget Sound, Washington. The other birds were collected as chicks in August 1983 from St. Lawrence Island, Alaska.

In 1986, there were 3 Atlantic, 38 tufted, and 10 horned puffins, 7 rhinoceros auklets, 6 pigeon guillemots, one razor-billed au, and 19 common murres.

Observation Methods
We timed dives, using a digital stopwatch. We measured only those dives by birds apparently searching for prey and excluded dives when prey were present and active feeding was taking place. We also excluded dives that were interrupted by aggression. We recorded the number of wing beats during timed dives or visible portions of dives of each species. We avoided timing successive dives of the same bird and spread our observations over a week to reduce the chances of disproportionately sampling individuals.

We observed foraging locations at 10-second intervals during dives until five sightings had been recorded. Three foraging “zones” were recognized: “near surface” (within 0.3 m of the surface); “benthic” (within 0.7 m of the substratum or rock walls); and “midwater” (the water column between the two). We made unquantified observations on the underwater propulsion of each species.

We observed interspecific interactions during “searching” and during active feeding. The latter occurred when live anchovy Engraulis mordax were released into the enclosure from a side tank or when meal-worms were introduced directly from above. We scored two types of observations: “aggressive displacement” (one species chasing another), and “kleptoparasitism” (one bird stealing or attempting to steal prey from another).

RESULTS

Behavior Underwater

Foraging behavior of the Pigeon Guillemot was very different from those of the other alcids. This species typically foraged by hanging head-down, probing the bottom, while using both wings and feet to maintain position.

Common murres also foraged near the bottom or on the sides of the tank, along the underwater artificial-rock wall (Table 1). Probing of the substratum was usually done horizontally or even facing upwards. This species used only its wings for propulsion. Tufted puffins also used only their wings underwater, usually traveling considerable distances back and forth across the full length of the tank in the midwater zone (Table 1). Tufted puffins rarely pecked at debris in the water, except when large prey were present. This contrasted with the frequent probing by bottom-feeding common murres and pigeon guillemots. Horned and Atlantic puffins had similar diving behavior to that of the tufted puffin, but were much less active during the observation period.
TABLE 1. Percentage habitat use by foraging alcids in an artificial environment at Sea World Inc, San Diego*

<table>
<thead>
<tr>
<th>Species</th>
<th>Observations</th>
<th>Percentage use of</th>
<th></th>
<th></th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td></td>
<td>Surface</td>
<td>Midwater</td>
<td>Bottom</td>
</tr>
<tr>
<td>Common murre</td>
<td>105</td>
<td>5</td>
<td>82</td>
<td>13</td>
</tr>
<tr>
<td>Tufted puffin</td>
<td>141</td>
<td>6</td>
<td>72</td>
<td>22</td>
</tr>
<tr>
<td>Horned puffin</td>
<td>66</td>
<td>14</td>
<td>83</td>
<td>3</td>
</tr>
<tr>
<td>Rhinoceros auklet</td>
<td>105</td>
<td>8</td>
<td>91</td>
<td>1</td>
</tr>
<tr>
<td>Atlantic puffin</td>
<td>31</td>
<td>6</td>
<td>87</td>
<td>6</td>
</tr>
<tr>
<td>Pigeon guillemot</td>
<td>97</td>
<td>2</td>
<td>11</td>
<td>88</td>
</tr>
</tbody>
</table>

*See text for definition of habitats.

The single Cassin’s auklet also fed primarily in the near surface and midwater zones, changing direction frequently and not making the long straight passages of puffins. Few feeding jabs were made, except immediately after meal-worms had been introduced into the tank. The bird did not join in foraging groups when anchovy were present.

Rhinoceros auklets rarely dived but padded along on the surface, dipping their heads below the surface for several seconds at a time as if searching for food. These birds remained near the surface or in the midwater when they dived (Table 1).

Rhinoceros auklet, tufted, horned, and Atlantic puffins all captured additional prey while holding one or more fish in their mandibles. The most frequent multiple-fish carrying behavior was by tufted puffins, which carried a mean $2.4 \pm 1.1$ (n = 16) fish during multiple loads.

**Durations of Dives**

Although large-bodied birds tended to remain submerged longer than small birds, the relationship was not consistent ($r_s = 0.46; N = 7$ species; $P > .05$; Table 2). Pigeon guillemots had relatively long dives. If this species, the only one which used both wings and feet for propulsion, is excluded, body mass was a much better predictor of duration of dive ($r_s = 0.89; P = .05$); N = 6 species. Rhinoceros auklets, near-surface feeders, had shorter dives than expected for their weight.

The wing-beat rate was inversely related to body mass: the heavier species had fewer beats per unit time than did lighter ones (Table 2; $r_s = 1.0, P < .05, N = 4$ species).

**Interspecific Interactions**

Interspecific interactions were frequent, especially when food was present. In 1984, tufted puffins frequently chased rhinoceros auklets and the Cassin’s auklet. A single common murre attacked conspecifics, tufted puffins, pigeon guillemots and a Cassin’s auklet, which approached the passage through which anchovy were released into the tank. This aggressive bird spent more than 10 minutes foraging near the passage and chasing other birds. In 1986, tufted puffins were the most aggressive species, chasing or attempting to steal prey from common murres (3), rhinoceros auklets (4), pigeon guillemot (1), and conspecifics (8). Common murres attempted to steal prey from rhinoceros auklets (2) and from a conspecific. A rhinoceros auklet attacked a tufted puffin. All these interactions took place underwater.
DISCUSSION

While some aspects of the foraging of alcids have been well documented [Bradstreet and Brown, 1985], their submarine behavior remains little known. Direct studies are difficult to make in the field: observations from the surface are only feasible in the upper few meters of the water column and under relatively calm conditions. The use of SCUBA or underwater television is similarly restricted, because of the short horizontal visibility in temperate waters [Tyler, 1969]. Devices for measuring foraging depth and speed [Kooyman, 1975; Kooyman et al, 1982; Wilson and Bain, 1984a,b] have been used for alcids (R.P. Wilson, personal communication), but they are useful only during the breeding season, when recapture of experimental birds is possible.

The artificial nature of the experimental environment imposed several obvious constraints on foraging. The depth of the tank was only 1.7 m, well within the depths reached by foraging alcids. Dives of up to 180 m appear possible, based on net-drowned birds [Piatt and Nettleship, 1985]. In addition, pelagic and benthic-foraging species were limited to an inshore habitat where they interacted with species with which they do not usually occur. Finally, the artificially provided food may have contributed to abnormally intense interactions between species. On the other hand, many food sources in marine environments are patchily distributed [reviewed by Brown, 1980]. Alcids frequently forage in multispecies feeding assemblages at such patches [cf. Hoffman et al, 1981; Porter and Sealy, 1981, 1982], so aggressive interactions should be common in nature.

In natural situations, common murre, rhinoceros auklet, tufted and horned puffins, and Cassin’s auklet appear to be primarily midwater foragers [Baltz and Morejohn, 1977; Ogi and Tsujita, 1977; Vermeer, 1980; Wehle, 1982; Vermeer and Westheim, 1984], whereas the pigeon guillemot is a demersal feeder [Drent, 1985; Thoresen and Booth, 1958]. Measurements of dive times by Cody [1973] in the wild were substantially greater than ours for three of five species. Given the greater depths available to birds foraging naturally, this is not surprising. However, times for tufted penguin and Cassin’s auklet were virtually identical in both studies (Table 2), suggesting that the artificial conditions at Sea World did not completely constrain normal
foraging. These two species may use dives primarily for horizontal rather than vertical movement. Cody's [1973] dive times for common murre and Rhinoceros Auklet were much longer than expected for species that frequently feed on surface shoals of prey [Hoffman et al., 1981; Porter and Sealy, 1981]. Other observers recorded even longer dives: Thoresen [1964] found that Cassin’s auklets submerged for 45–60 seconds, and Piatt and Nettleship [1985] report common murre dives lasting up to 231 seconds. On the other hand, Atlantic puffins dive durations were well within the 5–37-second ranges summarized by Bradstreet and Brown [1985] and almost identical with Lockley’s [1953] value (21 sec, N = 45).

The artificial situation was of considerable use in demonstrating the aberrant foraging behavior of the pigeon guillemot, which used both its feet and wings for propulsion. Thrusting with feet would facilitate probing the substratum, because use of wings may hinder entrance into crevices. Wing strokes may provide too powerful a pulse of forward propulsion, compared to alternating paddling with the feet.

Differences in diving behavior leading to differences in the use of patchy prey may play a role in the partitioning of foraging habitats [cf. Ashmole and Ashmole, 1967; Hoffman et al., 1981; Porter and Sealy, 1981, 1982]. Underwater interspecific interactions, both aggressive and kleptoparasitic, might also help space foraging individuals in the wild and exclude smaller species from foraging aggregations.

Competition for food within alcid species may occur [Cody, 1973], but studies of competition, like foraging itself, must take place underwater if we are to understand segregating mechanisms and their importance. Until techniques improve sufficiently to allow direct observation in the field, artificial environments provide the best means of studying seabirds underwater. Observations under artificial conditions allow comparison of species-specific behavior against controlled conditions of depth, food abundance, and benthic habitat, which would not be possible in nature. Problems caused by weather and sea-surface state are eliminated. Observation time is essentially unlimited. Finally, the types and abundances of prey and the species exploiting them can be manipulated. Sanford and Harris [1967] and Swennen [1977] illustrate other aspects of alcid behavior that can be examined through studies of captive individuals.

Captive environments have often been regarded as unnatural and useless for the study of marine animals. While this may be true for some species and captive arrangements, we believe that with the right environments and research questions, captive facilities are essential to an improved understanding of birds and other animals underwater.

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REFERENCES


