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4 **1 Lay Summary**  
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7 2 Tried and true or in with the new may all depend on spatial scale in home-hunting frogs.  
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9 3 Animals use two information sources when making decisions: prior information from  
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11 4 instinct or experience, and current information gathered in the moment. Our experiment  
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13 5 suggests frogs use prior information when choosing nest-sites at broad scales, but  
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15 6 switch to current information as the search refines. Thus, spatial scale may play an  
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17 7 important role in how individuals process information.  
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4 8 **Reduction in site-fidelity with smaller spatial scale may**  
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7 9 **suggest scale-dependent information use**  
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10 Running Title: Site-fidelity and spatial scale

11 **Animals change the strategy that they use to select breeding sites at the spatial**  
12 **scales of habitat, patch and microhabitat. In this regard, breeding site-fidelity is**  
13 **expected to vary according to environmental predictability, which, in turn, is**  
14 **expected to differ between each spatial scale. However, whether or not animals**  
15 **change their degree of site-fidelity at different spatial scales remains unclear. We**  
16 **captured and released males of the terrestrial frog *Pseudophryne bibronii* into**  
17 **alternative patches within a breeding habitat and determined the extent to which**  
18 **site-fidelity influenced individual nest-site choice. We found that males tended to**  
19 **return to their original patch rather than re-settle in an alternative patch.**  
20 **However, males were unlikely to return to their original nest-sites within the**  
21 **patch. We suggest that site fidelity in this species may be scale dependent because**  
22 **information from previous breeding seasons can predict the quality of patches, but**  
23 **not nest-sites. This behavioural variation is consistent with a hypothetical**  
24 **relationship between spatial scale and environmental predictability, which may**  
25 **have important implications for decision making processes that extend over**  
26 **multiple spatial scales.**

27  
28 **Key-words** habitat selection, current and prior information, spatial and temporal  
29 scale, uncertainty, site-fidelity, breeding behaviour, anuran

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4 31 Oviparous animals choose the best available habitat in which to lay their eggs  
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6 32 (Fretwell and Lucas 1970; Calsbeek and Sinervo 2002; Refsnider and Janzen 2010),  
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8 33 with decisions depending on environmental cues that indicate an area's reproductive  
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10 34 suitability (Krebs 1971). Furthermore, individual responses to these cues can be scale-  
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12 35 dependent. For instance, yellow headed blackbirds (*Xanthocephalus xanthocephalus*)  
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14 36 choose breeding sites based on assessments of food productivity at broad spatial scales,  
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16 37 but vegetation density at finer scales (Orians and Wittenberger 1991). Because available  
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18 38 cues can never completely predict the environment, animals often develop adaptive  
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20 39 responses to the inherent level of uncertainty. However, it is unclear how animals adjust  
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22 40 breeding-site decisions in relation to environmental unpredictability at different spatial  
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24 41 scales, despite this process being crucial for understanding habitat selection (Lima and  
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26 42 Zollner 1996; Schmidt, Dall, and van Gils 2010; Schmidt and Whelan 2010).

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30 43 One way animals can reduce uncertainty in their decision making is by  
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32 44 expressing stereotyped behavioural or physiological responses to specific environmental  
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34 45 triggers, or by using information from previous experience (Switzer 1993; Maynard  
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36 46 Smith 2000; Wagner and Danchin 2010). In many cases, 'prior information' allows an  
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38 47 individual to exploit patterns that are predictable over time. However, continued  
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40 48 exploitation of a pattern on the basis of prior information is vulnerable to changes in the  
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42 49 environment. Individuals can instead benefit by updating their information through  
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44 50 exploration of their environment, although gathering 'updated information' comes at a  
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46 51 cost (Dall and Johnstone 2002; Dall et al. 2005; Dall 2010). The optimal response to the  
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48 52 trade-off between the use of prior and updated information is partly determined by the  
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50 53 predictability of the environment (Gould 1974; Stephens 1989; Mangel 1990; Dall and  
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52 54 Cuthill 1997; Luttbegg and Warner 1999; Dall et al. 2005). In this respect, a decrease in  
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4 55 predictability is expected to reduce the benefits of using prior information in relation to  
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6 56 updated information because previous experience has less relevance to current  
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8 57 conditions.  
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10 58 Environmental predictability varies across different spatial scales, and  
11  
12 59 information use is expected to vary accordingly. There are at least two mechanisms that  
13  
14 60 could generate scale-dependent information use. First, the timescale of environmental  
15  
16 61 and ecological patterns and processes are longer at larger spatial scales (Wiens 1989).  
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18 62 Thus, prior information may provide a better basis for adaptive decisions at larger  
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20 63 spatial scales than smaller spatial scales, as previous conditions can serve as an adequate  
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22 64 approximation for the current state. Second the predictive ability of prior information  
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24 65 can decrease at smaller spatial scales because it becomes more difficult to build  
25  
26 66 dynamic models (e.g. behavioural assessment and response) as the scale being  
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28 67 considered decreases (Costanza and Maxwell 1994). This trend arises because the  
29  
30 68 uncertainties involved in small scale components can be averaged out when they are  
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32 69 considered at larger scales. Therefore, we can hypothesise that the use of prior  
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34 70 information will decrease, and the use of updated information will increase, at smaller  
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36 71 spatial scales.  
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42 72 We can study the use of prior and updated information through the expression of  
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44 73 site-fidelity, in which an individual is faithful to a previously used breeding-site over  
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46 74 multiple breeding attempts (Burger 1982; Switzer 1997; Ringler, Ursprung, and Hödl  
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48 75 2009). Site-fidelity may allow individuals to use prior information from previous  
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50 76 breeding attempts to exploit predictable conditions. However, continued exploitation of  
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52 77 the same site can result in lost opportunities for finding better quality sites. Individuals  
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54 78 can instead invest in updated information by exploring whether a superior site exists  
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4 79 (Johnson and Gaines 1990; Switzer 1993; Switzer 1997; Doligez et al. 2003; Piper  
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6 80 2011). If an animal's decision to be site-faithful can be scale dependent, this would  
7  
8 81 suggest that individuals adjust their decisions to the level of uncertainty at a given  
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10 82 spatial scale. However, many studies of breeding site choice base their conclusions on  
11  
12 83 patterns of distribution and abundance, and are unable to separate the decision to be  
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14 84 site-faithful from coarse ecological processes (e.g. resource limitation, competition) that  
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16 85 could also result in the re-use of nest sites (Parrish and Edelstein-Keshet 1999; Doligez  
17  
18 86 et al. 2003; Boulinier et al. 2008). Thus, manipulative field experiments that distinguish  
19  
20 87 between pattern and process will enable us to determine whether site-fidelity varies with  
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22 88 spatial scale.  
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26 89 We performed a novel patch-swap experiment on an entire male population of  
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28 90 the terrestrial toadlet *Pseudophryne bibronii*, and measured site-fidelity during re-  
29  
30 91 settlement. Our aim was to determine if individuals choose to be site-faithful if they are  
31  
32 92 presented with the opportunity to settle in an alternative breeding site. Following re-  
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34 93 settlement, we compared the use of site-fidelity at different spatial scales to determine if  
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36 94 there was a decrease in site-fidelity at smaller spatial scales.  
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## 41 96 **Materials and methods**

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### 43 98 *Study species*

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48 99 The brown toadlet *Pseudophryne bibronii* is a Myobatrachid frog that is  
49  
50 100 endemic to temperate regions of south-eastern Australia (Tyler and Knight 2009). *P.*  
51  
52 101 *bibronii* are terrestrial breeders, with males entering breeding sites at the beginning of  
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54 102 autumn and establishing shallow burrows in moist soil underneath leaf litter in dry creek  
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4 103 lines and drainage pans. Males advertise their presence to females and mediate  
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6 104 competitive interactions with acoustic signals (Pengilley 1971; Woodruff 1976;  
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8 105 Mitchell 2001; Byrne 2008; Heap, Stuart-Fox, and Byrne 2012; Heap and Byrne 2013).  
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10 106 Females oviposit directly into the burrow, after presumably assessing the quality of the  
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12 107 nest-site and/or the resident male (Pengilley 1971; Woodruff 1976; Byrne and Keogh  
13  
14 108 2007; Byrne and Keogh 2009). Females are extremely polyandrous and sequentially  
15  
16 109 split their clutch amongst the nests of two to eight males (Byrne and Keogh 2009; Byrne  
17  
18 110 and Roberts 2012). Consequently, around 80 percent of the males in the chorus can gain  
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20 111 mating success (Byrne and Keogh 2009). Typically, males remain with their eggs over  
21  
22 112 the course of the breeding season, which continues until winter rainfalls inundate the  
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24 113 habitat and eggs hatch into ephemeral pools. Heavy rain events that temporarily flood a  
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26 114 nest-site often lead to its abandonment, at which point males either establish a new nest  
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28 115 in an area that hasn't flooded, return to their original site after waiting for the water to  
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30 116 recede, or leave the chorus entirely. Such displacement can happen several times a  
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32 117 season (approximately 2-4 times) before the site remains flooded and toadlets establish  
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34 118 a new nest or leave altogether (P.G. Byrne, unpublished data). Males may or may not  
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36 119 provide some level of care for their eggs (Woodruff 1977). There is also evidence for  
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38 120 alternative reproductive strategies, including males fertilising eggs in other nests and  
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40 121 maintaining multiple nest-sites (Mitchell 2005; Byrne and Keogh 2009). Between  
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42 122 seasons toadlets move into the bush surrounding the breeding site and overwinter under  
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44 123 rocks or logs, and males are likely to experience at least five separate breeding seasons  
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46 124 over their lives (P.G. Byrne, unpublished data).  
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126 *Field protocol*

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4 127 The patch-swap experiment was performed on a population of toadlets in Bream  
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6 128 Beach, Australia, between 19 April and 20 May 2010. We divided the breeding habitat  
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8 129 into three distinct patches, referred to as the north, east and south patch, based on the  
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10 130 intersection of two ephemeral streams (Figure 1). We collected every calling male in  
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12 131 each patch approximately 4-6 weeks after the commencement of a 3-4 month breeding  
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14 132 season. Collections were made over three consecutive nights, with toadlets captured  
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16 133 from the north patch on night one (19/4/2010; n = 13 males), the east patch on night two  
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18 134 (20/4/10; n = 23 males), and the south patch on night three (21/4/10; n = 16 males). At  
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20 135 the time of collection, nest sites were marked with an ID flag and males were placed  
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22 136 into plastic zip-lock bags and transported to a field station (located approximately 1km  
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24 137 from the study site), where they were then housed in individual plastic containers (175 x  
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26 138 125 x 50mm). Containers each held a moist sponge to ensure frogs remained fully  
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28 139 hydrated and were kept in a room with windows that permitted frogs to receive natural  
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30 140 light: dark cycles. On the day after collection frogs were weighed using a digital balance  
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32 141 and photographed. Because *P. bibronii* have unique individual ventral patterns, the  
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34 142 photographic identification method (PIM; Bradfield 2004; Mitchell 2005; Kenyon,  
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36 143 Phillott, and Alford 2009; Kenyon, Phillott, and Alford 2010) provided a reliable and  
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38 144 unambiguous form of identification (identifications conducted by SMH and PB).

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44 145 We aimed to test the expression of patch-fidelity by comparing the fidelity of  
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46 146 individuals placed in an alternative patch with those placed in their original patch. We  
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48 147 kept each group of males at the field station for two nights in order to temporally  
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50 148 dislocate them from their original site selection attempt. Males from the north and east  
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52 149 patches were randomly chosen to be used in the patch-swap treatment, whereas males  
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54 150 from the south patch were chosen as a control. We released north males into the east  
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4 151 patch, east males into the north patch and south males into the south patch on three  
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6 152 successive nights (21-23/4/10). We released males at a centralised location within their  
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8 153 release patch (Figure 1), which was  $23 \pm 1$  m from their original capture site. Prior to  
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10 154 release, we arranged containers into a circle, with lids facing outwards, and after 5  
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12 155 minutes of acclimation opened each lid. Exactly 29, 30 and 31 days after the initial  
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15 156 collection we re-captured calling males from the north (17/5/10;  $n = 11$ ), east (18/5/10;  
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17 157  $n = 17$ ) and south (19/5/10;  $n = 12$ ) patches, respectively. We repeated the procedure of  
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19 158 the original capture and used the photographic identification method (PIM) to identify  
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21 159 the occupant of each nest site. Three new frogs were captured during this second  
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23 160 capture period, but were not included in analyses as they were not part of the  
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25 161 experiment. We laid lines of string through the chorus to serve as the axes of a  
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27 162 coordinate system and noted the Cartesian coordinates for original and re-settled nest-  
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29 163 sites.  
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### 35 *Statistical analyses*

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37 166 We considered the expression of site fidelity at the patch scale by using Fisher's  
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39 167 tests to determine whether the proportion of males that settled in their release patch  
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41 168 differed between treatment groups. Additionally, we explored the occurrence of site  
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43 169 fidelity at the nest-site scale and the change in site-fidelity between scales by using chi-  
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45 170 squared tests to determine the proportion of males that returned to i) their original patch  
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47 171 (patch-fidelity), ii) their original nest-site (strict site-fidelity) and iii) within 1 m of their  
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49 172 original nest-site (coarse site-fidelity). We calculated the 95% confidence intervals at  
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51 173 each scale and inferred whether there were any changes across scales by considering  
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53 174 whether the confidence intervals were overlapping.  
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4 175 We also tested for patch-fidelity by considering the directions and distances  
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6 176 travelled by males following displacement in relation to their original nest-sites, under  
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8 177 the hypothesis that these values will be similar if patch-fidelity was being expressed.  
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10 178 Specifically, we tested whether the distance each male travelled was equivalent to the  
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12 179 distance it was displaced by using linear regression and paired t-tests, analysing the  
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14 180 males of each patch separately. The direction of travel was analysed using a Hotelling  
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16 181 test, following the guidelines of Zar (1999). This test can determine whether there is a  
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18 182 significant difference between the azimuths of a male's original and re-settled nest-sites  
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20 183 (using the release site as the reference point). As a check on our methodology, we also  
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22 184 tested whether there was any linear relationship between an individual's change in nest-  
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24 185 site location (i.e. the distance between its original and resettled nest-site) and the  
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26 186 distance that it was transported to the release site from its original nest-site.  
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## 33 **Results**

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35 189 We first determined whether males expressed fidelity at the patch scale. The  
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37 190 frequency of males that settled in the release-patch depended on the treatment (Fisher's  
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39 191 test:  $p < 0.001$ ; Table 1). Specifically, males from the control were significantly more  
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41 192 likely to re-settle in the release patch than males from the patch-swap treatment  
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43 193 (Fisher's test:  $p < 0.001$ ; Table 1). This analysis included twelve males that were not re-  
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45 194 captured, who were classified as not having re-settled in the release patch. Furthermore,  
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47 195 the distances from the release site to original and re-settled nest-sites were strongly  
48  
49 196 correlated for the control males ( $F_{1, 10} = 10.63$ ,  $r^2 = 0.47$ ,  $p = 0.001$ ) and those captured  
50  
51 197 from the east patch ( $F_{1, 15} = 92.79$ ,  $r^2 = 0.85$ ,  $p < 0.001$ ). In comparison, there was no  
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53 198 significant correlation for males collected from the north patch ( $F_{1, 9} = 0.02$ ,  $r^2 < 0.01$ ,  $p$   
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4 199 = 0.901). However, paired t-tests indicate that there were no significant differences  
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6 200 between displacement and travel distances for males collected from the south ( $t_{11} =$   
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8 201 1.71,  $p = 0.116$ ), east ( $t_{16} = 0.37$ ,  $p = 0.719$ ) or north patches ( $t_{10} = 0.83$ ,  $p = 0.425$ ).  
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10 202 Additionally, the direction males travelled after release was not significantly different  
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12 203 from the direction of their original nest-site (Figure 2) for males from the south ( $F_{2, 10} =$   
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14 204 1.96,  $p = 0.191$ ), east ( $F_{2, 15} = 0.50$ ,  $p = 0.618$ ) or north ( $F_{2, 9} = 0.43$ ,  $p = 0.665$ ). Thus, it  
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16 205 appears that the scale of resettlement is equivalent to the scale of displacement. The lack  
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18 206 of correlation between the distances for the northern males may be due to the small  
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20 207 patch and sample sizes.

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24 208 We then considered changes in the expression of site fidelity between spatial  
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26 209 scales by comparing the proportions of individuals that re-settled in the same spatial  
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28 210 location at each scale. We only considered the forty males that re-settled for this  
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30 211 analysis, as we were interested in whether the males that decided to re-settle were site-  
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32 212 faithful or not. There were no significant differences in the proportion of individuals  
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34 213 that settled in their original patch between the three treatment groups (Fisher's test:  $p =$   
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36 214 0.739), or between the control and pooled patch-swap treatment groups (Fisher's test:  $p$   
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38 215 = 1.000). Thus, we pooled males from all three treatment groups together to consider  
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40 216 patch-fidelity. Overall, 38 of the 40 recaptured males (95%) were found in their original  
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42 217 patch (Figure 1, 3; Table 2). We are 95% confident that the proportion of males that  
43  
44 218 express patch-fidelity lies between 82 and 99% when all males are pooled (Figure 3,  
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46 219 Table 2).

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50 220 By comparison, only 3 of the 40 males (proportion: 0.08; 95% CI: 0.02 - 0.21)  
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52 221 that held a nest-site decided to re-settle at the same nest location (strict site-fidelity;  
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54 222 Figures 1, 3; Table 2). Even if the criterion for site-fidelity is relaxed to 1m surrounding  
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4 223 the original nest site (coarse site-fidelity), only eight individuals (proportion: 0.20, 95%  
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6 224 CI: 0.10 - 0.36) expressed site-fidelity (Figures 1, 3; Table 2). There were significant  
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8 225 differences in the proportions of males that expressed strict site-fidelity (Fisher's test:  $p$   
9  
10 226 = 0.017) and coarse site fidelity (Fisher's test:  $p = 0.030$ ) between treatment groups.  
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12 227 Specifically,  $\chi^2$  components indicate that nest-site fidelity was more common for males  
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14 228 that were collected from, and re-settled within, the northern patch (Table 2).  
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16 229 Comparison of each patch separately indicates that site-fidelity decreased between the  
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18 230 patch and nest-site scale for males from the southern and eastern patches, but not for  
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20 231 males in the northern patch (Figure 3).  
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23  
24 232       Importantly, there was no significant correlation between an individual's change  
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26 233 in nest-site location and the distance of the release site from its original nest-site (linear  
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28 234 regression:  $F_{1, 38} = 0.06$ ,  $p = 0.803$ ,  $r^2 < 0.01$ ), indicating that lack of nest site-fidelity  
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30 235 was not because males were released too far from their original nest site to be able to  
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32 236 return. In general, males re-settled in a nest-site not encountered during the original  
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34 237 survey and capture (presumably having constructed a new burrow). However, there  
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36 238 were a few exceptions. First, two pairs of individuals were found within a single nest  
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38 239 upon recapture, with one of these individuals having expressed site-fidelity. No eggs  
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40 240 were found in this nest. Second, one individual was found in a nest-site that was  
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42 241 inhabited by another during the original capture. Again, this nest did not contain any  
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44 242 eggs. The original resident had a new nest 2.5m away, and the new resident was found  
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46 243 3.2m from its original nest. Third, four original nest-sites appeared to have been  
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48 244 occupied for some period during re-settlement, but were unoccupied at the time of  
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50 245 recapture. This was determined by measuring the occurrence of calling activity during  
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52 246 the re-settlement period as part of a related study (Heap and Byrne 2013). Although the  
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4 247 identity of the callers could not be determined, the original occupants of these nests  
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6 248 were found 1.2m, 1.8m and 9.3m away from their original site by the end of the study.  
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8 249 The fourth male was not recaptured. Finally, there were three males that were  
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10 250 recaptured in their original nest-site. There were nests before and after capture that  
11  
12 251 contained eggs, and we have analysed the presence of eggs in another study (Heap and  
13  
14 252 Byrne 2013). This analysis found no correlation between nest-site location and egg  
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16 253 presence, or any correlation between breeding success before and after re-settlement.  
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## 255 **Discussion**

256 Males showed a strong preference for their original patch over an alternative  
257 patch. Furthermore, males moved in the direction of their original nest-sites following  
258 release and travelled an equivalent distance to that of displacement to reach a new nest-  
259 site. Together, these results imply that males display site-fidelity at the patch scale. In  
260 contrast, relatively few males returned to within one metre of their original nest-site.  
261 Additionally, males appear to be aware of the location of their original nest-site, judging  
262 by the direction and distance of movement after release, yet they do not tend to re-settle  
263 in the same location. Thus, these results suggest that the expression of site-fidelity for  
264 choosing breeding sites may be scale dependent (Figure 4). That is, returning to familiar  
265 patches may improve reproductive success, but fidelity to nest-sites may provide little  
266 additional benefit. However, changes in the expression of site-fidelity with spatial scale  
267 appeared to depend upon the patch that males were captured from because we can not  
268 be confident that the males that re-settled in the north patch showed an equivalent  
269 decrease in site-fidelity at smaller spatial scales compared to the east and south patches.

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4 270 Breeding habitat selection involves responding to information that predicts  
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6 271 reproductive success at multiple spatial scales. Previous studies have shown that the  
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8 272 cues that allow reliable assessment of site quality can vary with spatial scale (Krebs  
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10 273 1971; Orians and Wittenberger 1991). Our results suggest that the general manner in  
11  
12 274 which information is used can also vary between spatial scales. In particular, if we  
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14 275 consider site-fidelity to indicate the use of prior information, and occupation of new  
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16 276 sites to indicate the use of updated information (Johnson and Gaines 1990; Switzer  
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18 277 1993; Switzer 1997; Doligez et al. 2003; Piper 2011), then our results suggest that the  
19  
20 278 nature of information used to choose nest sites varies with spatial scale. Specifically,  
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22 279 male *P. bibronii* may benefit from using prior information when choosing patches, but  
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24 280 benefit from responding to updated information when choosing nest-sites within the  
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26 281 patch (Figure 4).  
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30 282 These results conform to theory that predicts the value of prior information (in  
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32 283 terms of the net benefit that responding to the information would provide) to increase as  
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34 284 spatial scale increases, whilst the value of updated information to increase as spatial  
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36 285 scale decreases (Wiens 1989; Costanza and Maxwell 1994; Figure 4). In the case of  
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38 286 toadlets, flooding patterns are an important factor in determining reproductive success  
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40 287 (Woodruff 1976; Bradford and Seymour 1988; Geiser and Seymour 1989; Byrne and  
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42 288 Keogh 2009), and variation in flooding patterns at different spatial scales may partly  
43  
44 289 explain why the value of prior information is greater at the patch scale than the nest-site  
45  
46 290 scale. Patches in this system occur around ephemeral bodies of water such as streams  
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48 291 and ponds. The climatic and topographical patterns that allow these bodies to exist may  
49  
50 292 be predictable across years, such that an individual can be relatively certain that a  
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52 293 similar body will exist in the current season based on its existence in a previous season.  
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4 294 However, whether or not a given nest-site floods to an appropriate level is likely to be  
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6 295 more variable (less predictable) between years than the presence of a suitable body of  
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8 296 water in the patch due to fine scale differences in drainage patterns over space and time.  
9  
10 297 Thus, prior information may be reliable at the patch scale but not at the nest-site scale.  
11  
12 298 This notion could be tested by measuring reproductive success at nest sites over  
13  
14 299 multiple years, with the prediction that variation in the average patch reproductive  
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16 300 success across years is less than variation at a given nest site. Additionally, the  
17  
18 301 hydrodynamic properties of the substrate can be measured and compared between years.  
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22 302 The lack of site fidelity at the nest-site scale suggests that males must gather  
23  
24 303 information on their current surroundings to find a suitable nest site within the patch. In  
25  
26 304 this regard, males appear to partly respond to information on the local spatial  
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28 305 arrangement of other males more than physical properties such as soil moisture when  
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30 306 establishing a nest-site (Heap and Byrne 2013). However, such physical properties may  
31  
32 307 influence male calling behaviour, and in turn, spatial arrangements. For example, in a  
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34 308 manipulative field experiment in which nest sites were artificially wetted, Mitchell  
35  
36 309 (2001) demonstrated that male *P. bibronii* call more from wetter nests presumably  
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38 310 because there is less risk of desiccation.  
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41 311 The response to other males may largely be driven by the need to alleviate  
42  
43 312 competition over acoustic space, as males tend to abandon sites in denser areas (Heap  
44  
45 313 and Byrne 2013). Although there is no apparent correlation between density and  
46  
47 314 breeding success in *P. bibronii* at these sites during the observed breeding season (Heap  
48  
49 315 and Byrne 2013), the evidence that competition for space is critical in finding mates  
50  
51 316 across frog species is overwhelming (Wells 2007). Competition aside, the previously  
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53 317 reported pattern that males have tendencies to avoid isolated and peripheral areas  
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4 318 provides an indicator that uncertainty as to nest-site quality is high within patches (Heap  
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6 319 and Byrne 2013). Specifically, this pattern of conspecific attraction suggests that males  
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8 320 copy each other's breeding site decisions, and individuals are expected to only prefer  
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10 321 using social cues over non-social cues when either i.) the costs of acquiring personal  
11  
12 322 information are too great (i.e. trial and error in reproductive success, coupled with the  
13  
14 323 risk of nest-site failure), or ii.) non-social cues are unreliable or uninformative (Dewar  
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16 324 2004; Coolen et al. 2005; Kendel et al 2005). That is, if uncertainty was not an issue  
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18 325 within patches then males should perhaps prefer acquiring personal information over  
19  
20 326 using social cues. In any case, the information that males use to choose a nest-site  
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22 327 remains an open question. That being said, any evidence that the use of social cues  
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24 328 within patches is driven by uninformative non-social cues (rather than the costs of  
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26 329 acquiring personal information) would strongly support the hypothesis that there is  
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28 330 scale-dependent uncertainty.  
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33         The higher variance in behaviour of males in the northern patch, who showed a  
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35 332 greater average degree of site-fidelity at the nest-site scale than males from other  
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37 333 patches, is consistent with this overall explanation. Males in the northern patch mostly  
38  
39 334 settled on the edge of a small pond that floods to the same extent almost every year  
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41 335 (P.G. Byrne, personal observation). By contrast, males in the southern and eastern  
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43 336 patches settled along the banks of small ephemeral streams that are less consistent in  
44  
45 337 their flooding patterns. Thus, prior information on nest-site quality may be more  
46  
47 338 relevant in the northern patch than the southern and eastern patches, and hence site-  
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49 339 fidelity more common at the nest-site scale. However, it is important to note that there  
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51 340 was greater variance in site-fidelity for northern males, and this could be due to either  
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53 341 the characteristics of the patch or the smaller sample size.  
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4 342           There is, however, an alternative explanation to a spatio-temporal scaling  
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6 343 relationship underlying changes in behaviour at different spatial scales. Males may have  
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8 344 actually gathered information about novel patches and decided that they were unsuitable  
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10 345 breeding sites. Males may also have avoided returning to their original nest-site due to  
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12 346 experimental handling. Thus, our explanation requires support from experiments that  
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14 347 demonstrate prior information is consistently used over current information to select  
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16 348 patches, and from a full qualification of the degree to which males show site fidelity at  
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18 349 the nest-site scale. These gaps can be addressed by conducting an experiment that tests  
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20 350 whether males prefer familiar patches over alternative patches that present more  
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22 351 favourable information on quality than the empty patches used in this experiment (e.g.  
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24 352 settled patches or evidence of females). Furthermore, an experiment in which males are  
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26 353 captured and returned to their original nest-site or returned to another male's nest-site  
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28 354 within the same patch can determine if site-fidelity is expressed at the nest-site scale.  
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30 355 Finally, a complete understanding of site-fidelity would require observations to be made  
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32 356 over multiple breeding seasons.

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37 357           In conclusion, our patch-swap experiment showed that terrestrial toadlets  
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39 358 displayed reduced breeding site-fidelity at smaller spatial scales, presumably due to  
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41 359 decreased environmental predictability. These patterns are consistent with changes in  
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43 360 the use of prior and updated information. A consideration of changes in information use  
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45 361 with spatial scale may be important when studying behaviours that take place over  
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47 362 multiple scales, such as habitat selection and foraging behaviour. Furthermore, a  
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49 363 relationship between spatial scale and the timescale of ecological processes may  
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51 364 influence how animals adapt to uncertainty beyond the use of prior and updated  
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53 365 information. For instance, the adaptive level of forgetting (Mangel 1990) may be longer  
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4 366 with regards to cues available at large spatial scales than small spatial scales.  
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6 367 Additionally, variation in information use between and within species can have  
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8 368 implications for population dynamics and community interactions (Schmidt, Dall, and  
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10 369 van Gils 2010). Thus, scaling relationships regarding information use can influence  
11  
12 370 broader ecological patterns. Future research may benefit from considering relationships  
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14 371 between environmental predictability and spatial scale as these associations are likely to  
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16 372 be critical for developing a theory of ecological information use (Schmidt, Dall, and van  
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18 373 Gils 2010).  
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4 487 **Figures**  
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8 488 Figure 1: Map of the habitat, showing the three patches (north, east, south). Arrows  
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10 489 between patches indicate where captured males were released, with a cross representing  
11  
12 490 the release site. The location of each male's original nest (grey circle) and re-settled nest  
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14 491 (black circle) are connected by a dotted line. Males that returned to their original nest  
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16 492 are represented by a black box. Males that did not re-settle are marked with a grey  
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18 493 triangle. The scale in the upper-right is marked at 1m intervals.  
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23 495 Figure 2: The mean angle of original (grey) and re-settled (black) nest-sites in relation  
24  
25 496 to the site of release displayed on a unit circle, for males captured from the southern  
26  
27 497 control, and experimental northern and eastern patches. The length of the vector  
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29 498 associated with the mean angle varies inversely with the dispersion of individual nest-  
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31 499 site angles, and is thus a measure of concentration in the direction of nest-sites from the  
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33 500 release site.  
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36 501  
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38 502 Figure 3: Estimated proportion (symbols) and 95% confidence interval (whiskers) for  
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40 503 males expressing patch, coarse and strict site-fidelity for males captured from the  
41  
42 504 southern control (circle; black; n = 12), northern (triangle; light grey; n = 11) and  
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44 505 eastern (square; dark grey; n = 17) patches.  
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49 507 Figure 4: The hypothesised relationship between spatial scale and the value of  
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51 508 information (in terms of the net benefit of responding to the information) for current  
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53 509 (solid line) and prior (dashed line) information. Site-fidelity is a response to prior  
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55 510 information. As such, superimposed over the curve for prior information are diagrams  
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511 of the two spatial scales considered in this study and the frequency of site-fidelity  
512 expressed by male toadlets.  
513

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514 **Tables**

515 Table 1: Frequency of individual male terrestrial toadlets (n = 52) that either:

516 established a calling site within the patch in which they were released, or moved to a

517 different patch.

settled in patch of release	control	patch-swap	
		N→E	E→N
yes	12	0	1
no	4	13	22

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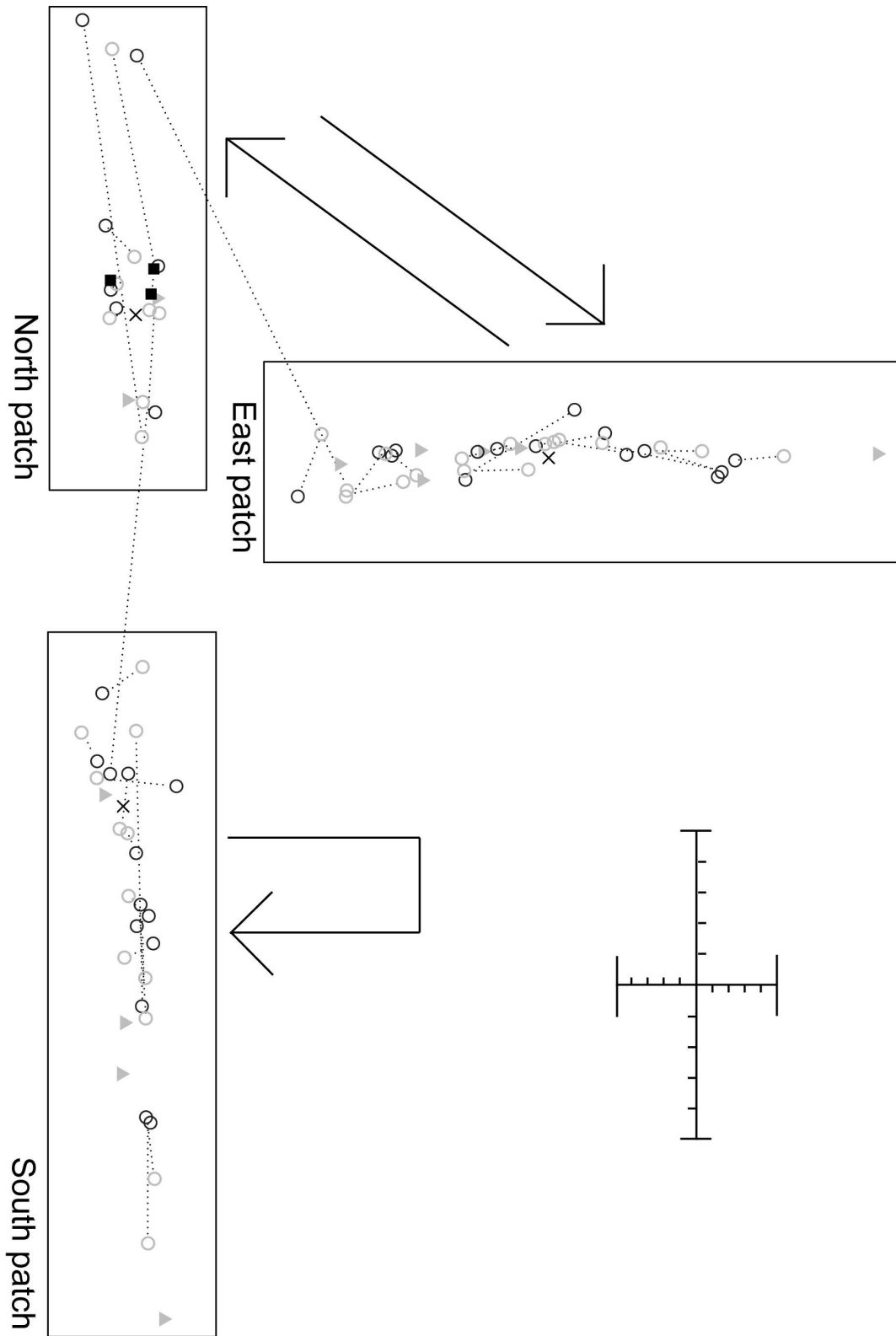
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519 Table 2: Frequency of re-settled individuals (n = 40) that established their re-settled  
 520 nest-site in a given location.  
 521

location	control	patch-swap	
		N→E	E→N
original patch	12 (0.03)	10 (0.02)	16 (0.00)
different patch	0 (0.60)	1 (0.37)	1 (0.03)
original nest-site	0 (0.90)	3 (5.73)	0 (1.28)
different nest-site	12 (0.07)	8 (0.46)	17 (0.10)
< 1m of original nest-site	2 (0.07)	5 (3.56)	1 (1.69)
> 1m of original nest-site	10 (0.02)	6 (0.89)	16 (0.42)

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 523 Chi-squared components indicated parenthetically.  
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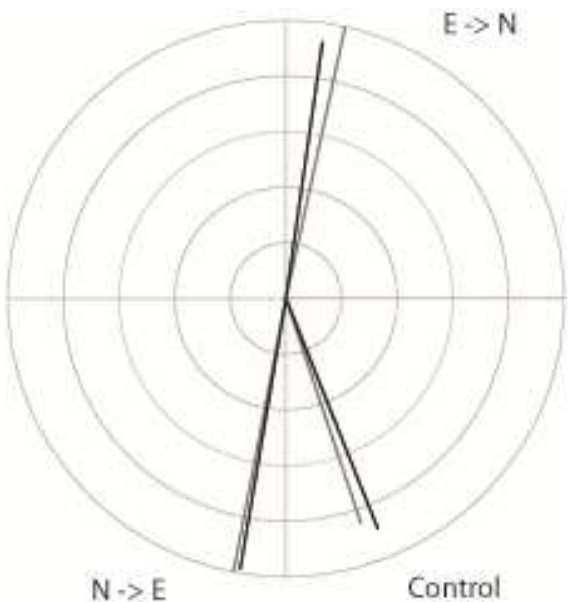


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Figure 1

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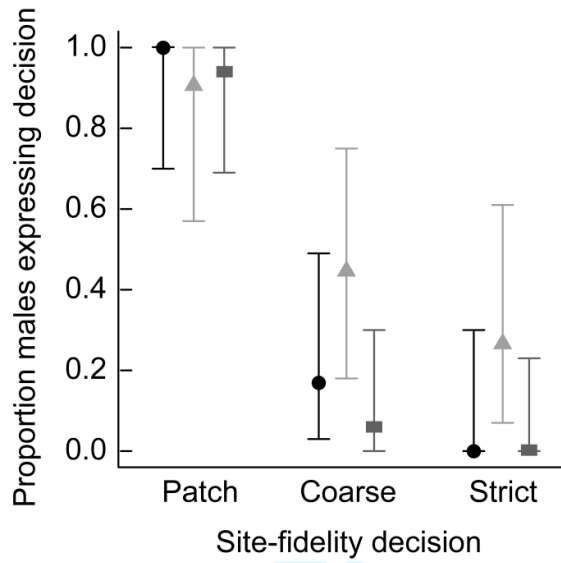
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Figure 2

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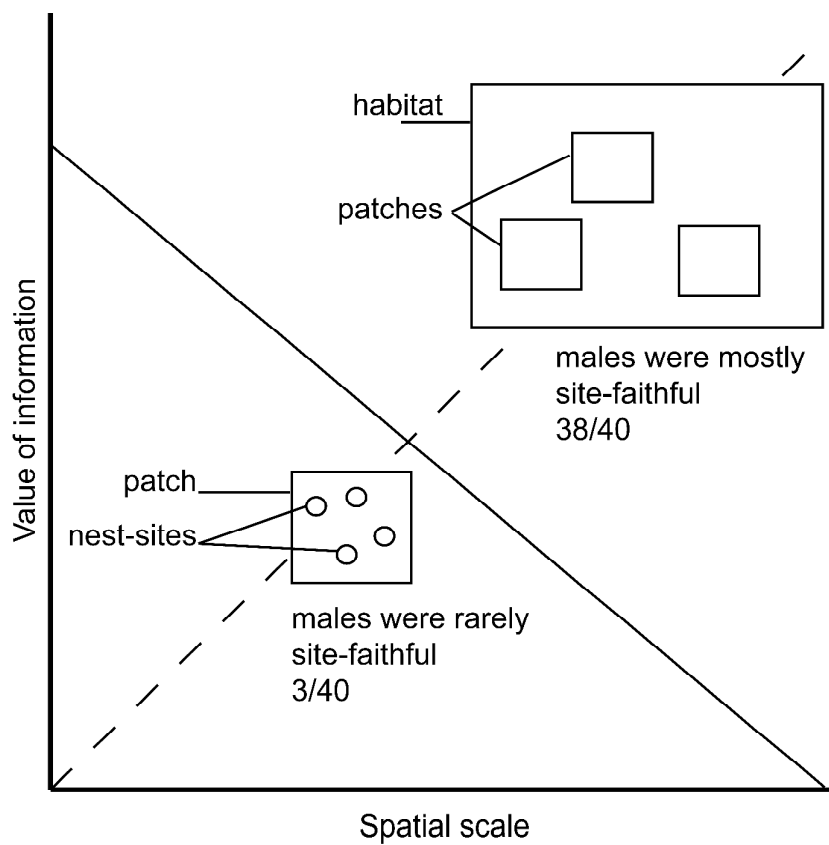


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Figure 3

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538 Figure 4

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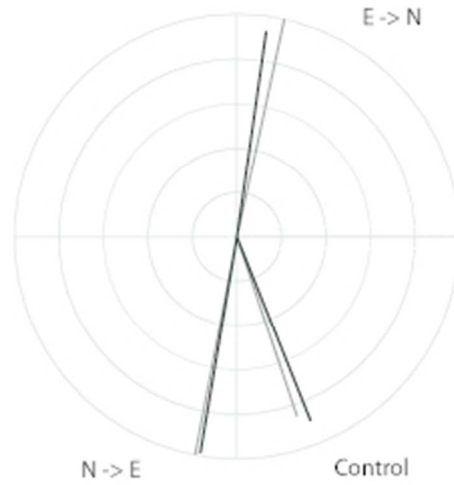
The dimensions of this image (in pixels) are too large to be converted. For this image to convert, the total number of pixels (height x width) must be less than 40,000,000 (40 megapixels).

Map of the habitat, showing the three patches (north, east, south). Arrows between patches indicate where captured males were released, with a cross representing the release site. The location of each male's original nest (grey circle) and re-settled nest (black circle) are connected by a dotted line. Males that returned to their original nest are represented by a black box. Males that did not re-settle are marked with a grey triangle. The scale in the upper-right is marked at 1m intervals.

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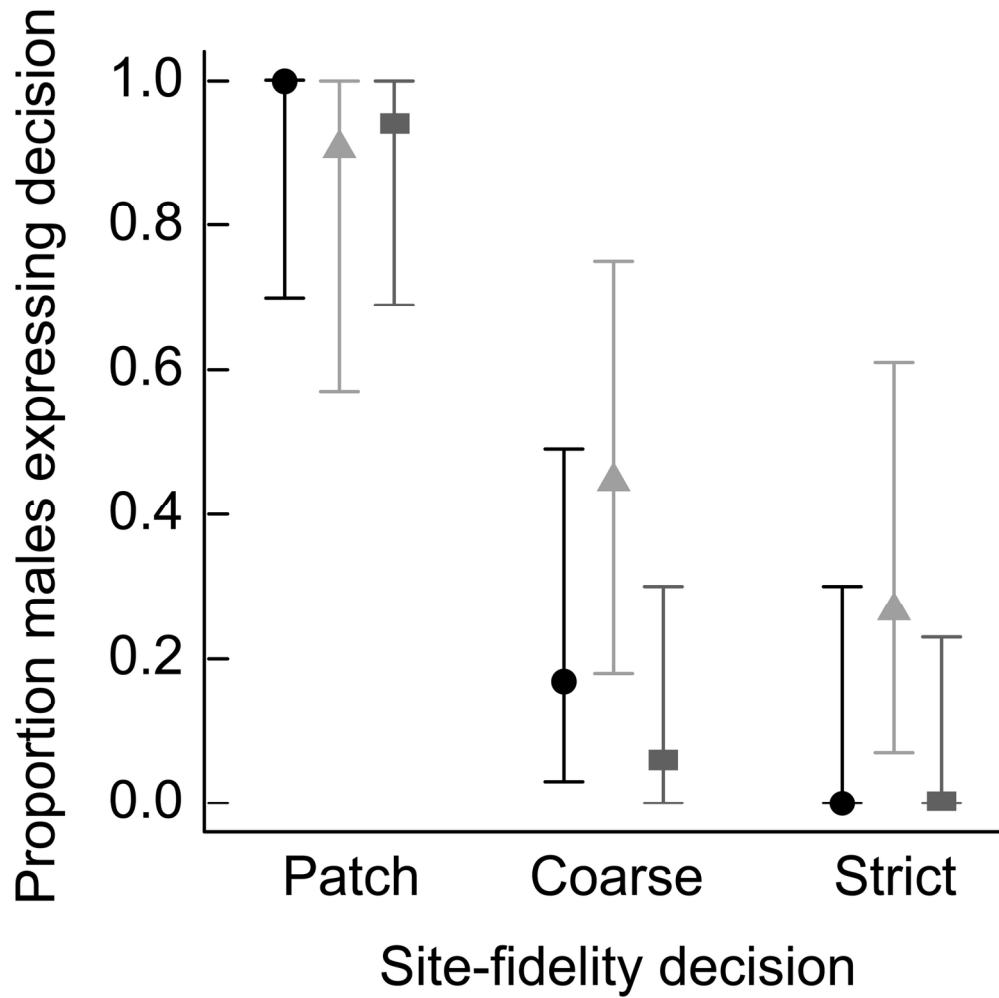
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The mean angle of original (grey) and re-settled (black) nest-sites in relation to the site of release displayed on a unit circle, for males captured from the southern control, and experimental northern and eastern patches. The length of the vector associated with the mean angle varies inversely with the dispersion of individual nest-site angles, and is thus a measure of concentration in the direction of nest-sites from the release site.

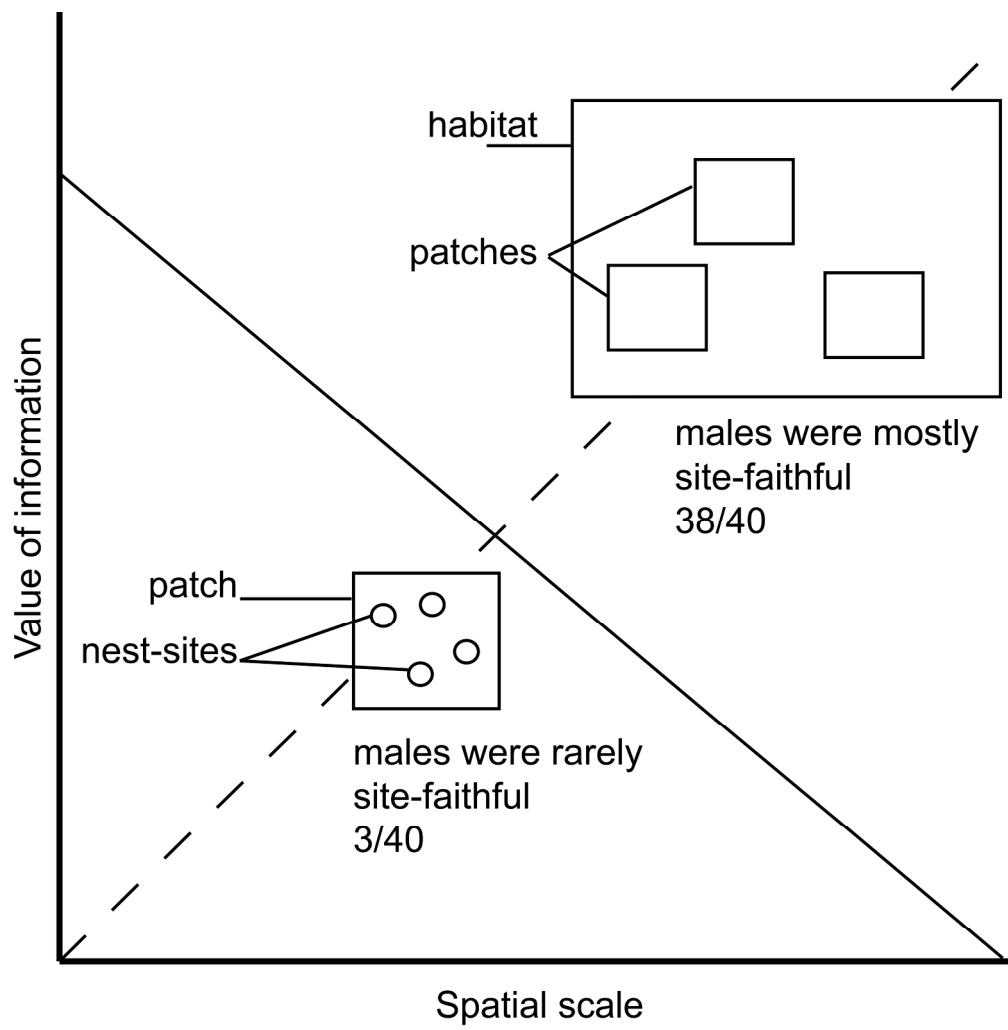
79x84mm (72 x 72 DPI)

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Estimated proportion (symbols) and 95% confidence interval (whiskers) for males expressing patch, coarse and strict site-fidelity for males captured from the southern control (circle; black;  $n = 12$ ), northern (triangle; light grey;  $n = 11$ ) and eastern (square; dark grey;  $n = 17$ ) patches.  
78x77mm (600 x 600 DPI)

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The hypothesised relationship between spatial scale and the value of information (in terms of the net benefit of responding to the information) for current (solid line) and prior (dashed line) information. Site-fidelity is a response to prior information. As such, superimposed over the curve for prior information are diagrams of the two spatial scales considered in this study and the frequency of site-fidelity expressed by male toadlets.  
117x119mm (600 x 600 DPI)

site-fidelity decision	control	patch-swap	
		N->E	E->N
strict site fidelity	0	3	0
coarse site fidelity	2	2	1
patch fidelity	10	5	15
different patch	0	1	1
frogs not recaptured	4	2	6
total frogs	16	13	23

Frequency of individual male terrestrial toadlets (n=52) that expressed strict, coarse or patch fidelity. Also included is the frequency of individuals that were not recaptured, and those that settled in a different patch to the original.

Note that this is not the frequency table that was used for analysis, but a summary.

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