

Elasmobranch cognitive ability: using electroreceptive foraging behaviour to demonstrate learning, habituation and memory in a benthic shark

JOEL A. KIMBER*[†], DAVID W. SIMS[†], PATRICIA H. BELLAMY*, ANDREW B. GILL*

* Department of Environmental Science and Technology, Cranfield University, Cranfield, Bedfordshire, MK43 0AL, UK

[†]Marine Biological Association of the United Kingdom, The Laboratory, Citadel Hill, Plymouth, Devon, PL1 2PB, UK

*[†]*Author for correspondence* (Email: joel@cmacsltd.co.uk; Tel: 0151 3277177)

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4 45 **ABSTRACT**

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6 46 Top predators inhabiting a dynamic environment, such as coastal waters, should
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9 47 theoretically possess sufficient cognitive ability to allow successful foraging despite
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11 48 unpredictable sensory stimuli. The cognition-related hunting abilities of marine mammals
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14 49 have been widely demonstrated. Having been historically underestimated, teleost
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16 50 cognitive abilities have also now been significantly demonstrated. Conversely, the
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19 51 abilities of elasmobranchs have received little attention, despite many species possessing
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21 52 relatively large brains comparable to some mammals. The need to determine what, if any,
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24 53 cognitive ability these globally distributed, apex predators are endowed with has been
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26 54 highlighted recently by questions arising from environmental assessments; specifically
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29 55 whether they are able to learn to distinguish between anthropogenic electric fields and
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31 56 prey bioelectric fields.

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33 57 We therefore used electroreceptive foraging behaviour in a model species,
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36 58 *Scyliorhinus canicula* (small-spotted catshark) to determine cognitive ability by analysing
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39 59 if elasmobranchs are able to learn to improve foraging efficiency and remember learned
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41 60 behavioural adaptations.

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43 61 Positive reinforcement, operant conditioning was used to study catshark foraging
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46 62 behaviour towards artificial, prey-type electric fields (Efields). Catsharks rewarded with
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49 63 food for responding to Efields throughout experimental weeks were compared with
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51 64 catsharks that were not rewarded for responding in order to assess behavioural adaptation
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53 65 via learning ability. Experiments were repeated after a three week interval with
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56 66 previously rewarded catsharks this time receiving no reward and *vice versa* to assess
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58 67 memory ability.
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68 Positive reinforcement markedly and rapidly altered catshark foraging behaviour.
69 Rewarded catsharks exhibited significantly more interest in the electrical stimulus than
70 unrewarded catsharks. Furthermore, they improved their foraging efficiency over time by
71 learning to locate and bite the electrodes to gain food more quickly. In contrast,
72 unrewarded catsharks showed some habituation, whereby their responses to the
73 electrodes abated and eventually entirely ceased, though they generally showed no
74 changes in most foraging parameters. Behavioural adaptations were not retained after the
75 interval suggesting learned behaviour was not memorised beyond the interval. Sequences
76 of individual catshark search paths clearly illustrated learning and habituation
77 behavioural adaptation.

78 This study demonstrated learning and habituation occurring after few foraging
79 events and a memory window of between twelve hours and three weeks. These cognitive
80 abilities are discussed in relation to diet, habitat, ecology and anthropogenic Efield
81 sources.

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83 *Key words: Scyliorhinus canicula, Efield, electroreception, behavioural adaptation,*
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91 **INTRODUCTION**

92 Cognitive ability is fundamental for optimising crucial animal behaviours such as
93 locating and acquiring food and mates, navigating and avoiding predators. It is especially
94 important for animals that inhabit complex, dynamic environments with unpredictable
95 sensory stimuli. Recent research suggests that relative brain size in vertebrates is linked
96 with the ability to adapt and persist in novel and changing environments (Reader and
97 MacDonald 2003; Sol et al. 2005, Maklakov et al. 2011). Coastal environments are
98 particularly changeable, both spatially and temporally, due to the convergence of
99 dynamic marine, freshwater, terrestrial, atmospheric and, increasingly, anthropogenic
100 factors. Organisms that inhabit such an environment should theoretically exhibit
101 behavioural flexibility to enable them to function and survive by adapting to changing
102 conditions and thereby maximise ecological fitness (Dill 1983). Learning and memory
103 are crucial means with which to facilitate such adaptation.

104 The cognitive ability and adaptability of marine mammals when foraging is well
105 supported (Schusterman and Kastak 2002) as evidenced by, for example, development of
106 intentional stranding (Guinet and Bouvier 1995), herding (Similä and Ugarte 1993), vocal
107 learning (Shapiro et al. 2004) and cooperation (Visser et al. 2008). The current, general
108 consensus is that many teleosts (bony fish) also possess significantly more cognitive
109 ability than previously believed (reviewed in Laland et al. 2003; Brown et al. 2006) with,
110 for example, foraging adaptability demonstrated by learning in sticklebacks (Croy and
111 Hughes 1991), salmon (Brown et al. 2003) and mosquito fish (Brown and Braithwaite
112 2005), and memory in trout (Bryan and Larkin 1972) and sticklebacks (Mackney and
113 Hughes 1995).

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4 114 Conversely, chondrichthyans (cartilaginous fish) have received relatively little
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6 115 attention with respect to cognitive ability. This is surprising given that certain
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9 116 elasmobranchs (sharks, skates and rays) possess brain to body mass ratios that overlap
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11 117 those of some mammals and birds (Demski and Northcutt 1996). Until very recently, the
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14 118 few examples of investigations into elasmobranch cognitive ability were relatively old,
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16 119 and involved visual discrimination to gain food rewards (Clarke 1959 and 1961; Wright
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19 120 and Jackson 1964; Aronson et al. 1967; Graeber and Ebbesson 1972; Graeber et al.
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21 121 1978). More recently, Schluessel and Bleckmann (2005) demonstrated spatial memory of
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24 122 environment in juvenile freshwater stingrays, Kuba et al. (2010) demonstrated tool use in
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26 123 a similar species, Meyer et al. (2010) suggested tiger sharks may use cognitive maps to
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29 124 navigate between distant foraging areas, and Guttridge et al. (2012) demonstrated social
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31 125 learning in juvenile lemon sharks. Based on this limited evidence for cognitive ability in
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34 126 elasmobranchs, we hypothesised that when using their primary sensory mode,
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36 127 electroreception, the cognitive abilities of benthic elasmobranchs would be clearly
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39 128 demonstrable and behaviourally adaptive.

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41 129 Electroreception is the last in a hierarchy of senses utilised by elasmobranchs
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43 130 whilst foraging (Kalmijn 1971); it aids precise location of prey and jaw orientation and
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46 131 has been demonstrated to override all other senses over short distances (Kalmijn 1971;
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48 132 Heyer et al. 1981). It is particularly crucial for the foraging success of benthic species that
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51 133 forage for inconspicuous prey owing to burial, refuging or crypsis (see Tricas and
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53 134 Sisneros 2004 for review). As such, it can be considered fundamental for the feeding
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56 135 success and subsequent somatic and gonadal growth of these predators. Electroreception
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58 136 can also be utilised during the location of and communication with conspecifics, the
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4 137 detection of predators and possibly in aiding navigation (Tricas and Sisneros 2004).
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6 138 Flexibility in their responses to electric stimuli within their environment via learning and
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9 139 memory should provide tangible ecological benefits to the life processes of these
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11 140 predators. When considered in conjunction with the repeatability of the behaviour under
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13 141 laboratory conditions (Kalmijn 1971), the importance of electroreception makes it an
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15 142 ideal tool to attempt to measure behavioural adaptation. Furthermore, the need to assess
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17 143 the cognitive ability of elasmobranchs has been accentuated recently amid questions
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19 144 raised by environmental assessments in coastal waters worldwide. Given the burgeoning
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21 145 deployment of subsea electric cables (e.g. associated with offshore renewable energy and
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23 146 grid connection development), suggestions of electromagnetically ultra-sensitive
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25 147 elasmobranchs potentially being affected have arisen (Gill et al. 2005; Sutherland et al.
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27 148 2008). The principal question relates to whether the elasmobranchs will be able to learn
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29 149 about electrical stimuli to enable them to distinguish between those that provide an
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31 150 energetic return (such as prey located via their bioelectric fields) and those that are
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33 151 anthropogenic in origin and that provide no food return (Kimber et al 2011).

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35 152 The objective of this study was therefore to investigate the ability of a model
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37 153 species of benthic elasmobranch, the small-spotted catshark (*Scyliorhinus canicula*), to
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39 154 learn to adapt its electroreceptive foraging behaviour towards profitable (in terms of food
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41 155 gain) and non-profitable (i.e. no food gain) electrical stimuli and remember learned
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43 156 adaptations. Such results would support the growing body of evidence that cognitive
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45 157 ability is beneficial in novel and changing environments among a variety of predators,
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47 158 and provide useful information for environmental assessments.
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4 159 In this context, laboratory studies were designed to study catshark behaviour
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6 160 using operant conditioning. Experiments investigated the foraging behaviour of catsharks
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9 161 rewarded with food for operant responses to an electrical stimulus. Contrasting treatment
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11 162 experiments were undertaken during which no food rewards were provided for responses
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14 163 to the electrical stimulus. Experiments were then repeated after an interval with
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16 164 previously rewarded catsharks receiving no food and *vice versa* to assess memory.
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166 **METHODS**

167 **Animals and Apparatus**

168 Twenty four size-matched (mean total length = 61.8 ± 4.8 cm standard deviation),
169 mixed-sex small-spotted catsharks (*S. canicula*) were caught on a Marine Biological
170 Association of the U.K. (MBA) research vessel off Plymouth, southwest England (station
171 L4: 50°15'N, 4°13'W). They were randomly assigned to one of four groups (1 to 4) and
172 tagged just below their dorsal fin with different coloured, individually numbered T-bar
173 anchor tags (FLOY TAG Inc., Seattle, Washington USA) following licensed UK Home
174 Office animal welfare regulations. Catsharks were maintained in 2,242 litre holding
175 aquaria (1.83m diameter x 0.43m depth) supplied by a sea water flow and return system
176 at the MBA in which they acclimatised for three weeks. Twice weekly, they were each
177 fed a 20g food ration equivalent to 3 % wet body mass per feed to standardise feeding
178 motivation (Sims and Davies 1994). Food consisted of mixed squid (*Loligo forbesi*),
179 whiting (*Merlanguis merlangus*) and marine pellets with liposome spray (New Era
180 Aquaculture Ltd., Thorne, UK).

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4 181 Salt-bridge electrode circuits and apparatus were used to present catsharks with
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6 182 prey-type electric fields (*sensu* Kimber et al. 2009). A trap-door mechanism and hidden
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9 183 food compartment were attached to the underside of an opaque, raised and gently ramped
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11 184 electrode plate. The food compartment was positioned against the plate and sealed with
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14 185 silicone gel to prevent food scent seepage. A hydraulic system of BD Luer Lok syringes
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16 186 and Nalgene 380 PVC tubing allowed the food compartment to be opened and closed
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19 187 remotely, smoothly, quickly and silently by the observer. This permitted presentation of
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21 188 food rewards to catsharks in close proximity to the dipole, immediately after a response
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24 189 to an electric field, and with minimal disturbance.
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27 28 191 **Experimental Procedure**

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31 192 Six 792 litre, acrylic aquarium tanks supplied with filtered seawater were used as
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33 193 behavioural arenas (1.65m L x 0.80m W x 0.60m D). The six catsharks from group 1
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36 194 were transferred to randomly chosen arenas (one catshark per arena) and allowed to
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38 195 acclimatise for 60 hours. Each catshark was then presented with an Efield produced by a
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41 196 9 μ A direct current twice per day for five days, a total of 10 experimental sessions,
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43 197 forming an experimental week. The Efield was chosen due to its similar strength to prey
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46 198 bioelectric fields and demonstrated elicitation of voluntary (operant) feeding responses in
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48 199 these benthic sharks (Kalmijn 1971; Kalmijn 1972). These feeding responses consist of
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51 200 rapidly turning towards and biting upon the electrodes (often repeatedly) once the Efield
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53 201 is detected. Three randomly selected catsharks were positively reinforced by rewarding
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55 202 them with offer of approximately 1.3 g of food immediately after their first bite upon the
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58 203 electrodes in each experimental session. Catsharks not consuming all of their rewards
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204 were fed the remainder of their weekly 13 g ration after the experimental week was
205 completed. This reduced feeding ration (approximately 2 % wet body mass per week:
206 Sims and Davies 1994) ensured satiation was not reached and hunger and normal
207 foraging behaviour persisted during the week. The other three catsharks acted as
208 contrasting treatments, whereby they were not rewarded for biting the electrodes, but
209 were instead fed a 13 g food ration after the experimental week was completed.

210 On completion of the experimental week, the group 1 catsharks were transferred
211 back to the holding aquaria and replaced with the catsharks from group 2. After 60 hours
212 acclimatisation, group 2 then underwent a similar experimental week. This procedure was
213 repeated for groups 3 and 4. Once group 4's experimental week was complete, each
214 group (1 to 4 in turn) then underwent a second experimental week (with each catshark in
215 different, randomly assigned arenas), similar except that those previously rewarded were
216 not rewarded and *vice versa*. There was therefore a three week interval between each
217 group's two experimental weeks.

218 Prior to each particular experimental session, a salt-bridge apparatus was
219 introduced into a randomly chosen arena, and at a randomly chosen end (to ensure
220 catsharks were not simply learning to associate the food with a particular location), with
221 the power switched off and water flow halted to allow the catsharks to settle down. After
222 20 minutes, the power was switched on and 20 ml of food scent (sieved squid and whiting
223 added to water) was introduced into the arena approximately 7.5 cm from the dipole.
224 Since one of the first hierarchical senses used during foraging by elasmobranchs is
225 olfaction (Hodgson and Mathewson 1971), it is necessary to use a dose of scent to
226 stimulate foraging behavior and attract the catsharks towards the electrode plate (*sensu*

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227 Kalmijn 1971). Once in close proximity of the electrodes, electroreception is known to
228 override all other senses. For the relatively small, benthic *S. canicula* this predominantly
229 occurs within approximately 5cm to 10cm (Dawson et al. 1980; Kimber et al. 2009) in
230 comparison to up to 30cm for larger, pelagic species (Kalmijn 1971; Heyer et al. 1981).

231 Sessions lasted for no more than 15 minutes and were recorded using overhead
232 cameras. The following hierarchical response variables of each catshark were compiled
233 by reviewing video footage: (a) the number of times the catsharks passed within 5-cm of
234 the electrodes, (b) the latency of turns towards and bites upon the electrodes, (c) the
235 frequency of turns towards and bites upon the electrodes, (d) after which bite (i.e. first,
236 second *etc.*) and what latency a food reward was taken (note rewards were not always
237 taken immediately), and finally (e) the search paths the catsharks undertook from their
238 starting position (when scent detected) to their first response at the electrode dipole. The
239 latter were traced from video footage on a large monitor. These traces were then
240 converted to JPEG files using an HP Designjet 815mfp scanner and subsequently
241 converted to polyline shape files and geo-referenced to arena size using ArcGIS software.
242 An index of the path directness to the dipole was then calculated by dividing search path
243 lengths by the direct distance between starting position and the electrodes.

244 Upon completion of all experiments, tags were removed from catsharks and the
245 attachment points treated. The catsharks were held in holding aquaria and after a short
246 period of observation were certified for release to the sea off Plymouth.

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4 **250 Data analysis**

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7 251 Statistica 8.0 and Genstat 10.0 software were used to run the statistical models
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9 252 that analysed differences in electroreceptive foraging behavioural parameters (a to e)
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11 253 between rewarded (R) and not rewarded (N) catsharks, between experimental weeks 1
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14 254 and 2, and also changes in the parameters throughout experimental sessions (i.e. within
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16 255 experimental weeks). Depending upon the hypothesis being tested and data type (count,
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18 256 continuous or path directness index), either hierarchical generalized linear mixed models
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21 257 (HGZLMM), hierarchical general linear models (HGLM) or general linear models
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23 258 (GLM) were used with relevant distributions (poisson, log link, identity or normal). Fixed
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26 259 effects were reward (yes or no) and experimental week (1 or 2) for tests between
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28 260 rewarded and unrewarded catsharks and between experimental weeks 1 and 2, and
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31 261 experimental session (1 to 10) or individual number for tests within experimental weeks.
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33 262 This ensured that each data point for each catshark was used only once during each
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35 263 analysis. If replication (non-independence) was not already accounted for within these
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38 264 models, the relevant random effects (individual number and/or session) or continuous
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41 265 predictors (session) were also used. These carefully formulated models robustly and
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43 266 powerfully dealt with the complex data to generate accurate descriptions of biologically
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46 267 relevant effects (*sensu* Nakagawa and Cuthill 2007).

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48 268 Estimates of effects generated by modeling and presented here represent either
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51 269 relative differences between means (whereby rewarded catshark effects are compared to
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53 270 the zero reference, unrewarded catsharks between experimental weeks) or regression
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55 271 coefficients (within experimental weeks). The latter were back-transformed to the units of
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58 272 original measurement to enable fitted curve plots to be produced (raw data was omitted
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4 273 owing to the effects of individual catsharks being partially confounded with experimental
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6 274 session). For all model results reported, the distributions of residuals (using
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9 275 transformations as required), were close to Normal and therefore the models were
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11 276 assumed to be satisfactory. Residual degrees of freedom ranged between approximately
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14 277 215 and 460 unless otherwise stated.

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17 18 19 279 **RESULTS**

20 21 280 **Learning and habituation**

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23 281 Averaged over all ten experimental sessions, rewarded catsharks passed within 5-
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26 282 cm of the electrodes significantly more than unrewarded catsharks (relative difference
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28 283 between means = 0.725, standard error (S.E.) = 0.141, $t = 5.15$, $P \ll 0.0001$).
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31 284 Throughout an experimental week, the high number of passes rewarded catsharks made
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33 285 before their first response to the electrodes significantly decreased (regression coefficient
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35 286 = -0.0678, S.E. = 0.0148, $t = 4.59$; $P < 0.001$; Figure 2). There was no change in the low
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38 287 number of passes unrewarded catsharks made before their first response to the electrodes
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41 288 (regression coefficient = -0.0001, S.E. = 0.0328, $t = 0.00$; $P = 1.0$; Figure 2).

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43 289 Throughout an experimental week, the time latency of first response to the
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45 290 electrodes of rewarded catsharks significantly decreased (regression coefficient = -
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48 291 0.0677, S.E. = 0.0274, $t = 2.47$, $P = 0.014$; Figure 3). There was no change in the time
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51 292 latency of first response of unrewarded catsharks (regression coefficient = -0.0039, S.E. =
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53 293 0.0366, $t = 0.11$, $P = 0.91$; Figure 3). Averaged over all ten experimental sessions,
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55 294 rewarded catsharks turned towards and bit the electrodes significantly more than
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58 295 unrewarded catsharks (relative different between means = 0.866 and 0.851, S.E. = 0.162

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4 296 and 0.153, $t = 5.35$ and 5.57 respectively, both $P \ll 0.0001$). Throughout an
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6 297 experimental week, the higher number of turns and bites made by rewarded catsharks
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8 298 significantly decreased (regression coefficient = -0.0547 and -0.0940 , S.E. = 0.00816 and
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10 299 0.0114 , $t = 6.70$ and 8.27 respectively, both $P < 0.0001$; Figure 4). So, too, did the lower
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12 300 number of turns and bites made by unrewarded catsharks, but more sharply (regression
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14 301 coefficient = -0.151 and -0.205 , S.E. = 0.0140 and 0.0206 , $t = 10.77$ and 9.93
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16 302 respectively, both $P < 0.0001$; Figure 4), such that on average, they ceased to bite upon
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18 303 the electrodes altogether after approximately six or seven experimental sessions.
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23 304 As the catsharks swam and searched for food rapidly, they did not always manage
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25 305 to take food rewards immediately after being offered them following their first bite upon
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27 306 the electrodes. If this was the case, however, they would almost invariably turn back
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29 307 swiftly (and repeatedly) to bite the electrodes again (rewarded catsharks responded to the
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31 308 electrodes greater than once in more than 97% of treatments). The bite after which they
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33 309 took the food reward was therefore not necessarily the first. The bite number and time
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35 310 after which rewarded catsharks managed to attain the food reward throughout an
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37 311 experimental week decreased significantly (regression coefficient = -0.0716 and -0.0844 ,
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39 312 S.E. = 0.0182 and 0.0294 , $t = 3.94$ and 2.87 respectively, $P = 0.0001$ and 0.004
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41 313 respectively; Figure 5). The search paths undertaken by rewarded catsharks throughout an
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43 314 experimental week also significantly decreased (regression coefficient = 1.904 , S.E. =
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45 315 0.0288 , $SS = 5.91$; $P < 0.019$; Figure 6 and 7). In contrast, on average, the paths
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47 316 undertaken by unrewarded catsharks did not change throughout an experimental week
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49 317 (regression coefficient = 1.61 , S.E. = 0.0347 , $SS = 0.137$; $P = 0.69$; Figure 6 and 7).
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4 **320 Memory**

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6 321 Table 1 shows that when rewarded and unrewarded catshark data were grouped
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9 322 together and compared between experimental weeks before and after the three week
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11 323 interval, there were no significant differences in any behavioural parameters other than a
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14 324 slight difference in the latency of first response to the electrodes. Neither were any
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16 325 interactions observed between reward (yes/no) and week (1 and 2) for any of the
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19 326 parameters (Table 1). Therefore, on average, foraging behaviour was independent of
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21 327 whether a catshark was rewarded before the interval and unrewarded after the interval or
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24 328 vice versa. These results suggest that behavioural alterations were not retained beyond the
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26 329 interval.

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31 **331 DISCUSSION**

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33 332 All catsharks were of similar size and maturity, from the same geographic
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36 333 location, acclimatised to the study conditions for equal time periods and fed on equal,
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39 334 minimum rations. Previous experience and initial motivation to feed was therefore
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41 335 assumed to be standardised among experimental animals. Rewarded catsharks
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43 336 consistently foraged and ingested rewards suggesting the small size of rewards prevented
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46 337 satiation and ensured continued motivation to respond to feeding opportunities.
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48 338 Unrewarded catsharks also showed continued, but not increasing motivation to feed.

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50 339 Water temperature varied with natural conditions during experimental procedures
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53 340 (18.22 °C +/- 0.98 S.D.). However, this small level of variation has previously been
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56 341 shown to have little effect on electroreceptive behaviour (Kimber et al. 2009). All
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58 342 experimental animals were subjected to the same experimental conditions in stable,

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4 343 predator free environments and the large sample size and powerful modelling provided
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6 344 the confidence that differences and trends observed were accountable to the experience
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9 345 and behavioural flexibility of the catsharks.

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11 346 Reinforcement of the operant foraging response to an electric stimulus by
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14 347 rewarding with food clearly altered the behaviour of catsharks. As would be expected,
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16 348 rewarded catsharks showed more interest in the electrodes than the contrasting treatment,
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19 349 unrewarded catsharks, demonstrated by more passes by, turns towards and bites upon the
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21 350 electrodes. Crucially, rewarded catsharks exhibited a number of behavioural alterations
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24 351 that suggest they were learning how to obtain food. The number of times they passed
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26 352 within close proximity of the electrodes before responding to them and the time latency
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29 353 of first response decreased. The bite number and time after which they managed to
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31 354 acquire the food reward from the trap door compartment decreased. Therefore, they did
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34 355 not need to respond further, and consequently, the number of times they turned towards
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36 356 and bit the electrodes also decreased. Furthermore, the length of search path they
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39 357 employed to first respond to the electrodes also decreased (see Figure 7 for clear
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41 358 examples of individual catshark search paths decreasing). Effectively, these results
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44 359 strongly suggest these catsharks were learning that when stimulated to forage, by rapidly
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46 360 locating the electrodes and biting them, food would appear in close proximity of the
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49 361 electrodes. Furthermore, the substantial changes in behaviour elicited by so few rewards
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51 362 (a maximum of ten per catshark, but often requiring just a few) demonstrate impressively
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53 363 rapid learning. Behavioural alterations improved the foraging efficiency of these
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56 364 catsharks over time and theoretically would have reduced energetic costs per unit food
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58 365 attained.

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366 Conversely, in the contrasting treatment, unrewarded catsharks exhibited less
367 interest in the electrodes, and less behavioural adaptation; no change in the number of
368 times they passed in close proximity of the electrodes, no change in latency to respond to
369 the electrodes and no change in the length of their search paths. They did, however,
370 markedly reduce the amount of times they turned towards and bit upon the electrodes
371 throughout an experimental week (even more so than their rewarded counterparts), and
372 even stopped biting altogether, which suggests they habituated to the electric stimulus
373 since they did not obtain any food by biting it. Theoretically, such adaptations would also
374 have reduced energetic and opportunity costs by reducing wasted effort. Figure 7 shows
375 examples of typical search path sequences of unrewarded catsharks, with no apparent
376 pattern or clearly habituating (eventually failing to respond to the electrodes and scent).

377 Whilst the results clearly demonstrate striking learning in the catsharks, according
378 to classical cognition theory there is a possibility that non-contingency might explain
379 some behavioural alterations (differences elicited by the food rather than being a
380 consequence of the contingency between bites to the electrodes and subsequent food
381 reward). A further control condition in which food is delivered non-contingently might
382 help to address this question, ideally involving a yoked procedure whereby two catsharks
383 in separate tanks are both offered concurrent rewards when one (the executive) responds
384 to an Efield, regardless of the other, yoked catshark's responses (*sensu* Church 1964).
385 Such a control would be a significant challenge in itself, especially considering the
386 complex, hierarchical stimulus modality inherent when studying elasmobranch
387 electroreceptive foraging behaviour. However, since the experiment was designed to
388 involve operant conditioning under positive reinforcement and to investigate ability to

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4 389 learn to distinguish between anthropogenic Efields and prey bioelectric fields in the
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6 390 natural environment, the behavioural adaptations observed demonstrate significant
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9 391 learning nonetheless.

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11 392 The average learning behavioural adaptations revealed by statistical analysis were
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13 393 exhibited by most, but not all catsharks. For example, 70 and 76% of rewarded catsharks
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15 394 exhibited trends associated with learning; decreasing reward attainment bite time and bite
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17 395 number respectively. Hence 30 and 24% did not exhibit such trends associated with
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19 396 learning. Therefore learning ability apparently varied between individuals. However, both
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21 397 sexes exhibited similar behavioural adaptations. It is possible that differences between the
22
23 398 adaptations of the sexes might become apparent if groups of catsharks were studied,
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25 399 rather than individuals, since sexual conflict (specifically male harassment and female
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27 400 avoidance) have been demonstrated to affect foraging behaviour (Kimber et al. 2009).

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29 401 The fact that none of the learned and habituated behaviours were continued after a
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31 402 three week interval and that behaviour levels were independent of whether rewards were
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33 403 offered before or after the interval suggests that the memory window for these
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35 404 elasmobranchs is less than three weeks. Having returned to the experimental arenas after
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37 405 the interval, the catsharks behaved as if they had not been subjected to the previous
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39 406 experimental sessions, regardless of whether rewarded or unrewarded. They then began
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41 407 to swiftly adapt their foraging behaviour over the subsequent experimental weeks
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43 408 accordingly.

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45 409 Like many other marine predators, elasmobranchs often inhabit highly variable,
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47 410 shallow coastal waters (Compagno et al. 2005) and many are therefore opportunistic
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49 411 predators (Lyle 1983; Ellis et al. 1996; Laptikhovsky et al. 2001). When considering
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4 412 populations of these elasmobranchs in their natural habitats, the impressive cognitive
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6 413 abilities demonstrated here make ecological sense. In essence, the sharks seem able to
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9 414 rapidly learn to improve their electroreceptive foraging efficiency towards profitable
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11 415 stimuli (in terms of food gain) over short periods (and presumably within small spatial
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13 416 scales). Equally, within similar temporal and spatial limits, they can rapidly habituate to
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16 417 (or learn to ignore) non-profitable stimuli (i.e. no food gain). This swift flexibility would
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19 418 therefore allow, for example, the predators to focus their efforts on easily caught, edible
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21 419 or nutritious prey (Dill 1983; Stephens and Krebs 1986; Kaiser et al. 1992). Similarly,
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23 420 efforts towards inedible, nutrient lacking and difficult to catch prey could be reduced,
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25 421 which would permit focussing elsewhere and minimising missed opportunities. For
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28 422 example, greater modification of foraging behaviour has been demonstrated in crabs
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31 423 (Micheli 1997) and sticklebacks (Girvan and Braithwaite 1998) when encountering
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33 424 variable prey in less stable habitats. Greater adaptability, inferred from larger brain size,
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35 425 has also been suggested to enable success in novel, complex or variable environments in
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38 426 passerine birds (Maklakov et al. 2011), primates (Reader and MacDonald 2003) and
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41 427 marine mammals (Kuczaj et al. 2009).

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43 428 The coastal zone is especially variable due to both natural and anthropogenic
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45 429 factors. In such an environment, therefore, remembering these electroreceptive foraging
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48 430 adaptations over longer temporal periods and larger spatial scales may not be of benefit
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51 431 (*sensu* Hirvonen et al. 1999). Possessing a memory window of less than three weeks for
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53 432 these skills is reasonable when considering prey diversity and distributions, in addition to
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55 433 physical habitat, may well change over relatively short time periods and over small
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58 434 distances. It would be interesting to determine exactly where this memory window lies in
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4 435 these benthic elasmobranchs. The results suggest it lies somewhere between 12 hours
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6 436 (learned behaviour was obviously remembered between experimental sessions each day)
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9 437 and 3 weeks (the experimental interval period). Longer memories have been
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11 438 demonstrated in teleost fish inhabiting relatively stable environments (e.g. up to 6 months
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14 439 in trout: Bryan and Larkin 1972; 3 months in cod: Nilsson et al. 2008) compared to
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16 440 shorter memories in those inhabiting more variable environments (e.g. 3 hours in paradise
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19 441 fish: Csanyi et al. 1989; from minutes to days in sticklebacks: Mackney and Hughes
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21 442 1995; Hughes and Blight 1999).

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24 443 Cognitive abilities are also likely to vary between elasmobranch species. For
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26 444 example, one may expect better memory windows in species inhabiting more stable
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29 445 habitats than more variable habitats (c.f. teleost fish; Odling-Smee and Braithwaite 2003).
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31 446 Inter-specific differences in visual learning have previously been observed between
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34 447 lemon and nurse (Clarke 1959) and lemon and bull sharks (Wright and Jackson 1964).
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36 448 Variation in brain to body mass ratios and in the relative mass of the major brain
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39 449 divisions can be used to postulate the capacities of different species' senses and cognition
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41 450 (Demski and Northcutt 1996). *Scyliorhinus canicula* have average brain to body mass
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44 451 ratios (Ridet et al. 1973) compared to higher and lower examples such as scalloped
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46 452 hammerheads (*Sphyrna lewini*) and Greenland sharks (*Somniosus microcephalus*)
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49 453 respectively (Northcutt 1978; Myagkov 1991). Interestingly, the former range widely
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51 454 throughout a number of markedly different coastal habitats, while the latter remain
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53 455 predominantly in cold, stable, deep arctic waters (Compagno et al. 2005).

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55 456 In addition to ecological considerations, the results of this study also have
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58 457 important implications regarding growing interest in possible interactions between
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4 458 electroreceptive fish and anthropogenic sources of Efields in the coastal environment that
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6 459 are within the range detectable and attractive to elasmobranchs (such as subsea cables:
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9 460 Gill et al. 2005; Gill and Kimber 2005; Sutherland et al. 2008; Boehlert and Gill 2010).
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11 461 Given the results of this study, it appears that within small temporal and spatial scales the
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14 462 sharks may be able to learn to ignore anthropogenic Efields and focus upon bioelectric
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16 463 fields by behavioural adaptation (assuming they can differentiate the sources; Kimber et
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18 464 al. 2011). However, they may well forget these adaptations over larger scales (e.g. when
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21 465 travelling between foraging areas) and respond to both types of Efield again. The balance
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24 466 between learning and forgetting would ultimately dictate long term effects on individual
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26 467 success and ecological fitness.

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29 468 In conclusion, we have measured rapid learning and habituation adaptation but
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31 469 relatively short memory in a fundamental behaviour for a model, benthic elasmobranch
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33 470 species. These cognitive abilities ideally suit a predator inhabiting a variable environment
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36 471 by improving foraging efficiency, but preventing missed opportunities, and support
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38 472 studies of other taxa that suggest relatively large brain size and behavioural adaptability
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41 473 correlates with habitat stability.

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487 **REFERENCES**

488 Aronson LR, Aronson FR, Clarke E (1967) Instrumental conditioning and light-dark
489 discrimination in young nurse sharks. *B Mar Sci* 17:249-256

490

491 Boehlert GW, Gill AB (2010) Environmental and ecological effects of ocean renewable
492 energy development – a current synthesis. *Oceanography* 23:68-81

493

494 Brown C, Braithwaite VA (2005) Effects of predation pressure on the cognitive ability of
495 the poeciliid *Brachyraphis episcopi*. *Behav Ecol* 16:482-487

496

497 Brown C, Markula A, Laland K (2003) Social learning of prey location in hatchery reared
498 Atlantic salmon. *J Fish Biol* 63:738-745

499

500 Brown C, Laland K, Krause J (2006) *Fish cognition and behaviour*. Blackwell Publishing
501 Ltd, Oxford

502

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56
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58
59
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62
63
64
65

503 Bryan JE, Larkin PA (1972) Food specialization by individual trout. Journal Bull Fish
504 Res Board Can 29:1615-1624
505
506 Centre for Marine and Coastal Studies (CMACS) (2003) A baseline assessment of
507 electromagnetic fields generated by offshore wind farm cables (COWRIE Stage 1).
508 Report number COWRIE-EMF-01-2002
509
510 Church RM (1964) Systematic effect of random error in the yoked control design.
511 Psychol Bull 62(2):122-131
512
513 Clark E (1959) Instrumental conditioning of lemon sharks. Science 130:217-218
514
515 Clark E (1961) Visual discrimination in lemon sharks. In: Tenth Pacific science congress,
516 University of Hawaii, Honolulu, USA, 21 August – 6 September 10:175-176
517
518 Compagno L, Dando M, Fowler, S (2005) Sharks of the world. HarperCollins Publishers
519 Ltd, London
520
521 Croy MI, Hughes RN (1991) The role of learning and memory in the feeding behaviour
522 of the fifteen-spined stickleback, *Spinachia spinachia* L. Anim Behav 41:149-159
523
524 Csanyi V, Csizmadia G, Miklosi A (1989) Long-term memory and recognition of another
525 species in the paradise fish. Anim Behav 37:908-911

1
2
3
4 526
5
6
7 527 Dawson BG, Heyer GV, Eppi R, Kalmijn AJ (1980) Field experiments on electrically
8
9 528 evoked feeding responses in the dogfish shark, *Mustelus canis*. Biol Bull 159:482
10
11 529
12
13
14 530 Demski LS, Northcutt RG (1996) The brain and cranial nerves of the white shark: An
15
16 531 evolutionary perspective. In: Klimley AP and Ainley DG (eds) White sharks: The biology
17
18 532 of *Carcharodon carcharias*. Academic Press, pp 121-131
19
20
21 533
22
23
24 534 Dill LM (1983) Adaptive flexibility in the foraging behavior of fishes. Can J Fish Aquat
25
26 535 Sci 40:398-408
27
28
29 536
30
31 537 Ellis JR, Pawson MG, Shackley SE (1996) The comparative feeding ecology of six
32
33 538 species of shark and four species of ray (Elasmobranchii) in the North-east Atlantic. J
34
35 539 Mar Biol Ass UK 76:89-106
36
37
38 540
39
40
41 541 Gill AB, Kimber JA (2005) The potential for cooperative management of elasmobranchs
42
43 542 and offshore renewable energy development in UK waters. J Mar Biol Ass UK 85:1075-
44
45 543 1081
46
47
48 544
49
50
51 545 Gill AB, Gloyne-Phillips I, Neal KJ, Kimber JA (2005) The potential effects of
52
53 546 electromagnetic fields generated by sub-sea power cables associated with offshore wind
54
55 547 farm developments on electrically and magnetically sensitive marine organisms.
56
57
58 548 (COWRIE stage 1.5). Report number COWRIE EMF 06-2004
59
60
61
62
63
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65

1
2
3
4
5
6
7
8
9
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564
565
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567
568
569
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571

Gill AB, Huang Y, Gloyne-Philips I, Metcalfe J, Quayle V, Spencer J, Wearmouth V (2009) COWRIE 2.0 Electromagnetic Fields (EMF) Phase 2: EMF-sensitive fish response to EM emissions from sub-sea electricity cables of the type used by the offshore renewable energy industry. Commissioned by COWRIE Ltd. Report number COWRIE-EMF-1-06

Girvan JR, Braithwaite VA (1998) Population differences in spatial learning in three-spined sticklebacks. Proc R Soc Lond B 265:913-918

Graeber RC, Ebbesson SO (1972) Visual discrimination learning in normal and tectal-ablated nurse sharks (*Ginglymostoma cirratum*). Comp Biochem Physiol A 42:131-139

Graeber RC, Ebbesson SO, Jane JA (1978) Visual discrimination following partial telencephalic ablations in nurse sharks (*Ginglymostoma cirratum*). J Comp Neurol 180:325-344

Guinet C, Bouvier J (1995) Development of intentional stranding hunting techniques in killer whale (*Orcinus orca*) calves at Crozet Archipelago. Can J Zool 73:27-33

Guttridge TL, van Dijk S, Stamhuis EJ, Krause J, Gruber SH, Brown C (2012) Social learning in juvenile lemon sharks, *Negaprion brevirostris*. Anim Cogn 16(1):55-64

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64
65

572 Heyer GW, Fields MC, Fields RD, Kalmijn AJ (1981) Field experiments on electrically
573 evoked feeding responses in the pelagic blue shark, *Prionace glauca*. Biol Bull 161:345-
574 346
575
576 Hirvonen H, Ranta E, Rita H, Peuhkuri (1999) Significance of memory properties in prey
577 choice decisions. Ecol Model 115:177-189
578
579 Hodgson ES, Mathewson RF (1971) Chemosensory orientation in sharks. Ann NY Acad
580 Sci 188:175-182
581
582 Hughes RN, Blight CM (1999) Algorithmic behaviour and spatial memory are used by
583 two intertidal fish species to solve the radial maze. Anim Behav 58:601-613
584
585 Kaiser MJ, Westhead AP, Hughes RN, Gibson RN (1992) Are digestive characteristics
586 important contributors to the profitability of prey? A study of diet selection in the fifteen-
587 spined stickleback, *Spinachia spinachia* (L.). Oecologia 90:61-69
588
589 Kalmijn AJ (1971) The electric sense of sharks and rays. J Exp Biol 55:371-383
590
591 Kalmijn AJ (1972) Bioelectric fields in sea water and the function of the ampullae of
592 Lorenzini in elasmobranch fishes. SIO Ref Ser 72-83:1-21
593

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54
55
56
57
58
59
60
61
62
63
64
65

594 Kimber JA, Sims DW, Bellamy PH, Gill AB (2009) Male-female interactions affect
595 foraging behaviour within groups of small- potted catshark, *Scyliorhinus canicula*. Anim
596 Behav 77:1435–1440

597

598 Kimber JA, Sims DW, Bellamy PH, Gill AB (2011) The ability of a benthic
599 elasmobranch to discriminate between biological and artificial electric fields. Mar Biol
600 158(1):1-8

601

602 Kuba MJ, Byrne RA, Burghardt GM (2010) A new method for studying problem solving
603 and tool use in stingrays (*Potamotrygon castexi*). Anim Cogn 13(3):507-513

604

605 Kuczaj SA, Gory JD, Xitco MJ (2009) How intelligent are dolphins? A partial answer
606 based on their ability to plan their behavior when confronted with novel problems. Jap J
607 Anim Psychol 59:99-115

608

609 Laland KN, Brown C, Krause J (2003) Learning in fishes: from three-second memory to
610 culture. Fish Fish 4:199-202

611

612 Laptikhovskiy VV, Arkhipkin AI, Henderson AC (2001) Feeding habits and dietary
613 overlap in spiny dogfish *Squalus acanthias* (Squalidae) and narrowmouth catshark
614 *Schroederichthys bivius* (Scyliorhinidae). J Mar Biol Ass UK 81:1015-1018

615

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56
57
58
59
60
61
62
63
64
65

616 Lyle JM (1983) Food and feeding habits of the lesser spotted dogfish, *Scyliorhinus*
617 *canicula* (L.), in Isle of Man waters. J Fish Biol 23:725-737
618
619 Mackney PA, Hughes RN (1995) Foraging behaviour and memory window in
620 sticklebacks. Behaviour 132:1231-1253
621
622 Maklakov AA, Immler S, Gonzalez-Voyer A, Ronn J, Kolm N (2011) Brains and the
623 city: big-brained passerine birds succeed in urban environments. Biol Lett 7(5):730-732
624
625 Meyer CG, Papastamatiou YP, Holland KN (2010) A multiple instrument approach to
626 quantifying the movement patterns and habitat use of tiger (*Galeocerdo cuvier*) and
627 Galapagos sharks (*Carcharhinus galapagensis*) at French Frigate Shoals, Hawaii. Mar
628 Biol 157:1857-1868
629
630 Micheli F (1997) Effects of experience on crab foraging in a mobile and a sedentary
631 species. Anim Behav 53:1149-1159
632
633 Myagkov NA (1991) The brain sizes of living elasmobranchii as their organization level
634 indicator. I. General analysis. J Brain Res 32:553-561
635
636 Nakagawa S, Cuthill IC (2007) Effect size, confidence interval and statistical
637 significance: a practical guide for biologists. Biol Rev 82:591-605
638

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54
55
56
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58
59
60
61
62
63
64
65

639 Nilsson J, Kristiansen TS, Fosseidengen JE, Ferno A, van den Bos R (2008) Learning in
640 cod (*Gadus morhua*): long trace interval retention. Anim Cogn 11:215-222
641
642 Northcutt RG (1978) Brain organization in cartilaginous fishes. In: Hodgson ES and
643 Mathewson RF (eds) Sensory biology of sharks, skates and rays. U.S. Office of Naval
644 Research, Arlington, Virginia, pp 117-193
645
646 Odling-Smee L, Braithwaite VA (2003) The influence of habitat stability on landmark
647 use during spatial learning in the three-spined stickleback. Anim Behav 65:701-707
648
649 Reader SM, MacDonald K (2003) Environmental variability and primate behavioural
650 flexibility. In: Reader SM and Laland KN (eds) Animal innovation Oxford University
651 Press, Oxford, UK
652
653 Ridet J-M, Bauchot R, Delfini C, Platel R, Thireau M (1973) L'encephale de *Scyliorhinus*
654 *canicula* (Linne) (Chondrichthyes, Slacii, Scyliorhinidae). Recherche d'une grandeur de
655 reference pour des etudes quantitatives. Cah Biol Mar 14:11-28
656
657 Schluessel V, Bleckmann H (2005) Spatial memory and orientation strategies in the
658 elasmobranch *Potamotrygon motoro*. J Comp Physiol A 191:695-706
659
660 Schusterman RJ, Kastak D (2002) Problem solving and memory. In: Hoelzel R (ed)
661 Marine mammal biology: an evolutionary approach. Blackwell Science Ltd, pp 371-388

1
2
3
4 662
5 663
6 664 Shapiro AD, Slater PIB, Janik VM (2004) Call usage learning in gray seals (*Halichoerus*
7
8
9 665 *grypus*). J Comp Physiol 118:447-54
10
11 666
12 667
13 668 Similä T, Ugarte F (1993) Surface and underwater observations of cooperatively feeding
14
15
16 669 killer whales in Northern Norway. Can J Zool 71:1494-1499
17
18
19 670
20
21 671 Sims DW, Davies SJ (1994) Does specific dynamic action (SDA) regulate return of
22
23 672 appetite in the lesser spotted dogfish, *Scyliorhinus canicula*? J Fish Biol 45:341-348
24
25
26 673
27
28 674 Sol D, Bacher S, Reader SM, Lefebvre L (2008) Brain size predicts the success of
29
30 675 mammal species introduced into novel environments. Am Nat 172:S63-S71
31
32
33 676
34
35
36 677 Stephens DW, Krebs JR (1986) Foraging theory. Princeton University Press, Princeton,
37
38 678 New Jersey
39
40
41 679
42
43 680 Sutherland WJ, Bailey MJ, Bainbridge IP, Brereton T, Dick JTA, Drewitt J, Gilder PM,
44
45 681 Green RE, Heathwaite AL, Johnson SM, MacDonald DW, Mitchell R, Osborn D, Owen
46
47 682 RP, Pretty J, Prior SV, Prosser H, Pullin AS, Rose P, Stott A, Tew T, Thomas CD,
48
49 683 Thompson DBA, Vickery JA, Walker M, Walmsley C, Warrington S, Watkinson AR,
50
51 684 Williams RJ, Woodroffe R, Woodroof HJ (2008) Future novel threats and opportunities
52
53 685 facing UK biodiversity identified by horizon scanning. J Appl Ecol 45:821-833
54
55
56
57 686
58
59
60
61
62
63
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2
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687 Tricas TC, Sisneros JA (2004) Ecological functions and adaptations of the elasmobranch
688 electrosense. In: von der Emde G, Mogdans J and Kapoor BG (eds) The senses of fishes:
689 Adaptations for the reception of natural stimuli. Narosa Publishing House, New Delhi,
690 India, pp 308-329
691
692 Visser IN, Smith TG, Bullock ID, Green GD, Carlsson OG, Imberti S (2008) Antarctic
693 peninsula killer whales (*Orcinus orca*) hunt seals and a penguin on floating ice. Mar
694 Mammal Sci 24:225-234
695
696 Wright T, Jackson R (1964) Instrumental conditioning of young sharks. Copeia 2:409-
697 412

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TABLES

Table 1. Results when comparing hierarchical response parameters between week before (1) and week after (2) a three week interval and interactions between reward (R) and not-reward (N) and week 1 and 2

Behaviour parameter	Week 1 and 2				Interaction R/N and Week 1/2			
	Effect*	S.E.	Stat**	<i>P</i>	Effect*	S.E.	Stat**	<i>P</i>
Passes within 5cm	-0.117	0.149	0.78	0.44	0.169	0.260	0.65	0.52
Latency to 1 st response	-0.487	0.245	1.99	0.05	0.582	0.387	1.90	0.21
Turn frequency	0.264	0.166	1.59	0.11	0.047	0.306	0.15	0.88
Bite frequency	0.038	0.163	0.23	0.82	0.119	0.273	0.44	0.66
Reward time (d.f.=139)	0.005	0.211	0.00 (<i>w</i>)	0.98	n/a	n/a	n/a	n/a
Reward bite (d.f.=170)	0.037	0.115	0.32	0.75	n/a	n/a	n/a	n/a
Path directness	0.020	0.079	0.06 (<i>SS</i>)	0.80	-0.091	0.065	2.18 (<i>SS</i>)	0.16

* Estimate of effect (relative difference between means)
 ** *t* statistic, unless otherwise stated (*w* = Wald; *SS* = sum of squares)
 S.E. = standard error
 n/a = model not well fitting due to lack of data
 d.f. = degrees of freedom

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4 **717 FIGURE LEGENDS**

5 718
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8 **720 Fig. 1.** Plan view of experimental apparatus upon electrode plate

9 721
10 **722 Fig 2.** Changes in the number of passes within 5cm of electrodes throughout
11 723 experimental week plotted by back-transforming estimates of effects to original units of
12 724 measurement for fitted curve (Rewarded: constant = 1.72, regression coefficient = 0.068,
13 725 error = 0.015; Unrewarded: constant = 0.12, regression coefficient = 0.0001, error =
14 726 0.033)

15 727
16
17 728 **Fig 3.** Changes in the latency of first response to the electrodes throughout experimental
18 729 week plotted by back-transforming estimates of effects to original units of measurement
19 730 for fitted curve (Rewarded: constant = 8.18, regression coefficient = 0.068, error = 0.027;
20 731 Unrewarded: constant = 8.43, regression coefficient = 0.004, error = 0.037)

21 732
22
23 733 **Fig. 4a and b.** Changes in number of turn and bite responses to electrodes throughout
24 734 experimental week plotted by back-transforming estimates of effects to original units of
25 735 measurement for fitted curve (Turns - Rewarded: constant = 1.98, regression coefficient =
26 736 0.005, error = 0.008; Unrewarded: constant = 1.72, regression coefficient = 0.151, error =
27 737 0.014; Bites - Rewarded: constant = 1.67, regression coefficient = 0.094, error = 0.011;
28 738 Unrewarded: constant = 1.39, regression coefficient = 0.205, error = 0.021)

29 739
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31 740 **Fig. 5a and b.** Changes in the time and bite number after which rewarded catsharks
32 741 acquired food reward throughout experimental week plotted by back-transforming
33 742 estimates of effects to original units of measurement for fitted curve (Time: constant =
34 743 7.18, regression coefficient = 0.084, error = 0.029; Bite: constant = 1.64, regression
35 744 coefficient = 0.072, error = 0.018)

36 745
37
38 746 **Fig. 6.** Changes in path directness to electrodes throughout experimental weeks plotted
39 747 by back-transforming estimates of effects to original units of measurement for fitted
40 748 curve (Rewarded: constant = 1.90, regression coefficient = 0.068, error = 0.029;
41 749 Unrewarded: constant = 1.61, regression coefficient = 0.014, error = 0.035), * index
42 750 calculation provided in methods.

43 751
44
45 752 **Fig. 7.** Examples of individual catshark search paths throughout experimental week (i to v)
46 753 when rewarded and unrewarded. C = catshark start position; E = electrode position; P.D. =
47 754 path directness (rounded figures)

Figure 1

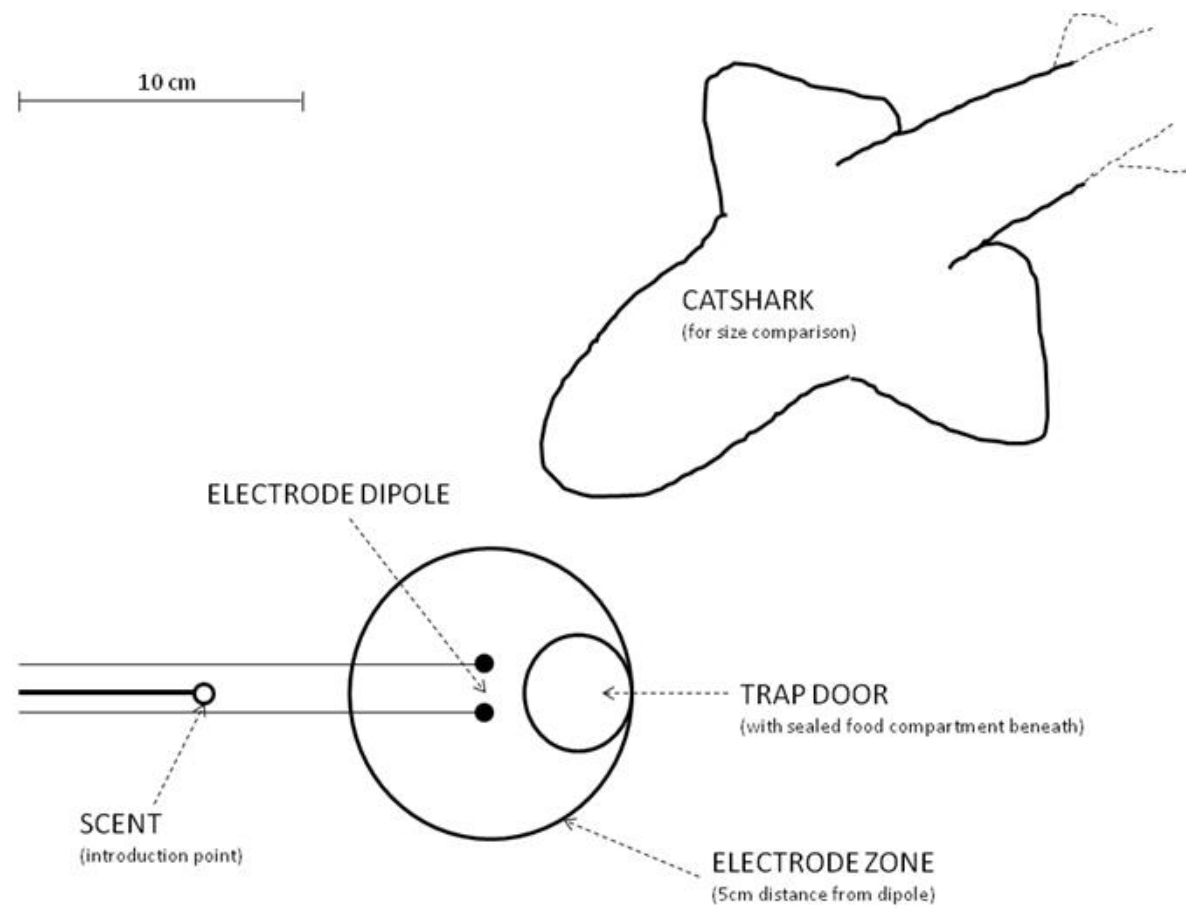


Figure 2

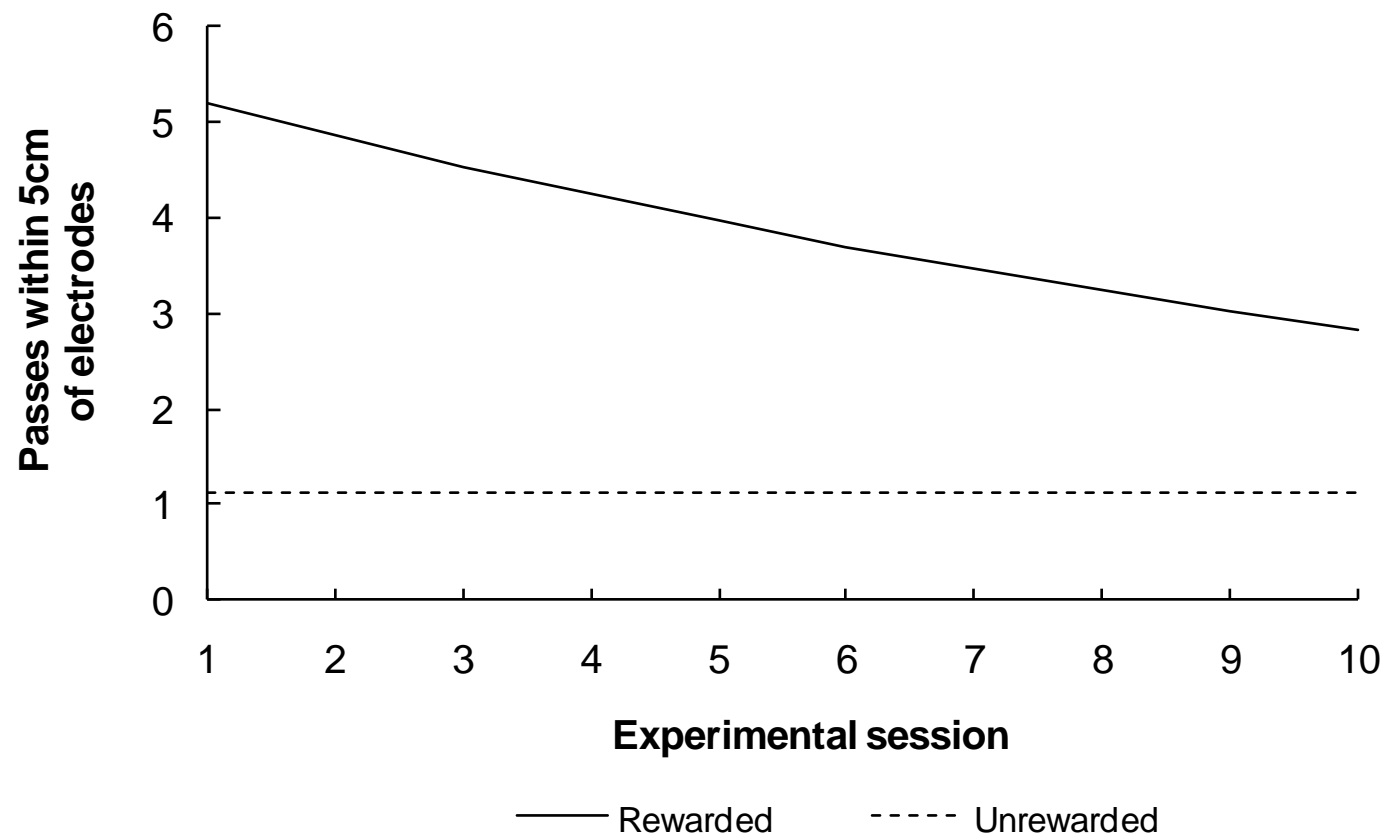


Figure 3

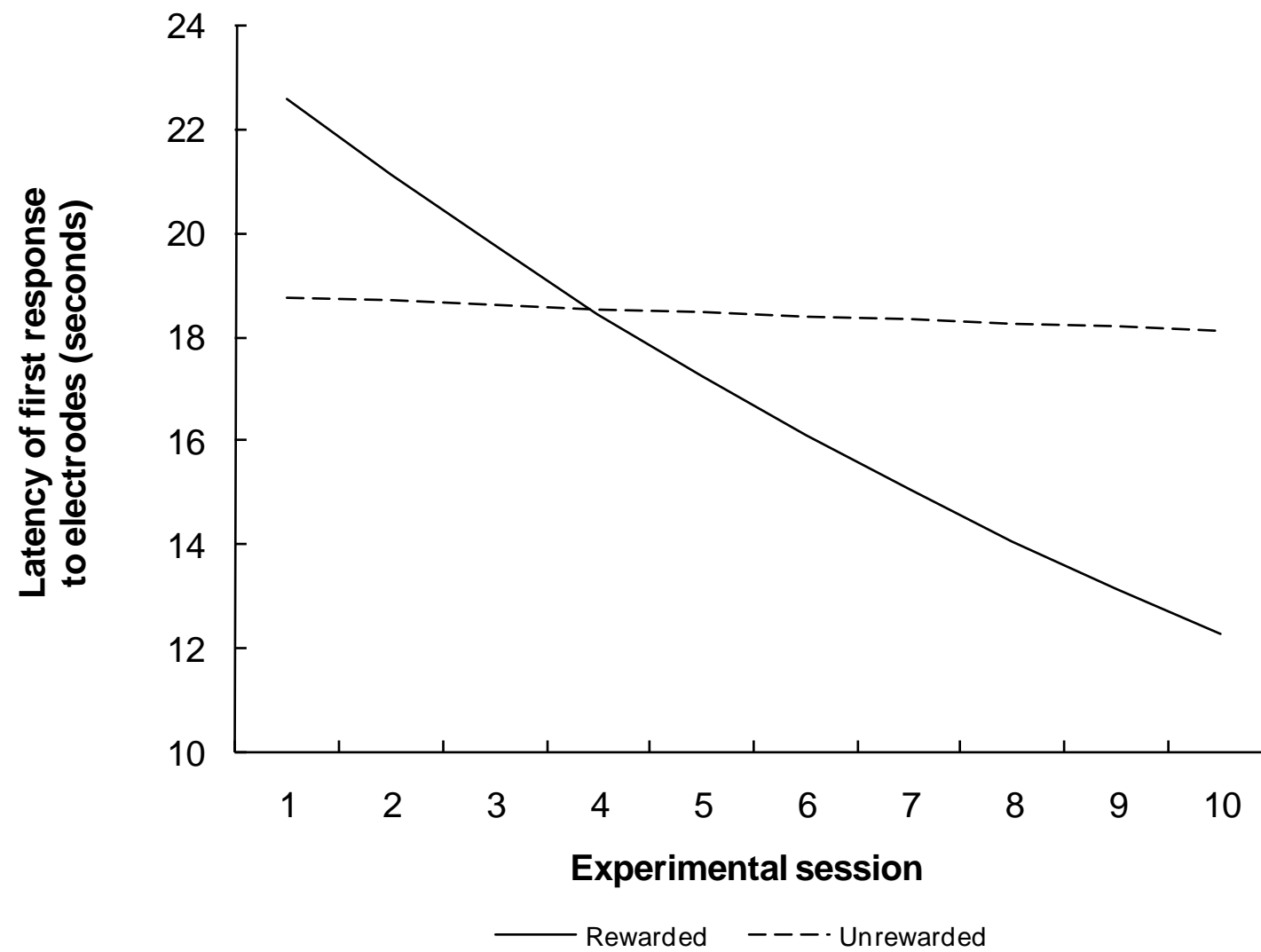


Figure 4

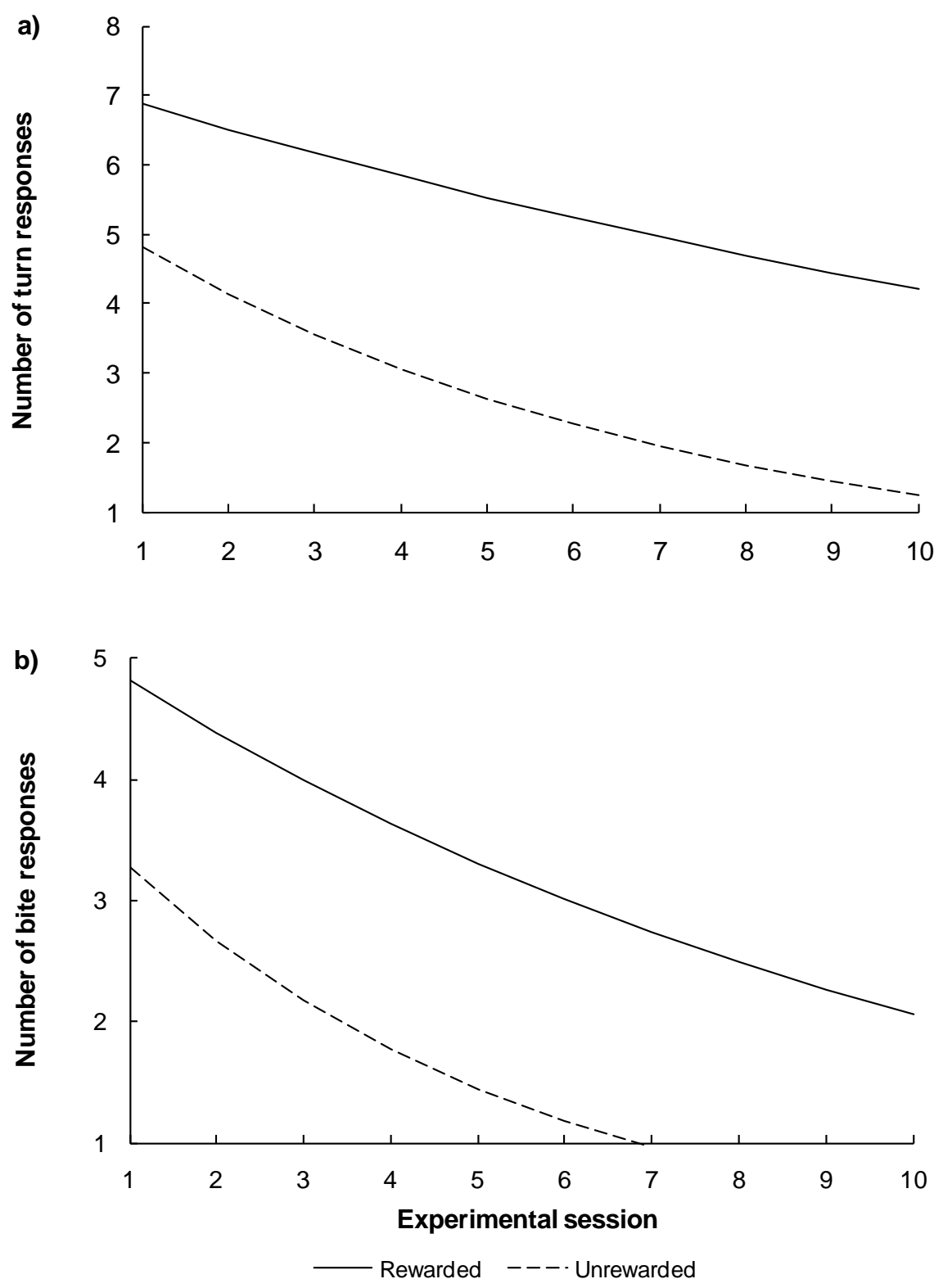


Figure 5

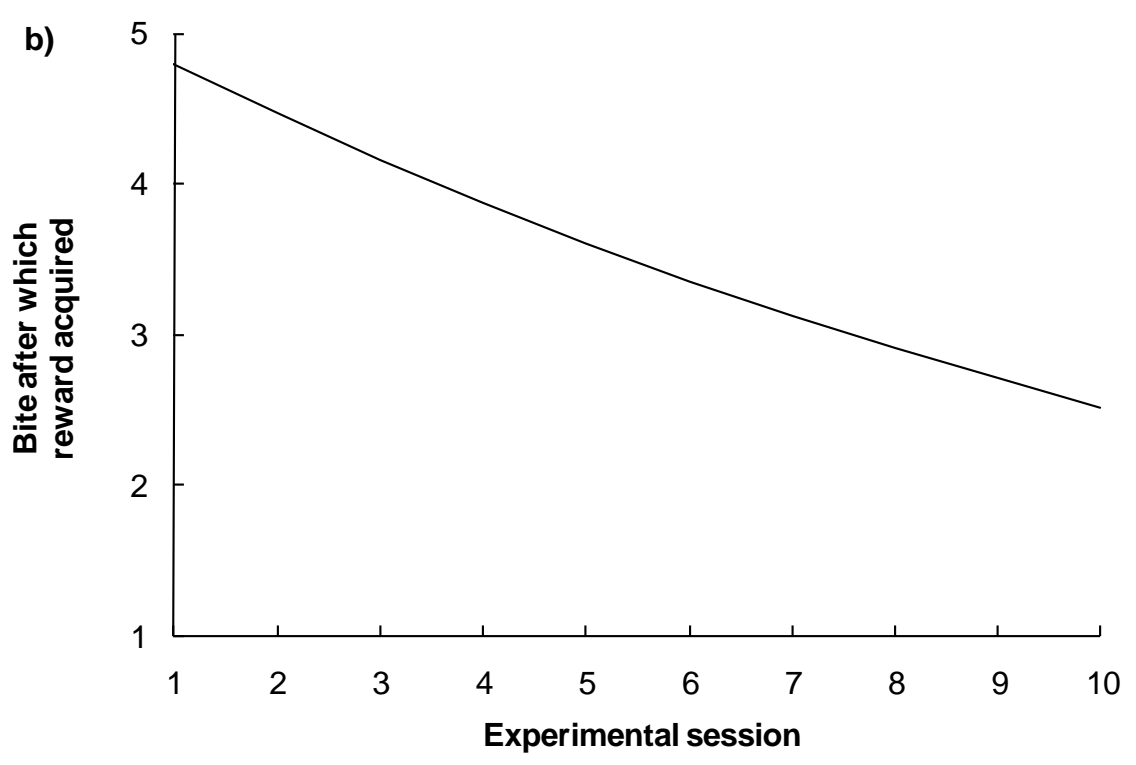
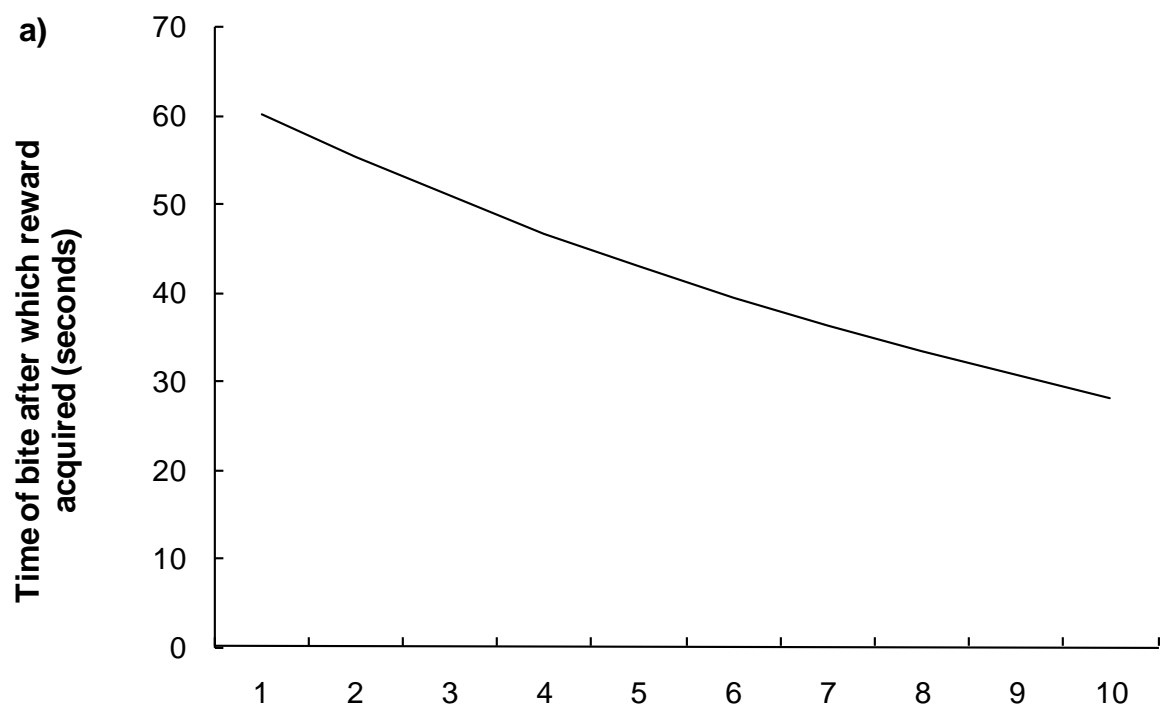


Figure 6

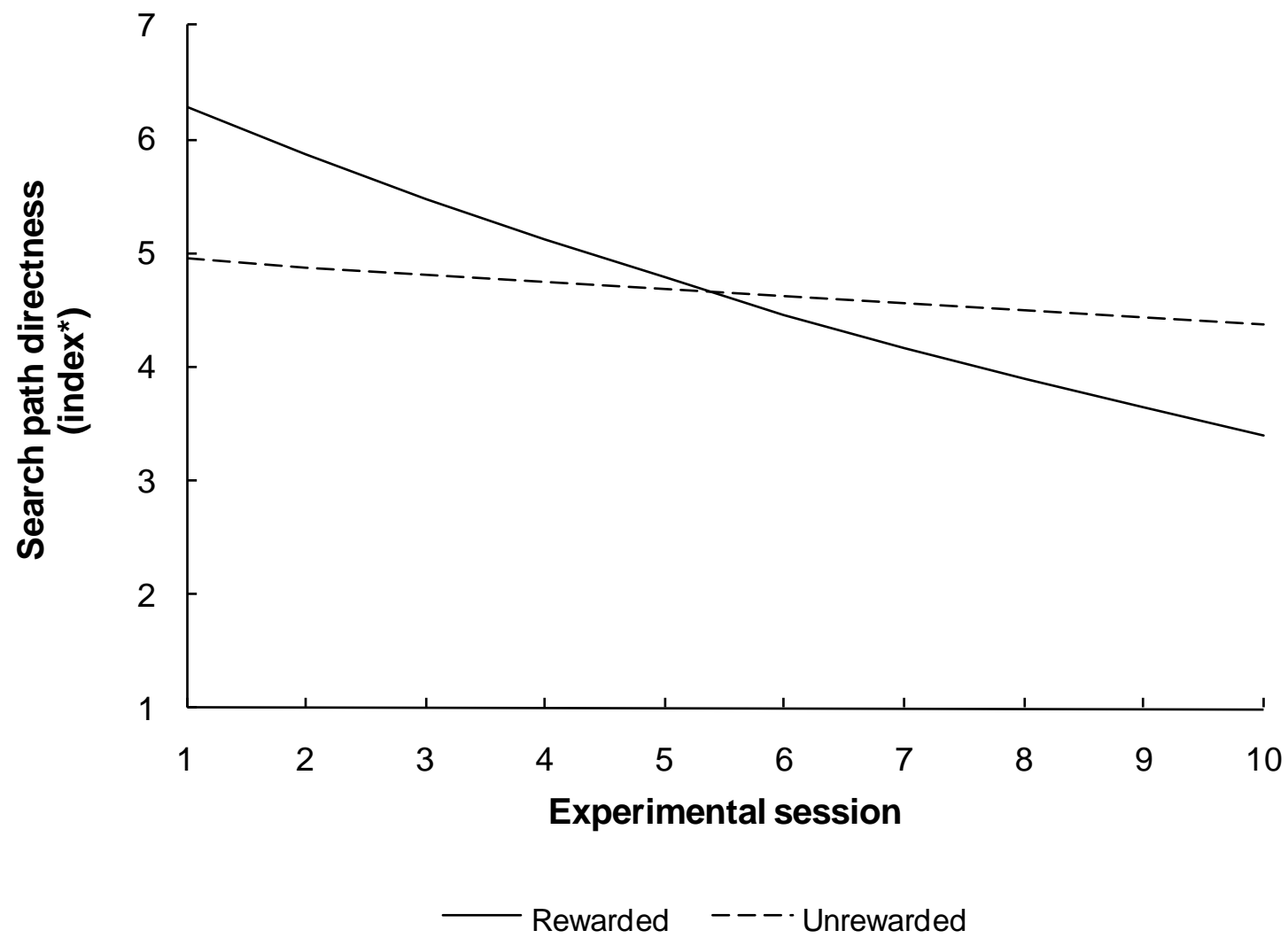
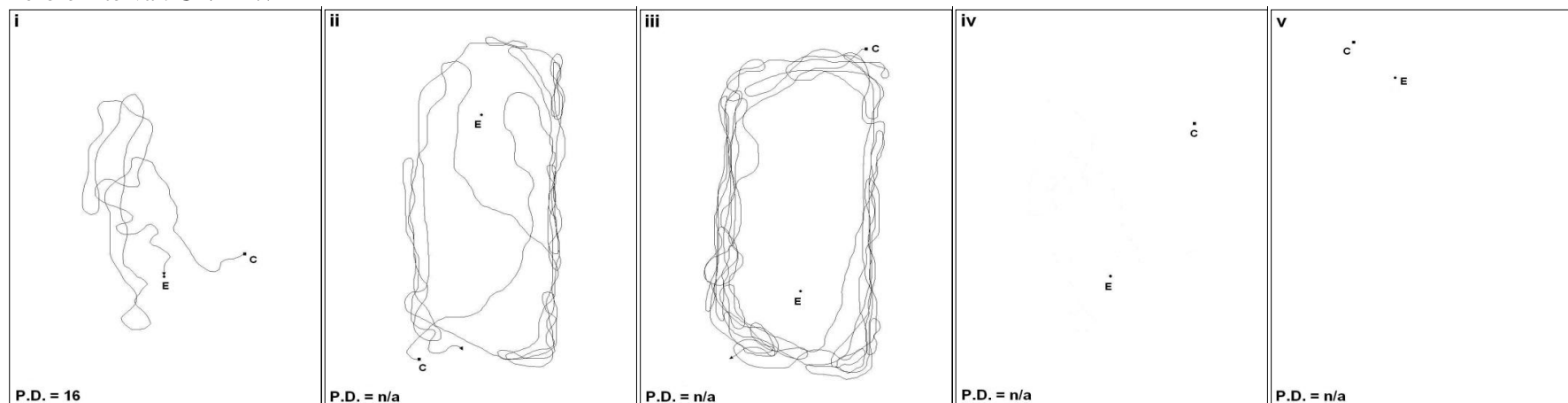
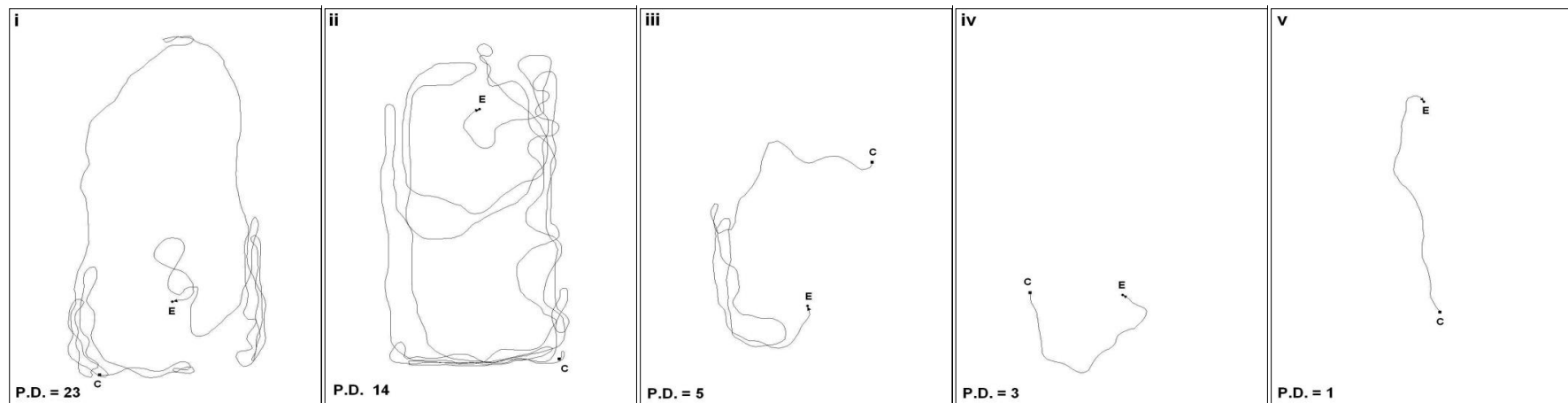


Figure 7

Before interval: **UNREWARDED**

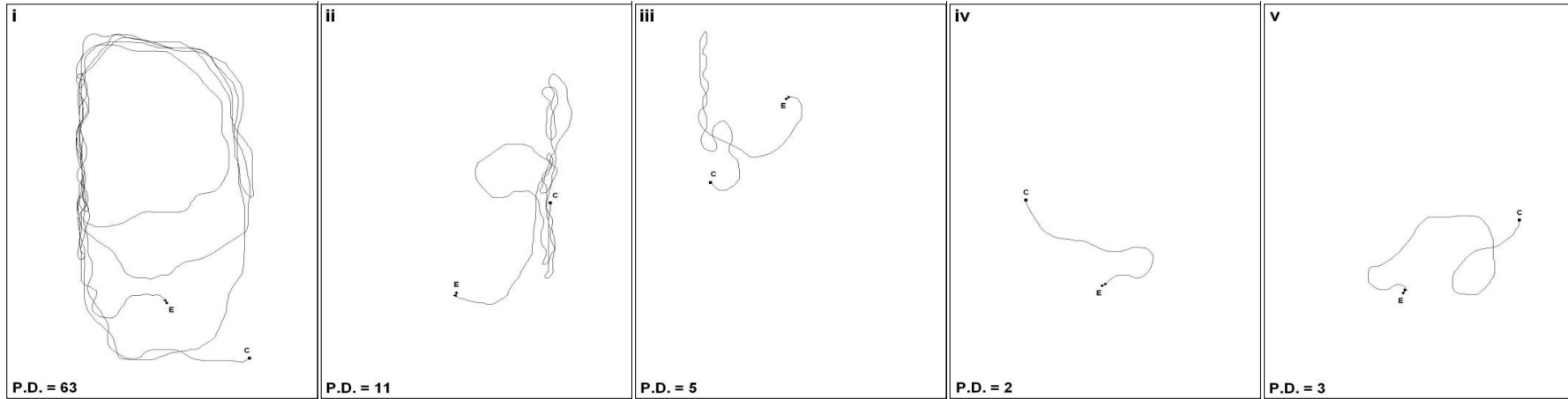


After interval: **REWARDED**

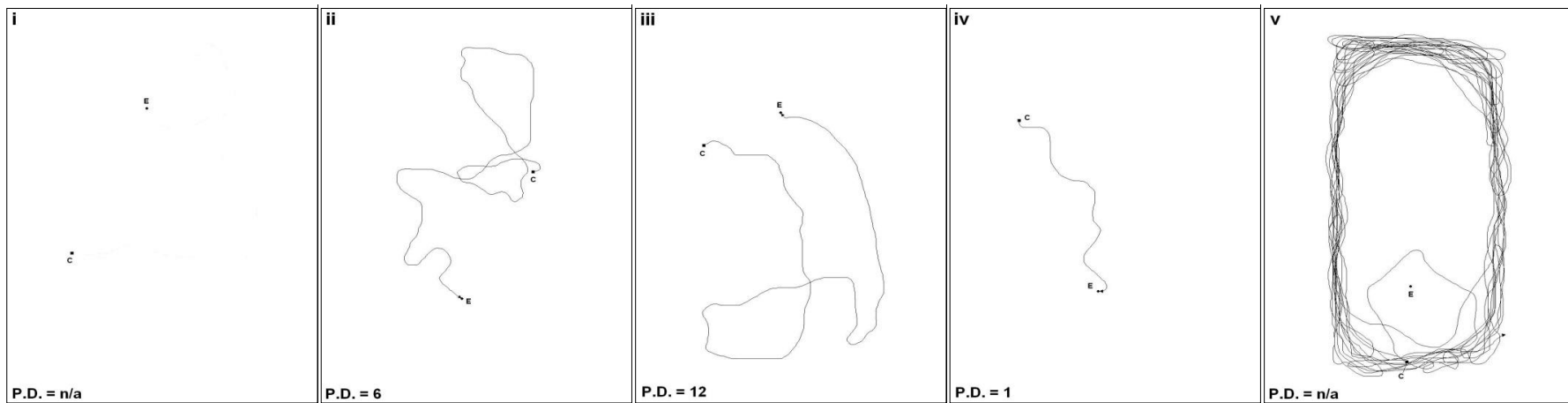


Catshark Blue 1501

Before interval: **REWARDED:**



After interval: **UNREWARDED:**



Catshark Green 230

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Elasmobranch cognitive ability: using electroreceptive foraging behaviour to demonstrate learning, habituation and memory in a benthic shark

Kimber, Joel A.

Springer Science Business Media

Joel A. Kimber, David W. Sims, Patricia H. Bellamy and Andrew B. Gill. Elasmobranch cognitive ability: using electroreceptive foraging behaviour to demonstrate learning, habituation and memory in a benthic shark. *Animal Cognition*, 2014, Vol. 17, No. 1, pp. 55-65

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