

Dermal bite wounds as indicators of reproductive seasonality and behaviour in the Atlantic stingray, *Dasyatis sabina*

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Synopsis

Elasmobranch fishes exhibit a series of complex courtship and mating behaviours in which males inflict significant bite wounds to the body of female mates. However, the variety and frequency of mating wounds are not known across a full reproductive season for any species. We examined the distribution and abundance of dermal wounds in adult Atlantic stingrays, *Dasyatis sabina*, which have a protracted and defined mating season to determine (1) if dermal wounds can be used as indicators of mating activity, (2) whether different categories of bite wounds can be associated with specific mating behaviours, and (3) whether the skin thickness in females is sexually dimorphic. Adults of both sexes showed fresh wounds during the full duration of the mating season (October–June) and there was no relationship between ray size and wound density. Females had more total wounds than males in every month with a maximum average of 20.2 wounds per female in April. Mating wounds were categorized into five distinct forms: single track, double track, bite, margin abrasion and excision. Wounds were randomly distributed over the body of males but concentrated on the posterior half of the disc in females. Each wound type occurred in approximately equal proportions among sexes with the exception of the precopulatory and copulatory-induced margin abrasions which accounted for 13.7% of the total wounds in females but only 3.1% in males. We suggest that the pronounced and concurrent appearance of single track, double track and bite wounds among males results from random premating courtship attacks by males because females cannot be visually discriminated. However, the concentration of wounds on the posterior disc of females is consistent with the possible presence of olfactory cues (e.g. pheromones) that are released at the cloaca. The pectoral fin dermis of females was 50% thicker than that of males, which eliminated the excision of margins during male grasping and functions to reduce female injury. The temporal occurrence of wounds from October through June and peak in April is consistent with previous reproductive studies that show fresh sperm in the reproductive tract of females over the protracted mating period and also ovulation in late March or early April. The importance of social reproductive biting is discussed in relation to the reproductive induction hypothesis proposed to possibly explain the protracted mating of this species. Monitoring of dermal wounds provides a useful non-invasive technique to determine reproductive activity and a means for inference of social relationships in elasmobranch populations.

Introduction

He jests at scars, that never felt a wound.
Romeo & Juliet, II ii

All known elasmobranch fishes exhibit a complex series of reproductive behaviours which involve the use of the mouth by males. During early courtship the male closely follows and aggressively bites the fins and body of the female (e.g. Klimley 1980, Tricas 1980, Uchida et al.¹, Carrier et al. 1994, Nordell 1994). Such pre-mating behaviour was suggested to function as a precopulatory releasing mechanism that facilitates cooperation of the female to mate (Springer 1960). In most species the male must grasp the pectoral fin of the female with his mouth to provide leverage for clasper insertion. The male then continues to grasp the female's pectoral fin with the mouth throughout copulation in order to maintain body alignment of the pair (Tricas & LeFeuvre 1985). A major result of these male biting behaviours is the infliction of wounds, abrasions or permanent scars on female sharks and rays (Stevens 1974, Pratt 1979, McCourt & Kerstitch 1980, Tricas 1980, Reed & Gilmore 1981, Nordell 1994).

Many batoid species have a pronounced sexually dimorphic dentition. It has long been known that the teeth of male skates are sharp and narrow while those of females are molariform in shape (e.g. Bigelow & Schroeder 1953). This dimorphic dentition in skates was originally proposed to function in differential food habits (Feduccia & Slaughter 1974) but was discounted because similar prey items are taken by both sexes (McEachran 1975). Recent work on the Atlantic stingray, *Dasyatis sabina*, shows that this dental dimorphism is not a permanent, static morphology but rather occurs on a seasonal basis (Kajiura & Tricas 1996). In the non-mating season male stingrays have female-like molariform teeth which are relatively inefficient for grasping. These are replaced by rows of sharp cuspidate teeth over the entire reproductive season and then revert to the molariform shape when the mating season ends. The sharp dentition provides males with an improved grip when biting on female pectoral fins during courtship and copulation.

¹ Uchida, S., M. Toda & Y. Kamei. 1990. Reproduction of elasmobranchs in captivity. pp. 211–237. In: H.L. Pratt, S.H. Gruber & T. Taniuchi (ed.) Elasmobranchs as Living Resources: Advances in the Biology, Ecology, Systematics, and the Status of the Fisheries, US Dep. Commer., NOAA Tech. Rep. 90. 518 pp.

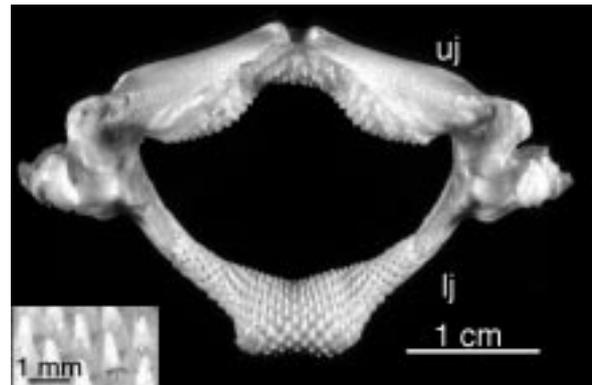


Figure 1. Jaws of a mature male Atlantic stingray sampled during the mating season. Teeth of the upper jaw (uj) form a prominent biting surface mid-way between the symphysis and jaw hinge. Teeth of the lower jaw (lj) form a single large median pad. This differential arrangement of teeth on the jaws enables discrimination of which jaw element created a bite wound. Inset shows close up of lower jaw teeth.

When a male stingray bites the dorsal surface of a female, the small pointed teeth cut narrow tracks through the pigmented epidermis to expose the underlying white dermal layer. Since male stingrays only inflict wounds when they possess the cuspidate dentition, the presence of these injuries can theoretically be used to determine the onset, duration and intensity of courtship and mating activity. In addition, the different morphology of the upper and lower jaws permits the determination of how each wound is created (Figure 1).

The significance of this vigorous reproductive biting behaviour is evident in some species which have also evolved a sexually dimorphic skin morphology. For example, the dermal layer of the skin in female blue sharks, *Prionace glauca*, is twice as thick as that of males of comparable size. This enhancement in female skin thickness likely functions to reduce the risk of serious injury from wounds inflicted during mating activity (Pratt 1979). However, the temporal relationships between dental and dermal sexual dimorphisms are unknown for any species.

The Atlantic stingray has the longest preovulatory mating period reported for any elasmobranch. Females mate continuously from October through April, bear numerous fresh mating wounds and possess active sperm in their reproductive tracts during this entire period (Lewis 1982, Snelson et al. 1988, Maruska et al. 1996). However, egg development occurs throughout this seven month period until females ovulate almost synchronously near the end of

March (Maruska et al. 1996). The lack of evidence for female sperm storage or arrested embryonic development in this species has led to the question of what function, if any, the preovulatory mating activity serves. Maruska et al. (1996) proposed the hypothesis that the protracted mating activity may serve to stimulate oogenesis or some other aspect of female reproduction. Thus, an understanding of the nature of male–female interactions during the reproductive season may provide important information to answer this question.

This study provides the first detailed analysis of fresh mating wounds in an elasmobranch fish population across an entire reproductive season. The Atlantic stingray provides an excellent study species because of its widespread abundance, well studied reproductive biology and protracted mating season. This study tests the hypotheses that (1) the presence of dermal wounds can be used as an indicator of mating activity, (2) dermal wounds reflect different social reproductive behaviours, and (3) dermal thickness of rays is both sexually and seasonally dimorphic.

Methods

Sexually mature Atlantic stingrays, *D. sabina* (males > 22.0 cm DW (disc width), females > 24.0 cm DW), were collected monthly from the Indian River Lagoon, Brevard County, Florida from August 1993 to July 1994. These collections were used for other reproductive studies on this species (Kajiura & Tricas 1996, Maruska et al. 1996). Rays were encircled with a 6 m soft nylon seine, captured individually with a hand net, euthanized and placed on ice for transport to the laboratory. Each individual was rinsed of excess mucus, fixed in 4% formaldehyde then preserved in 40% isopropanol. A minimum of six males and six females was examined from each month over the one year sampling period.

Wounds were categorized into one of five classes that are described in detail in the Results. Only fresh wounds in which the underlying white dermis was exposed were included in the analysis. The ventral surface of each ray was examined but the lack of pigmented epidermis precluded visualization of any wounds which might have been present. Therefore, only wounds on the dorsal surface were included in this study.

The location of each wound on the body was recorded as an angular vector on the dorsal surface of the disc. To standardize the measurements and

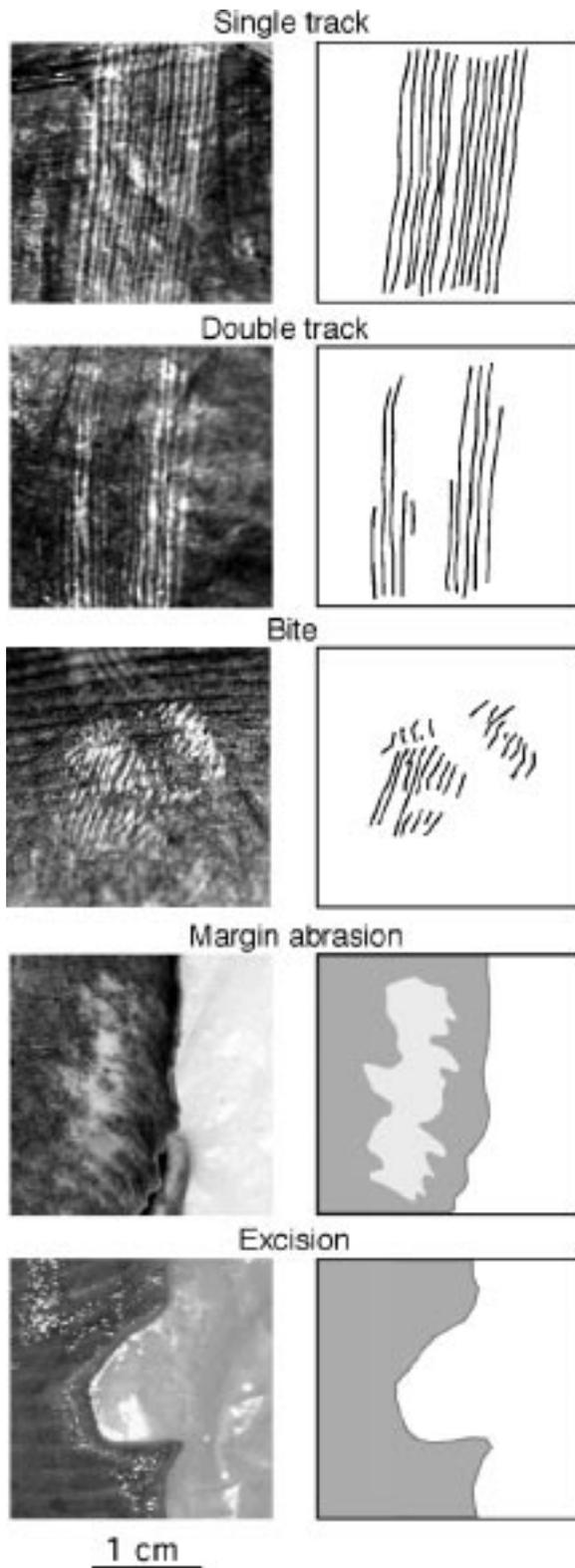
compensate for varying body size, all measurements were taken relative to the centre of gravity (centroid) which is on the mid-line of the body at approximately 54% of the disc length. The rostrum was designated as 0° and angular deviation measured in a counterclockwise rotation. Radial distances from the centroid to the nearest edge of individual wounds and the corresponding angle from the rostrum were recorded. For wounds in which parallel tooth tracks were visible (single track, double track, bite) the orientation of the wound relative to the centroid was also measured. This data format permitted reconstruction of the type, location and orientation of all wounds on any individual.

The wounds on the body were categorized into one of four dorsal disc quadrants of equal area: left anterior, left posterior, right posterior and right anterior. The scars in each quadrant were summed and a χ^2 test performed to determine if number of scars varied spatially on the surface of the disc.

To determine whether females possess a thicker dermis, ten individuals of each sex were sampled from July 1993 (non-mating season) and January 1994 (mating season). A section of the disc margin (approximately 5 mm wide by 20 mm long) was removed from the left side of the disc at a position 135° from the rostrum. A video image of each section was viewed in cross section under a compound microscope, digitized and stored on disc. Dermal thickness was measured at 9–11 mm from the edge of the disc which corresponds to the depth of the fin which would be grasped by the mouth of a male. Measurements were taken at positions where there were no wounds or scars to avoid confounding effects of scar tissue. A 2-way ANOVA was applied to determine if dermal thickness differed between sexes and seasons. An analysis of covariance (ANCOVA) was also used to determine if dermal thickness varied as a function of ray size.

Results

Over the twelve month sampling period 702 wounds were examined on 75 females and 259 wounds on 73 males. Five distinct categories of wounds were observed in both sexes and classified as a (1) single track, (2) double track, (3) bite, (4) margin abrasion, or (5) excision (Figure 2). A ‘single track’ wound was defined as a single set of parallel tooth tracks that result from a scrape of the lower jaw across the skin. A ‘double track’ wound consisted of two sets of parallel tooth tracks in close proximity which were formed



by a scrape of the palatoquadrate dentition across the skin. A 'bite' formed a distinctive triangular pattern that consisted of opposing single and double tracks formed by teeth of the lower and upper jaws, respectively. We confirmed these wound patterns using male jaws which possessed the cuspidate dentition applied to the disc of a fresh dead specimen. A 'margin abrasion' was a light coloured patch of skin that had lost its pigmentation. Margin abrasions were isolated to the 2-cm wide edge around the disc margin, showed no distinct tooth tracks and most likely resulted from prolonged grasping of the fin margin. In an 'excision' wound, tissue along the disc margin was removed presumably by extreme biting. The size and shape of the excision wound closely matched the dimensions of the male lower jaw.

Dermal wounds were observed in both sexes over a consecutive monthly period from October to June. Single track wounds were the most frequent class and accounted for 69% of total wounds in females and 74% in males (Figure 3). Percent abundance of the other wound types was also similar between the sexes with the exception of margin abrasions which accounted for 13% of the total wounds in females but only 3% in males. Only six excisions were found out of a total of 961 wounds, and all were found in males.

Females showed a greater mean number of total wounds than males in every month with the exceptions of August and September in which wounds were rare for both sexes (Figure 4). Wounds were very uncommon in rays during the non-reproductive summer months of July, August and September. Total number of wounds on females differed among month of the year (ANOVA $F = 7.17$, $df = 11, 61$, $p < 0.001$). Females showed an increase in number of wounds in October that remained at an elevated level for the next five months before the peak in April. Following the April maximum, wound frequency declined to summer low values. April had the greatest number of wounds compared with the summer minima (Tukey's Multiple Comparisons Test, $p < 0.001$).

The number of wounds per individual male covaried with that for females, but male monthly means were usually less than half that of females (Figure 4). Like females, average wound density in males also changed

Figure 2. Classification of dermal bite wounds on Atlantic stingrays observed during the one year sampling period. Five classes of wounds were identified: (1) single track, (2) double track, (3) bite, (4) margin abrasion, and (5) excision. A photographic image of each wound type is shown on the left and a schematic representation to the right.

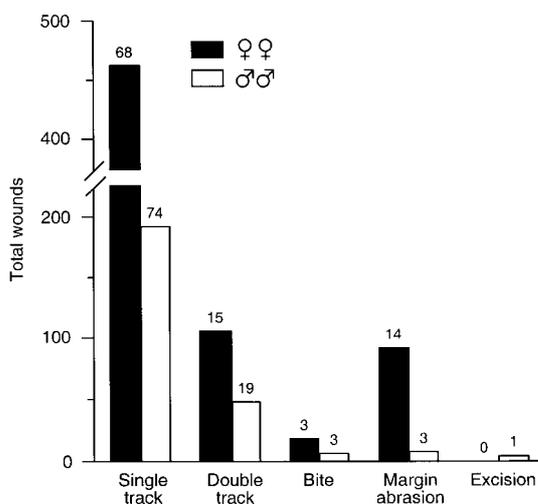


Figure 3. Total number of wounds for each of the five bite categories in male and female Atlantic stingrays. The percentage of each wound type is shown above each bar for both sexes. Female rays ($n = 75$) received approximately twice as many bites in each class compared to males ($n = 73$) with the exception of margin abrasions which occurred primarily in females.

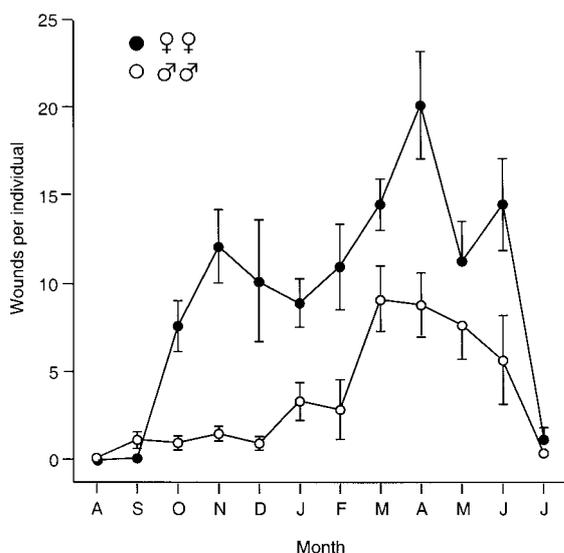


Figure 4. Number of wounds ($\bar{x} \pm SE$) for males and females sampled over a consecutive 12 month period from August 1993 to July 1994. Wound density in females increased in the fall, remained high throughout the winter and peaked in April before the return to summer minima. Monthly wound densities covaried among the sexes, but male densities were usually less than half that of females. A total of 6 males and 6 females was sampled each month of the study with the exceptions of February (males $n = 7$) and December (females $n = 9$).

across the year (ANOVA $F = 5.97$, $df = 11$, 61 , $p < 0.001$) with rays sampled in March and April having more wounds than rays sampled in July through December (Tukey's Multiple Comparisons Test, $p < 0.05$). In addition, males sampled in May had more wounds than males sampled in July, August, October and December (Tukey's Multiple Comparisons Test, $p < 0.05$).

The temporal abundance of each of the five wound types is illustrated in Figure 5. For females, single track wounds are the most abundant type in all months except August and September (Figure 5a). Double track wounds covary in monthly abundance with single track wounds while margin abrasions are relatively high from the onset of mating activity and show no clear pattern. Although single track wounds are also the most common wound found in male rays, they occur in relatively low abundance compared to females (Figure 5b). However, increases in both single and double track wounds are also seen in March and last for 3–4 months. The remaining wound types found in males account for only a small portion of the total throughout the year.

Wounds were randomly distributed across the body of males as seen by an expected 25% in each quadrant ($\chi^2 = 0.747$, $df = 3$, $0.5 < p < 0.9$) (Figure 6). However, there was a greater number of both total wounds ($\chi^2 = 51.53$, $df = 3$, $p < 0.001$) and also margin abrasions ($\chi^2 = 74.78$, $df = 3$, $p < 0.001$) in the posterior half (90° – 270°) of the female discs. Over 96% of margin abrasions in females were located in the posterior half of the body and abundance did not differ between left and right sides ($t = 0.872$, $p = 0.393$). Total number of wounds was not associated with size of the ray for either sex (males $R^2 < 0.001$, females $R^2 < 0.005$) which indicates that larger females are not courted more than smaller females.

The dermis of females is thicker than that of males in both mating and non-mating seasons (2-way ANOVA, $F = 60.8$, $df = 1$, 36 , $p < 0.001$) (Figure 7). However, we could not demonstrate a difference in dermal thickness between mating and non-mating seasons for either sex ($F = 0.928$, $df = 1$, 36 , $p = 0.34$). Although mean female disc width was greater than that of males, an ANCOVA revealed that dermal thickness was greater in females and independent of body size ($F = 186.9$, $df = 1$, $p < 0.05$).

Discussion

This study reveals new information about the mating behaviours in batoid elasmobranchs and the utility

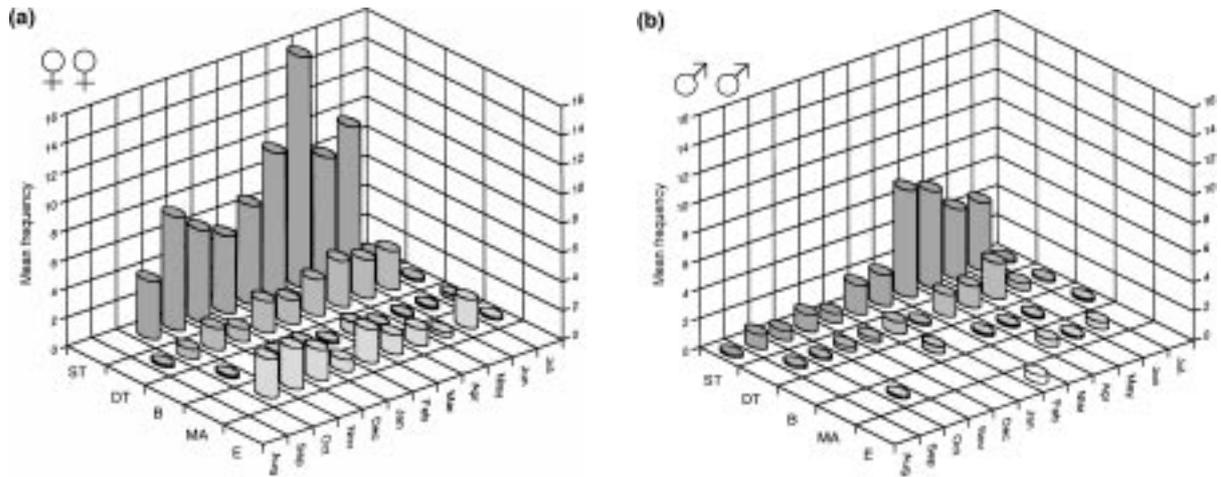


Figure 5. Monthly abundance of each wound category for the Atlantic stingray. Single track wounds were the most common for both sexes and peaked in abundance in April for females (a) and March for males (b). Sample sizes are the same as Figure 4. Wound categories: single track (ST), double track (DT), bite (B), margin abrasion (MA), excision (E).

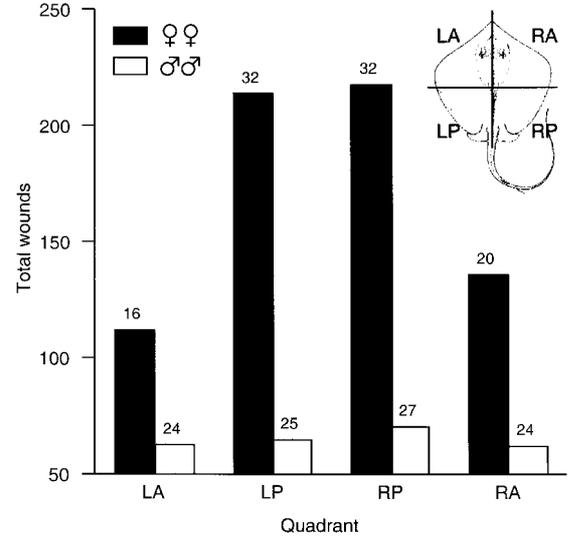


Figure 6. Distribution of wounds for male and female Atlantic stingrays in the four quadrants of the body disc. Males (n = 73) exhibited an even distribution of wounds in the left anterior (LA), left posterior (LP), right posterior (RP), and right anterior (RA) quadrants, whereas females (n = 75) had more wounds on the posterior half of their discs. Percentage of total wounds in each quadrant is indicated above each bar.

of quantifying mating wounds over the reproductive season. The presence of fresh wounds on *D. sabina* indicates that, like most elasmobranchs, this species exhibits biting behaviour during courtship and mating. Two functions are known for biting behaviour in sharks

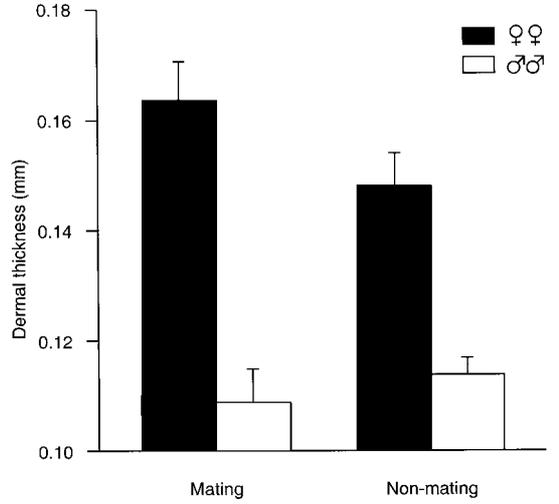


Figure 7. Dermal thickness ($\bar{x} \pm SE$) of male and female Atlantic stingrays sampled during the mating and non-mating seasons. The dermis is thicker in females than males in both the mating and non-mating seasons but dermal thickness does not vary across seasons for either sex; n = 10 for each sample.

that can also be applied to batoids. Biting by male sharks functions as a precopulatory releasing mechanism in females that facilitates cooperation to mate (Springer 1960). Tricas (1980) described courtship wounds inflicted to the dorsum of a female by two wild male spotted eagle rays, *Aetobatus narinari*. Excessive biting activity during courtship can inflict serious wounds and may even be lethal in captive cownose rays,

Rhinoptera javanica (Uchida et al.¹). Biting also serves to maintain contact during copulation in sharks (Tricas & LeFeuvre 1985) and this appears to apply to some species of batoids (McCourt & Kerstitch 1980, Nordell 1994). For those species which exhibit size dimorphisms, it might be impossible for the male to grip the leading edge of the female's pectoral fin during copulation. Small male clearnose skates, *Raja eglanteria*, initiate mating by using their jaws to grip the trailing edge of the pectoral fins of larger females and maintain this grip throughout copulation which can last for several hours (Luer & Gilbert 1985).

Previous studies of elasmobranch mating wounds and scars showed that bite wounds occur primarily on females (Pratt 1979, Stevens 1974) but the specific behavioural contexts in which they were inflicted were not addressed. While female stingrays receive more bites than males, our results show that male stingrays are also the target of substantial intrasexual biting. Biting activity among males may be due to their inability to distinguish females during the precopulatory phase of mating behaviour. It is highly unlikely that male rays visually discriminate female rays by their lack of claspers. In addition, visual identification of either sex is not possible in turbid waters, at night or when a ray is buried in the bottom substrate. We believe that the occurrence of bite wounds on males usually results from chance encounters in this sex-mixed species. Random premating encounters would explain the high number of courtship scrapes on the dorsal surface of males and rare frequency of margin abrasions which are presumed to occur during copulation. However, some wounds on males may also be the result of aggressive interactions between conspecifics for access to females. Increased intrasexual aggression among males during female ovulation might contribute to the highest occurrence of wounds in March and April (Figure 4). However, this hypothesis would also require a means for recognition of other males, perhaps at a specific phase of male competition during courtship.

The seasonal pattern of mating wounds corresponds with the seasonal change in male tooth morphology. The dentition of male Atlantic stingrays is known to change from a female-like molariform shape in the non-mating months to a sharp cuspidate morphology during the mating season (Kajiura & Tricas 1996). During the early phases of the mating season, rows of male teeth become increasingly pointed and correlate to the increase in female wound frequency that is maximum in April. This sharpened dentition imparts an enhanced grip tenacity and also an increased capacity to damage

the skin of females (Kajiura & Tricas 1996). As the mating season ends and female wounds decrease, male teeth become less pointed and lose their capacity to scar. While male-initiated aggressive interactions in the summer months may continue to occur, the molariform male tooth morphology would not create wounds (Kajiura & Tricas unpublished data). Thus, the frequency of male aggressive behaviour during summer months remains unknown. Similarly, the constant dull molariform dentition of females does not permit the use of dermal wound patterns to quantify levels of female aggression during the year.

The absence of excision wounds on females might be attributed to their thicker dermis which presumably provides more protection than the thinner dermis of males (Figure 7). As a result, bites which would be stimulatory to a female might actually sever tissue from a male.

Bite wounds are distributed randomly on the body of males while in females wounds are concentrated in the posterior half of the disc. This finding is in agreement with other reports that male rays grip females on the posterior margin of their pectoral fins during courtship (Uchida et al.¹, Luer & Gilbert 1985, Reed & Gilmore 1981, Tricas 1980). The greater number of wounds in the posterior half of female discs is due partly to the large number of margin abrasions. Margin abrasions are nearly five times as abundant on females as on males which would be consistent if they result from copulatory grips rather than precopulatory courtship bites. However, the greater number of margin abrasions in the posterior half of the disc of *D. sabina* is inconsistent with observations of *Urolophus halleri* (Nordell 1994) where the male grips the anterior margin of the female's disc during intromission. The high frequency of posterior margin abrasions is more likely caused by vigorous grasping of the posterior margin prior to copulation as reported for *U. halleri* by Nordell (1994) and Tricas et al. (1995). While one of us (TCT) has observed presumed courtship, which involved following, nudging and biting by male *D. sabina*, the only published account of mating activity is provided by Snelson et al. (1988) but no details on behaviour were provided.

The concentration of scars on the posterior half of the female body may be the result of olfactory cues that originate at the cloaca. Organic molecules such as sex steroids or other specific compounds may function as pheromones that provide information to males about the reproductive condition of the female. Johnson & Nelson (1978) suggested that olfactory cues

were responsible for pair formation in the blacktip reef shark, *Carcharhinus melanopterus*. Similar pairing of rays in which the male orients behind the female was reported for many species (Tricas 1980, Reed & Gilmore 1985, Nordell 1994) and is consistent with this hypothesis.

Even if mating cannot be easily observed, inferences can be made about the mating behaviour by examination of the wound morphologies. Single track wounds are inflicted by a scrape from the lower jaw. The long, linear single track wounds could be formed by male rays diving to gouge the dorsum of females with their lower jaw as described in the myliobatid eagle ray by Tricas (1980). In *D. sabina* double track wounds are formed by the teeth of the upper jaw and were less abundant than lower jaw single track wounds. This is in contrast to the blue shark in which tooth cuts on the body are made almost exclusively by teeth of the upper jaw (Pratt 1979). It may be that the profuse and massive mating wounds seen in carcharhinid sharks result from damage inflicted by the serrated teeth of the upper jaw whereas the relatively narrow teeth of the lower jaw function to anchor the lower jaw during the bite action. Thus, differences in dental morphology among species may be important determinants of their reproductive behaviour.

The presence of mating wounds provides a useful, non-invasive method to determine periods of mating activity. Fresh wounds are formed during periods of active courtship and copulation, and can thus serve as indicators of mating activity even when it is not directly observed. However, future studies should refine the definitions and chronology of wounds inflicted during courtship and mating behaviours. For example, the term mating scar, which was used in many studies, actually refers to fresh wounds. In fact, mating wounds should be distinguished from mating scars. We define wounds as recently inflicted tissue trauma which has not yet healed. These are distinct from scars which represent a later stage at which the wound has healed. In addition, future use of this technique should include a determination of the time for wound healing so that the temporal aspects of wound persistence can be addressed. In our study, only wounds in which the white dermal layer was clearly seen were counted and we confirmed that wounds on stingrays which were maintained in captivity heal completely within two weeks (unpublished data). Klimley & Nelson (1981) found that recently inflicted white patch abrasions on female scalloped hammerhead sharks

would transform to black patches as they partially healed.

The continuous appearance of fresh wounds from October through June is coincident with the protracted mating season described for *D. sabina* by Snelson et al. (1988). The consistent presence of live sperm in the reproductive tract of females, and also the clasper grooves of males, indicates that males copulate and inseminate females continuously for 7–8 months during which time male sperm stores are depleted (Maruska et al. 1996). Despite this protracted mating period, females ovulate nearly synchronously at the end of March or early April. Thus, the *reproductive induction hypothesis* was proposed by Maruska et al. (1996) to possibly explain this protracted mating activity which does not involve fertilization of eggs until the very end of the mating season. In many mammalian vertebrates, courtship or copulation behaviours are important to induce reproductive events such as ovulation (Pearsons 1944, Enders 1952) but this process is not examined in elasmobranch fishes. If reproductive induction of females occurs in *D. sabina*, it could be mediated by stimulation of the cutaneous receptors in the skin by aggressive male attacks. Experimental manipulation studies, where the sexes are isolated and female egg development monitored, are necessary to test this proposal.

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