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Female impersonation as an alternative reproductive strategy in giant cuttlefish

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Out of all the animals, the cephalopods possess an unrivalled ability to change their shape and body patterns. Our observations of giant cuttlefish (*Sepia apama*) suggest this ability has allowed them to evolve alternative mating strategies in which males can switch between the appearance of a female and that of a male in order to foil the guarding attempts of larger males. At a mass breeding aggregation in South Australia, we repeatedly observed single small males accompanying mating pairs. While doing so, the small male assumed the body shape and patterns of a female. Such males were never attacked by the larger mate-guarding male. On more than 20 occasions, when the larger male was distracted by another male intruder, these small males, previously indistinguishable from a female, were observed to change body pattern and behaviour to that of a male in mating display. These small males then attempted to mate with the female, often with success. This potential for dynamic sexual mimicry may have played a part in driving the evolution of the remarkable powers of colour and shape transformation which characterize the cephalopods.

Keywords: alternative mating strategy; cephalopod; giant cuttlefish; mimicry; *Sepia apama*; Spencer Gulf

1. INTRODUCTION

Alternative male mating strategies have become the textbook example of evolutionarily stable strategies. Examples of different males employing different behaviours and/or life histories are known from many animal groups, including all vertebrate classes (Arak 1984) and a number of invertebrates (Forsyth & Alcock 1990; Sauer *et al*. 1997). A common situation has males which are either large and able to guard females or resources, or small and reliant on 'sneaky' matings (Taborsky 1998). One method by which sneaks escape detection by larger males is to impersonate a female, something which typically requires males to have a life history that makes them physically similar to females. Theoretical models (Owens & Hartley 1991) suggest that constraints on males' ability to vary their phenotype may be necessary for 'honest signalling' of male quality to evolve, giving opponents the opportunity to assess competitive ability. If males are able to change their appearance facultatively, then the system will be less stable, increasing the likelihood of an arms race between impersonators and males attempting to avoid deception.

2. STUDY ANIMAL AND METHODS

The giant cuttlefish (*Sepia apama*) lives in the shallow temperate waters of southern Australia, from southern Queensland to north-west Western Australia. No detailed studies have been undertaken into the biology, behaviour and reproduction of this cuttlefish. The species is sexually dimorphic with males possessing longer arms than females, these arms being fringed by wide, banner-like webs off the ventral margins (figure 1*a*). Mating consists of males courting females with elaborate colour displays (dark zebra stripes rapidly pulsing across the dorsal mantle with extended white banner-like webs off the arms). Copulation occurs by coupling head to head, with the male transferring sperm packets to a pouch below the beak of the female (figure 1*b*). During most of this process, the female displays a mottled body pattern of dark blotches on a white background (figure 1*b*). Following copulation, the female then proceeds to lay large eggs singly, attaching them to the undersurface of rock crevices or boulders. Eggs are fertilized by being passed over the sperm receptacle below the mouth. The male remains in attendance, mate guarding the female from other suitors. In larger breeding aggregations of giant cuttlefish, males frequently engage in ritualized display combat with other males. Disparate size typically results in the loser fleeing without physical combat. In more even contests, battles can escalate to seizing and biting opponents. Many males exhibit bite scars or missing arm tips.

In Spencer Gulf, South Australia, extensive soft sediment substrates and limited rocky reefs have resulted in massive and unique breeding aggregations of giant cuttlefish. Every year between April and July, these animals congregate in their thousands on small shallow rocky reefs in the region to spawn (Moran 1998). Breeding animals can be easily approached and will mate, lay eggs, mate guard and fight within centimetres of observing divers.

3. RESULTS

While investigating male mate-guarding behaviour during spawning, we repeatedly observed male–female

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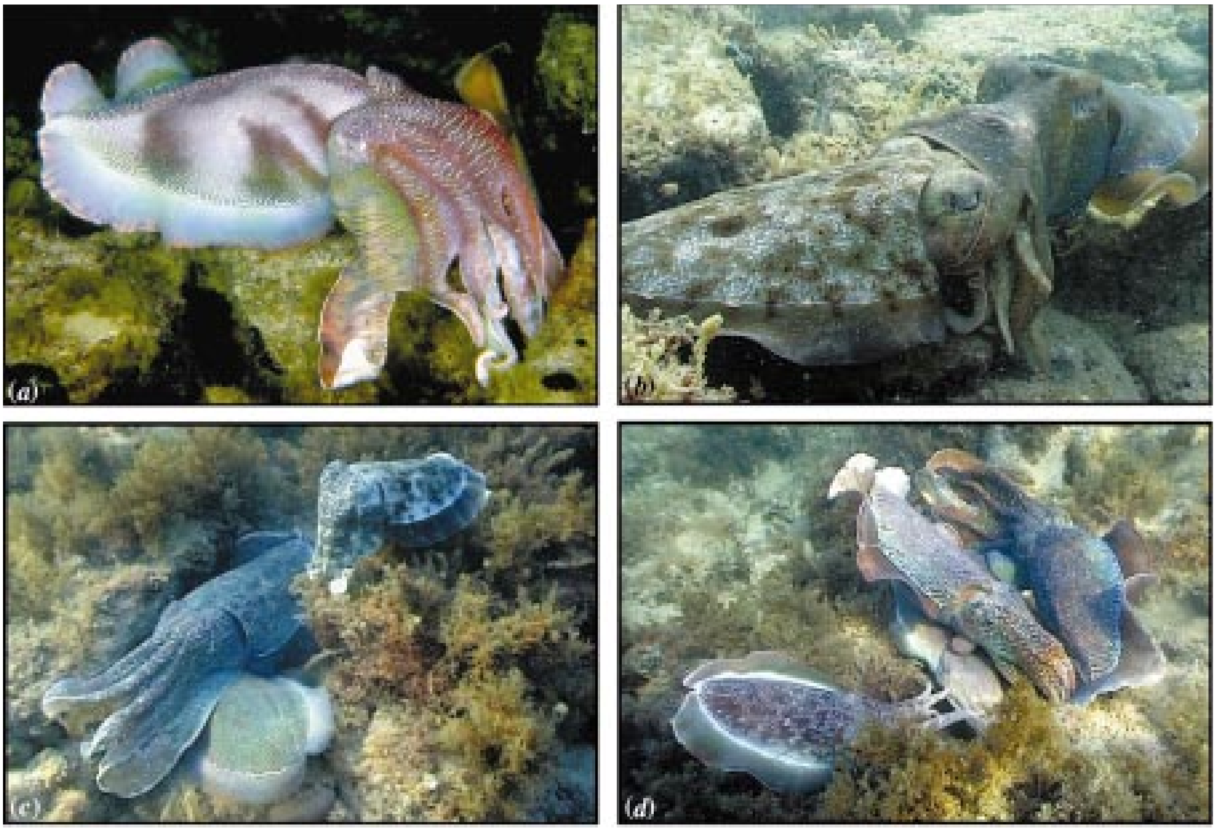

Figure 1. (*a*) Male giant cuttlefish in typical courtship display, characterized by extended banner-like web margins off the arms and fast-moving, black zebra stripes across the mantle. (*b*) Mating couple with female (left) showing mottled body pattern. (*c*) Satellite male (right) with retracted web banners and mottled body pattern in attendance with large mate-guarding male and egg-laying female. (*d*) Mottled satellite male (left) attempting to mate with guarded female while larger males are in display combat. As this combat escalated to physical attacks between the larger males, the satellite male went on to mate successfully with the female.

pairs being shadowed at close proximity by what appeared to be a second female (on the basis of short arms without banners and the mottled body pattern typical of females; figure 1*c*). However, on occasions when the large male of the pair was engaged in display or physical combat with other large males, the satellite individual frequently moved towards the female and attempted to mate with the female (figure 1*d*), often with success. In approaching the female and during mating, the behaviour of smaller males varied, with some showing male displays of banners and moving stripes and others remaining in female guise. Returning large males had varied responses ranging from ignoring the mating couple to aggressive separation of the pair. On separation, satellite male behaviour varied from attempts to mate guard the female (using typical male displays and extended web banners) to repeated female impersonation. The satellite male typically remained close to the large male and female. When the satellite male donned the mottled body pattern (figure 1*c*), agonistic behaviour of the large male immediately ceased. In contrast, large males would chase displaying males considerable distances away from the female they were guarding. In the absence of rivals, males previously observed mimicking females displayed typical male body patterns and shape and courted females in identical fashion to larger males.

4. DISCUSSION

Due to the remote location of this breeding aggregation, its exposure to adverse weather conditions and the limited breeding season of giant cuttlefish (April–June), the authors have not yet been able to undertake detailed quantitative surveys of the behaviour described. At this stage, information on dynamic female mimicry in giant cuttlefish remains qualitative. However, our direct observations and video footage noted more than 20 examples of such mimicry in satellite males, suggesting that the behaviour is relatively widespread in this large breeding aggregation and possibly within the species as a whole. As there is no information on ageing in *S. apama*, it remains unclear whether the behaviour observed in the smaller males is a strategy of younger males or is an alternative strategy for undersized males of equivalent age to their larger competitors.

Few studies have examined cephalopod mating behaviour in the wild (see the summary in Hanlon & Messenger (1997)). None of these studies have reported female impersonation as a mating strategy. However, the paucity of such studies means that it is entirely possible that similar behaviour occurs in other cephalopods, particularly shallow and clear-water species.

Cephalopods are less constrained in their ability to vary their physical appearance than perhaps any other group. It is likely that pressure from visual predators and the need to avoid detection by visual prey were the primary driving forces in the evolution of cephalopod skin. The sexual mimicry behaviour reported here may make 'honest signalling' less likely (Owens & Hartley 1991), raising the intriguing possibility that the benefits of dynamic sexual mimicry may also have contributed to the evolution of these transformation abilities, particularly in the most dramatic colour-changing groups such as the cuttlefish.

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