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## THE IMPRINTING HYPOTHESIS AND SEA TURTLE REPRODUCTION

DAVID W. OWENS, MARK A. GRASSMAN, AND JOHN R. HENDRICKSON

**ABSTRACT:** Carr proposed that sea turtles learn characteristic components of their natal beach early in life. Keen olfaction and possibly other senses would then be used for the return to their natal beach for nesting. Verification of this hypothesis, using experiments designed to "artificially imprint" turtles to a new beach, has been hampered by several aspects of sea turtle life-history. Laboratory tests suggest that loggerheads (*Caretta caretta*) will acquire a food preference and that this preference has an olfactory component, but that food imprinting does not occur because preference for the initial food is lost rapidly. A preliminary laboratory attempt at "artificially imprinting" on chemical cues is equivocal. An alternative to the imprinting hypothesis is a "social facilitation model" proposed by Hendrickson. This hypothesis supposes sociality for maturing turtles in which first-time nesters encounter and follow experienced adults to the nesting beach, which they "learn" by olfactory and other navigation systems. The latter model appears to have parsimonious attributes, thus warranting increased consideration for at least some populations.

*Key words:* Reptilia; Testudines; Cheloniidae; Imprinting; Olfaction; Sociality

THE imprinting hypothesis which was first discussed widely in the late 1950's by Carr (1967), stated that turtles learn an identifying cue or set of cues characteristic of the natal beach. The process would occur during a sensitive period in the nest or as the hatchling enters the sea and swims away. At sexual maturity, the return navigation to the natal beach is facilitated by orientation to the cue or cues. It is an intriguing model which would help to explain the unusual reproductive pattern seen in sea turtles. Initially, it was thought by Carr and his associates that experiments involving relocation of hatchlings would provide both the proof for the hypothesis and an active conservation tool. Beginning 28 yr ago, extensive relocations of hatchling green turtles (*Chelonia mydas*) from Tortuguero, Costa Rica, were made to several locales throughout the Caribbean and Gulf of Mexico. It became apparent in the 1960's and 1970's that these and other similar experiments were probably flawed by several problems: (1) A probable high mortality rate for hatchlings (Hirth and Schaffer, 1974) would have necessitated the introduction of many thousands of hatchlings at each beach in order to realize recruitment. Although thousands of

hatchlings were introduced over a 5 yr period (Carr, 1967; Rudloe, 1979), efforts were spread over several beaches. (2) A recent concern is the unanticipated long developmental period which may occur in green turtles. Although captive-reared females may reach sexual maturity at as early as 8-9 yr of age (Wood and Wood, 1980), under natural conditions there is some indication that 15-40 yr may be required (Balazs, 1980; Limpus and Walter, 1980). Possibly some of the turtles relocated in the 1950's may still return to surrogate nesting sites. (3) An additional consideration is the inability to recognize a given turtle if and when it does return. Tagging an animal that grows from 20 g to 200 kg and which might not be seen again for many years remains a significant problem. A living tag procedure, involving auto-grafting, may yet provide a method for marking hatchlings permanently (Hendrickson and Hendrickson, 1981). (4) Some conservation programs incorporating nest transplantation over long and short distances may have inadvertently altered sex ratios in a detrimental way. This suggestion has arisen because temperature-dependent sex differentiation occurs in many turtles (Yntema and Mrosovsky, 1980). (5) A fur-

ther complication which has not been considered is the role of timing in an animal's life history. First, if imprinting occurs, there are no clues as to when the "critical period" or optimum learning phase occurs. Second, the importance of seasonality in offshore currents has not been evaluated. Currents may be critical in distributing hatchlings to eventual feeding grounds, especially considering recent discoveries of apparent population-specific hatchling-frenzy in *C. mydas* (Dalton, 1979a,b). (6) Finally, the potential importance of adult sociality has never been considered in conservation programs. Hirth (1971) proposed that navigation may involve a multiplicity of cues. Herein, we suggest that social encounters may play a role in locating nesting beaches, particularly for virgin females. Should sociality be important in nesting migration, the lack of "experienced" females would reduce markedly the chances of establishing a new nesting colony. Rather, one would predict recruitment only to established nesting beaches.

In short, due to one or more of the above problems or to other as yet unidentified difficulties, there are no data from any conservation program which demonstrate recruitment to an existing or proposed new nesting beach. Nevertheless, the practice of attempting "artificial imprinting" appears to be on the increase around the world.

#### OLFACTORY IMPRINTING

The most appropriate model for sea turtle imprinting is not the classic sexual or filial imprinting of nidifugous birds, but rather the olfactory or chemical imprinting found in salmonid fishes. The importance of olfactory imprinting to salmon was carefully demonstrated by Hasler and his associates in the mid-1970's using an "artificial imprinting" protocol (Cooper et al., 1976). Even an inorganic component such as calcium ion is of potential importance in migratory behavior of sockeye salmon, *Oncorhynchus nerka* (Bodznick, 1978).

In salmon, as in sea turtles, it is unlikely that chemical imprinting can explain the entire migration; however, the demonstration of such a system in other oceanic wanderers is indeed the strongest argument for continued consideration of the imprinting hypothesis in sea turtles.

Olfactory involvement in sea turtle navigation has been discussed on many occasions (Carr, 1967; Koch et al., 1969) and reviewed recently by Manton (1979). Manton et al. (1972a,b) used operant conditioning to demonstrate olfactory acuity and discriminatory ability of young green turtles. They were also able to show that taste is not the chemical sense involved, because chemically anosmic animals could make none of the discriminations that were possible in animals with functional olfactory epithelia. Olfaction has also been implicated as a possible homing mechanism in the wood turtle, *Clemmys insculpta* (Carroll and Ehrenfeld, 1978).

Our suggestion of a central importance for olfaction does not rule out other cuing systems. In fact, sea turtles would be very unusual if they depended on a single orientation system. For example, Ridgway et al. (1969) demonstrated an acuity for low frequency sound in *C. mydas*. Using cochlear potentials, maximum sensitivity was seen in the region of 300–400 Hz. Wave sound on beaches could therefore be used as a cue. The ability of three species of turtles to perform true navigation feats was shown recently by DeRosa and Taylor (1980). Both a sun-compass and an internal biological clock were demonstrated in *Trionyx spiniferus*, *Chrysemys picta*, and *Terrapene carolina*. The old suggestion of magnetic cuing has also been resurrected recently with the report of the ferrous material magnetite in the brain of *Caretta caretta* but not in that of the snapping turtle *Chelydra serpentina* (Kirschvink, 1980). Unfortunately, space will not permit a thorough evaluation of each of these potentially important systems. Rather,

we have chosen to concentrate our discussion on chemoreception, where there is a modest literature.

#### CHEMICAL IMPRINTING IN TURTLES

A form of imprinting analogous to filial imprinting of nidifugous birds has been proposed for *Pseudemys scripta* and *C. serpentina* (Evans et al., 1973, 1974). Sibling pairs of juvenile turtles kept together in the same tank spent more time together in test situations than siblings kept in separate tanks. Olfaction was found to play an integral part in this social interaction. An alternative explanation is that animals may have become conditioned to their olfactory environment, associating it with feeding or home territory. Thus, in test situations a turtle might be expected to spend more time in association with a familiar tank mate because the mate had contributed to an olfactory environment associated with food or home site. Further experimentation is needed in this poorly studied area.

The food preferences of hatchling snapping turtles may be affected by early feeding experience (Burghardt, 1967; Burghardt and Hess, 1966), an observation which these authors called "food imprinting." Turtles fed 2 wk on a particular diet preferred the initial food when presented a choice between three foods. This preference persisted for as long as 12 d after the animals were changed to other diets. However, Mahmoud and Lavenda (1969) fed *P. scripta* a particular diet for 30 d and found the initial preference to be extinguished after 16 d on a new food. If food imprinting is defined by a primacy effect as Burghardt (1967) suggested, these animals could be said to have been food imprinted. However, irreversibility or at least the persistence of entrained behavior has been historically considered to be an important characteristic of imprinting (for review see Sluckin, 1972).

The suggestion that early feeding experience in hatchlings may affect later

feeding behavior raises an important question related to conservation. Could the efforts dedicated to head-starting, which is the practice of raising turtles to a larger size prior to release (Pritchard, 1979), be nullified by producing animals that are imprinted on inappropriate food materials? For example, many of the projects use commercial pelleted food.

An additional concern with respect to early feeding involves migration. It has been proposed that hatchling sea turtles imprint to chemical cues at the beach or in the water (Carr, 1972) and return many years later to nest. Presumably, the currents passing each nesting beach have characteristic biota on which the hatchlings would feed. These foods might constitute an important component of the early chemosensory learning. If turtles imprint in a manner analogous to salmon, these early feeding experiences might provide specific chemical cues for their eventual return for nesting.

An experiment was conducted to test food imprinting in sea turtles (Grassman and Owens, 1982). Loggerhead turtles (*C. caretta*) developed a preference for foods they were fed for 14 d beginning approximately 5 d after hatching (Fig. 1). Turtles conditioned to a particular food were able to select that food over two other choices both when the food was visible as well as when it was covered by a piece of cloth. This indicates that chemoreception is involved in food selection. These preferences were, however, extinguished after 14 d of feeding on alternate foods. Because preferences were ephemeral under laboratory conditions, it seems unlikely that headstarting would affect adversely the feeding behavior of turtles by feeding them pellets or other unnatural diets. Extinction of early feeding preferences in these experiments does not eliminate the possibility that sea turtles imprint to their natal beach or that early feeding experience might play a role in imprinting. One might expect reproductive hormones to play a role in nesting migrations of turtles. Juvenile

turtles, such as those used in these experiments, might not be expected to show behavioral responses to "home" odors until they are in an appropriate reproductive condition.

To investigate further the olfactory imprinting hypothesis, a laboratory experiment was conducted which was modeled after studies of Hasler and co-workers on salmonids (Cooper et al., 1976). A preliminary report of the work has been published previously (Grassman and Owens, 1981). *Caretta caretta* eggs were divided into four treatment nests of equal size. The following treatments were used: (1) The nest was kept moist with  $5 \times 10^{-5}$  M morpholine dissolved in 0.9% Instant Ocean® until after hatching, when the turtles were placed in a tank of  $5 \times 10^{-5}$  M morpholine in artificial sea water (MPP treatment). (2) The nest was kept moist with artificial sea water (0.9%) alone and hatchlings were placed in a tank of  $5 \times 10^{-5}$  M morpholine in Instant Ocean (MPO treatment). (3) The nest was kept moist with  $5 \times 10^{-5}$  M 2-phenylethanol in 0.9% Instant Ocean and the hatchlings were placed in a tank of  $5 \times 10^{-5}$  M 2-phenylethanol in artificial sea water (PPP treatment). (4) The nest and hatchlings were exposed only to Instant Ocean (UNT, untreated). Treatments were continued in tank water until testing was completed. Nest treatments included 2–5 d during which hatchlings were emerging from the broken shells and absorbing yolk sacs. Testing began approximately 5 mo after hatchlings were placed in tanks and continued for another 5 mo.

Each test involved placing a single turtle in an electronic monitoring tank (Fig. 2) and presenting the animal with a simultaneous choice between four compartments containing either  $5 \times 10^{-5}$  M morpholine,  $5 \times 10^{-5}$  M 2-phenylethanol, or two controls. The monitoring tank recorded amount of time an animal spent and number of entries it made into each compartment. After an 0.5 h acclimation period, each run lasted 4.5 h. The partic-

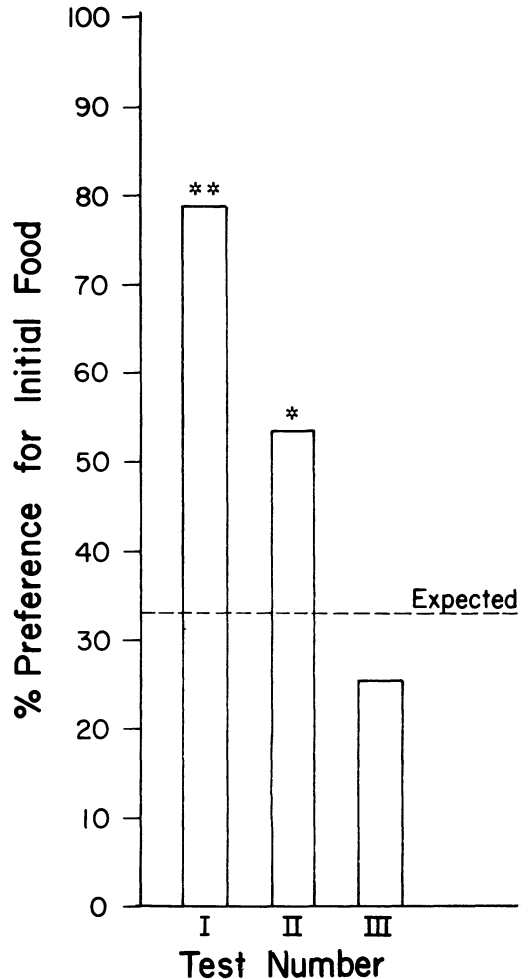


FIG. 1.—Responses of *Caretta caretta* to foods they were fed for 2 wk after hatching (from Grassman and Owens, 1982). (I) Response to initial food 1 day after the initial 2 wk training period. (II) Response to initial food when covered with cloth to eliminate visual cues. (III) Response to initial food after 2 wk of feeding on an alternate diet. \*\* $P < 0.001$  different from expected. \* $P < 0.01$  different from expected.

ular infusion that a compartment received was varied to eliminate compartment bias. Analysis of variance, followed by a Duncan's multiple range procedure (Sokal and Rohlf, 1969), was used to analyze data ( $\alpha = 0.05$  in all cases). To meet assumptions of ANOVA, analyses were performed on data transformed by arcsin.

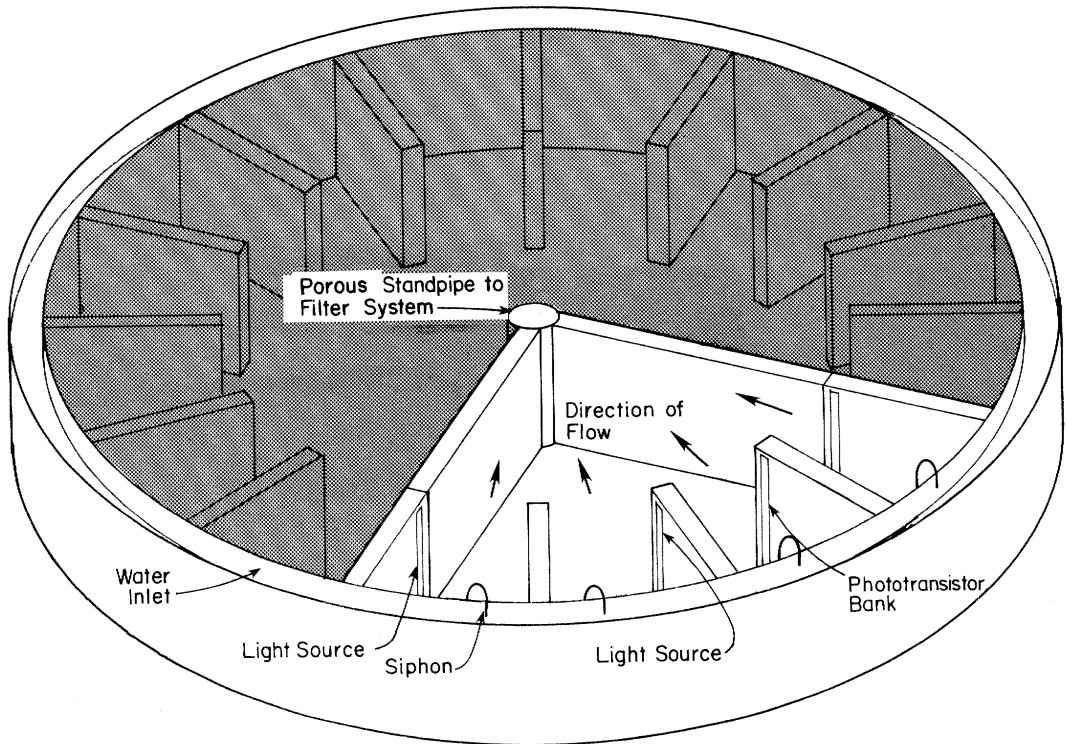


FIG. 2.—Schematic representation of the electronic monitoring tank (Kleerekoper, 1977) as modified for imprinting studies of turtles. Precise volumes of chemicals were pumped into compartments to maintain appropriate concentrations.

We hypothesized that each group of turtles might respond to the environment most similar to that of their holding tank, associating it with feeding or “home” water. However, only MPP turtles showed a significant increase in percent entries to a compartment containing a chemical they had experienced previously—morpholine in this case (Fig. 3). Superficially, this result suggests that the chemical nature of the nest environment may affect the animal’s orientation behavior later in life. Time spent in the different compartments was similar to percent entries (Grassman and Owens, 1981).

UNT animals showed significantly greater percent entries comparing morpholine to 2-phenylethanol and the entire pattern of their response was similar to the MPP group (Fig. 4). Their re-

sponses to chemical treatments did not differ significantly from their responses to untreated compartments. Although it might appear that morpholine is inherently more “attractive” to turtles than 2-phenylethanol, the suggestion is not supported by the results obtained with MPO and PPP animals (Figs. 5, 6). The failure of PPP turtles, which were treated in a fashion parallel to MPP, to respond to 2-phenylethanol is also unexplained. Salmonids have been imprinted to 2-phenylethanol (Scholtz et al., 1976). Manton et al. (1972*a,b*) demonstrated that green turtles can detect and remember 2-phenylethanol cues in conditioning experiments. Therefore, it seems unlikely that loggerhead turtles would be unable to imprint to 2-phenylethanol if they do in fact imprint to morpholine.

A treatment (UNT, MPP, MPO, and

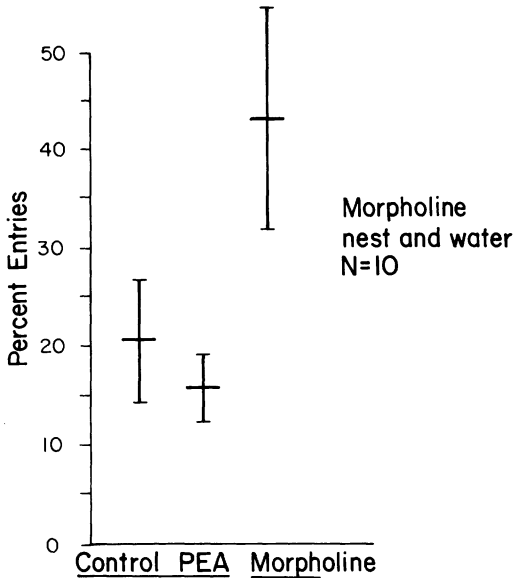


FIG. 3.—Percent entries into control compartments and into compartments treated with 2-phenylethanol (PEA) and morpholine by turtles receiving morpholine in the nest and in water of the holding tank. Horizontal bar represents the mean, vertical bar the SEM. Compartment environments underscored with the same line are not significantly different (Duncan's,  $P < 0.05$ ).

PPP) by infusion (morpholine, 2-phenylethanol, and control) factorial ANOVA was performed to determine if there was significant interaction between treatment group responses and environments presented to animals in the monitoring tank. Because the interaction was not significant ( $P = 0.08$ ), there are no statistical differences in UNT, MPP, MPO, and PPP in these test situations.

Why would we expect a juvenile turtle to orient to a cue even if it had been imprinted to that cue? Normally one would predict the response to be evident only in the adult. Because the motivation to orient to the chemical cue cannot be reproductive, maturity being many years away, we felt that a response might still be shown to be due to a substituted motivation. Because the turtles were unfed, food searching in the monitor tank would possibly be elicited in place of the repro-

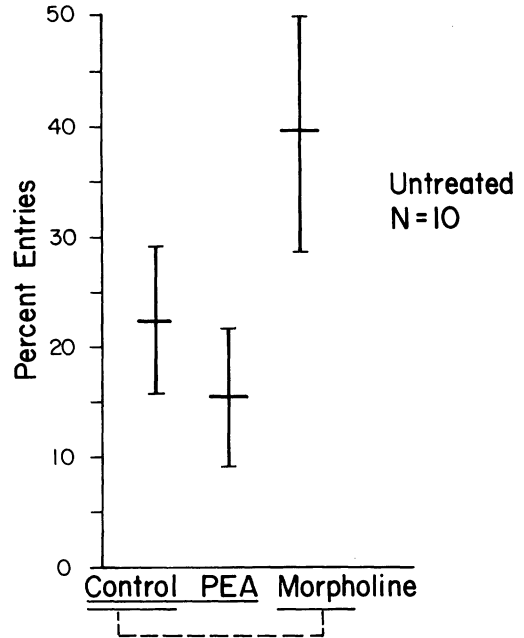


FIG. 4.—Percent entries into control compartments and into compartments treated with 2-phenylethanol (PEA) and morpholine by turtles receiving no chemical treatment. Horizontal bar represents the mean, vertical bar the SEM. Compartment environments underscored with a solid line, or solid lines connected by a dashed line, are not significantly different (Duncan's,  $P < 0.05$ ).

ductive responses normally associated with the stimulus in adults. If a group of animals had been imprinted during the critical period in our experiment, they would potentially exhibit a prolonged orientation to the stimulus. Thus, recognition of the cue might be demonstrated without attempting the logistically difficult experiment on migratory adults. These data are preliminary and do not constitute proof that any form of imprinting has occurred. However, we are encouraged that this form of experimentation is worth pursuing.

#### SOCIAL FACILITATION MODEL

Although the imprinting hypothesis has received virtually all of the experimental attention, at least one other hypothesis deserves consideration. Hendrickson (1958) outlined the "social

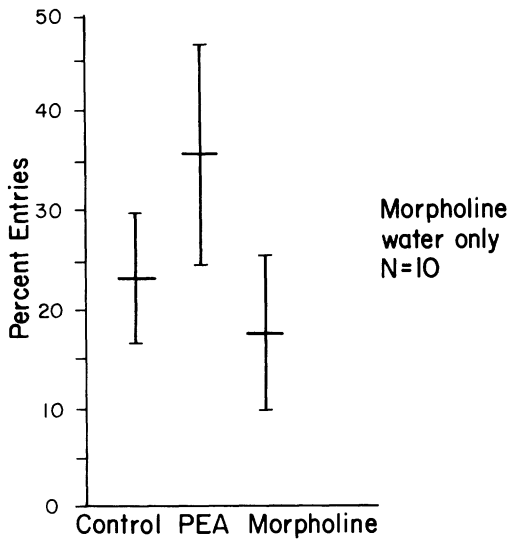


FIG. 5.—Percent entries into control compartments and into compartments treated with 2-phenylethanol (PEA) and morpholine by turtles receiving morpholine only after removal from the nest. Horizontal bar represents the mean, vertical bar the SEM. Compartment environments underscored with the same line are not significantly different (Duncan's,  $P < 0.05$ ).

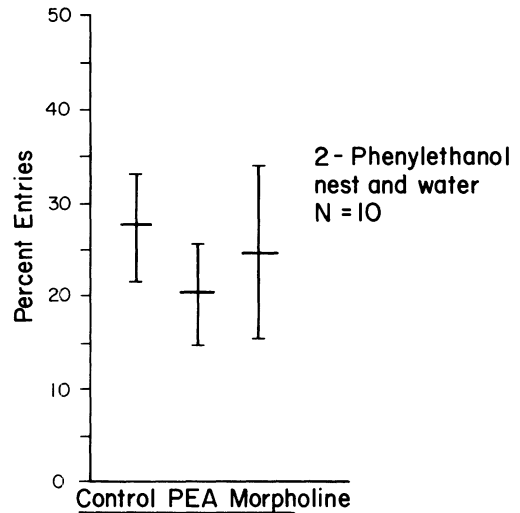


FIG. 6.—Percent entries into control compartments and into compartments treated with 2-phenylethanol (PEA) and morpholine by turtles receiving 2-phenylethanol in the nest and in their holding tank. Horizontal bar represents the mean, vertical bar the SEM. Compartment environments underscored with the same line are not significantly different (Duncan's,  $P < 0.05$ ).

facilitation model" (Fig. 7) in which no specialized information would be acquired by hatchlings. Rather, the critical point in the animal's life history would be a time of increased stochastic movement as the young animal reaches sexual maturity. These turtles would then have a greater likelihood of encountering other conspecifics, most of which would be "experienced." Onset of this behavior would probably be controlled by the same endocrine changes that induce sexual maturation. The net effect would be that virgin females or males would join groups and follow them on a particular migration to the nesting beach. If favorable mating and nesting experiences occur, young animals would then "learn" this particular nesting beach and acquire such characteristics as site fixation.

Crucial to this hypothesis is a form of sociality for sea turtles which is not well documented. Regarding all turtles, Eh-

renfeld (1979) concluded that "sociality is neither well-developed nor an indispensable feature of the various behaviors associated with nesting." There are indications that this statement may not be appropriate for some species of sea turtle. In particular, *Lepidochelys* appears to exercise a great deal of sociality in coordination of the massive "arribada" nestings. There are numerous reports in the popular literature of turtles moving in schools (Carr, 1967), although these are not well documented. Booth and Peters (1972) observed nesting reserves offshore from the nesting beach where groups of inter-nesting females would wait until time for subsequent nestings. This aggregation of females in the reserve area appeared to provide protection for nesters from the aggressive pursuits of amorous males. Although similar phenomena have not been described elsewhere, this situation suggests sociality.



In fish and marine mammals, schooling is facilitated by such sensory adaptations as the lateral line and sonar systems respectively. Do sea turtles have comparable sensory capabilities? As discussed earlier in regard to chemical imprinting, we believe that olfaction could be the critical key once again. A plausible model for sea turtle schooling involves a loose aggregation of animals in which the individuals would be up to hundreds of meters apart swimming on the same heading. If the turtles can smell each other, olfactory-gradient recognition could keep the loose school together. In this case, tight schooling would not be necessary. Pritchard (1969) suggested that Rathke's glands on the plastron could provide a pheromone system of communication. Ehrenfeld and Ehrenfeld (1973) have shown these to be typical exocrine glands. Histochemical data suggested that a glycoprotein secretion is present. Because they examined only immature specimens and did not evaluate the secretion itself, more work is needed before the potential of these glands in pheromone production can be evaluated. If a pheromone system is to be demonstrated, considerable behavioral research will be necessary. Pheromonal involvement in navigation and homing has been suggested in the char, *Salmo alpinus* (Nordeng, 1971), and Atlantic salmon, *Salmo solar* (Solomon, 1973). Such a system in sea turtles would be particularly valuable in recruiting novice animals into the migratory population.

Homing over great distances is a legendary capability of sea turtles which is often recounted by fishermen (Carr, 1967; Rudloe, 1979). The recent work of Ireland (1979a,b) has substantiated this capability on a limited scale using immature *C. mydas* in Bermuda. The animals made complex return trips in relatively short times after displacements of up to 6.8 km. Reports of sea turtle homing lend some support to the hypothesis that as adults these species can learn a com-

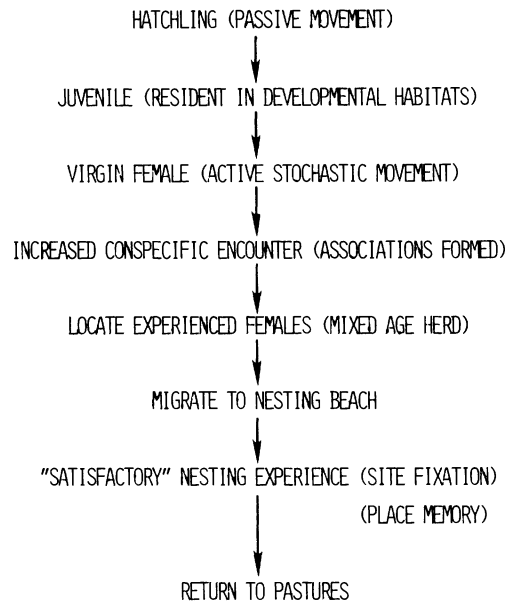


FIG. 7.—The model of social facilitation, modified after Hendrickson (1958). The model refers specifically to female *Chelonia mydas*.

plex navigation pattern such as would be required for a nesting migration.

#### GENETIC COMPONENTS

A final possible contribution to migration patterns seen in each population may be behavioral genetic-coding. In specific populations of sockeye salmon, characteristic directional or compass preferences are innately exhibited. These preferences correlate well with future migratory requirements of the population (Ross et al., 1980). Dalton (1979a,b) studied rhythmic components and duration of hatchling frenzy using *C. mydas* hatchlings from Ascension and Costa Rica, and found distinctive and characteristic activity patterns. She suggested that these patterns may be adaptive for current systems adjacent to specific nesting beaches. Thus, if the primary current is a great distance offshore, the hatchling frenzy would be precoded for a longer initial active swim. If this is genetic coding,

migration patterns may also have a genetic component specific to a population.

#### DISCUSSION

The evolution or development of long-range migration patterns is a question that has generated considerable interest and speculation. Carr and Coleman (1974) have proposed a gradual development based on patterns of plate tectonics and olfactory imprinting (Koch et al., 1969). Hirth (1978) proposed a continuum of migrations from simple to complex patterns over geological time. Gould (1978) objected to these gradualistic explanations and agreed with Carr's earlier theory that the initial migration could have happened very suddenly. Whether stated or implied, each of these theories appears to relate back to the imprinting hypothesis.

Although attention has been given to the possibility of turtle imprinting, implications of the social facilitation model (SFM) have not been considered. The ability of adults to learn and remember the location of a nesting area seems to be a more parsimonious hypothesis than hatchling imprinting. With the SFM in *C. mydas*, for example, memory of cues would have to persist for 1–4 yr, whereas an imprinted turtle would have to remember cues for 15–45 yr. For this reason the SFM deserves attention and may even be easier to test than imprinting. For example, the SFM implies that younger turtles would be less adept at nesting than older animals (Hendrickson, 1958) in that improvement or modification of nesting site over time would be more likely to occur than in imprinting. This suggests that first nesters might be more likely to choose less desirable nest sites. The SFM hypothesis could be tested, since neophyte nesters might have smaller clutch sizes or eggs which would be identifiable. This is the case with new *C. mydas* nesters at Cayman Turtle Farm (Wood and Wood, 1980). Pritchard used this line of reasoning to argue that new females of Kemp's ridley (*Lepidochelys*

*kempi*) may be recruiting to the nesting beach in Tamaulipas, Mexico (Pritchard, 1980). Scientists may have overlooked these nesters since research efforts have been concentrated on prime nesting beaches. Possibly the hundreds of *C. caretta* nesting areas along the east coast of the United States could be examined for this type of neophyte nesting. Stoneburner and Ehrhart (1981) noted an extremely long-range change in nesting site for a single loggerhead. Captive breeding programs that have utilized wild-caught green turtles at Grand Cayman (Ulrich and Owens, 1974), Miami, and Hawaii verify the flexibility built into whatever cuing system is used.

With regard to testing the SFM, a strong argument can be forwarded in support of the joint Mexican–United States experiment which is attempting to establish a new nesting beach in Texas (see below). If the SFM has credence, one would predict that, despite elaborate efforts to “artificially imprint” the ridleys to Padre Island, they would probably join the main fleet nesting in Tamaulipas, Mexico. If current tagging procedures on the head-started animals are satisfactory, the test should produce some results in from 3–5 yr. This assumes a sexual maturity at from 7–10 yr, which may still be optimistic.

If the SFM is part of the migration system, development of new nesting beaches would not be difficult to imagine. Under high nesting densities, crowding might induce subgroups to split off and seek new nesting beaches. Similarly, storms driving migrators off course could leave fleets of animals on untested shores. In either of these situations two events must then occur under SFM conditions to establish a new nesting beach. First, a favorable experience would lead the turtle back to the same nesting area in subsequent years. Second, some of the hatchlings would by chance have to be recruited into the adult group at the feeding ground. It is possible that a rookery could develop in an area with unfavor-

able currents. Hatchlings might then drift away and be lost or recruited to yet another population's feeding grounds. Persistence of such a situation would seem unrealistic except under very high population densities where the original parent population would continue to lose neophytes to the new migration group.

The most intensive sea turtle conservation effort currently underway is an international cooperative project designed to save the critically endangered *L. kempii*. Since 1966 the Mexican government has provided special beach guards and moved nests into protected enclosures at Rancho Nuevo in Tamaulipas, Mexico, the only known nesting locale for the species. In 1978 the United States joined the project with an "artificial imprinting" program in an attempt to establish a new nesting colony on Padre Island, Texas (Klima and McVey, 1982). This program is taking special care to avoid many of the problems listed above (particularly 1-4). Ehrenfeld (1980) has, however, criticized this form of sea turtle conservation, particularly with regard to the Kemp's ridley. He does not think that the unproven techniques of artificial imprinting and head-starting should be employed with this species. Supporters of the project disagree with this objection and believe that continuation of the experiment is an acceptable strategy for the following reasons: (1) Only about 2% of the population's egg production is siphoned off for the Padre Island program (e.g., 1855 of 85,217 eggs during 1979; Pritchard, 1980). The 1461 head-started turtles that survived weighed an average of 900 g each when released a year later. This is far greater survivorship than would be predicted for the entire remainder of the eggs for that year. McVey and Wibbles (pers. comm.) report that approximately 2.8% of the 1979 and 1980 releases have been recaptured. Of the more than 60 returns, only one animal had lost weight and it was recovered after only one month. Because 90% of the captures were of live, healthy animals, most

of which had doubled or tripled in weight, the preliminary results are very encouraging. The radio-tracking methodology used in the initial turtle release has recently been described by Timko and DeBlanc (1981). (2) This "artificial imprinting" experiment, because of its magnitude and increased attention to detail, is the only reasonable field test of the imprinting hypothesis being conducted anywhere in the world today. Because hatchlings cannot be marked adequately, only the onset of nesting at a new "imprint" site can substantiate the hypothesis. Recruiting to existing nesting rookeries cannot substantiate the imprinting hypothesis because new recruits may have followed experienced nesters to breeding grounds, as discussed above. Thus, the Padre Island relocation study is critical to the entire experiment in that it attempts to produce a distinct nesting locale. (3) The project has greatly increased public awareness of the problem, which may ultimately affect decision making with regard to improving the protection afforded this species in the wild. (4) A few of the head-started turtles are being maintained in captivity at larger aquaria. Should the wild population ultimately collapse, these individuals may provide a reserve gene pool for a future captive-breeding program. In the meantime, much can be learned about the reproductive biology of this species by studying these captive individuals (Owens, 1982). For example, we have recently determined the sex ratio of a set of the first year's animals which are being held in Galveston and Miami (Morris et al., 1981).

Although the conservation program for Kemp's ridley has attempted to correct the earlier suspected problems for this type of experiment, all participants and observers readily admit that there may still be many additional factors in need of consideration. An increased research effort in this area, as well as a more thorough evaluation of past and present projects, remains a critical need if we are to

ever understand sea turtle behavior and reproduction.

As Carr pointed out (1980), it is an unfortunate oversimplification to attempt to explain the diverse life-history patterns of all sea turtles based on his work with the Ascension and Tortuguero populations of *C. mydas*. Certainly imprinting, adult learning, and genetics could play varying roles within each of the genera of marine turtles. Even population-specific differences in the relative importance of the components might be expected. In populations of *Dermochelys*, *Chelonia*, and *Lepidochelys*, where complex migrations are evident, one might expect more complicated adaptations such as hatchling imprinting. The question of how a sea turtle chooses its nesting beach is of central importance to all conservation projects involving these species. Despite the inherent difficulties in studying these problems, we hope that both conservationists and scientists will persist in their efforts.

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