returns south. Turtles departing from French Frigate Shoals to return to the main islands during July could therefore set a course each morning directly into the rising sun.

Another navigational aid that could possibly be used by Hawaiian Chelonia is the subtle color differences that are present in clouds due to reflections from shallower ocean depths where banks occur. However, the use of visual cues may not be essential considering that two males found with extensive fibropapillomas on their eyes were believed to have been recent migrants to French Frigate Shoals (section 3.34).

Ascension Island is thought to be an adaptation to the gradual separation of South America and West Africa resulting from seafloor spreading (Carr 150, 151; Hirth 265). Similar geophysical mechanisms may also help to account for evolution of the Hawaiian Chelonia pattern with respect to voyages occurring between the geologically older northwestern areas of the Hawaiian Archipelago and the more recently formed French Frigate Shoals. This migratory component appears to be equivalent to the Ascension Island pattern. As new islands progressively appeared and disappeared, ancestors of Hawaiian Chelonia may also have gradually extended their traveling distances between resident foraging areas and aggregate breeding grounds. This theory does not, however, provide an explanation for reproductive migrations occurring from the main islands, which are known to be geologically younger than French Frigate Shoals.

While at French Frigate Shoals, nesting turtles demonstrate a distinct preference for a certain island and, to a lesser extent, show some favoritism for certain areas on that island (section 3.15). The retention of this island fixity between breeding seasons in the 21 remigrations of females thus far documented (section 3.16) suggests the presence of a refined memory system for short-range orientation. Direct vision as well as olfactory cues are undoubtedly major components of this discrimination process. The orientation of turtles underwater at night prior to emergence for nesting could be expected to involve some of the same sensory cues used by turtles foraging at night in the resident areas (section 3.42).

3.6 Basking

Hawaiian green turtles exhibit the behavioral trait of coming ashore to bask or rest at certain undisturbed sites in the NWHI. This includes adults of both sexes and, to a lesser extent, immature turtles of all sizes larger than 35 cm. The land basking habit is rare among marine turtles, with Hawaiian and Galapagos Chelonia being the only two populations in which it has been well documented in the historical literature. However, basking in the Galapagos Archipelago has not been observed for a number of years and therefore may no longer be a characteristic of the population. There is no historical evidence of Hawaiian Chelonia basking on any of the main islands. However, an observation made at Johnston Atoll suggests that on rare occasions green turtles may bask at this location (Amerson and Shelton 31; Balazs 78). At the Wellesley Isles in Australia's Gulf of Carpentaria, female green turtles alone are known to come ashore during the breeding season to avoid males. The 27 December 1777 log of

the Resolution states that at Christmas Island green turtles were turned on their backs while "asleep," and that this was a common method of capture (Beaglehole 105). In addition, previously unreported basking behavior by green turtles has been observed at Lizard Island on the Great Barrier Reef (W. Anderson and J. Leis, personal communications) and at North West Cape, Western Australia (J. Bradley, personal communication).

The presence of basking turtles in the NWHI was noted by many of the early visitors during the 1800's (Brooks, 135, 136; Farrell 220; Hornell 271; Lisiansky 335; Morrell 360; Munro 365-370; Paty 402; Read 429; Rothschild 435; Walker 531; Anonymous 564, 566). However, widespread knowledge of this behavior did not occur until publication of an account of the 1923 Tanager Expedition in a 1925 issue of National Geographic Magazine (Wetmore 542). A photograph from this article of a basking turtle at Lisianski Island was republished shortly thereafter in the New York Zoological Society Bulletin, along with further descriptive information by Dr. Alexander Wetmore (Mellen Several other authors subsequently mentioned the occurrence of basking by Hawaiian Chelonia as a rarity among marine turtles (Carr 150, 152; Grant 238; Loveridge 336; Pope 415). During aerial censuses of Hawaiian monk seals in 1957 and 1958, Kenyon and Rice (288) regularly observed turtles basking along the shorelines of the NWHI (see also Parsons 400). From 1950 to 1973, basking turtles were at various times recorded and counted in conjunction with biological surveys by the Pacific Ocean Fisheries Investigation (386-398), the HDFG (Brock 133; Kramer 308, 309; Kramer and Beardley 310; Walker 532, 533; Woodside 554; Woodside and Kramer 555), the Pacific Ocean Biological Survey Program (see Subject Index), and the USFWS (Kridler 311-327; Olsen 380-385). Summaries of these observations and censuses have been published by Amerson (30); Amerson et al. (32); Clapp and Wirtz (171); Clapp and Kridler (172); Clapp et al. (173); Ely and Clapp (211); and Woodward (556). During recent years, photographs of basking Hawaiian Chelonia have appeared along with articles and reports by Altonn (6); Balazs (55 with Monachus, 57, 61 with Ocypode, 62, 78); Eliot (208); Hirth (265); Lipman (333); Moake (358 with Chelonibia); and Anonymous (642, 657, 667).

Basking in the NWHI takes place on calcareous sand beaches of varying particle size and composition located at French Frigate Shoals, Laysan and Lisianski Islands, Pearl and Hermes Reef, Kure and, on a single reported occasion, Midway (Balazs 78). At Laysan (P. and B. Johnson, personal communication) and Lisianski Islands, some turtles also emerge on calcareous beachrock slabs. At Nihoa, two turtles have been seen on a single occasion basking on a rock at the base of the island's northwest cliff (Clapp et al. 173; Kridler 326). At Necker Island, basking turtles regularly use a small sloping rock ledge measuring approximately 4 by 5 m. During periods of large westerly and northwesterly ocean swells, some turtles bask at an alternate protected shoreline area a short distance away that is comprised of smooth waterworn boulders. The resident aggregation of green turtles that basks and feeds at Necker Island is undoubtedly one of the most interesting, unusual, and fragile components of the Hawaiian Chelonia population (Balazs 72).

Although basking occurs principally in the daytime between approximately 1000 and 1830 h (variable with season), turtles at Necker Island have

been found to also commonly emerge at night. At times this nocturnal emergence appears to be correlated with the setting of a bright moon (Balazs 72). The author has also observed small numbers of turtles resting along the shoreline at night at French Frigate Shoals and Laysan Island, but not at Lisianski Island. Amerman (24), Kridler (319), and Sibley (444, 445) frequently found turtles resting at night on Southeast Island at Pearl and Hermes Reef. Amerson $et\ al.$ (32) attributed nighttime emergence to the disturbing activities of research personnel during the daytime. However, this seems unlikely in view of the fact that, for the September 1967 visit to Southeast Island by USFWS personnel, Kridler (319) stated "When the island was first landed upon, there were no turtles present on the beach. At dusk the first day, however, one after another hauled up on the beach on the lagoon side near camp until 19 were present."

With the exception of La Perouse Pinnacle, basking occurs on all of the islands at French Frigate Shoals (Figure 2), as well as on several unnamed seasonally occurring sandbars. The northern shore of Trig Island and the northeastern shore of Whale-Skate Island are the most heavily utilized during all months of the year by the resident aggregation. At East Island, basking tends to coincide more with the breeding season (April-September). Turtles use the entire coastline, but higher concentrations consistently occur at the southeastern end (Figure 6, areas 8-9). As with nesting, turtles display a fixity for basking on a particular island and, to a lesser extent, for regularly basking at the same site on that island. The greatest numbers of basking turtles are found throughout French Frigate Shoals during late May and June due to the presence of the migratory breeding assemblage. The incidence of basking then declines as the breeding season progresses (Figure 11). The greatest number of basking turtles seen by the author at any one time was 52 (18 males, 18 females, and 16 unknown) along the northeastern shore of Whale-Skate on 12 June 1978 at 1630 h. It is of interest to note that turtles have never been observed entering into nesting activity directly from a basking position.

Some adult Hawaiian *Chelonia* apparently do not bask. During each breeding season at French Frigate Shoals since 1973, approximately 46% (range 32.7%-56.2%) of the turtles identified with painted numbers on their carapace while nesting were subsequently never seen basking. Some of these females are undoubtedly among the 40% that only lay a single clutch of eggs in a breeding season (section 3.15). Consequently, after nesting the turtles may not be present to bask because they have either departed on the return trip to their resident area, or have been eliminated by tiger sharks. Females that attempt to nest but no not lay eggs and are subsequently not seen again (section 3.15) also constitute some of the turtles that are not seen basking. It is possible, however, that turtles in both of these categories do bask, but only during the time prior to first coming ashore to nest or make nesting attempts.

No differences were found between the lengths of the internesting intervals of basking and nonbasking turtles observed during the 1974 and 1975 breeding seasons. This indicates that basking does not significantly hasten the *in vivo* development of eggs for oviposition as might be expected.

It is important to note that at least some members of the seasonal breeding aggregation that are from resident areas in the main islands do, in fact, bask while they are at French Frigate Shoals. This is a significant point in that the 54% recorded basking each season could conceivably consist of only those females from Laysan and Lisianski Islands and Pearl and Hermes Reef where basking is a regular occurrence. Both males and females observed basking at French Frigate Shoals have been among the tagged turtles recovered in the main islands (Table 15). In addition, basking has been displayed at French Frigate Shoals by three turtles that were returned to the wild after extended periods in captive facilities where emergence for basking was not possible (Table 16).

Investigations of the thermal ecology of basking Hawaiian Chelonia are currently being conducted by Whittow and Balazs (549). Results of this work to date have shown that the surface temperature of the carapace measured with a radiometer can attain values as great as 42°C. The large areas of black pigmentation present in most adult Hawaiian Chelonia undoubtedly contribute to high surface temperatures during periods of intense solar radiation. The greatest internal body temperature recorded through the cloaca was 31.3°C at a time when the ambient seawater temperature was 26.3°C. Shortly after coming ashore to bask, some turtles open their mouth to a wide position and regurgitate small amounts of liquid (see Anonymous 670 for photograph). This is probably a result of compression of the stomach due to the body weight pressing on the plastron while on land. Turtles exhibit very little activity while basking except for occasionally flipping sand on their carapace for thermoregulation (see Tinker 492 for photograph). They do not, however, seem to orient their position in relation to the sun. In males, the tail will frequently be curled close to the body rather than fully extended. The length of time spent basking appears to be inversely related to the black-globe temperature. Respiration patterns while basking have been found to consist of breath-holds averaging 3.6 min, followed by a single shallow breath.

Basking in freshwater turtles (and other poikilotherms) is principally a behavioral strategy to raise body temperature and accelerate metabolic processes such as digestion and growth. Other motivating factors or benefits that have been suggested include synthesis of Vitamin D from skin sterols (Pritchard and Greenhood 419), removal of epizoics through drying, and social interaction (Boyer 132). These factors could also be applicable to basking by Hawaiian green turtles.

With respect to socialization (Hirth 265), considerable gregarious behavior is displayed while basking at French Frigate Shoals, with turtles often in direct contact or even partially on top of one another (Balazs 57). This is, of course, consistent with the other life activities of *Chelonia* such as feeding together, breeding together in large aggregations, and probably even traveling together across the open ocean. Hawaiian monk seals sometimes show gregarious tendencies toward basking turtles, both at French Frigate Shoals and at Necker. This has involved seals of all sizes from young pups to adults. Mothers with newborn pups may, however, make aggressive gestures and vocalizations at turtles emerging to bask in the immediate shoreline area.

One of the advantages to Hawaiian *Chelonia* obtained from basking is the reduction in exposure to predation by tiger sharks. In some cases, this could even be the motivating factor for basking (section 3.33). Emergence to land at

night may be especially advantageous, considering that tiger sharks are believed to be principally nocturnal predators. Resting along the shoreline at night could, however, also be due to a scarcity of acceptable resting sites located underwater. A further advantage to resting on land would be the conservation of energy by not having to periodically swim to the surface for respiration.

Hawaiian *Chelonia* will bask under captive conditions if they are provided with a sloping area suitable for emergence (Balazs and Ross 88). Both Sea Life Park and the Kahala Hilton Hotel on Oahu have display facilities in which Hawaiian green turtles regularly bask. However, hawksbills and loggerheads in the same pool at Sea Life Park never exhibit this behavior. A subadult green turtle of Hawaiian origin at the Kewalo Marine Laboratory, University of Hawaii, also regularly basks on a wooden ramp installed in its concrete tank (Whittow and Balazs 549). There are no reports in the literature of green turtles from other populations basking in captivity. However, most facilities where marine turtles are maintained do not have sloping areas where emergence can occur.

The basking behavior of Hawaiian *Chelonia* could very well be an inherited characteristic that evolved as a protective mechanism against tiger sharks and as a method for gaining body heat at locations where seawater temperatures were marginal. The mean temperature of 20.5°C in February at the northwestern end of the Hawaiian Archipelago (section 3.43) could consitute such an environment at the present time, and perhaps cooler ocean conditions prevailed during the early development of the population. The survival value of basking, however, declined significantly with the first arrival of humans in the NWHI in the late 1700's. The extensive exploitation of turtles that subsequently took place can be attributed mostly to the basking behavior which provides accessibility for easy harvesting in the terrestrial environment.

In addition to the unique research opportunities for tagging (section 3.52) and depth recordings (section 3.15), the basking behavior of Hawaiian Chelonia offers considerable potential for investigations of hearing and vision on land under natural conditions. The author is particularly interested in the aspect of vision, due to the fact that green turtles are believed to be myoptic when out of the water (see Hirth 265). This would appear to be an unusual evolutionary development considering that the turtle's eyes leave the water each time a breath is taken. Observations to date have indicated that Hawaiian Chelonia display considerable visual sensitivity while basking.

4. POPULATION

4.1 Structure

4.11 Sex ratio

The inability to distinguish immature males from females on the basis of external characteristics is a limiting factor in determining natural sex ratios in populations of *Chelonia* and other marine turtles. Observations at French Frigate Shoals during June of 1973, 1978, and 1979 on days when relatively large numbers of adult basking turtles were ashore revealed a sex ratio of 66% females and 34% males (range 50%-81% females, 23%-50% males). As the breeding season progresses, the percent of basking males has been found to decline considerably. Of the 33



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