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Diving rhythms and diurnal roosting times of Pelagic Cormorants.—Insight into the foraging ecology of diving birds such as cormorants may be gained by timing their diving sequences. In particular, the ratio of dive times to pause times (D/P) can reveal a species' physiological diving abilities (Dewar, The Bird as a Diver, Witherby, London, England, 1924; Dow, Auk 81:556–558, 1964). Possible differential physiological limitations may in turn explain the ecological separation of some cormorant species into shallow and deeper feeding zones (e.g., Stonehouse, Ibis 109:600–605, 1967). Other variables such as foraging success and the duration of foraging and diurnal roosting are useful in understanding variation in foraging behavior between species and among individuals of different ages within a species (Morrison et al., Wilson Bull. 90:414–422, 1978). Detailed observations of foraging have been made for only a few species of cormorants and the ways in which diving variables differ among species, age groups, and habitat types remain largely unknown. In this paper we present our findings on diving sequences and the intervals between bouts of feeding and diurnal roosting in Pelagic Cormorants (*Phalacrocorax pelagicus*). The data were obtained as part of a broader ecological study of this species in Barkley Sound, British Columbia.

Study area and methods.—From 1 July to 5 September 1982 and 1 July to 15 August 1983 we observed cormorants as they foraged near a diurnal roosting site off Taylor Island in the Deer Group Islands, Barkley Sound. The study site is typical of coastal habitat on the west coast of Vancouver Island (see Carter et al., Colonial Waterbirds 7:25–34). The bottom was rocky and water depth ranged from 0.5 to 20 m. Approximately 15 individuals, mostly immatures and non-breeders, regularly foraged in this area. We identified immature birds by their generally brown plumage and the lighter coloration of the breast and neck (see Palmer, Handbook of North American Birds, Vol. 1, Yale Univ. Press, New Haven, Connecticut, 1962). The exact age of the immatures was not known but they were likely in their first year because no young had yet fledged in either year from local breeding sites and because adult plumage is apparently acquired by the second year (Palmer 1962).

Dive and pause times were recorded with a stopwatch to the nearest sec from land 25 to 300 m from the birds. Pause times were recorded only when they were terminated by a dive and did not include periods after dives when prey was handled or birds swam to other foraging locations. Diving sequences of 10 or more dives were used in our calculations. We considered a foraging bird to be successful if it surfaced with prey in its bill; as this may not always be the case, our estimates of success are minimal. We calculated percent success only for complete foraging bouts. Length of the entire foraging bout was from the time the first dive began to the start of typical post-feeding behavior, e.g., vigorous plumage shaking, splashing, and often head dipping.

Birds were not marked, and thus, we could only occasionally record the time each spent roosting during the day between foraging bouts. In these cases we distinguished individuals by plumage characteristics (e.g., white flank patches), or by their position on the roosting site. Weather and tidal conditions were recorded during each observation bout, and water depth was estimated using hydrographic charts corrected for tidal level.

Results and discussion.—Seventy percent of the observed foraging sequences of adult and immature cormorants were in water 2–5 m deep, although birds sometimes foraged at depths down to 20 m. While prey may be encountered in the water column, we suspect that most of these dives were to the bottom. Robertson (Condor 76:346–348, 1974) reported that near Mandarte Island, British Columbia, Pelagic Cormorants fed mostly on prey characteristic of the littoral-benthic zone. Ainley et al. (Condor 83:120–131, 1981) reported that Pelagic Cormorants fed primarily on prey that "remain in close contact with, and even conceal

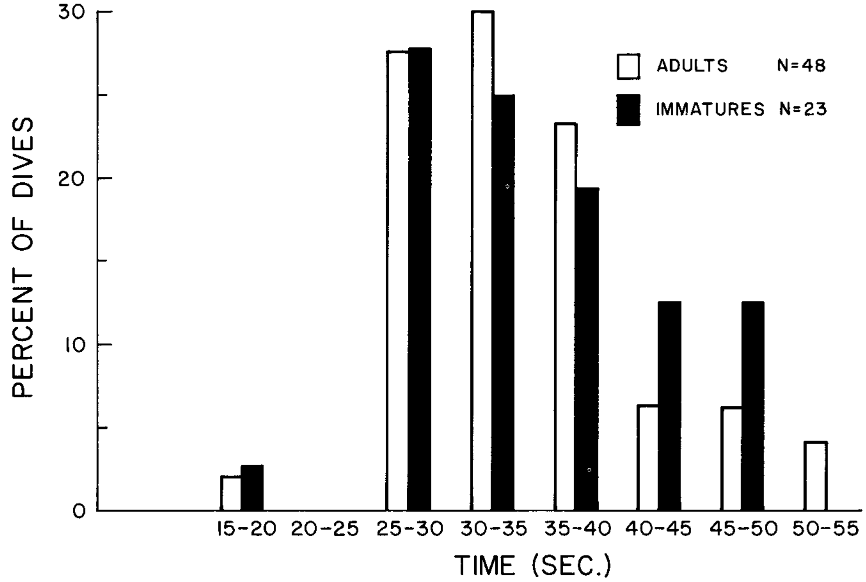

FIG. 1. Duration of dives of adult and immature Pelagic Cormorants in water 2–5 m deep.

themselves in, the rock and kelp substrate." Twice we identified prey as gunnel (Pholidae) and sculpin (Cottidae), both benthic fishes. Depths to 20 m are well within the physiological diving limits of this species (see Palmer 1962).

Diving sequences were recorded for 48 adults and 23 immatures foraging in water 2–5 m deep (these may include some repeat observations of the same birds). The distributions of diving times and pause times are given in Figs. 1 and 2, respectively. The mean diving time of adults (34.9 ± 4.1 sec, N = 1328) was significantly lower ($P < 0.05$, $t = 2.105$) than that for immatures (35.5 ± 7.8 sec, N = 474). We also found that the mean adult pause time (15.2 ± 3.2 sec, N = 460) was significantly lower ($P < 0.001$, $t = 5.76$) than that for immature birds (16.9 ± 3.9 sec, N = 190). Occasionally we were able to record pause time immediately following a measured dive time. For these paired values, the mean D/P ratio for adults foraging in water 2–5 m deep (2.3 ± 0.5, N = 390) differed significantly ($P < 0.001$, $t = 3.563$) from that of immatures (2.1 ± 0.7, N = 132). These D/P values nevertheless are sufficiently close to reveal similar diving abilities between these age groups (see Morrison et al. 1978).

Our D/P values agree closely with the value of 2.0 that Dow (1964) reported for a Pelagic Cormorant diving in depths between 1.5 and 6.1 m. Morrison et al. (1978) reported a D/P ratio of 2.1 for Olivaceous Cormorants (*P. olivaceous*) foraging in a shallow estuary and compared it to a value of 2.0 for Double-crested Cormorants (*P. auritus*) foraging in coastal waters. Stonehouse (1967) reported D/P ratios of 2.3–3.0 for four species of shags in New Zealand. Morrison et al. (1978) suggested that similarities in D/P ratios between various habitats and water depths indicates that the optimum diving rhythm among cormorant species is similar.

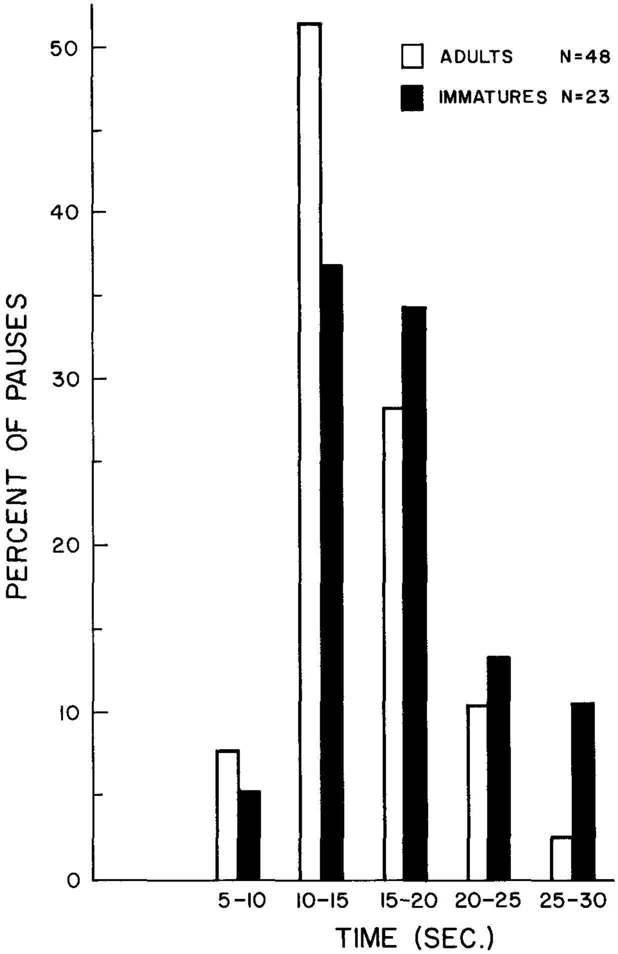

FIG. 2. Duration of pauses of adult and immature Pelagic Cormorants in water 2–5 m deep.

Water depth may be an important influence on the duration of dives and pauses (Simmons, Br. Birds 63:300–302, 1970; Batulis and Bongiorno, Auk 89:665–667, 1972; Morrison et al. 1978). Dewar (1924) and Stonehouse (1967) reported that the D/P ratios increase with depth to a critical value, and then fall as a physiological limit is reached. We observed that the D/P ratio for adults and subadult Pelagic Cormorants did not change significantly as depth increased to 20 m ($P > 0.05$, $t = 1.721$). This supports Dow's suggestion (1964) that if the dive and pause times are mainly functions of water depth, the D/P ratio for a species should remain approximately constant.

We found no significant difference ($P > 0.2$, $t = 0.063$) in capture rate for complete for-

TABLE 1

FORAGING AND DIURNAL ROOSTING TIMES FOR ADULT AND IMMATURE PELAGIC CORMORANTS

	Adult		Immature		
	$\bar{x}$ ± SD	N	$\bar{x}$ ± SD	N	
Foraging time (min)	25.9 ± 15.3	30	23.1 ± 15.8	15	$P > 0.2$, $t = 0.573$
Diurnal roost time (min)	86.0 ± 39.1	22	84.6 ± 32.7	15	$P > 0.2$, $t = 0.114$
R/F[1]	3.3		3.7		

[1] Ratio of time spent at diurnal roosting sites (i.e., out of water) to the time spent foraging.

aging bouts by adults (10.8 ± 8.4%, N = 30) and immatures (11.0 ± 13.3%, N = 16). Morrison et al. (1978) reported that Olivaceous Cormorants entering their first winter could dive as well as adults (as reflected by similar D/P ratios), but captured prey less successfully. They suggested that capture technique, maneuverability, and the development of a search image affect the capture rate of individuals of different ages. Our data indicate that in certain habitats Pelagic Cormorants can acquire adult diving ability and capture success by at least their first summer.

Adults and immatures had similar diurnal roosting and foraging times (Table 1). These values may be affected by environmental factors, which influence prey availability and capture rate, and by physiological factors. Rijke (J. Exp. Biol. 48:185–189, 1968) demonstrated that the physical structure of cormorant feathers renders them less water repellent than those of ducks. This may reduce buoyancy and enhance underwater feeding (Owre, Ornithol. Monogr. No. 6, 1967; but see Elowson, Auk 101:371–383, 1984). The increased wetability of cormorants and anhingas (*Anhinga* spp.) has led to speculation that wing drying may play a role in the spread-wing postures typical of this family (see Clark, Auk 86:136–138, 1969; Berry, Madoqua 8:5–55, 1976). Siegfried et al. (Zool. Afr. 10:183–192, 1975) suggested that poor water repellency impairs the birds' thermoregulatory properties and results in relatively short foraging bouts in non-breeding birds. Mahoney (pp. 461–470 *in* Proc. Symp. on Birds of the Sea and Shore, J. Cooper, ed., African Seabird Group, Cape Town, South Africa, 1979) further suggests that thermal physiology may influence species distribution. The ratio of time spent out of water to the time spent foraging (R/F) may thus be expected to differ between species and habitats. We recorded an R/F value of 3.3 for adult birds (Table 1). This value was 5.4 for adult Olivaceous Cormorants (calculated from the data in Morrison et al. [1978]) and 0.7–3.0 for four species of cormorants inhabiting freshwater and marine habitats in South Africa (calculated from data in Siegfried et al. [1975]). Our understanding of the factors affecting these R/F values is incomplete and the continued documentation of diving variables and diurnal roost times is needed to provide further insight into the ecology and physiology of these diving birds.

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