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What should I eat? Experimental evidence for prey selection in grey seals

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Understanding the responses of predators, such as seals, to variations in prey availability is key to understanding their role in marine ecosystems. Individual variation in prey preference is likely to be important but we have little information on this aspect of predator behaviour. Operant conditioning techniques and an underwater feeding apparatus were used to test the prey species and size preferences of five captive grey seals, *Halichoerus grypus*, in a series of paired choice trials. The experimental procedure was designed to present simple foraging choices to remove as many potentially confounding variables as possible. Results suggest that individual grey seals exhibit prey preferences. When presented with different numbers of items of the same species, seals generally selected the larger number of prey items. When presented with choices between two species, seals apparently showed consistent preferences for particular species. However, the apparent species preferences may be simply explained in terms of size selection.

Through top-down control, predators can be an important determinant of ecosystem structure and function in the marine environment (Baum & Worm, 2009). The role of predators, such as seals, in marine ecosystems has been central to studies investigating predator–prey relationships and interactions with fisheries (Boyd, 2002; Harwood & Croxall, 1988; Matthiopoulos et al., 2008). Incorporating individual variation into models of marine ecosystems is challenging (Matthiopoulos et al., 2008) and ideally requires information on individual preference for different types of prey.

Prey selection has been examined using both experimental and observational approaches (Sih & Christensen, 2001). Experiments to examine prey selectivity are usually confined to small organisms that are relatively easy to handle (Magnhagen, 1985; Sih, Crowley, McPeek, Petranka, & Strohmeier, 1985; Walton, Hairston, & Wetterer, 1992; Woolnough & Carthew, 1996). For larger animals, in particular large carnivores, prey selectivity is primarily investigated using observational field studies that compare predator diets with measures of prey abundance (Bowen & Harrison, 1994; Sih & Christensen, 2001). This approach, however, is based upon estimates of the abundance of prey that are unlikely to be at a sufficiently fine scale to translate directly to either prey availability or encounter rates between predators and prey (Sih & Christensen, 2001). Such estimates of prey preference may also reflect other aspects of foraging behaviour, such as habitat choice, rather than a direct comparison between prey per se.

Optimal foraging theory predicts that predators should prefer prey that maximize gain per unit handling time (MacArthur & Pianka, 1966) and for a given predator size there should be an optimal prey size at which prey value is at a maximum (Davies, 1977; Elner & Hughes, 1978). Terrestrial carnivores usually show a preference for large prey (Karanth & Sunquist, 1995; Paltridge, 2002); however, such results may not be applicable to marine mammals that feed at depth but are constrained to return to the surface to breathe. These animals usually consume small prey whole at the capture site but are often seen eating part or all of large prey items at the surface (Brown & Mate, 1983; Hauser, Allen, Rich Jr & Quinn, 2008).

Little is known about prey choice in marine mammals because examining predation decisions within the context of their immediate environment is difficult (Bowen, Read, & Estes, 2002). Bowen and Harrison (1994) examined prey selection in grey seals, *Halichoerus grypus*, by combining a large-scale diet study with

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coordinated, specifically targeted fish abundance surveys. Although they found a general relationship between abundance and presence in the diet it was not possible to directly characterize prey preferences because abundance estimates calculated from fishing surveys did not provide information on the availability of prey to individual seals. In addition, although seals are known to be generalist and opportunistic predators at the population level (Hammond, Hall, & Prime, 1994; Hammond & Prime, 1990; Harkonen, 1987; Thompson et al., 1996) individual specialization in diet is widespread among generalist predators and many generalist populations are made up of individual specialists (Bolnick et al., 2003; Woo, Elliott, Davidson, Gaston, & Davoren, 2008).

In view of this paucity of information at the individual level, here we took an experimental approach to investigate prey choice in grey seals. By using an experimental approach, we were able to control the availability of prey to individual seals and test the hypothesis that they show preferences for particular prey species.

METHODS

Study Animals

Five grey seals were used in this study, one adult female ('Flora'), three female pups ('Hannah', 'Daisy' and 'Emma') and one male pup ('Ivan'). Experiments were conducted in 2005 and 2006 with seals being fed on various combinations of available species during the experiments: herring, *Clupea harengus* (2005 and 2006), sprat, *Sprattus sprattus* (2005 and 2006), whiting, *Gadus merlangus* (2005), mackerel, *Scomber scombrus* (2006) and haddock, *Melanogramnus aeglefinus* (2006), all of which are found in the diet of wild seals in the U.K. (e.g. Hammond et al., 1994; Hammond & Prime, 1990; Wilson, 2015). To exclude the possibility that prey selection was simply the result of avoidance of novel prey, for 8 weeks prior to experiments seals were offered the same species and size ranges of fish that were subsequently offered during experiments. Seals were fasted from the evening prior to the experiment to ensure a similar state of hunger within and among animals at the beginning of all sessions. Trials were carried out between 1000 and 1600 hours and after experiments the seals were given additional fish to ensure that they got their predetermined maintenance daily food intake.

Prey Choice Experiment

An underwater feeding apparatus was designed and built to present fish to seals in the feeding experiment. The apparatus was fixed at the side of a 5 m diameter pool and constructed in Perspex with a one-way screen to hide the experimenter from the seal's view while allowing the seal's behaviour to be observed (Fig. 1). A paired presentation design was used where fish were inserted manually into two clear plastic tubes (50 cm long, 18 cm diameter) and presented to the seal.

Operant conditioning was used to train the seals to use the prey choice apparatus. The desired operant was for the seals to select the contents of one of the tubes by touching the relevant tube with its nose and was shaped by selective food reinforcement of successive approximations to the required behaviour. Using the shaping and conditioning procedures, seals were trained to station away from the apparatus between presentations of fish and to perform an operant response upon presentation of fish in the apparatus.

In 2006, the duration of the session, handling time and the time taken to eat the prey, were also recorded. Handling time was recorded as the time between opening the chosen tube to the seal either having eaten all of the prey or when it had come to the surface and moved away from the feeder. For each seal, Kruskal–Wallis tests were used to detect differences in the handling times between the prey species. To account for the differences in the sizes of the different prey species, the handling times were first converted to a rate (time to consume 100 g of fish) before the comparisons were undertaken.

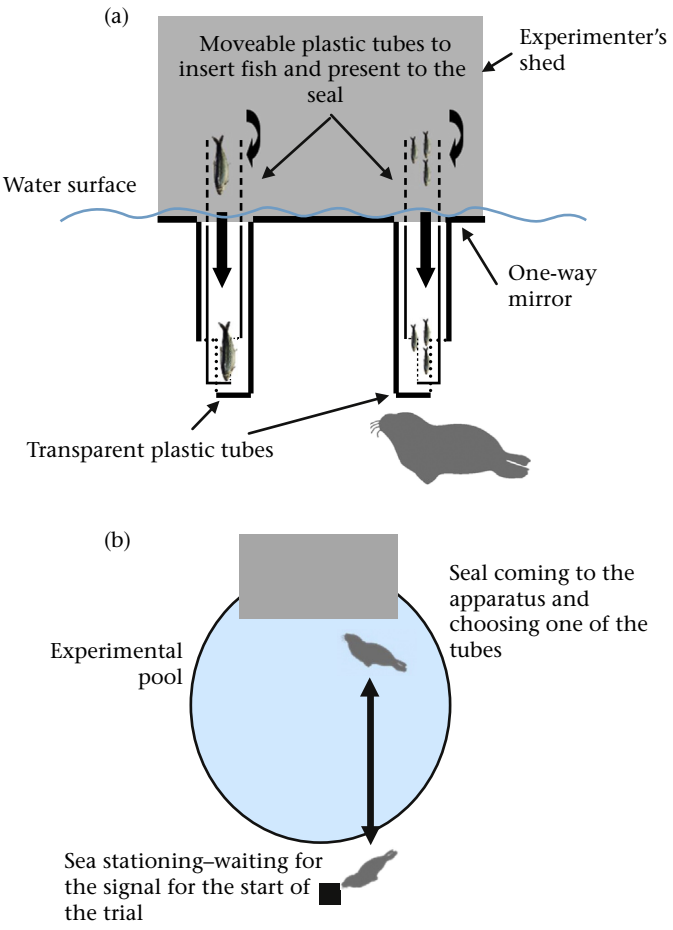

Figure 1. Diagram of (a) the prey choice apparatus and (b) plan of the experimental pool showing the prey choice apparatus position and the stationing area (see Methods for more details).

During a session, the choices offered to the seals in each individual trial were randomized so that there were no obvious patterns in which tube contained which prey species or the largest weight of prey. The ratio of weights presented in each trial varied, and overall this was balanced within each prey combination (i.e. the weight of herring was not always the greatest when presented together with sprat). During a week of experiments, two species of fish were used in different proportions each day, while the fish used during training and maintenance feeding could vary. Between five and 32 presentation trials were carried out on a single day, depending on the weight of fish presented. Individual seals were tested on 30–69 days giving a total of 246 seal-trial days. The number of trials undertaken with each seal/prey combination was a function of the seasonal availability of prey and the use of seals in other experimental procedures (Sparling, Thompson, Fedak, Gallon, & Speakman, 2008).

Prey Choice Analyses

Discrete choice analysis was used to investigate the prey preference of the seals in the study, with all analyses undertaken in R