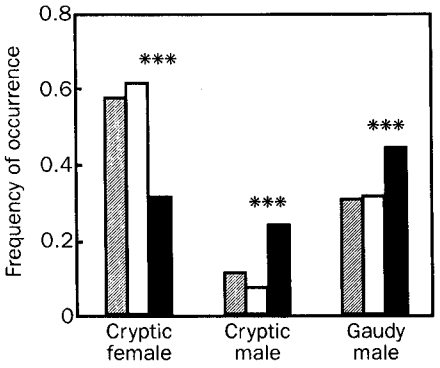
Risks of alternative mating tactics

SIR — Bright colours and conspicuous mating tactics may reduce survival by attracting predators[1,2]. Evolutionary theory proposes that trade-offs between mate attraction and predator avoidance can promote the development of inconspicuous, safer, 'alternative' mating strategies[3,4]. Our study of predation on different male colour morphs of the parrotfish, *Sparisoma radians*, challenges the generality of this supposition.

S. radians is a common inhabitant of Caribbean seagrass meadows. Like many other sex-changing fishes, females give rise to different male morphs that display a range of mating tactics[5]. Gaudy males of *S. radians* defend territories in which they actively court and mate singly with females, whereas cryptic males (that resemble females) form small, compact schools ($\bar{x}$ = 7 fish; n = 37 schools) that persistently follow and spawn with single females.

S. radians is the primary prey of the yellow jack, *Caranx bartholomaei*, representing 44 per cent numerically and 65 per cent by weight of 991 recognizable prey from 396 jack stomachs we collected in Panama between 1988 and 1992. Before the mid-afternoon spawning period of *S. radians*, females and both male morphs were eaten in relation to their availability in the population. In sharp contrast, both gaudy and cryptic males were found much more frequently than expected in the stomachs of jacks collected during the spawning period. Unexpectedly, cryptic males were 2.3 times more likely to be eaten than gaudy males when compared with their relative abundance. These differences were due neither to size-selective predation by jacks (data and analyses in the figure) nor to differential experience or predator avoidance by older gaudy males: the size range of gaudy males spans that of cryptic males, and large (> 11 cm) gaudy males are actually taken more frequently than small (6–11 cm) ones (χ^2 = 13.8; $P < 0.001$).

This shift over the course of the day from non-selective predation on sexually inactive *S. radians* to selective predation on spawning males, particularly cryptic males, provides a unique demonstration not only of sexual differences in the predation costs of mating but also of differences in such costs for different male mating tactics. Male mating behaviour, rather than colour pattern, must drive these predation patterns, since both types of males suffered higher predation only when sexually active. Conspicuous courtship and territorial behaviour probably draw attacks on gaudy males. We think that schooling invites predation upon cryptic males because schools are visually conspicuous and easy to exploit: jacks search for fish hiding in the seagrass and schools of cryptic males produce rich, male-biased 'patches' of prey. Preoccupation with obtaining females and repeated daily spawning by males may also boost their overall risk of being eaten.



Frequency of occurrence of *S. radians* in the population (n = 1,269 fish from 18 trawls in 1992; open bars) and in the stomachs of jacks collected by handspear before (shaded bars) and during (filled bars) the spawning period of *S. radians* (n = 52 *S. radians* from 44 jacks and n = 262 *S. radians* from 180 jacks, respectively). The relative abundances of females and the two male morphs of *S. radians* in the population did not differ from those in 'pre-spawning' stomachs (χ^2 = 0.65; P = 0.72), but did differ from those in 'spawning-period' stomachs (asterisks, binomial comparison of proportions by fish type for population versus spawning period: $Z \geq 6.81$; $P < 0.0001$). More cryptic and fewer gaudy males than expected were found within jacks collected during the spawning period (n = 194 males; χ^2 = 13.6; d.f. = 1; $P < 0.001$). Yellow jacks tend not to eat *S. radians* smaller than 6 cm, regardless of sex or colour, but consume *S. radians* larger than 6 cm in direct proportion to their availability (208 *S. radians* in six size classes; χ^2 = 4.22; d.f. = 5; P = 0.52).

To conclude, our data strongly support the general prediction that conspicuous male courtship imparts substantial risks[6]. They also reveal, however, that 'alternative' mating tactics by cryptically coloured individuals may actually be the riskiest of those available. This latter result is counterintuitive, given that both schooling and the expression of alternative mating tactics by cryptic morphs are generally thought to lower the relative risk of predation.

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