

## Searching prey in 3D environment: hierarchical foraging behaviour of northern elephant seals

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Predators are expected to adjust their movement path according to the spatial distribution pattern of prey. In the marine environment, diving predators exploit three-dimensional (3D) environment where small-scale prey patches are often nested within large-scale patches (hierarchical distribution). However, few studies examined the fine-scale foraging behaviour of deep divers in three dimensions. Here we applied spherical first-passage time (SFPT) analysis on 3D diving path of four female northern elephant seals during their foraging migrations. We also examined prey encounter events along the 3D diving path using mandible accelerometers. SFPT analysis showed that area-restricted search (ARS) behaviour occurred at the small spatial scale of 8-10 m (i.e. radius of sphere), which was nested within the larger ARS scale of 17-19 m. Small- and large-scale ARS behaviour occurred 4.7 and 5.9 times in a single dive on average, respectively, and covered only the small proportion (9 and 22%, respectively) of the total distance traveled during the bottom phase of dives. However, a large proportion of prey encounter events (71 and 84%) occurred during the small- and large-scale ARS behaviour, respectively. These results suggest that elephant seals effectively use nested ARS behaviour to enhance foraging success in the hierarchically structured 3D marine environment.