A seasnake's colour affects its susceptibility to algal fouling

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Evolutionary transitions from terrestrial to aquatic life modify selective forces on an animal's coloration. For example, light penetrates differently through water than air, and a new suite of predators and visual backgrounds changes the targets of selection. We suggest that an aquatic animal's coloration may also affect its susceptibility to algal fouling. In a colour-polymorphic field population of seasnakes (*Emydocephalus annulatus*) in New Caledonia, black individuals supported higher algal cover than did banded conspecifics. In experimental tests, black snake models (plastic tubes) accumulated more algae than did banded models. Algal cover substantially reduced snake activity (in the field) and swimming speeds (in the laboratory). Effects of algal cover on a snake's hydrodynamic efficiency and/or its rate of cutaneous gas exchange thus may impose selection on the colours of aquatic organisms.

Keywords: algal settlement; aquatic; biofouling; constraints; marine; snake

1. INTRODUCTION

An organism's colour can affect its fitness via many pathways. Some species have evolved colours that camouflage them against the local habitat, thereby preventing detection by predators or prey; others have bright colours that attract mates, intimidate rivals or mimic toxic species (Savage & Slowinski 1992; Andersson 1994; Baube 1997; Houde 1997; Marshall 2000). An extensive literature reveals many examples of subtle modifications of colour and pattern that enhance organismal fitness (e.g. Endler 1983; Whiting *et al.* 2009). In this paper, we suggest another potential selective force: in aquatic animals, rates of algal fouling may depend upon (and hence impose selection upon) an animal's colour.

Selective forces on coloration of aquatic animals differ from those acting on their terrestrial counterparts. For example, murky water impedes light transmission; specific wavelengths of light attenuate at different rates with water depth; visual backgrounds differ (especially, predators may view the animal from below rather than above); and much of the background may be in motion owing to water currents (Fuller 2002; Johnsen & Sosik 2003). Another change accompanying the transition to aquatic habitats involves the costs of fouling by algae and invertebrates, which can substantially reduce hydrodynamic efficiency (by modifying the boundary layer around the organism's body; e.g. Subramanian *et al.* 2004; Swift *et al.* 2006) and hence impose significant fitness costs (Wahl 1996, 1997). Rates of algal settlement and growth are influenced by substrate colour, with higher rates of settlement on darker substrates (Dahlem *et al.* 1984; Henschel *et al.* 1990; Hodson *et al.* 2000; Swain *et al.* 2006). If the same phenomenon occurs with living organisms, we might expect an animal's colour to affect its susceptibility to algal fouling.

Evolutionary transitions from terrestrial to aquatic life have occurred in many phylogenetic lineages, providing a robust opportunity to compare the characteristics of

related taxa in each habitat type, and hence identify selective forces unique to each of those habitats (e.g. Kooyman 1989; Boyd 1997; Shine & Shetty 2001). Snakes are well-suited to such analyses, because they display multiple independent transitions to aquatic life (Heatwole 1999; Aubret *et al.* 2007; Aubret & Shine 2008). Many of the distinctive phenotypic attributes of aquatic snakes are readily interpretable as adaptations to the challenges of underwater existence; for example, flattened paddle-like tails, large lungs, valvular nostrils and relatively anterior clutch position (Shine 1988; Heatwole 1999). Another consistent attribute of aquatic snakes (hydrophiid seasnakes, laticaudid seasnakes, acrochordid filesnakes, homalopsine colubrids) involves coloration: most are banded rather than unicoloured, blotched or striped. The same tends to be true of highly aquatic species within other lineages (e.g. water cobra *Boulengerina annulata*, American water-snakes of the genus *Nerodia*; Pough 1976; Pauwels *et al.* 2008). However, many terrestrial snakes are also banded, weakening any argument for a functional link between coloration and aquatic habits (e.g. Jackson *et al.* 1976; Pauwels *et al.* 2008). Fouling by algae has been reported in several taxa of seasnakes (*Aipysurus laevis*: Heatwole 1999; *Astrotia stokesii*: Smith 1926; *Acalyptophis peroni*, *Aipysurus duboisii*, *Hydrophis coggeri*: Ineich & Laboute 2002; *H. melanocephalus*: Ohba *et al.* 2005; *Aipysurus foliorum*, *A. fuscus*, *A. aepraefrontalis*, *A. laevis*, *Disteira kingii*: Zann *et al.* 1975), suggesting that a snake's colour might influence its susceptibility to biofouling.

Polymorphic traits (i.e. those seen in multiple forms within a single population) offer an unusually robust opportunity to identify correlates (and thus, potentially, costs and benefits) of alternative trait values (Roulin 2004). During fieldwork on a colour-polymorphic population of the turtle-headed seasnake (*Emydocephalus annulatus*) in the Noumea Lagoon of New Caledonia, we noticed that free-ranging snakes were often heavily coated in algae (myrionematoid brown algae, tentatively identified as *Streblonema* spp.; but with occasional red algae [Ceremiales] and cyanobacteria also; figure 1a). In this

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Figure 1. (a) A free-ranging turtle-headed seasnake in the Noumea Lagoon, showing heavy algal fouling (5 January 2009). (b) Two extremes of colour phase in turtle-headed seasnakes from the Noumea Lagoon; both snakes were collected at the same site.

population, snakes range in colour from jet black to brightly black-and-white banded, with many intermediate patterns also (Shine *et al.* 2003; see figure 1b). We predicted that if a snake's colour influences its vulnerability to algal fouling, darker snakes should carry more algae. The same hypothesis predicts that algal settlement and growth should be higher on black objects than on banded or pale ones. Plausibly, algal fouling may affect a snake's activity levels and/or locomotor abilities. Below, we provide data to evaluate all of these predictions.

2. MATERIAL AND METHODS

(a) Incidence of algal fouling on free-ranging snakes in the field

In the course of a mark–recapture study conducted each January from 2004 to 2009, we hand-captured turtle-headed seasnakes at Anse Vata in the Noumea Lagoon. Snakes were returned to the laboratory to be weighed, measured and individually marked (with a microchip) prior to release at their site of capture less than 60 min later. We dichotomously scored two traits for each snake: snake coloration (black versus at least partially banded) and algal cover (zero or light versus moderate to heavy). At the time of collection (by hand, while snorkelling), we also scored whether snakes were inactive (hidden among the coral) or actively moving (presumably foraging; Shine *et al.* 2003).

All analyses below are based on the first time each snake was captured, to avoid pseudoreplication.

(b) Experimental study of algal fouling

As model snakes, we used plastic centrifuge tubes, shorter than adult *E. annulatus* (9 cm versus 32–72 cm) but similar in diameter (3 cm). To create different colours without affecting surface texture, we placed rolled-up sheets of paper inside the clear plastic tubes, such that the coloured surface was applied to the innermost surface of the plastic tube. We constructed six snake models: two black, two white and two black-and-white banded (band width 2 cm). These were set out in random order inside the mesh cage that protects the Noumea Aquarium's pumping station (to avoid algal grazing from herbivorous organisms). The tubes (full of air) were suspended and were freely floating in the water column (50 cm deep at low tide). These snake models were left under water for 29 days. Because the algae grow on the tubes as small (less than 5 mm diameter) circular colonies, we assessed the degree of algal fouling by counting the number of algal colonies along two transects randomly placed along the length of each tube.

(c) Effects of algal cover on snake locomotor ability

We quantified swimming speeds of *E. annulatus* ($n = 102$) in a large raceway (30 × 500 cm, 50 cm deep) within a tank filled with fresh (circulating) sea water at 25.1–26.0°C. Each snake was placed in a holding tank for at least 30 min to recover from handling and measuring, and then released at one end of the 5 m raceway, and the time in which it travelled successive 1 m lengths was recorded. The snake was turned around at the end of each run, and the trial repeated in the other direction. Analysis was based on 12 trials per snake.

(d) Survival rates as a function of snake colour

We used the program MARK (White & Burnham 1999) to estimate survival rates of snakes of different colour morphs. We modelled four groups (banded males, black males, banded females, black females) and allowed full time-dependence for both the recapture and survival parameters (to give a total of 16 models; Nichols 2005).

3. RESULTS

(a) Incidence of algal fouling on free-ranging snakes in the field

Likelihood ratio tests from a logistic regression with algal score as the dependent variable showed significant annual variation in algal cover ($\chi^2 = 15.61$, d.f. = 4, $p < 0.004$; figure 2a), but with banded snakes averaging less algal cover than their black conspecifics in every year of the study ($\chi^2 = 10.15$, d.f. = 1, $p < 0.002$; figure 2a). The interaction term between year and snake colour was non-significant ($\chi^2 = 1.56$, d.f. = 4, $p = 0.82$). Analyses in which we added additional covariates suggested that this colour-associated difference in algal cover was not a secondary consequence of other factors. For example, larger snakes tend to have more algal cover (mass effect $\chi^2 = 10.10$, d.f. = 1, $p < 0.002$), but the association between colour and algal cover persisted even if snake body size (mass) is incorporated into the analyses: at the same size, banded snakes had less algal cover than did melanistic conspecifics ($\chi^2 = 10.25$, d.f. = 1, $p < 0.002$). When encountered in the field, snakes with a

Figure 2. (a) Algal cover on free-ranging turtle-headed seasnakes (*Emydocephalus annulatus*) from Anse Vata, New Caledonia, over a 5-year period. Algal cover was scored as being heavy or light, and snakes were scored as either black (black circles with continuous line), or at least partially banded (white circles with dashed lines). (b) Number of algal colonies along two random transects on the surface of snake models (plastic tubes of three different colours) after the models had been deployed in shallow water in New Caledonia for 29 days in March–April 2008. (c) Swimming speeds of turtle-headed seasnakes with and without a heavy cover of algae in standardized laboratory trials. Black circles with continuous lines, heavy algae; white circles with dashed lines, no algae.

heavy covering of algae were often inactive and hidden among the coral, whereas snakes with less or no algal cover were almost invariably found while they were actively foraging (50% versus 19% inactive: $\chi^2 = 3.54$, d.f. = 1, $p < 0.0001$).

(b) Experimental study of algal fouling

The colour of a snake model affected the amount of algal cover on that model after a 29-day deployment (figure 2b; ANOVA on the number of algal colonies along two random transects per tube, $F_{2,9} = 13.15$, $p < 0.003$). Less algae settled and grew on banded tubes than on black tubes, and even less on white tubes (Fisher's PLSD *post hoc* tests show that all three colours differ from each other at $p < 0.05$).

(c) Effects of algal cover on snake locomotor ability

The presence of heavy algae reduced a snake's speed by about 20 per cent (figure 2c; repeated-measures ANOVA with algal cover as the factor and speed (snout-vent lengths per second) as the repeated measure: $F_{1,100} = 5.78$, $p < 0.02$). This conclusion was unchanged if we incorporated other factors (such as snake body size and colour) into the analyses.

(d) Survival rates as a function of snake colour

Our mark–recapture data reveal temporal stability in morph frequencies; the percentage of banded snakes ranged from 17.8 to 35.6 per cent over the 6 years of the study, but was within the range of 27.5 to 35.6 per cent in 5 of those years (logistic regression shows $p = 0.37$, likelihood ratio $\chi^2 = 6.45$, d.f. = 6). Also, the frequencies of banded versus black snakes did not change with age for 111 snakes for which we could confidently assess ages based on mark–recapture histories (logistic regression, ages 1–6 years, $p = 0.77$, likelihood ratio $\chi^2 = 0.08$, d.f. = 1). Similarly, the survival rates of snakes did not differ depending on their colour. The best-supported MARK models have a constant probability of survival regardless of sex or colour ($= 0.69 \pm 0.28$ per annum), but with a variable probability of recapture through time (from 0.39 to 0.78 per annum). The Akaike Information Criterion (AIC) weight for the best model (0.37) was 30 per cent better than for the next best model (which allows survival to vary among groups). Thus, a snake's colour does not appear to affect its survival.

4. DISCUSSION

Polymorphisms involving melanistic versus banded colour phases in terrestrial snakes typically have been attributed to the effects of dorsal colour on rates of thermal exchange. That is, darker dorsal colour facilitates heat uptake, perhaps at the cost of increased conspicuousness and, thus, vulnerability to predation (Andren & Nilson 1981; Gibson & Falls 1988; Madsen & Stille 1988; Luiselli 1992; King 1993; Shine & Madsen 1994; King & Lawson 1995; Lindell & Forsman 1996; Zaidan 2001; Bittner *et al.* 2002). However, thermal-based explanations cannot be applied to the case in *Emydocephalus*, because (unlike on land) colour does not affect the body temperatures of a snake under water (Shine *et al.* 2003). Our data suggest another potential fitness consequence of colour in

seasnakes (and potentially other aquatic animals): susceptibility to algal fouling.

Our results support two key predictions from the hypothesis that body coloration affects algal fouling. First, black snakes were more heavily algae-covered than were banded conspecifics. This correlation does not provide unequivocal evidence for causation, however—for example, black individuals may spend more time in habitats (shallower water?) that enhance rates of algal growth, or may slough their skins less frequently. We have no data on these topics, although we note that an adjacent population in an area with less nutrient inflow from the land (Baie des Citrons) has a higher proportion of melanistic snakes, as expected from the hypothesis that melanism may be disadvantageous in areas of high algal growth rates. More direct evidence for a causal link comes from our experiments, in which the colour of a snake-shaped model affected the rate at which it became covered in algae. The mechanistic basis of this effect presumably involves cues for algal settlement: reflecting their phylogenetic affinity with invertebrates (rather than terrestrial plants), algal spores use a range of substrate-based cues to select sites when settling out of the water column at the end of their planktonic phase (Dahlem *et al.* 1984). Importantly, increased rates of settlement on darker substrates are seen in an array of marine biofouling taxa, including barnacles, abalone, pearl oysters, mussels, ascidians and algae (Dahlem *et al.* 1984; Henschel *et al.* 1990; Callow & Callow 2000; Hodson *et al.* 2000; Swain *et al.* 2006; Findlay *et al.* 2008).

If snake colour influences rates of algal accumulation, what are the consequences of such accumulation? The most obvious such consequence is increased drag. Mathematical modelling and empirical studies on a wide range of other systems suggest that a thick algal coating would reduce the snake's speed and/or efficiency of movement. By analogy, drag coefficients on fishing nets can more than double as a result of algal fouling (Swift *et al.* 2006), and increased drag owing to algal epibionts negatively affects growth in snails (Wahl 1996, 1997). Even minor disruptions to laminar flow across the skin surface of a seasnake have significant hydrodynamic consequences (Avolio *et al.* 2006). In keeping with this hypothesis, our locomotor trials revealed a 20 per cent reduction in swimming speeds in snakes covered with a heavy coating of algae.

A second effect of algal cover on a snake's skin involves cutaneous gas exchange. Seasnakes receive up to 33 per cent of their oxygen needs from the surrounding water and can excrete up to 94 per cent of respiratory carbon dioxide in this way (Graham 1974). Cutaneous respiration may be important to a snake's fitness by prolonging dive times, and thus reducing exposure to predators while surfacing (Heatwole 1999) and/or enhancing the effectiveness of underwater courtship (Avolio *et al.* 2006). If algal fouling reduces gas exchange across the skin, it may force an algae-covered snake to surface more frequently to breathe. However, studies on other marine systems suggest the reverse possibility. At least during daylight hours, algal fouling might increase rather than decrease oxygen concentrations at the snake's body surface, owing to algal photosynthesis (Larkum *et al.* 2003; Roberts *et al.* 2007). Especially, for a snake that was stationary for long periods (as

commonly occurs in algae-covered snakes; see above), heavy algal growth might confer a benefit (reduced rate of surfacing to breathe) rather than a cost. Even for a moving snake, skimming (low-turbulence) flow should develop over the algal cover towards the rear of the body, stabilizing the boundary layer and thus increasing oxygen levels close to the snake's body surface (Subramanian *et al.* 2004). Other benefits are also plausible—for example, algae-covered snakes are likely to be more difficult for visually hunting predators to detect (figure 1a) and/or predators could be deterred by secondary metabolites of the alga (Hay *et al.* 1990; Stachowicz & Hay 1999).

Might colour-related susceptibility to algal fouling explain the polymorphism seen in *E. annulatus* in the Noumea Lagoon? We cannot answer that question with the available data. If the fitness costs of fouling (e.g. reduced hydrodynamic efficiency) always exceed benefits (e.g. increased oxygen availability), we would expect all snakes to be banded (or, even better, white; see figure 2b) rather than black. The reality, however, will be more complex. For example, the balance between costs and benefits of algal accumulation might shift with a snake's sex and body size, reflecting factors such as sex-based or size-based divergence in: (i) the importance of locomotor efficiency or prolonged dive times for snake fitness (Avolio *et al.* 2006); (ii) sloughing frequencies (e.g. smaller snakes grow faster and thus shed more frequently, losing their biofouling cover more often); or (iii) direct consequences of differential activity patterns or larger body size (e.g. the oxygen availability benefits of algal cover might be seen only at large body size, if skimming flow does not occur in the first 50 cm or so of the snake's anterior body; see fig. 7 in Subramanian *et al.* 2004). A diverse array of other factors may also be at work, including other costs and/or benefits of colour. For example, algae-covered individuals might be better camouflaged visually (figure 1) and chemically (Hay *et al.* 1990; Stachowicz & Hay 1999) from predators. Our analyses of survival rates do not reveal any overall (net) fitness benefit to either colour morph, consistent with models for balanced polymorphism.

The generality of our findings for other aquatic snakes, and other marine organisms, remains unclear. Our study species, *E. annulatus*, inhabits shallow-water tropical coral reefs during daylight hours (Shine *et al.* 2003, 2004). These conditions would encourage algal settlement and growth. Snakes (or other taxa) that are nocturnally active, and/or spend most of their time in deeper and/or murkier water, will probably experience less intense selection on resistance to algal accumulation. However, our data on *E. annulatus* support the hypothesis that in the evolutionary transition from terrestrial to aquatic life, one of the significant new selective forces that has arisen involves the effects of an animal's colour on the rate that its body surface is colonized by algae.

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