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COURTSHIP AND MATING-RELATED BE-HAVIORS IN MYLIOBATID RAYS.—Direct observations of courtship and mating behavior is elasmobranch fishes are rare. This paucity of information stems primarily from logistic problems associated with extended underwater observations and the wide-ranging habits of these large fishes. Consequently, published descriptions generally cite fortuitous observations made on captive individuals. This paper describes probable mating-related behaviors observed in two species of rays (Myliobatidae) in their natural habitat.

The spotted eagle ray, Aetobatis narinari, is a circumtropical species common in coral reef and sand habitats where it feeds primarily on benthic mollusks (Bigelow and Schroeder, 1953). During a recent visit to Enewetak Atoll, Marshall Islands, I observed possible courtship and premating behavior on two separate occasions. The first observations were made from a pier at the southwest end of Enewetak Island on 20 October 1976 approximately 15 min after sunset. Just beneath the surface in waters adjacent to the pier, two males (all sexes determined by the presence or absence of claspers) of similar size (approximately .75-m wing span) swam juxtaposed behind the flanks of a larger female (approximately 1.5-m wing span). The trio, arranged in a wedge-shaped formation, moved in a clockwise pattern parallel to the length of the pier. From their positions behind the female, the two male rays both alternatively and collectively dashed forward and nipped at the posterior margin of the female's pectoral fins. In response, the female surfaced, raised her back out of the water, and vigorously

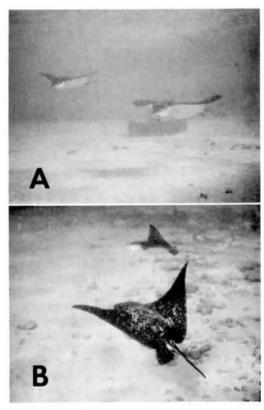


Fig. 1. Possible courtship-related behaviors in the spotted eagle ray Aetobatis narinari. A) Following behavior. Male (left) follows at rear flank of female (right). Male may also orient closer to female's pelvic region. B) Circling behavior. Male (in background) swims ahead and circles completely around female before returning to original follow position. Abrasions on female's dorsal surface inflicted by male during some dorsal mounts.

slapped her wings on the surface. The males briefly ceased their impingement upon the female but continued to follow (and nip) after the female resumed swimming a few seconds later. Occasionally, one of the males swam forward and circled completely around the swimming female before he returned to his original flank position behind the female. The three rays continued combinations of these behaviors: follow (\mathfrak{F}) , nip (\mathfrak{F}) , surface and splash (\mathfrak{P}) , and circle (\mathfrak{F}) at the pier for approximately 15 min until they moved south along the shoreline and out of view.

The second observations were made on 11 December 1976 beginning at 0900 h from a partially-submerged barge on the lagoon side

of Enewetak Island. On this occasion there was single male (approximately .90-m wing span) and a large female (approximately 1.25-m wing span) swimming together in a formation and pattern similar to that observed earlier at the pier. From the surface, I observed the following recurrent sequence of behaviors. Typically, the male approached the female from slightly above either the right or left rear quarter and positioned himself onto the female's dorsal surface. The female, however, was uncooperative and repeatedly shied away to one side after each mount. The male continued to press until, after three or four mounts, the female swam to the surface and prevented any dorsal approach by the male. Once the female was at the surface, the pursuant male began to alternatively 'bob' (swim along a sinuous path in the vertical plane of its forward motion; total vertical displacement = approximately 2 m) and 'sway' (swim along a sinuous path in the horizontal plane of its forward motion; total horizontal displacement = approximately 2 m) behind and below the female but made no further physical contact. The female cruised slowly at the surface for approximately 30 sec and then submerged to a depth of about 1 m. The male then immediately resumed further mounting attempts. Occasionally the male circled around the front of the female in the same manner as observed at the pier.

After 15 min of surface observations, I entered the water to take photographs. The pair continued swimming in formation (Fig. 1A), and showed no noticeable changes in behavior in response to my presence. However, the clearer underwater view soon revealed that during some mounts the male 'gouged' the female's dorsal surface with his lower dental plate and inflicted relatively large skin abrasions on her back (Fig. 1B). The female continued to avoid the male by veering away or swimming to the surface for a few seconds (at which the male began to 'bob' and 'sway'). After the female submerged the male continued to mount, gouge and intermittently circle the female (Fig. 1B). Approximately 10 min after I had entered the water, the female swam quickly toward the lagoon and out of sight, possibly in response to my relatively close approaches. Within seconds after the female had departed, the male began to swim in a wide circular pattern (radius = 10-15 m) while making approximately 45°-angle dives and ascents between the surface and bottom (an exaggerated 'bobbing' behavior). This

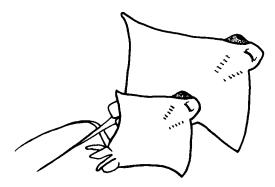


Fig. 2. Premating position in bat rays, Myliobatis californica, as viewed by author from below. Smaller ray (male) has tail flexed dorsally at 90° and right clasper erected at 45°. Male repeatedly bumped underside of female possibly in attempts to insert clasper into her cloaca. Redrawn from photograph.

behavior produced brilliant flashes of his white underside that could be seen even after the outline of the ray had disappeared from view.

A brief observation was made on the bat ray, Myliobatis californica, on 17 July 1977 while diving at the seaward edge of a bed of giant kelp, Macrocystis pyrifera, near the Isthmus at Santa Catalina Island, California. A male bat ray (approximately .75-m wing span) was positioned just ventral and behind a larger female (approximately 1.25-m wing span) as the pair swam slowly through the water column with synchronized beats of their wings. The male ray's tail was erected dorsally at 90° and one clasper flexed dorsally at approximately 45° in a parallel plane (Fig. 2). The male then moved slightly forward and began to bump his back against the underside of the female in what might have been an attempt to insert his clasper into her cloaca. Unfortunately, poor visibility prevented verfication of intromission if it did occur. The pair turned around in a wide circle and swam past once again in the same position before they disappeared from view.

Information on courtship and mating in sharks and skates is incomplete, and for rays almost non-existent. Wourms (1977) summarized the literature on mating in chondrichthyan fishes and suggested that rays use similar methods to copulate as small skates. Evidence presented for skates of the genus *Raja* by Richards et al. (1963) indicates that the larger species make either a dorsal or ventral approach to females for copulation. For the bat

ray, Myliobatis californica, the ventral approach is used by the male in a swimming mode, although it is not necessarily the sole method of copulation. The dorsal erections of the tail and clasper observed in M. californica are similar to those reported for the clear-nosed skate, R. eglanteria, by Libby and Gilbert (1960). In their observations, the male bent his tail 75° beneath hers and inserted one clasper (flexed medially 90°) into the female's cloaca. Unlike the bat ray, however, copulation occurred while the skates rested on the bottom and the male used his alar spines to gain purchase for ventral insertion. Alar spines undoubtedly facilitate reposed sedentary copulation in larger skates, thus myliobated rays which have a similar gross morphology but lack alar spines may resort to copulation while swimming as a primary mating mode. In the second observation made on eagle rays at Enewetak, the male mounted the female via a dorsal approach, but because he sometimes 'gouged' the female and no clasper flexion was seen, it is difficult to determine whether these were actual copulatory mounts rather than premating courtship behavior. Larger sharks have been described in copulo while swimming (Clark, 1963) and smaller sharks while at rest where the male wraps himself around the female (Dempster and Herald, 1961; Gilbert and Heath, 1972). Skates mate in resting positions on the bottom (Libby and Gilbert, 1960; Richards et al., 1963) and generally are not known to swim during copulation. Like large sharks, eagle rays (Randall, 1968) and bat rays (pers. obs.) are relatively active and often are encountered in the water column. Likewise, their mating-related behaviors might include relatively mobile modes when compared to the more demersal Rajidae and Dasyatidae.

There are similarities in courtship behaviors between different groups of elasmobranch fishes. Following, for example, where males closely follow a female from behind as observed in the eagle ray, was reported for the bat ray, Myliobatis californica, by Feder et al. (1974). They reported two separate observations of a female closely followed by two smaller males, with one male pushing the female in her genital region. Johnson and Nelson (1978) described close-following behavior in the blackfin reef shark, Carcharhinus melanopterus, and the reef whitetip shark, Triaenodon obesus, and suggested that this was an olfaction-mediated behavior where the male orients to the female's vent. Following behavior also occurred in the bonnethead shark, Sphyrna tiburo, (Myrberg and Gruber, 1974) and during mating season for gray reef sharks, Carcharhinus amblyrhynchos, at Enewetak (pers. obs.). Individual gray reef sharks in these follow formations at Enewetak also circled around the lead female and returned to a posterior position in a similar manner as observed for eagle rays. Such circling might function as a visual reinforcement between a leading female and following potential mates. Biting behavior, that results in tooth cuts and wounds usually on the dorsal surface of female sharks, has been hypothesized as a precopulatory releaser by Springer (1960) and is supported by observations of biting during courtship in the horn shark, Heterodontus francisci (Dempster and Herald, 1961; Taylor, 1971); and in the clearnosed skate, Raja eglanteria (Libby and Gilbert, 1960). Similarly, gouging and nipping behavior might have a related function during courtship for the spotted eagle ray.

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