

Natural History Miscellany

The Adaptive Significance of Sexually Dimorphic Scale Rugosity in Sea Snakes

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ABSTRACT: In terrestrial snakes, rugose scales are uncommon and (if they occur) generally are found on both sexes. In contrast, rugose scales are seen in most sea snakes, especially in males. Why has marine life favored this sex-specific elaboration of scale rugosity? We pose and test alternative hypotheses about the function of rugose scales in males of the turtle-headed sea snake (*Emydocephalus annulatus*) and conclude that multiple selective forces have been involved. First, rugosities may aid male positioning during courtship, because histology shows that tubercles are more highly innervated than adjacent flat areas of each scale and hence are presumably more sensitive to tactile cues, and because biomechanical tests show that rugosities enhance friction between the bodies of males and females. Second, the occurrence of rugosities over the entire body of males and (albeit less well developed) in females as well suggests that rugosities also play a hydrodynamic role by modifying water flow across the snake's surface. Flow tank tests show that rugosities reduce the thickness of the boundary layer by almost 50% and create turbulent flow that should massively enhance rates of cutaneous oxygen uptake and hence prolong maximal courtship duration by males.

Keywords: biomechanics, courtship, marine, mate recognition, sexual selection.

Ecomorphological research aims to understand the selective forces responsible for the evolution of phenotypic diversity, but the task is a challenging one because any single trait may be subject to many selective forces (Endler 1986; Wikelski and Romero 2003) and because a single selective

force can simultaneously act on a broad suite of correlated traits, making it difficult to tease apart the fitness consequences of any single trait (e.g., Arnold 1983). The search for links between function and morphology can be expedited by selecting an appropriate “model system” in which relationships between environment and morphology are particularly clear and for which only a limited set of potential selective forces are relevant. For example, the study of adaptive evolution can be facilitated by choosing a system that involves invasion of a new habitat (Huey et al. 2000; Carroll et al. 2001; Reznick and Ghalambor 2001) and/or sexual dimorphism (Katsikaros and Shine 1997; Lee 2001). This article provides information on a “model system” that fulfils both of these criteria: sex-specific scale rugosities in sea snakes.

Hydrophiid snakes evolved from terrestrial Australian elapids and invaded the ocean relatively recently (Wallach 1985; Keogh et al. 1998). The scales of sea snakes differ from those of their terrestrial relatives in at least two ways. First, scale rugosity is more common overall in sea snakes (occurring in at least 11 of 16 genera) than in terrestrial snakes (Heatwole 1999; Avolio 2004; Avolio et al. 2006). Second, scale rugosity in sea snakes is more highly developed in males than in females, whereas sexual dimorphism in scale rugosity is rare in terrestrial snakes (Gritis and Voris 1990; Shine 1993; Greer 1997; Avolio 2004; Avolio et al. 2006). Why, then, has the invasion of oceanic habitats stimulated the evolution of sex-specific scale rugosities in snakes?

Recent studies have identified an ideal model system with which to test such ideas. Male turtle-headed sea snakes (*Emydocephalus annulatus*) in New Caledonia are smooth scaled during summer but display obvious rugosities on virtually every body scale during the winter breeding season; females are comparatively smooth scaled year-round (Shine et al. 2003b; see fig. 1). Thus, scale rugosity attains its fullest development only in males and only during the breeding season, suggesting that this trait may enhance mating success in males (Lande 1980). We set out to test this prediction by posing and evaluating a

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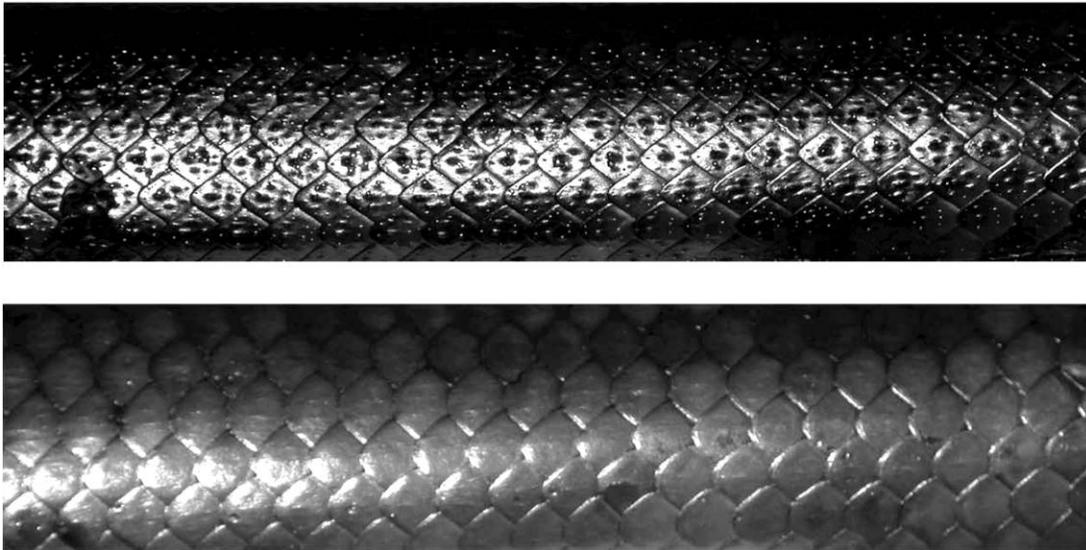


Figure 1: Lateral surfaces of the bodies of an adult male turtle-headed sea snake (*Emydocephalus annulatus*; top) from the Noumea Lagoon compared with an adult female (bottom) captured in the same area at the same time of year (June). Males are much more rugose. Color version of figure available in the online edition of the *American Naturalist*.

series of hypotheses about the functional significance of scale rugosity for aquatic snakes.

Possible Functions of Sexually Dimorphic Scale Rugosities

Scale rugosity might influence male fitness via one or more of the following pathways.

During Physical Interactions between Males and Females

If rugosities provide sensory information to a courting male, we predict that rugosities will be concentrated on those parts of the male's body that contact females during courtship and that rugosities will be more highly innervated than are nonrugose areas of the scale. If rugosities help to maintain body contact between the sexes during courtship or copulation, we predict that rugose scales will generate more friction than nonrugose scales and that courtship and copulation involve extensive body contact. If females use rugosities as a cue for choosing a high-quality mate, we predict that females will accept copulation more readily from males with larger rugosities.

During Physical Interactions between Rival Males

If rugosities enhance success in male-male combat (by increasing grip when grappling with an opponent), we predict that males engage in physical combat and that

rugose scales generate more friction than nonrugose scales. If rugose scales facilitate sex recognition (and thus reduce the frequency of misdirected courtship from other males; Rivas and Burghardt 2001; Shine et al. 2003a), we predict that male snakes will selectively court smooth as opposed to rugose partners.

During Mate-Searching Behavior of Males

Rugose scales may enable courting males to remain underwater longer by enhancing cutaneous uptake of oxygen. Sea snakes gain up to 20% of their oxygen needs through their skin (Seymour 1974; Heatwole and Seymour 1975), so enhanced oxygen uptake might prolong effective dive times. Courting males that surface to breathe frequently lose contact with their partners at this time (Shine 2005), so increased dive duration could contribute to more effective courtship. Rates of mass transfer (diffusion) of oxygen across the skin surface will be enhanced if rugosity reduces the thickness of the boundary layer and/or renders it more turbulent (Denny 1988; Bruno and Edmunds 1998).

Methods

Species and Study Area

Turtle-headed sea snakes (*Emydocephalus annulatus*) are small (males to 63 cm snout-vent length, females to 69

cm) hydrophiid snakes from the tropical Pacific (Ineich and Laboute 2002). We examined scale morphology using specimens of *Emydocephalus annulatus* from Ashmore Reef, Australia (12°12'S, 123°05'E) and held by the Australian Museum of Natural History. To test our ideas with live animals, we studied *E. annulatus* at adjoining beaches (Anse Vata and Baie de Citrons) in July 2004 in Noumea, New Caledonia (22°16'S, 166°26'E; see Shine et al. 2003b).

Do Rugose Scales Act as Tactile Receptors?

We removed dorsal and ventral midbody scales of 12 preserved *E. annulatus*, cut the scales in cross section (anterior-posterior), and embedded, sectioned (at 7- μ m thickness on a Leica microtome), and stained them for myelin and unmyelinated axons using Luxol Fast Blue and Holmes's Silver Nitrate, respectively (Fawcett et al. 1994). Four sections from each scale were examined under a microscope (Olympus, CH-2) to score the number of myelinated nerve bundles for each half-field (10 μ m²) and the distance of each nerve from the epidermis ($\times 40$) up to a depth of 0.5 mm. We also measured the height of rugosities and the thickness of the epidermis over rugosities and adjacent nonrugose areas ($\times 10$).

We used a three-way ANOVA with the fixed factors of sex, scale location (dorsal vs. ventral), and scale type (under tubercle vs. under flat area) to examine differences in the numbers of nerves per half-field and the depth of nerves. Before statistical analyses, we checked that data were normally distributed. Where our data failed to meet this assumption, we lowered the level of statistical significance from $P = .05$ to $P = .01$ (Underwood 1997). All statistical analyses were performed using Statview 5.1 (SAS Institute 1998).

Do Scale Rugosities Aid Sex Recognition by Male Snakes?

If male *E. annulatus* use scale rugosities for mate recognition, we expect that reproductive males will more readily approach and court smooth rather than rugose models. Thus, we exposed free-ranging mate-searching males to nylon ropes (50 cm long, 1.5 cm in diameter; see Shine 2005), half of which were smooth (via a plastic coating: Plasti-dip; Performix) and the others rugose. In each trial, either a rough ($n = 11$) or a smooth rope ($n = 11$) was pulled past a male snake at a distance of 30 cm from his head in a way that mimicked female movements (sinuous, head down, moving at 1 m min⁻¹), and we recorded whether the male approached the stimulus and whether he made contact, as well as the number of tongue flicks that he directed at the rope (complete cycles of tongue tip extrusion and withdrawal).

Do Rugose Scales Enhance Friction between Adjacent Snakes?

Live snakes were obtained from Noumea in June 2004 (midwinter) when females were relatively smooth scaled and males were rugose. Snakes were weighed and then laid flat (on their left side) in a rectangular Perspex box (fig. A1 in the online edition of the *American Naturalist*). A recently killed female snake (snout-vent length = 55 cm) was used as the lower snake, and live snakes were placed on top of this animal to measure the friction between the two animals. An adjustable lid containing lead weights rested on the upper snake's body, providing 245 g of mass to push the upper snake down against the immobile lower animal. The two snakes were aligned in the same direction and were in contact for a 10-cm length (from 10 to 22 cm above the cloaca). A spring scale (Pesola, 250 g capacity) clipped to the tail of the upper snake was used to pull the live animal backward (fig. A1). The spring scale reading at the onset of movement (static friction) was noted. Trials were repeated five times for each snake; seawater was sprayed on the snakes between trials to keep them moist. We used these measurements of static friction to calculate the snake's coefficient of friction $\mu = F/N$, where N is the mass of the top snake plus 245 g and F is the static friction.

Do Scale Rugosities Affect Thickness of the Boundary Layer?

We investigated the effects of flow regime and surface roughness on boundary layer characteristics using silicone replicas of rugose male ($n = 4$) and nonrugose female ($n = 4$) dorsal scales and using smooth silicone as a control ($n = 4$). To construct these replicas, live snakes from New Caledonia were dried thoroughly and laid down flat so that we could make impressions of the left side of the body (30 cm above the cloaca) using vinyl polysiloxane dental silicone (Express; light body regular set, 3M ESPE). These negatives were sprayed with silicone release agent (Rocket Release, Stoner), and silicone (Elastosil; M4470, manufactured by Wacker) was poured into the negative mold. The resulting cast (10 cm \times 3 cm) was allowed to set for 24 h before being glued to plastic cylinders (4 cm diameter \times 12 cm high) connected to lead weights. The plastic platforms were positioned within a recirculating flow tank (80 cm long \times 20 cm wide \times 30 cm high; Vogel 1988) 40 cm downstream from the flow straighteners (fig. A2 in the online edition of the *American Naturalist*). Flow speed in the tank was controlled with a variable-speed motor, with water temperature at $16^\circ \pm 1^\circ\text{C}$. Velocity gradients were determined at a range of heights above the silicone scale impressions exposed to steady unidirectional

flow at three velocities (mean \pm SD; 0.96 ± 0.19 m min⁻¹, $n = 537$; 2.45 ± 0.70 m min⁻¹, $n = 540$; 4.16 ± 1.13 m min⁻¹, $n = 537$) bracketing the speed range recorded for free-swimming *E. annulatus* (Shine et al. 2004).

Flow was visualized by seeding the water with neutrally buoyant dried brine shrimp cysts (200–250 μ m in diameter; Johnson and Sebens 1993) illuminated by a Leitz Pradovit 250 light projector shone at a mirror reflecting a thin beam of light vertically into the flow tank (fig. A2). The vertical light sheet 9 cm long \times 2 cm wide illuminated only particles flowing directly above the skin. A Sony DCR-TRV17 digital video camera recording at a frame rate of 30 Hz was positioned in lateral view of the models, with a ruler for scale. After recording flow for 2 min per model, we then recorded flow at the same position in the tank after the model had been removed to determine free stream velocity.

Video footage was analyzed using Adobe Premier Pro film editing software. Velocity of water flow was quantified by tracking one particle over three successive 1-cm distances, using frame-by-frame analysis. Flow speeds were estimated from cysts ($n = 3$) at five heights above each skin (0.0025, 0.005, 0.0075, 0.01, and 0.0125 m above the surface). If a repeated-measures linear regression on untransformed mean flow speeds (m min⁻¹) versus height above skin gave a significant fit to these data and met the statistical assumptions of randomly distributed residuals, the relationship was deemed to be linear. If the fit was not statistically significant or if the residuals were not distributed randomly, then hyperbolic functions were distinguished using simple linear regression of log-transformed data (Real 1977). When the fit of more than one function was significant and met all statistical assumptions, the function with the highest r^2 value was deemed the best fit. We used t -tests to compare slopes of the best fitting regressions among treatments.

Having found the best fitting function for a model, we calculated the height of the boundary layer as the height at which the velocity was 95% that of free stream velocity during the trial (Denny 1988). Differences between heights of the boundary layer were analyzed using two-way ANOVA models for the factors of sex and swimming speed.

Do Scale Rugosities Affect Whether Water Flow across the Skin Is Laminar versus Turbulent?

Flux of dissolved gases and metabolites between an organism and the surrounding water largely depends on the organism's size and shape, the water velocity, and whether the boundary layer is laminar or turbulent (Nakamura and van Woesik 2001). We distinguished between turbulent and laminar boundary layers with the roughness Reynolds number, defined as (Denny 1988)

$$Re^* = \frac{u^*h}{\nu}, \quad (1)$$

where u^* is the friction velocity (here assumed to be 10% of the free-stream velocity in m min⁻¹), h is the height of the rugosities (0.001 m vs. 0.0001 m for smooth skin), and ν is the kinematic viscosity of seawater. A fully rough surface ($Re^* > 60$) has a more turbulent boundary layer than a smooth surface ($Re^* < 5$).

The rate of diffusion of oxygen across the boundary layer can be calculated after Nakamura and van Woesik (2001):

$$K_c = \frac{cD_vW^{d-1}\rho^dU^d}{\mu^d}. \quad (2)$$

To solve equation (2), the input parameters were as follows: c (a constant), equal to 2 (Patterson 1992); D_v (the diffusion coefficient of the dissolved species), which for oxygen in water is equal to 2×10^{-9} m² s⁻¹; W (the organisms' characteristic dimension in meters), taken as the widest diameter of *E. annulatus* measured from live animals ($n = 86$) in New Caledonia; d (a flow size exponent), equal to 0.5 for mass transfer through a laminar boundary layer and to 0.8 for mass transfer through a turbulent boundary layer; ρ (the fluid's density, in this case seawater at 25°C), equal to 1,023.3 kg m⁻³; U (the water velocity), input at 0.02, 0.04, and 0.07 m s⁻¹ (equivalent to 1, 2.5, and 4 m min⁻¹); and μ (the dynamic viscosity of water, in this case seawater at 25°C), equal to 9.5×10^{-4} kg m⁻¹ s⁻¹.

Results

Do Rugose Scales Act as Tactile Receptors?

Under light microscopy, the rugose scales of *Emydocephalus annulatus* showed an epidermis with stratified squamous keratinizing epithelium. The dermis consisted of loose connective tissue with spindle-shaped cells, many blood capillaries, and nerve bundles (fig. 2). In cross section, rugosities were similar to nonrugose areas of the scale (cf. fig. 2A, 2B). Tubercles appeared elevated because of thickened epidermis, thickened dermis, or both (fig. 2C, 2D), depending on which region of the tubercle was sectioned (the middle of the tubercle consists of thickened dermis, whereas the edges are thickened epidermis).

We recorded more nerves per half-field (10 μ m²) under tubercles than under flat areas of the scale (fig. 3A; $F = 13.10$, $df = 1, 75$, $P < .001$; see table A1 in the online edition of the *American Naturalist*) and more nerves per half-field on ventral scales than on dorsal scales (fig. 3A; $F = 11.10$, $df = 1, 75$, $P < .002$; see table A1). However,

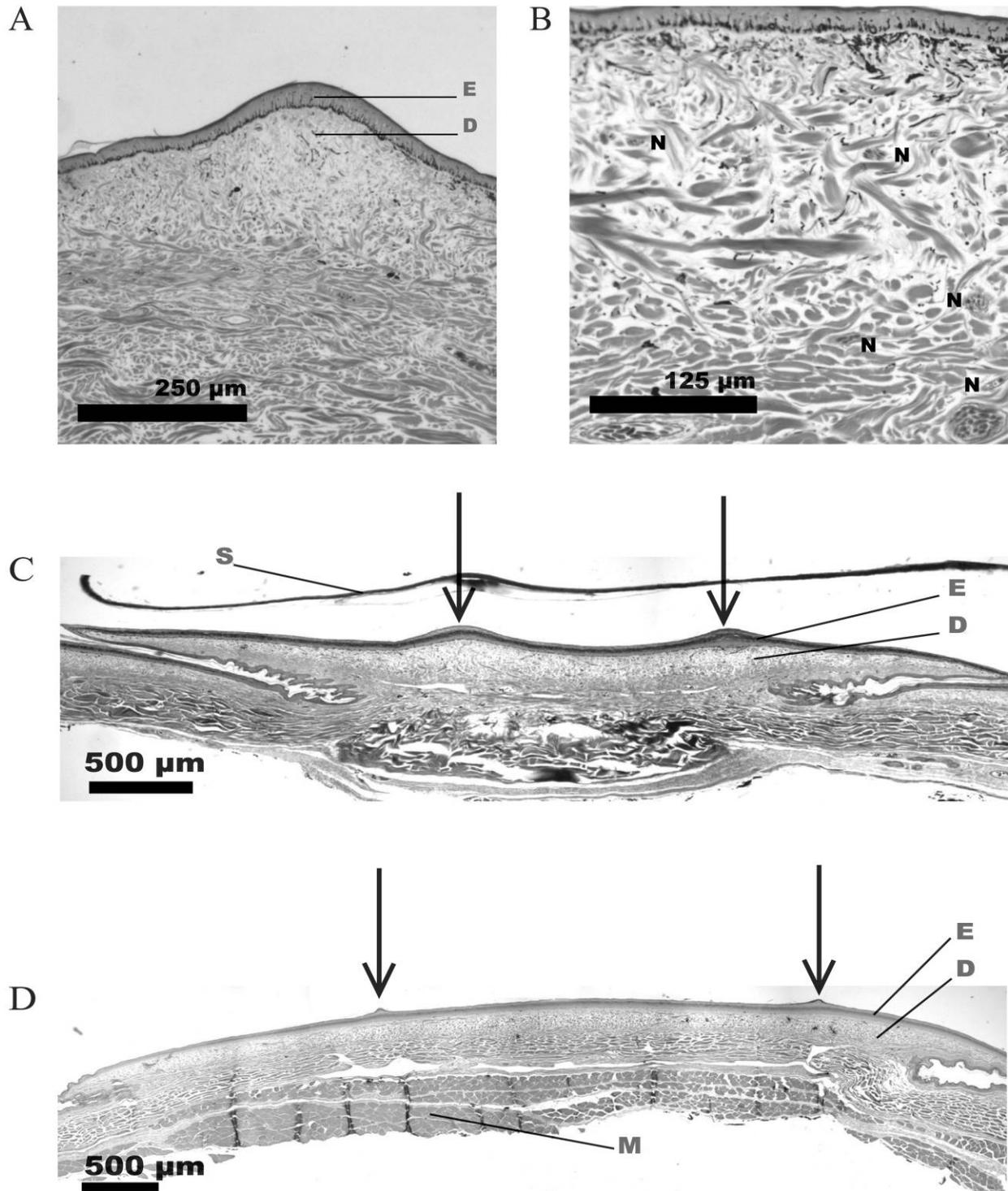


Figure 2: Light microscopic section ($7\ \mu\text{m}$ thick) through dorsal scale surface of *Emydocephalus annulatus* stained with LFBFAg. *A*, Tubercle on male scale. *B*, Nonrugose area of male scale showing myelinated nerve bundles in cross section. *C*, *D*, Micrographs showing rugosities on male (*C*) and female (*D*) scales. Abbreviations: *E* = epidermis, *D* = dermis, *N* = myelinated nerves, *M* = muscle, *S* = slough; arrows point to tubercles. Color version of figure available in the online edition of the *American Naturalist*.

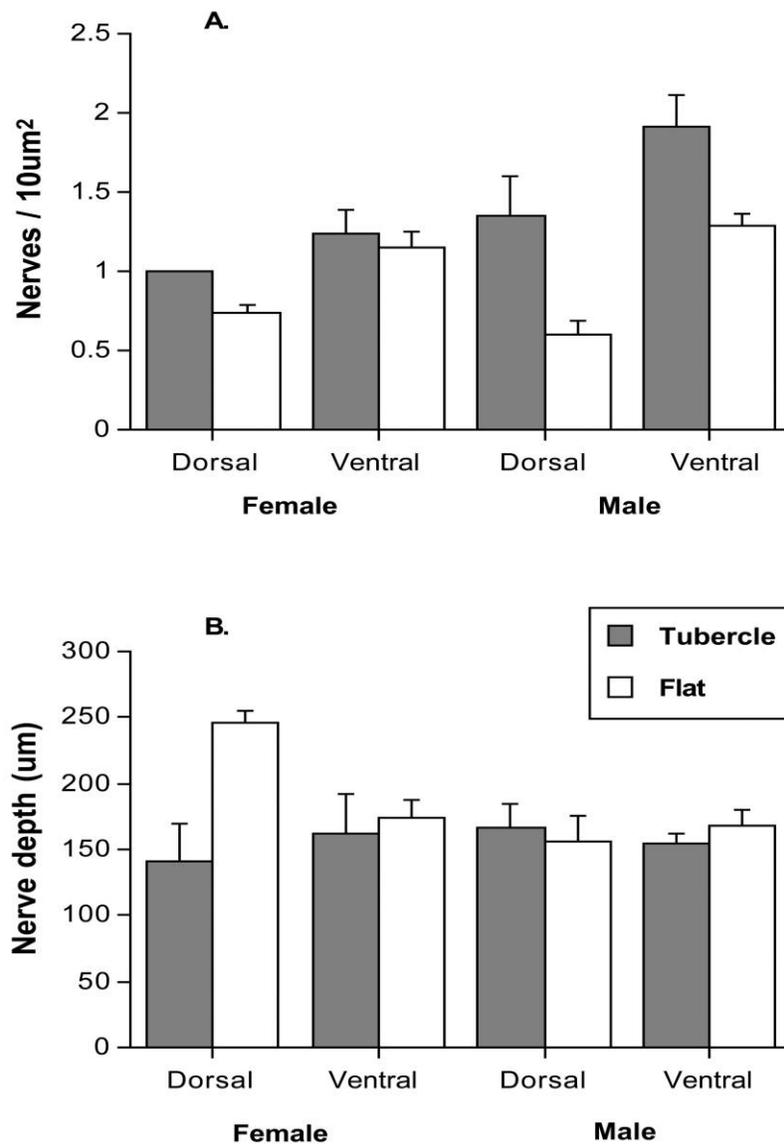


Figure 3: Sensory innervation of rugose and nonrugose scales of sea snakes *Emydocephalus annulatus*. Data are shown separately for scales from the dorsal and ventral surfaces of snakes of each sex, with $n = 12$ specimens for each group. The graphs show (A) mean number of nerves per half-field ($10 \mu\text{m}^2$) and (B) mean depth of myelinated nerves (distance from epidermis) in micrometers under tubercles and under flat areas of the scale. Error bars represent SEs.

males and females had similar numbers of nerves per half-field (fig. 3A; $F = 3.87$, $df = 1, 75$, $P = .05$; note that we lowered the significance level from $P = .05$ to $P = .01$ for this comparison). Nerves under rugosities averaged closer to the epidermis than did nerves in flat areas of the scale, but this result also fell short of statistical significance when we lowered the significance level to $P = .01$ (fig. 3B; $F = 4.58$, $df = 1, 75$, $P = .04$; table A2 in the online edition of the *American Naturalist*). Mean nerve depth did

not differ as a function of either sex or scale type, with no significant interactions (fig. 3B; all $P > .05$; table A2).

Do Scale Rugosities Aid Sex Recognition by Male Snakes?

Free-ranging male sea snakes directed similar numbers of tongue flicks toward smooth ropes ($n = 10$, mean = 2.91, $SD = 1.22$) as rough ropes ($n = 10$, mean = 3.55, $SD = 2.46$; paired t -test; $t = 1.10$, $df = 10$, $P > .05$) and

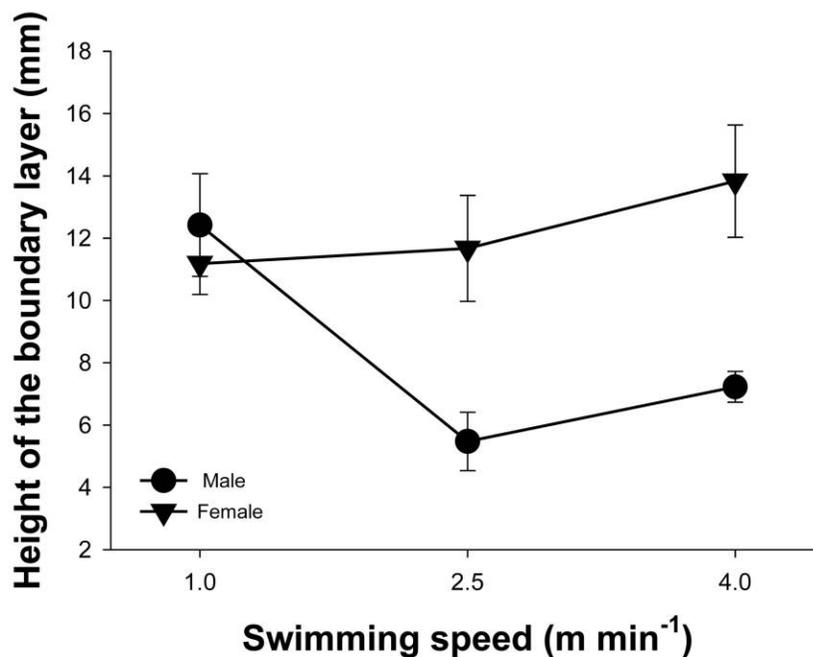


Figure 4: Mean height of the boundary layer over silicone models of male ($n = 3$) and female ($n = 3$) *Emydocephalus annulatus* skin. Boundary layer height was defined as the height at which 95% of the free stream velocity was obtained and empirically derived from best fit regressions for each model. Error bars represent SEs.

were equally likely to approach either stimulus (10 out of 11 males approached in each case). Thus, surface rugosity did not influence the likelihood of a male sea snake approaching or tongue flicking the stimulus.

Do Rugose Scales Enhance Friction between Adjacent Snakes?

The mean coefficient of static friction against the body of another snake was greater for live male *E. annulatus* than for live females (mean values 0.88 vs. 0.60; ANOVA, $F = 32.21$, $df = 1, 16$, $P < .0001$).

Do Scale Rugosities Affect Thickness of the Boundary Layer?

Most velocity profiles of water flowing over the silicone impressions as a function of height above the surfaces were better fitted by logarithmic rather than linear functions (tables A3–A5 in the online edition of the *American Naturalist*). The velocity of water flow did not increase with height from the substrate in most empty-flume trials, indicating that artefacts from the flow tank per se were minor. At swimming speeds typical of foraging *E. annulatus* (1 m min^{-1} ; Shine et al. 2004), the height of the boundary layer did not differ between male and female snakes. How-

ever, at swimming speeds typical of courting and mate-searching males ($2.5\text{--}4 \text{ m min}^{-1}$; Shine 2005), the boundary layer was almost 50% thinner over models of rugose skin than over models of nonrugose skin (fig. 4; tables A6–A8 in the online edition of the *American Naturalist*). The height of the boundary layer over nonrugose skin did not change over this range of swimming velocities (fig. 4). Thus, rugosities on male skin substantially decreased the thickness of the boundary layer at (and only at) the relatively rapid speeds associated with male reproductive activity in the field.

Do Scale Rugosities Affect Whether Water Flow across the Skin Is Laminar versus Turbulent?

The Reynolds number (Re^*) for rugose skin was >60 at all swimming speeds tested (range 95.5–382.0), whereas nonrugose skin had $Re^* < 5$ (range 1.0–3.8). Therefore, we deemed rugose skin to have a turbulent boundary layer and nonrugose skin to have a laminar boundary layer for the purpose of solving equation (2).

Do Scale Rugosities Influence Rates of Mass Transfer?

Solving equation (2) predicts that the rates of mass transfer (diffusion to and from a snake's body) are greatly en-

hanced by turbulent boundary layers (fig. 5). Theory predicts the following: at a velocity of 2.5 m min^{-1} , rates of passive diffusion of O_2 are 50% greater in turbulent boundary layers than in laminar boundary layers; water velocity is a rate-determining step in mass transfer, whereby greater velocities mean greater rates of passive diffusion in turbulent boundary layers (fig. 5). Rates of passive diffusion are low in laminar boundary layers regardless of velocity. Solving equation (2) suggests that eddy diffusion (in turbulent boundary layers) transports materials more rapidly than does molecular diffusion (in laminar boundary layers), resulting in increased rates of mass transfer. Thus, a more rugose surface will generate turbulent rather than laminar flow as well as result in a thinner boundary layer. These effects of scale rugosity should enhance rates of oxygen uptake for an aquatic snake, at least at high swimming speeds. Rugosities also may aid in diffusion by increasing surface area but are not vascularized in *E. annulatus* (Avolio et al. 2006) and hence are unlikely to have much effect in this regard.

Discussion

Our results support some of the hypotheses that we posed in the first section of this article and falsify others. In total,

our data suggest that the elaboration of sex-specific scale rugosity in the sea snake *Emydocephalus annulatus* (and, by inference, in other sea snakes with sex-linked rugosities; Avolio et al. 2006) has been driven by a series of selective forces. The most likely scenario is initial selection for exaggeration of a preexisting function (provision of tactile cues to courting males), followed by an increase in the size and number of tubercles to facilitate friction (and thus, grip) during mating attempts and, last, extension of the tubercles over most of the male's body because of hydrodynamic advantages that increase cutaneous oxygen uptake. We explain this interpretation.

The initial selective force for scale rugosity in male sea snakes likely was the same as that responsible for the (infrequent) cases of similar sex-specific scale rugosity in terrestrial snakes. Males of some natricine colubrid species have anal knobs with greater sensory innervation than nearby skin (Noble 1934), which are thought to provide males with sensory information regarding cloacal alignment during courtship (Blanchard 1931; Noble 1937; Pisani 1976). In sea snakes, scale rugosities in the cloacal region may have evolved under sexual selection to enhance sensory perception in males to compensate for reduced availability of chemosensory and visual cues in the marine environment (Shine 2005). In keeping with this putative

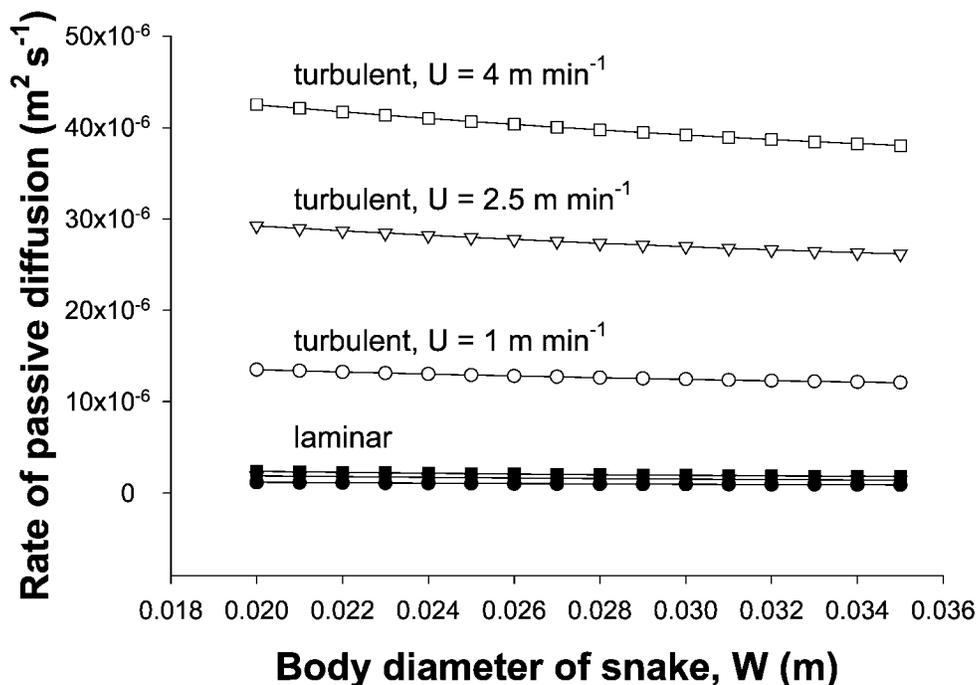


Figure 5: Calculated rates of mass transfer across snake skin as a function of snake body diameter and water velocity. The solid symbols are based on laminar flow of water above the skin surface, whereas the open symbols are based on turbulent flow of water over the skin surface.

sensory function, tubercles of male *E. annulatus* were more highly innervated than was adjacent nonrugose skin (figs. 2, 3). However, it would be useful to test sensitivity directly in this respect by measuring nerve impulses. Because tubercles have a thicker epidermal layer (fig. 2C), greater innervation may be required to achieve the same sensory input.

Our experiments with free-ranging *E. annulatus* suggest that males do not use scale rugosities to determine the sex of other snakes. Instead, mate-searching males approach snakelike stimuli based on visual cues and then use chemosensory traits to distinguish reproductive females (Shine 2005). In light of the poor visual acuity of these animals (Shine 2005), it is not surprising that our experimental manipulations of surface roughness did not modify mate-recognition behaviors. For the same reason, we doubt that females would use scale rugosity for mate choice. A role for male-specific scale rugosity to minimize courtship from other males also would require such courtship to be so common as to comprise a major cost to a less rugose male (Rivas and Burghardt 2001; Sherratt and Forbes 2001), which appears unlikely in *E. annulatus* (Shine et al. 2003b; Shine 2005).

The distribution of rugosities across the entire body of male *E. annulatus* suggests that tactile functions cannot be their only use. During courtship, the male's head and neck are the only parts of his body in regular contact with the female (Avolio et al. 2006). Enhanced friction during copulatory positioning (or male-male combat in species exhibiting this behavior, which *E. annulatus* does not show; Shine 2005) seems more plausible and fits well with the evolution of sexually dimorphic skin rugosities in some other lineages of animals. For example, males of some fish and amphibian taxa develop skin rugosities during the breeding season (Wiley and Collette 1970); in frogs, this trait is seen most often in species that spawn under conditions where physical contact between the male and female may be difficult to maintain (Duellman and Trueb 1986). Our friction trials confirmed that the rugose skin of males provided better resistance against the female's body than would nonrugose skin. If friction before and during copulation was the primary selective force for scale rugosity, we might expect rugosities to be most highly developed in parts of the body (e.g., posterior ventral region of the male) for which positioning next to the female is most important. In keeping with this prediction, males of some sea snake species have strongly differentiated scalation across their bodies, with tubercles (and sometimes spines) concentrated in such areas (Avolio et al. 2006).

Again, however, the wide distribution of rugosities across the bodies of male *E. annulatus*—as well as the trend for female sea snakes to display rugosities also, albeit

smaller than those of conspecific males (Avolio et al. 2006)—suggests that scale rugosity confers some more general advantage to an aquatic snake. Hydrodynamics offers a strong possibility in this regard. Both sexes may benefit from higher cutaneous oxygen uptake, but these benefits may be more important to males than to females because mate-searching male snakes typically move farther and faster than do females (Gregory et al. 1987; for *E. annulatus*, see Shine et al. 2004). Hence, increased oxygen uptake may be more important for males.

Our flume experiments showed that the rugosities of reproductive male *E. annulatus* do indeed modify the way in which water flows across the scale surface. Importantly, these effects depend on swimming speed, a factor that differs between mate-searching male *E. annulatus* and all other segments of the population (Shine et al. 2004). At their normal foraging speeds, male and female *E. annulatus* would experience similar hydrodynamic advantages, whereas at higher speeds (seen only in mate-searching males; Shine et al. 2004), the rugosities in male skin convey a clear advantage by reducing the boundary layer and making it more turbulent to enhance near-surface mixing.

Our measurements and modeling suggest that the mass transfer of oxygen is enhanced by surface rugosity. At courtship speed, males could increase cutaneous oxygen uptake because of the reduced boundary layer and the shorter distance across which oxygen molecules must diffuse. The boundary layer over rugose skin is only about half as thick as that over nonrugose skin, potentially increasing the passive rate of diffusion of oxygen by an order of magnitude (figs. 4, 5). Behavioral studies on free-ranging *E. annulatus* have shown that males often lose contact with females they are courting, especially when the male is forced to interrupt courtship to return to the surface to breathe (Shine 2005). Thus, enhanced cutaneous oxygen uptake might allow a male to maintain uninterrupted courtship for longer periods by prolonging dives (Feder and Booth 1992) and thus reduce the rate at which potential mates are lost.

In summary, our data suggest a complex scenario of multiple functions for the sexually dimorphic scale rugosities of marine snakes. The restricted availability of chemical and visual cues underwater may have been the initial stimulus for elaboration of the ancestral condition of small male-specific scale rugosities in the paracloacal region of some terrestrial snake taxa. However, advantages associated with friction during courtship then favored a spectacular increase in both the degree and distribution of scale rugosity in males. Last, hydrodynamic advantages of this rugosity provided a selective advantage for an even more dramatic development, whereby rugosity in some hydrophiid snakes (including *E. annulatus*) is evident on virtually every scale on the male's body as well as signif-

icantly developed on many females (Avolio et al. 2006). Sea snake scale rugosity thus may provide an unusually clear example of co-option and successive elaboration of morphological traits in a lineage that has been subject to novel selective forces as it has adapted to the challenges posed by exploitation of a new habitat type.

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