



Original Article

Reduction in site fidelity with smaller spatial scale may suggest scale-dependent information use

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

Key words: anuran, breeding behavior, current and prior information, habitat selection, site fidelity, spatial and temporal scale, uncertainty.

INTRODUCTION

Oviparous animals choose the best available habitat in which to lay their eggs (Fretwell and Lucas 1970; Calsbeek and Sinervo 2002; Refsnider and Janzen 2010), with decisions depending on environmental cues that indicate an area's reproductive suitability (Krebs 1971). Furthermore, individual responses to these cues can be scale dependent. For instance, yellow-headed blackbirds (*Xanthocephalus xanthocephalus*) choose breeding sites based on assessments of food productivity at broad spatial scales, but vegetation density at finer scales (Orians and Wittenberger 1991). Because available cues can never completely predict the environment, animals often develop adaptive responses to the inherent level of uncertainty. However, it is unclear how animals adjust breeding site decisions in relation to environmental unpredictability at different spatial scales, despite this process being crucial for understanding habitat selection (Lima and Zollner 1996; Schmidt and Whelan 2010; Schmidt et al. 2010).

One way animals can reduce uncertainty in their decision making is by expressing stereotyped behavioral or physiological responses to specific environmental triggers or by using information from previous experience (Switzer 1993; Maynard Smith 2000; Wagner and Danchin 2010). In many cases, "prior information" allows an individual to exploit patterns that are predictable over time. However, continued exploitation of a pattern on the basis of prior information is vulnerable to changes in the environment. Individuals can instead benefit by updating their information through exploration of their environment although gathering "updated information" comes at a cost (Dall and Johnstone 2002; Dall et al. 2005; Dall 2010). The optimal response to the trade-off between the use of prior and updated information is partly determined by the predictability of the environment (Gould 1974; Stephens 1989; Mangel 1990; Dall and Cuthill 1997; Luttbeg and Warner 1999; Dall et al. 2005). In this respect, a decrease in predictability is expected to reduce the benefits of using prior information in relation to updated information because previous experience has less relevance to current conditions.

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Environmental predictability varies across different spatial scales, and information use is expected to vary accordingly. There are at least 2 mechanisms that could generate scale-dependent information use. First, the timescale of environmental and ecological patterns and processes is longer at larger spatial scales (Wiens 1989). Thus, prior information may provide a better basis for adaptive decisions at larger spatial scales than smaller spatial scales, as previous conditions can serve as an adequate approximation for the current state. Second, the predictive ability of prior information can decrease at smaller spatial scales because it becomes more difficult to build dynamic models (e.g., behavioral assessment and response) as the scale being considered decreases (Costanza and Maxwell 1994). This trend arises because the uncertainties involved in small-scale components can be averaged out when they are considered at larger scales. Therefore, we can hypothesize that the use of prior information will decrease, and the use of updated information will increase, at smaller spatial scales.

We can study the use of prior and updated information through the expression of site fidelity, in which an individual is faithful to a previously used breeding site over multiple breeding attempts (Burger 1982; Switzer 1997; Ringle et al. 2009). Site fidelity may allow individuals to use prior information from previous breeding attempts to exploit predictable conditions. However, continued exploitation of the same site can result in lost opportunities for finding better quality sites. Individuals can instead invest in updated information by exploring whether a superior site exists (Johnson and Gaines 1990; Switzer 1993, 1997; Doligez et al. 2003; Piper 2011). If an animal's decision to be site-faithful can be scale dependent, this would suggest that individuals adjust their decisions to the level of uncertainty at a given spatial scale. However, many studies of breeding site choice base their conclusions on patterns of distribution and abundance and are unable to separate the decision to be site-faithful from coarse ecological processes (e.g., resource limitation, competition) that could also result in the reuse of nest sites (Parrish and Edelstein-Keshet 1999; Doligez et al. 2003; Boulinier et al. 2008). Thus, manipulative field experiments that distinguish between pattern and process will enable us to determine whether site fidelity varies with spatial scale.

We performed a novel patch-swap experiment on an entire male population of the terrestrial toadlet *Pseudophryne bibronii* and measured site fidelity during resettlement. Our aim was to determine if individuals choose to be site-faithful if they are presented with the opportunity to settle in an alternative breeding site. Following resettlement, we compared the use of site fidelity at different spatial scales to determine if there was a decrease in site fidelity at smaller spatial scales.

MATERIALS AND METHODS

Study species

The brown toadlet *P. bibronii* is a Myobatrachid frog that is endemic to temperate regions of southeastern Australia (Tyler and Knight 2009). *Pseudophryne bibronii* are terrestrial breeders, with males entering breeding sites at the beginning of autumn and establishing shallow burrows in moist soil underneath leaf litter in dry creek lines and drainage pans. Males advertise their presence to females and mediate competitive interactions with acoustic signals (Pengilly 1971; Woodruff 1976; Mitchell 2001; Byrne 2008; Heap et al. 2012; Heap and Byrne 2013). Females oviposit directly into the burrow, after presumably assessing the quality of the nest site and/or the resident male (Pengilly 1971; Woodruff 1976; Byrne

and Keogh 2007, 2009). Females are extremely polyandrous and sequentially split their clutch among the nests of 2–8 males (Byrne and Keogh 2009; Byrne and Roberts 2012). Consequently, around 80% of the males in the chorus can gain mating success (Byrne and Keogh 2009). Typically, males remain with their eggs over the course of the breeding season, which continues until winter rain-falls inundate the habitat and eggs hatch into ephemeral pools. Heavy rain events that temporarily flood a nest site often lead to its abandonment, at which point males either establish a new nest in an area that has not flooded, return to their original site after waiting for the water to recede, or leave the chorus entirely. Such displacement can happen several times a season (approximately 2–4 times) before the site remains flooded and toadlets establish a new nest or leave altogether (Byrne PG, unpublished data). Males may or may not provide some level of care for their eggs (Woodruff 1977). There is also evidence for alternative reproductive strategies, including males fertilizing eggs in other nests and maintaining multiple nest sites (Mitchell 2005; Byrne and Keogh 2009). Between seasons, toadlets move into the bush surrounding the breeding site and overwinter under rocks or logs, and males are likely to experience at least 5 separate breeding seasons over their lives (Byrne PG, unpublished data).

Field protocol

The patch-swap experiment was performed on a population of toadlets in Bream Beach, Australia, between 19 April and 20 May 2010. We divided the breeding habitat into 3 distinct patches, referred to as the north, east, and south patch, based on the intersection of 2 ephemeral streams (Figure 1). We collected every calling male in each patch approximately 4–6 weeks after the commencement of a 3- to 4-month breeding season. Collections were made over 3 consecutive nights, with toadlets captured from the north patch on night 1 (19 April 2010; $n = 13$ males), the east patch on night 2 (20 April 2010; $n = 23$ males), and the south patch on night 3 (21 April 2010; $n = 16$ males). At the time of collection, nest sites were marked with an ID flag and males were placed into plastic zip-lock bags and transported to a field station (located approximately 1 km from the study site), where they were then housed in individual plastic containers (175 × 125 × 50 mm). Containers each held a moist sponge to ensure frogs remained fully hydrated and were kept in a room with windows that permitted frogs to receive natural light:dark cycles. On the day after collection, frogs were weighed using a digital balance and photographed. Because *P. bibronii* have unique individual ventral patterns, the photographic identification method (PIM; Bradfield 2004; Mitchell 2005; Kenyon et al. 2009, 2010) provided a reliable and unambiguous form of identification (identifications conducted by S.M.H. and P.B.).

We aimed to test the expression of patch-fidelity by comparing the fidelity of individuals placed in an alternative patch with those placed in their original patch. We kept each group of males at the field station for 2 nights in order to temporally dislocate them from their original site selection attempt. Males from the north and east patches were randomly chosen to be used in the patch-swap treatment, whereas males from the south patch were chosen as a control. We released north males into the east patch, east males into the north patch, and south males into the south patch on 3 successive nights (21–23 April 2010). We released males at a centralized location within their release patch (Figure 1), which was 23 ± 11 m from their original capture site. Prior to release, we arranged containers into a circle, with lids facing outward, and after 5 min of acclimation opened each lid. Exactly 29, 30, and 31 days after the

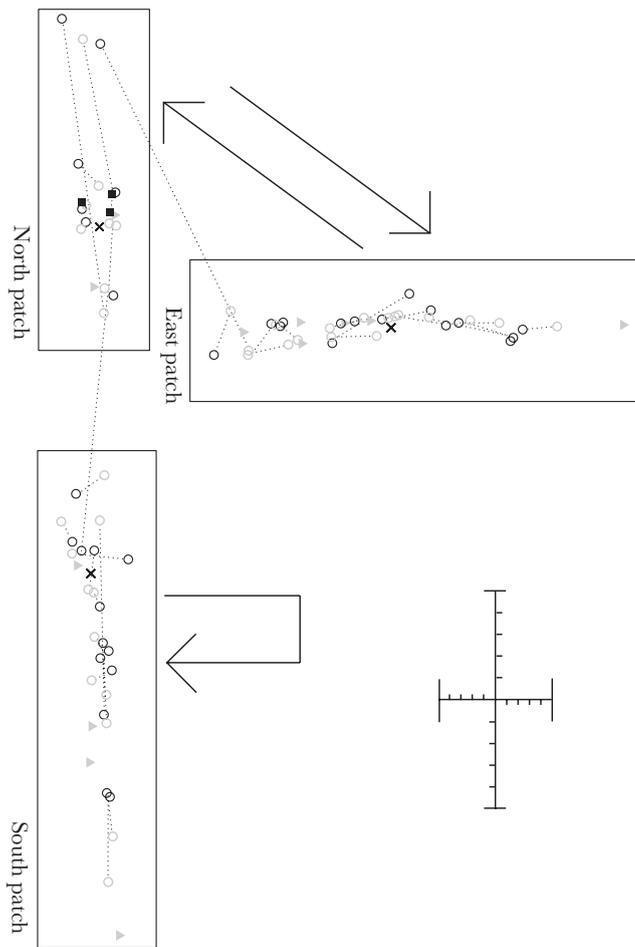


Figure 1
Map of the habitat, showing the 3 patches (north, east, and south). Arrows between patches indicate where captured males were released, with a cross representing the release site. The location of each male's original nest (gray circle) and resettled nest (black circle) is connected by a dotted line. Males that returned to their original nest are represented by a black box. Males that did not resettle are marked with a gray triangle. The scale is marked at 1-m intervals.

initial collection, we recaptured calling males from the north (17 May 2010; $n = 11$), east (18 May 2010; $n = 17$), and south (19 May 2010; $n = 12$) patches, respectively. We repeated the procedure of the original capture and used the PIM to identify the occupant of each nest site. Three new frogs were captured during this second capture period but were not included in analyses as they were not part of the experiment. We laid lines of string through the chorus to serve as the axes of a coordinate system and noted the Cartesian coordinates for original and resettled nest sites.

Statistical analyses

We considered the expression of site fidelity at the patch scale by using Fisher's tests to determine whether the proportion of males that settled in their release patch differed between treatment groups. Additionally, we explored the occurrence of site fidelity at the nest-site scale and the change in site fidelity between scales by using chi-square tests to determine the proportion of males that returned to 1) their original patch (patch-fidelity), 2) their original nest site (strict site fidelity), and 3) within 1 m of their original nest site (coarse site fidelity). We calculated the 95% confidence intervals

(CIs) at each scale and inferred whether there were any changes across scales by considering whether the CIs were overlapping.

We also tested for patch-fidelity by considering the directions and distances travelled by males following displacement in relation to their original nest sites, under the hypothesis that these values will be similar if patch-fidelity was being expressed. Specifically, we tested whether the distance each male travelled was equivalent to the distance it was displaced by using linear regression and paired t -tests, analyzing the males of each patch separately. The direction of travel was analyzed using a Hotelling test, following the guidelines of Zar (1999). This test can determine whether there is a significant difference between the azimuths of a male's original and resettled nest sites (using the release site as the reference point). As a check on our methodology, we also tested whether there was any linear relationship between an individual's change in nest-site location (i.e., the distance between its original and resettled nest site) and the distance that it was transported to the release site from its original nest site.

RESULTS

We first determined whether males expressed fidelity at the patch scale. The frequency of males that settled in the release patch depended on the treatment (Fisher's test: $P < 0.001$; Table 1). Specifically, males from the control were significantly more likely to resettle in the release patch than males from the patch-swap treatment (Fisher's test: $P < 0.001$; Table 1). This analysis included 12 males that were not recaptured, who were classified as not having resettled in the release patch. Furthermore, the distances from the release site to original and resettled nest sites were strongly correlated for the control males ($F_{1,10} = 10.63$, $r^2 = 0.47$, $P = 0.001$) and those captured from the east patch ($F_{1,15} = 92.79$, $r^2 = 0.85$, $P < 0.001$). In comparison, there was no significant correlation for males collected from the north patch ($F_{1,9} = 0.02$, $r^2 < 0.01$, $P = 0.901$). However, paired t -tests indicate that there were no significant differences between displacement and travel distances for males collected from the south ($t_{11} = 1.71$, $P = 0.116$), east ($t_{16} = 0.37$, $P = 0.719$), or north patches ($t_{10} = 0.83$, $P = 0.425$). Additionally, the direction males travelled after release was not significantly different from the direction of their original nest site (Figure 2) for males from the south ($F_{2,10} = 1.96$, $P = 0.191$), east ($F_{2,15} = 0.50$, $P = 0.618$), or north ($F_{2,9} = 0.43$, $P = 0.665$). Thus, it appears that the scale of resettlement is equivalent to the scale of displacement. The lack of correlation between the distances for the northern males may be due to the small patch and sample sizes.

We then considered changes in the expression of site fidelity between spatial scales by comparing the proportions of individuals that resettled in the same spatial location at each scale. We only considered the 40 males that resettled for this analysis, as we were interested in whether the males that decided to resettle were

Table 1
Frequency of individual male terrestrial toadlets ($n = 52$) that either established a calling site within the patch in which they were released or moved to a different patch

Settled in patch of release	Control	Patch-swap	
		N → E	E → N
Yes	12	0	1
No	4	13	22

site-faithful or not. There were no significant differences in the proportion of individuals that settled in their original patch between the 3 treatment groups (Fisher's test: $P = 0.739$) or between the control and pooled patch-swap treatment groups (Fisher's test: $P = 1.000$). Thus, we pooled males from all 3 treatment groups together to consider patch-fidelity. Overall, 38 of the 40 recaptured males (95%) were found in their original patch (Figures 1 and 3 and Table 2). We are 95% confident that the proportion of males that express patch-fidelity lies between 82% and 99% when all males are pooled (Figure 3 and Table 2).

By comparison, only 3 of the 40 males (proportion: 0.08; 95% CI: 0.02–0.21) that held a nest site decided to resettle at the same nest location (strict site fidelity; Figures 1 and 3 and Table 2). Even if the criterion for site fidelity is relaxed to 1 m surrounding the original nest site (coarse site fidelity), only 8 individuals (proportion: 0.20, 95% CI: 0.10–0.36) expressed site fidelity (Figures 1 and 3 and Table 2). There were significant differences in the proportions of males that expressed strict site fidelity (Fisher's test: $P = 0.017$)

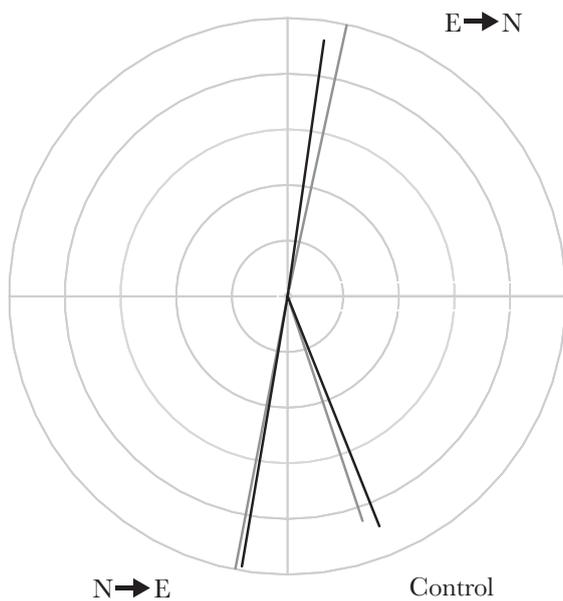


Figure 2

The mean angle of original (gray) and resettled (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.

Table 2

Frequency of resettled individuals ($n = 40$) that established their resettled nest site in a given location

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)
<1 m of original nest site	2 (0.07)	5 (3.56)	1 (1.69)
>1 m of original nest site	10 (0.02)	6 (0.89)	16 (0.42)

Chi-square components indicated parenthetically.

and coarse site fidelity (Fisher's test: $P = 0.030$) between treatment groups. Specifically, chi-square components indicate that nest-site fidelity was more common for males that were collected from, and resettled within, the northern patch (Table 2). Comparison of each patch separately indicates that site fidelity decreased between the patch and nest-site scale for males from the southern and eastern patches, but not for males in the northern patch (Figure 3).

Importantly, there was no significant correlation between an individual's change in nest-site location and the distance of the release site from its original nest site (linear regression: $F_{1,38} = 0.06$, $P = 0.803$, $r^2 < 0.01$), indicating that lack of nest-site fidelity was not because males were released too far from their original nest site to be able to return. In general, males resettled in a nest site not encountered during the original survey and capture (presumably having constructed a new burrow). However, there were a few exceptions. First, 2 pairs of individuals were found within a single nest on recapture, with one of these individuals having expressed site fidelity. No eggs were found in this nest. Second, one individual was found in a nest site that was inhabited by another during the original capture. Again, this nest did not contain any eggs. The original resident had a new nest 2.5 m away, and the new resident was found 3.2 m from its original nest. Third, 4 original nest sites appeared to have been occupied for some period during resettlement but were unoccupied at the time of recapture. This was determined by measuring the occurrence of calling activity during the resettlement period as part of a related study (Heap and Byrne 2013). Although the identity of the callers could not be determined, the original occupants of these nests were found to be 1.2, 1.8, and 9.3 m away from their original site by the end of the study. The fourth male was not recaptured. Finally, there were 3 males that were recaptured in their original nest site. There were nests before and after capture that contained eggs, and we have analyzed the presence of eggs in another study (Heap and Byrne 2013). This analysis found no correlation between nest-site location and egg presence or any correlation between breeding success before and after resettlement.

DISCUSSION

Males showed a strong preference for their original patch over an alternative patch. Furthermore, males moved in the direction of their original nest sites following release and travelled an equivalent distance to that of displacement to reach a new nest site. Together, these results imply that males display site fidelity at the patch scale. In contrast, relatively few males returned to within 1 m of their original nest site. Additionally, males appear to be aware of the location of their original nest site, judging by the direction and

distance of movement after release, yet they do not tend to resettle in the same location. Thus, these results suggest that the expression of site fidelity for choosing breeding sites may be scale dependent (Figure 4). That is, returning to familiar patches may improve reproductive success, but fidelity to nest sites may provide little additional benefit. However, changes in the expression of site fidelity with spatial scale appeared to depend on the patch that males were captured from because we cannot be confident that the males that resettled in the north patch showed an equivalent decrease in site fidelity at smaller spatial scales compared with the east and south patches.

Breeding habitat selection involves responding to information that predicts reproductive success at multiple spatial scales. Previous studies have shown that the cues that allow reliable assessment of site quality can vary with spatial scale (Krebs 1971; Orians and Wittenberger 1991). Our results suggest that the general manner in which information is used can also vary between spatial scales. In particular, if we consider site fidelity to indicate the use of prior information, and occupation of new sites to indicate the use of updated information (Johnson and Gaines 1990; Switzer 1993, 1997; Doligez et al. 2003; Piper 2011), then our results suggest that the nature of information used to choose nest sites varies with spatial scale. Specifically, male *P. bibronii* may benefit from using prior information when choosing patches but benefit from responding to updated information when choosing nest sites within the patch (Figure 4).

These results conform to theory that predicts the value of prior information (in terms of the net benefit that responding to the information would provide) to increase as spatial scale increases, whereas the value of updated information to increase as spatial scale decreases (Wiens 1989; Costanza and Maxwell 1994; Figure 4). In the case of toadlets, flooding patterns are an important factor in determining reproductive success (Woodruff 1976; Bradford and Seymour 1988; Geiser and Seymour 1989; Byrne and Keogh 2009), and variation in flooding patterns at different spatial scales may partly explain why the value of prior information is greater at

the patch scale than the nest-site scale. Patches in this system occur around ephemeral bodies of water such as streams and ponds. The climatic and topographical patterns that allow these bodies to exist may be predictable across years, such that an individual can be relatively certain that a similar body will exist in the current season based on its existence in a previous season. However, whether or not a given nest-site floods to an appropriate level is likely to be more variable (less predictable) between years than the presence of a suitable body of water in the patch due to fine scale differences in drainage patterns over space and time. Thus, prior information may be reliable at the patch scale but not at the nest-site scale. This notion could be tested by measuring reproductive success at nest sites over multiple years, with the prediction that variation in the average patch reproductive success across years is less than variation at a given nest site. Additionally, the hydrodynamic properties of the substrate can be measured and compared between years.

The lack of site fidelity at the nest-site scale suggests that males must gather information on their current surroundings to find a suitable nest site within the patch. In this regard, males appear to partly respond to information on the local spatial arrangement of other males more than physical properties such as soil moisture when establishing a nest site (Heap and Byrne 2013). However, such physical properties may influence male calling behavior and, in turn, spatial arrangements. For example, in a manipulative field experiment in which nest sites were artificially wetted, Mitchell (2001) demonstrated that male *P. bibronii* call more from wetter nests presumably because there is less risk of desiccation.

The response to other males may largely be driven by the need to alleviate competition over acoustic space, as males tend to abandon sites in denser areas (Heap and Byrne 2013). Although there is no apparent correlation between density and breeding success in *P. bibronii* at these sites during the observed breeding season (Heap and Byrne 2013), the evidence that competition for space is critical

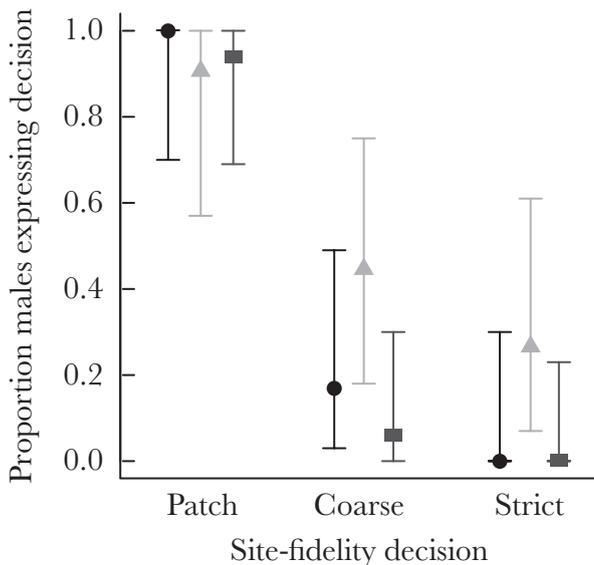


Figure 3 Estimated proportion (symbols) and 95% CI (whiskers) for males expressing patch, coarse, and strict site fidelity for males captured from the southern control (circle; black; $n = 12$), northern (triangle; light gray; $n = 11$), and eastern (square; dark gray; $n = 17$) patches.

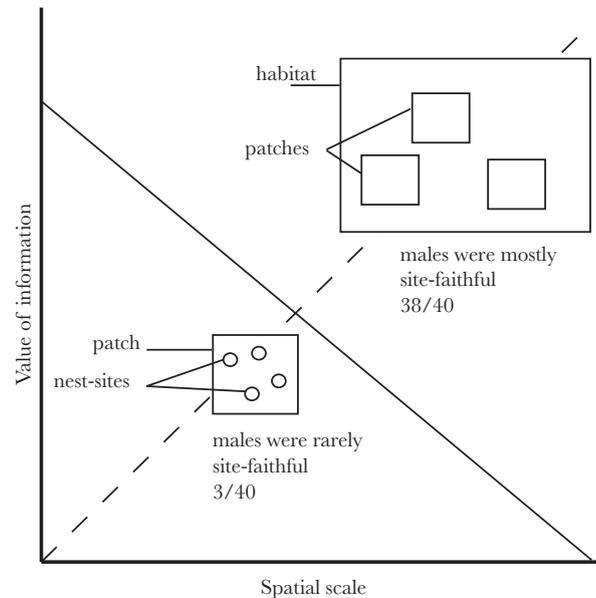


Figure 4 The hypothesized relationship between spatial scale and the value of information (in terms of the net benefit of responding to the information) for current (solid line) and prior (dashed line) information. Site fidelity is a response to prior information. As such, superimposed over the curve for prior information are diagrams of the 2 spatial scales considered in this study and the frequency of site fidelity expressed by male toadlets.

in finding mates across frog species is overwhelming (Wells 2007). Competition aside, the previously reported pattern that males have tendencies to avoid isolated and peripheral areas provides an indicator that uncertainty as to nest-site quality is high within patches (Heap and Byrne 2013). Specifically, this pattern of conspecific attraction suggests that males copy each other's breeding site decisions, and individuals are expected to only prefer using social cues over nonsocial cues when either 1) the costs of acquiring personal information are too great (i.e., trial and error in reproductive success, coupled with the risk of nest-site failure) or 2) nonsocial cues are unreliable or uninformative (Dewar 2004; Coolen et al. 2005; Kendal et al. 2005). That is, if uncertainty was not an issue within patches, then males should perhaps prefer acquiring personal information over using social cues. In any case, the information that males use to choose a nest site remains an open question. That being said, any evidence that the use of social cues within patches is driven by uninformative nonsocial cues (rather than the costs of acquiring personal information) would strongly support the hypothesis that there is scale-dependent uncertainty.

The higher variance in behavior of males in the northern patch, who showed a greater average degree of site fidelity at the nest-site scale than males from other patches, is consistent with this overall explanation. Males in the northern patch mostly settled on the edge of a small pond that floods to the same extent almost every year (Byrne PG, personal observation). By contrast, males in the southern and eastern patches settled along the banks of small ephemeral streams that are less consistent in their flooding patterns. Thus, prior information on nest-site quality may be more relevant in the northern patch than the southern and eastern patches, and hence, site fidelity more common at the nest-site scale. However, it is important to note that there was greater variance in site fidelity for northern males, and this could be due to either the characteristics of the patch or the smaller sample size.

There is, however, an alternative explanation to a spatiotemporal scaling relationship underlying changes in behavior at different spatial scales. Males may have actually gathered information about novel patches and decided that they were unsuitable breeding sites. Males may also have avoided returning to their original nest site due to experimental handling. Thus, our explanation requires support from experiments that demonstrate prior information is consistently used over current information to select patches and from a full qualification of the degree to which males show site fidelity at the nest-site scale. These gaps can be addressed by conducting an experiment that tests whether males prefer familiar patches over alternative patches that present more favorable information on quality than the empty patches used in this experiment (e.g., settled patches or evidence of females). Furthermore, an experiment in which males are captured and returned to their original nest site or returned to another male's nest site within the same patch can determine if site fidelity is expressed at the nest-site scale. Finally, a complete understanding of site fidelity would require observations to be made over multiple breeding seasons.

In conclusion, our patch-swap experiment showed that terrestrial toadlets displayed reduced breeding site fidelity at smaller spatial scales, presumably due to decreased environmental predictability. These patterns are consistent with changes in the use of prior and updated information. A consideration of changes in information use with spatial scale may be important when studying behaviors that take place over multiple scales, such as habitat selection and foraging behavior. Furthermore, a relationship between spatial scale and the timescale of ecological processes may influence how

animals adapt to uncertainty beyond the use of prior and updated information. For instance, the adaptive level of forgetting (Mangel 1990) may be longer with regard to cues available at large spatial scales than small spatial scales. Additionally, variation in information use between and within species can have implications for population dynamics and community interactions (Schmidt et al. 2010). Thus, scaling relationships regarding information use can influence broader ecological patterns. Future research may benefit from considering relationships between environmental predictability and spatial scale as these associations are likely to be critical for developing a theory of ecological information use (Schmidt et al. 2010).

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