and in maintaining balanced polymorphisms. In monogamous animals, variations in fitness at breeding time should provide a general mechanism by which a mating preference can produce a selective advantage.

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Ecological or Phylogenetic Interpretations of Crocodilian Nesting Habits

NESTING habits within the Crocodilia range from simple excavation of a hole for egg deposition (as in most reptiles) to the construction of mounds of vegetation or other materials in which the eggs are deposited. Nests constructed by some Crocodilia show a considerable advance over those of any other reptilian group; this ability of the Crocodilia has been widely discussed. Wermuth[1] interpreted the available data to indicate that all possible gradations from simple hole nesting to elaborate mound construction were represented. Greer[2], following Schmidt[3], believes that nesting habits may indicate relationships, and has recently divided the group into hole versus mound nesting categories and discussed the evolutionary significance of this dichotomy.

Neill[11] has argued that the nesting habits of crocodilians are ecologically related, with mound nesting habits associated with marshy environments and the hole nesting habit with nesting on banks. This view has subsequently been adopted by Greer[14] juxtaposed with his original phylogenetic argument. Although the value of such an ecologically responsive character as a phylogenetic indicator may be seriously questioned on logical grounds, additional complexities in the reproductive behaviour of crocodilians are now known which demonstrate that nest type is not necessarily a genetically fixed character in all species.

Fig. 1 Nest of *Crocodylus acutus* in Gatun lake, Canal Zone, Panama. Nest hole is approximately in the centre of the clearing.

Several species are now known to, or are suspected to, display both behaviours, both between populations and even within populations.

Crocodylus acutus, considered by Greer[2] and all other workers to be a hole-nesting crocodile[3,5–7], may display both hole and mound building behaviours in different portions of its range, and even within single populations. In some localities, Jamaica and some Central American areas, for example (Fig. 1), it deposits its eggs in a hole, but in other areas, such as some portions of Mexico[4] and southern Florida, it builds well defined mounds (Fig. 2).

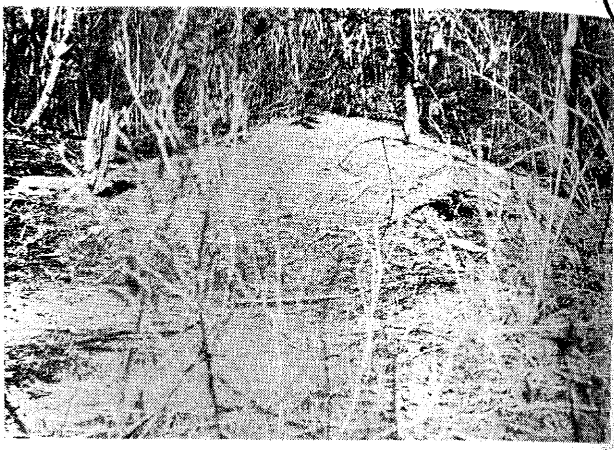

Fig. 2 Mound nest of *Crocodylus acutus* at Florida Bay, Florida.

In one locality, Florida Bay in the Everglades National Park, Florida, all nest types are utilized by the species (Ogden, personal communication). Some females construct mounds of large size (Fig. 2), some construct low, poorly differentiated, mounds, and some are known to lay their eggs in holes. Ogden, who is studying this population, reports that one female constructed a low mound and then laid her eggs in a hole dug in the trail leading to the mound. It will be interesting to learn of any differential hatching success or survival between the two nest types in this area.

There are several other species which display both nesting habits. *Crocodylus moreleti*, in Mexico, is a mound-nesting species (ref. 4 and personal observations of Powell and of Campbell) where it nests in swamp or marsh, but there is evidence that it uses nests in holes where it occurs along shallow forested streams with extensive sand banks. *Crocodylus rhombifer* of Cuba is a hole-nesting species[2,10], but there is evidence to suggest that this is only partly true (Fernandez). The term used to describe the nest of this species by the original source, "nido", can be translated either "hole" or "nest" and an error in translation is possible. Other species for which both nest types are indicated are noted in Table 1.

Table 1 shows a surprisingly good relationship between hole nesting and habitation in large rivers and lakes, and mound nesting and habitation in swamps, marshes, and other low-lying situations. It is not evident which specific environmental condition is most important in determining the nest type: position of the water table, availability of suitable substrate for digging holes, or probability of drastic unpredictable fluctuations in water level, and so on.

In the light of the crocodile's unusual, for a reptile, learning capacity[8] we may speculate that individual differences may be based on the ecological experience of specific females, but it may be more reasonable to expect that the particular nest type used, on the average, in a given area represents the most adaptive response to the particular set of environmental variables encountered in that area. But the phylogenetic scheme presented by Greer[2,14] is based on characters which are both ecologically responsive and intraspecifically variable and may

Table 1 Nest Type and Species Ecology

Species	Nest type	Habitat
Gavialis gangeticus	Hole	Large rivers
Crocodylus acutus	Hole or mound	Coastal marsh, larger rivers and lakes
Crocodylus intermedius	Hole	Large rivers and lakes
Crocodylus johnsoni	Hole or mound[11,13]	Savanna creeks and rivers, pools
Crocodylus niloticus	Hole	Large rivers and lakes
Crocodylus palustris	Hole or mound[15]	Diverse; marsh and swamp, lakes and rivers
Crocodylus rhombifer	Hole or mound *	Freshwater swamp and marsh
Crocodylus siamensis	Hole or mound[12]	Rivers and river swamps, lakes
Crocodylus cataphractus	Mound	Rainforest, savanna, wooded or grassy
Crocodylus novaeguineae	Mound	Freshwater swamps and marsh
Crocodylus porosus	Mound	Salt marsh, large rivers, lakes
Crocodylus moreleti	Mound[4] †	Savanna, river swamp, marsh-bordered lakes
Osteolaemus tetraspis	Mound	Rainforest streams, ponds
Alligator mississippieusis	Mound	Diverse; ponds, rivers, swamps, etc.
Alligator sinensis	Mound[9]	River flood plains, freshwater marsh and swamps
Caiman crocodilus	Mound	Diverse; marshes, swamps, ponds, lakes
Melanosuchus niger	Mound	Savannas, freshwater, marsh, grassy lakes
Paleosuchus palpebrosus	Mound	Swamp, forested pools and floodplains
Tomistoma schlegeli	Mound	Rivers and river swamps

* Fernandez (personal communication) reports that the nests of *C. rhombifer* are sand or soil mounds, or holes.

† Confirmed by Campbell and Powell.

Only species for which both data are available are included. References as in Greer[2] except as noted.

therefore be more properly interpreted as indicating ecological similarities rather than phylogenetic relationships.

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New Technique for the Study of Sperm Whale Migration

In the southern hemisphere, female and young male sperm whales (up to about 39 feet long) are not normally found in higher latitudes than 40° S while large males occur in Antarctic waters[1-3]; clearly many large bulls must migrate from the breeding areas into colder regions. Evidence of the return of large bulls to lower latitudes rests upon marking them in the Antarctic[4] or external infestation by Antarctic *Cocconeis* or *Cyamus*[5]. Only a single mark[5] has been recovered which provides direct evidence for the return north from Antarctic waters. This mark (USSR No. 650203) was fired on December 25, 1967, at 62° 22′ S 26° 25′ E and the whale was killed on May 13, 1968, off Durban. The small size of the male concerned (35 feet at death) makes this record rather surprising although Jonsgård[6] did mention that the smallest whales from Antarctic waters were about 35 feet. Marking can provide information on only a small part of the whale population at considerable cost, freshness of the whale restricts the value of infestation as an indicator but the study of food remnants in sperm whale stomachs provides another method without these disadvantages.

I have been studying the stomach contents of sperm whales for several years[7,8], including collections made in the Antarctic, at Durban and Donkergat, South Africa, and in Western Australia. The main food of sperm whales in these areas is cephalopod. Although cephalopod flesh is quickly digested by the whale, the chitinous jaws or beaks are retained in the second stomach and are, apparently, vomited periodically, as they are seldom found in the gut below that point. From studies on the flesh remains[8], it has proved possible to distinguish between cold water Antarctic cephalopods and those from temperate waters off Africa and Australia. Lower beaks from identified specimens have provided criteria for the identification of ingested lower beaks[7-9].

Stomach contents of some of the whales at Durban include beaks of Antarctic squid (Table 1). The majority of these are *Moroteuthis ingens*, *Mesonychoteuthis hamiltoni*, *Gonatus antarcticus* and an undescribed species of *Moroteuthis*.

Of twenty-two female whales about 64% contained no Antarctic cephalopod beaks in their complete stomach contents. Antarctic species contributed 1.3% or less of all beaks in each of the remaining stomachs. The northern limit of the Antarctic cephalopods is not known accurately, but their limited presence in female whales suggests that it must be close to 40° S. Near this latitude the subtropical convergence[10] probably acts as a faunal boundary[11].

Of twenty-nine male sperm whales examined at Durban, 17% had no Antarctic cephalopod beaks. In 50% of those with Antarctic beaks they contributed 1.7% or less of all lower beaks. Males 35 feet or less in length had few or no Antarctic beaks (Fig. 1), although in 60% of those over 37 feet Antarctic species contributed more than 9% of all lower beaks in each whale. This supports the observations that males less than 35 feet long do not normally go into Antarctic waters, and suggests that one male of only 37 feet did go far south. This male contained a greater percentage of an unidentified species of cephalopod than any other whale, and its previous movements may therefore have been rather unusual.

The percentage of Antarctic beaks in those males with more