



## Male–female interactions affect foraging behaviour within groups of small-spotted catshark, *Scyliorhinus canicula*

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To examine potential effects of male–female interactions on the sexes' foraging behaviour, we studied equal-sized, single- and mixed-sex groups of a benthic elasmobranch, the small-spotted catshark, in response to electric stimuli. A total of 88 size-matched, adult individuals were repeatedly presented with a range of artificial, prey type electric fields (E fields) under laboratory conditions in groups of (1) four males, (2) four females and (3) two of each sex. Females in single-sex groups were more responsive towards E fields than both single- and mixed-sex group males, despite showing similar activity levels. Equally, females in mixed-sex groups were more responsive than males in mixed groups, but showed similar activity levels. Furthermore, females in mixed-sex groups were less responsive to E fields than females from single-sex groups, despite showing similar activity levels. Males in mixed-sex groups were less responsive than males in single-sex groups, but were more active. These results indicate more intense foraging behaviour among females than males and significant reductions in foraging behaviour when grouped with the opposite sex. Both findings are probably associated with consequences of differing reproductive strategies and resultant sexual conflict (specifically male harassment and female avoidance).

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Monogamy is rare in animals (Birkhead 1997) and thus partnerships are often temporary. Consequently, lifetime reproductive success of partners is predominantly unequal (Arnqvist & Rowe 2005). Despite individuals of each sex sharing an interest in mutual offspring, their interest in many aspects of the 'economies' of reproduction differs (Parker 1979). Copulatory behaviour is often costly owing to, for example, energy expenditure, increased predation risk, reduced feeding opportunity and parasite transmission. Therefore, commonly, disparity between the sexes' investment in offspring (usually attributed to anisogamy but also potentially to parental care) means that reproductive success is maximized in males by increasing mating frequency, but that females benefit more by resisting multiple mates and choosing mates selectively. These different mating rate optima generate strong sexual conflict in a wide range of animals (e.g. insects, Parker

1979; teleost fish, Magurran 2001; lizards, Schutz et al. 2007; sea mammals, Chilvers et al. 2005). In sexually reproducing animals, females of many species have evolved strategies such as resistance/avoidance, aggression and segregation to counter such conflict (Arnqvist & Rowe 2005; Wearmouth & Sims 2008). In response, males have evolved strategies including guarding, sneaky mating attempts and aggressive harassment. In turn, these adaptations also incur significant costs. For females, resistance/avoidance can result in increased energy expenditure, increased predation risk and decreased foraging opportunity (Arnqvist & Rowe 2005). Female costs can also include injury (Blanckenhorn et al. 2002) or even death (Le Boeuf & Mesnick 1991). Research on reproductive strategy, sexual conflict and costs is expanding, but the field is still young and requires empirical evidence (Arnqvist & Rowe 2005), especially considering the potential implications of such sex-based interactions upon reproductive success, ecological fitness, and possibly even reproductive isolation and speciation (Parker & Partridge 1998), extinction and conservation (Caro 1998).

The benthic elasmobranch *Scyliorhinus canicula* is a useful species with which to investigate sexual interactions. Males are thought to be sexually active throughout the year (Sims 2005).

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Females can store sperm for long periods of time (Metten 1939), have a very extended, if not continuous, egg-laying season (Sumpter & Dodd 1979) and can lay eggs regularly (Harris 1952). Therefore, females have the potential to exert considerable choice over copulation partners. The sexes show markedly different behavioural strategies resulting in fine-scale sexual segregation (Sims et al. 2001). At a number of sites, males occupy deeper water areas during the day and forage at night in warmer, shallow water, whereas females aggregate in shallow-water, labyrinthine caves in the daytime and conduct nocturnal foraging in deep water (Sims 2005). This habitat segregation is thought to be driven primarily by aggressive courtship and mating behaviour of males towards females causing refuging behaviour in the latter (Sims 2005). This suggests that female foraging behaviour is in part influenced by males. Whether the presence of males affects the foraging behaviour of female catsharks has not been tested directly, principally because of the logistical difficulties of recording free-ranging behaviours of multiple individuals across the spatiotemporal scales over which foraging takes place.

While foraging elasmobranchs use a hierarchy of senses, electroreception is especially important as it overrides all other senses within close proximity (within centimetres) of a feeding stimulus (Kalmijn 1971; personal observation). It is a highly acute sense that enables the detection of prey bioelectric fields and is therefore crucial for predation success of benthic elasmobranchs, in particular, since they often forage for prey buried beneath the substratum (Tricas & Sisneros 2004). For relatively small, benthic elasmobranchs, such as *S. canicula*, electroreception operates predominantly within approximately 5–15 cm of stimuli (Kalmijn 1971; personal observation). Behavioural responses to artificial prey type electric stimuli are routinely repeatable and quantifiable (e.g. Kalmijn 1971; Filer et al. 2008) and therefore represent useful measures of foraging behaviour.

The effect of intersexual conflict on animal feeding has been little studied, despite the fact that fecundity is often strongly influenced by body mass in many taxa (especially in fishes) which is, in turn, determined by feeding success (Wootton 1998). Therefore the aim of the present study was to contribute important understanding on the topic by focusing on a model system, *S. canicula*. We used electroreceptive responsiveness as a behavioural proxy for foraging to examine whether there were differences between male and female foraging behaviour. We also tested whether the presence/absence of the opposite sex affects the electroreceptive foraging behaviour of males and females. Accordingly, we examined the behaviour of equal-sized, single- and mixed-sex groups of *S. canicula* towards artificial, prey type electric fields under laboratory conditions. Although stomach analysis suggests males and females possess similar diets (Lyle 1983), stomach content may result from prey abundance rather than predatory preference or sensory capability. Equally, prey bioelectric fields vary with size and species (Kalmijn 1972). Therefore we used a range of electric fields to ensure comparability of male and female electroreceptive behaviour.

## METHODS

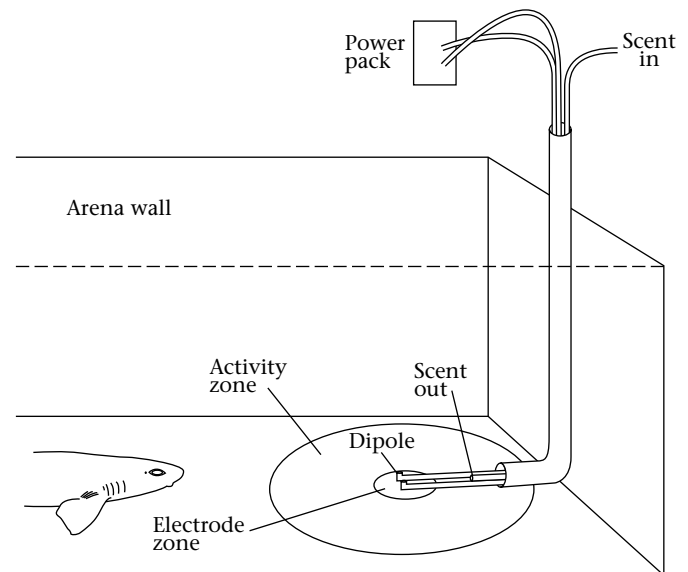
### Animals and Apparatus

Eighty-eight size-matched, adult *S. canicula* (hereafter referred to as catsharks) were caught on a Marine Biological Association of the U.K. (MBA) research vessel off Plymouth, southwest England (station L4: 50°15'N, 4°13'W). The 44 male and 44 female catsharks averaged  $66.5 \pm 3.3$  cm and  $59.7 \pm 2.7$  cm total length  $\pm$  SD, respectively. The catsharks were maintained in 2242-litre holding aquaria (1.83 m diameter  $\times$  0.43 m depth) supplied by a sea water

flow and return system at the MBA in which they acclimatized for 3 weeks. Twice weekly, they were each fed a 20 g ration (equivalent to 3% wet body mass per feed, Sims & Davies 1994) of mixed squid, *Loligo forbesi*, whiting, *Merlangius merlangus*, and marine pellets with liposome spray (New Era Aquaculture Ltd., Thorne, U.K.).

Seven 792-litre acrylic behavioural arenas (1.65  $\times$  0.80 m and 0.60 m deep) in isolated experiment rooms were supplied with filtered sea water. Four catsharks were transferred into each of these arenas with three arenas containing two of each sex, two arenas containing four males, and two arenas containing four females. Catsharks were tagged with a Petersen-type disk through the pectoral fin (2 cm diameter Floy Tag laminated discs; Floy Tag Inc., Seattle, Washington, U.S.A.) according to licensed Home Office animal welfare regulations. Tagging of different pectoral fins and use of black and white disks enabled each of four individuals per arena to be identified directly and on video recordings of subsequent trials.

To produce electric fields in the arenas, two 9 V, battery-powered, salt bridge electric circuits with 1 cm dipole electrodes were attached to transparent acrylic bases. The bases were marked with 20 cm and 5 cm radius circles centred on the dipoles which defined Activity and Electrode Zones, respectively (Fig. 1). For each apparatus, a transparent tube of 2 mm internal diameter terminated 7.5 cm before the salt bridge through which food-derived scent (sieved squid and whiting added to water) was introduced into the arena. The scent was required to invoke foraging behaviour (sensu Kalmijn 1971; Filer et al. 2008) and thus attract catsharks towards the Electrode Zone. The apparatus was portable allowing the electrodes to be placed at one of two randomly chosen locations at either end (on the bottom) of a randomly chosen arena (Fig. 1). The electrodes were used to present the catsharks with a range of biologically relevant E fields previously shown to be associated with prey bioelectric fields and attractive to elasmobranchs (Kalmijn 1972, 1982): approximately 0.095, 0.950 and 9.500  $\mu$ V/cm at the dipole. The E fields were produced by 0.9, 9.0 and 90.0  $\mu$ A currents, respectively, and were monitored during experiments. In addition, a control (power-disconnected, 0.0  $\mu$ A) was also incorporated into the experimental design. An elasmobranch's electroreceptive response towards an artificial E field closely resembles an attack on a prey animal (Kalmijn 1971). Activity levels rise following



**Figure 1.** Schematic diagram of the experimental apparatus showing the salt bridge circuit and electrode plate used to produce E fields in an arena (not to scale).

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