Microhabitat selection in an assemblage of crickets (Orthoptera: Ensifera) of a tropical evergreen forest in Southern India

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Abstract. 1. Habitat selection is a universal aspect of animal ecology that has important fitness consequences and may drive patterns of spatial organisation in ecological communities.

2. Measurements of habitat selection have mostly been carried out on single species and at the landscape level. Quantitative studies examining microhabitat selection at the community level are scarce, especially in insects.

3. In this study, microhabitat selection in a natural assemblage of cricket species was examined for the first time using resource selection functions (RSF), an approach more commonly applied in studies of macrohabitat selection.

4. The availability and differential use of six microhabitats by 13 species of crickets inhabiting a tropical evergreen forest in southern India was examined. The six available microhabitats included leaf litter-covered ground, tree trunks, dead logs, brambles, understorey and canopy foliage. The area offered by the six microhabitats was estimated using standard methods of forest structure measurement. Of the six microhabitats, the understorey and canopy accounted for approximately 70% of the total available area.

5. The use of different microhabitats by the 13 species was investigated using acoustic sampling of crickets to locate calling individuals. Using RSF, it was found that of 13 cricket species examined, 10 showed 100% selection for a specific microhabitat. Of these, two species showed fairly high selection for brambles and dead logs, which were rare microhabitats, highlighting the importance of preserving all components of forest structure.

Key words. Crickets, India, microhabitat selection, resource selection function, tropical evergreen forest, Western Ghats.

Introduction

Animals distribute in space for all their life processes. This distribution may be undirected or in response to opposing selective forces (such as predator presence, competitor or mate abundance), or a function of the patchiness of a resource (Rosenzweig, 1991). If the distribution of animals or use of a resource is merely proportional to the availability of the resource, then such a distribution or usage is not selective. If the use of a resource is disproportionate to its availability, then there is selection (Manly et al., 1993). Habitat selection has fitness consequences (Whitham, 1978; Townsend, 1989) and has been proposed as one of the drivers of distribution of species, resulting in patterns of biodiversity at different spatial and temporal scales (Morris, 2003). In acoustically communicating animals, microhabitat selection could also be driven by optimal calling site selection to derive sound transmission benefits for efficient communication.

There is a vast body of literature, both theoretical and empirical, which examines habitat selection (Rosenzweig, 1981; Cody, 1985). Studies have been carried out at different spatial scales and at different levels of community structure (within- and between-species). Studies on vertebrates deal with...
large-scale, often landscape level examination of selection that fall under the category of macrohabitat selection (McLoughlin et al., 2002, 2004; Liu et al., 2005; Morales et al., 2008). Such studies require mapping vegetation cover at the landscape level, placing the areas sampled under different categories of vegetation cover/type and subsequently quantifying use in each category. Compton et al. (2002) suggest that such an approach cannot be applied for animals with low mobility since the entire range of habitats may not even be available. It is necessary to measure use and availability at a scale that is biologically relevant to the study system. In the case of insects, investigation of both use and availability of resources needs to be carried out at a finer scale. Only a few studies have quantitatively demonstrated selection for microhabitats in insects (Whitham, 1978; Joern, 1982).

Irrespective of the spatial scale of the investigation, habitat selection studies are dominated by investigation of a single species (Petit & Petit, 1996; Hjermann, 2000; Ciarniello et al., 2007) or closely related competing species (Larson, 1980; Howard & Harrison, 1984; Schroder, 1987). Studies that examine habitat selection at the community level are few (Hallett, 1982; Joern, 1982; Martin, 1998). In this study, microhabitat selection has been examined for the first time in an assemblage of cricket species in a tropical evergreen forest using resource selection functions (RSF) based on quantitative estimates of microhabitat availability and use.

Crickets belong to the order Orthoptera (sub-order Ensifera) and use acoustic signals to attract mates over long distances. They are nocturnal and form an integral part of many species assemblages and are a dominant component of the dusk chorus. Stationary males call to attract conspecific females using species-specific calls. The tropical forests of Kudremukh National Park in Southern India have a species-rich assemblage of crickets (Diwakar & Balakrishnan, 2007a). Since they occupy the same habitat and their peak calling times overlap (Diwakar & Balakrishnan, 2007a), they are likely to compete for the same habitat and their peak calling times overlap (Diwakar & Balakrishnan, 2007a,b). Studies examining calling sites have been carried out in a patch of evergreen forest on either side of a 1-km transect (study area 1000 m × 60 m) in an area where all the study species were known to occur (Diwakar & Balakrishnan, 2007a; Diwakar et al., 2007).

Proportional use. Microhabitat use was measured by tracking calling individuals by ear and noting the microhabitat from which they were calling, once they were visually located. Sampling was carried out during the peak calling time (18.00–21.00 hours) along a 1-km transect. All calling individuals within 30 m on either side of the transect were located, and the height of the callers and the microhabitat from which they were calling was noted. Sampling was carried out in different patches of forest on different nights to minimise pseudoreplication. The proportion of use of each of the six microhabitats by each of the 13 species was calculated as follows:

\[
\text{Proportional use of microhabitat (h) by species (s)} = \frac{\text{number of individuals of species (s) found in microhabitat (h)}}{\text{total number of individuals of species (s) sampled}}
\]

Proportional availability. To characterise microhabitat and vegetation structure, six test quadrats (20 × 30 m) were randomly selected inside the study area such that no two quadrats were < 100 m apart. Six microhabitats were identified in each, namely, ground (covered by leaf litter), brambles (dense clump of dead twigs and dry leaves), dead logs, tree trunks, understory and canopy. Subsequently, detailed measurements were carried out to estimate the total sitting space offered by each microhabitat in each of the six test quadrats. In each test quadrat, every tree was marked and the girth at breast height (GBH) was measured. For the trees with GBH > 20 cm, the basal area was

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measured and the sum of the basal areas when subtracted from the total quadrat area gave the ground area covered by leaf litter. The height of first branching was measured for each tree (GBH > 20 cm). The GBH multiplied with the height gave the curved surface area of the trunks (assuming a cylindrical shape). The structure of dead logs was approximated to that of a solid cylinder and the total surface area was calculated using standard geometric formulae. To calculate total surface area offered by brambles, they were approximated to the shape of a cuboid and the length, breadth and height of the brambles were measured using a graduated stick.

To estimate the total sitting space in the understorey and canopy, the total leaf surface area needs to be measured. This may be obtained by multiplying foliage density with the volume of forest sampled. To this end, each quadrat was divided into 24 (5 × 5 m) sub-quadrats using rope grids. In each of the 24 sub-quadrats, a 1 × 1 m sub-plot was selected randomly. Sampling for understorey and canopy was carried out at the sub-plot level and the values were later extrapolated to the rest of the quadrat area.

For both understorey and canopy, foliage density was calculated using the chequered board technique described by Macarthur and Macarthur (1961), modified suitably (Jain et al., 2010) for greater reliability and efficiency. The foliage density was calculated using the proportion of sky/background that is not obscured by vegetation. The formula used is as follows:

\[ k = \ln(1/X)/D, \]

where \( k \) is the foliage density, \( X \) is the proportion of background unobscured and \( D \) is the height class interval.

In each of the 1 × 1 m sub-plots, measurement of foliage density was carried out in four different layers for the understorey: 0–1 m (lower understorey), 1–5 m (mid-understorey) and 5–8 m (upper understorey). We measured the height of the upper and lower bound of the layer being sampled to calculate D. Photographs of vegetation were taken using a Nikon digital camera (D40, AF-S Nikkor 18–55 mm lens; AF-S Nikkor 55–200 mm; Nikon Corporation, Japan), with a white board (1 m × 1 m) placed parallel to the ground acting as the background. For the upper understorey (5–8 m), for logistical reasons (raising the background board to 8 m), photographs were taken in only 12 sub-plots as opposed to 24 in the other two layers. For estimation of foliage density in the canopy, the height of the lower bound was measured manually and the upper bound of the canopy was estimated visually. We tried several measuring instruments to measure the height of the top of the canopy but the dense canopy precluded the use of a clinometer. Range finders including those using lasers gave large errors (in calibration trials) because it was difficult to focus them at the top of the canopy in the dense clutter of leaves. For canopy photographs, the frame area (area captured in one frame of the photograph, when taken from a certain distance) was previously calibrated on the ground for different distances (simulating different heights of the top of the canopy). Hence, for each canopy shot, we had a calibrated value of how much area of the canopy was covered in each frame. Each frame for the canopy covered approximately an area of 50 m² and so 12 frames rather than 24 were shot in each quadrat. The photographs were analysed using Image J (version 1.32j; Wayne Rasband, National Institutes of Health, Bethesda, MS, USA) and the foliage density in each plot was calculated as in the case of the understorey.

For each test quadrat, we obtained foliage density measurements for four layers (canopy and three layers of understorey). There were a total of 72 measurements of foliage density in each of the six test quadrats (24 each for layers 0–1 m and 1–5 m and 12 each for the 5–8 m layer and the canopy). Each foliage density measurement made at the sub-plot level was multiplied by the corresponding D value (upper bound of layer − lower bound) to get at the one-sided leaf surface area. The values were summed and then scaled up to the total area of the test quadrat. Total available area offered by the understorey and canopy was thus obtained for all six test quadrats. The average surface area contributed by each of the six microhabitats was calculated and summed to give the total available surface area in each quadrat. The proportional availability of the six microhabitats was calculated as follows:

Proportional availability of microhabitat \( (h) \)

\[ = \frac{\text{average surface area contributed by microhabitat } (h)}{\text{total area available (summed across all microhabitats)}} \]

**Resource selection functions**

The set of values of proportional availability of six microhabitats and their proportional use by 13 species of crickets was used to calculate the RSF as described by Mclooughlin et al. (2002). The first step involves calculation of the selection function \( \left( w_{h,s} \right) \) of a microhabitat \( (h) \) by a species \( (s) \). It gives the value of selection of a particular microhabitat for a species when we control for unequal availability:

\[ w_{h,s} = \frac{\text{proportion used}_h/\text{proportion available}_h} \]

The next step serves as a standardisation and gives a value on the scale of 0–1 such that the RSF value obtained for all species for different microhabitats can be compared with each other. It gives a probability value that indicates the likelihood that an individual of species \( s \) will choose microhabitat \( h \) over all other microhabitats that are equally available to it (Mclooughlin et al., 2002). The standardisation is carried out as follows:

\[ b_{h,s} = \frac{w_{h,s}}{\Sigma_{h=1\,to\,H} w_{h,s}} \]

for \( s = 1 \) to \( S \), where \( S \) is the total number of species and \( H \) is the total number of microhabitats.

**Results**

**Proportional availability of microhabitats**

The proportion of sitting space offered by each of the six microhabitats is shown in Fig. 1. The ground contributed about 15% of total sitting space. On average, 93% of the quadrat ground area was available as leaf litter-covered ground and only 7% of it was blocked by the bases of trees. A total of 230 trees were recorded across the six quadrats. The average GBH of trees was 0.84 m² ± 0.046 SE and the average height of first
branching was 11.27 m ± 0.354 SE. Dead logs and brambles were rare in occurrence across all six test quadrats sampled. On average, dead logs and brambles offered very little sitting space in a quadrat (1% each), whereas tree trunks accounted for 12% of available microhabitat. The canopy and understorey together accounted for approximately 70% of the total available area (Table 1; Fig. 1). The average surface area measured in the understorey across six test quadrats was highest in the mid-understorey (1–5 m; 593.92 m² ± 75.60 SE, \(n = 144\)) and least in the lower understorey (0–1 m; 165.53 m² ± 44.70 SE, \(n = 144\)). The top most layer of the understorey (5–8 m; although just 1 m less in depth than the mid-understorey) had a much lower average leaf surface area (303.74 m² ± 96.10 SE, \(n = 144\)) than the mid-understorey.

**Proportional use of microhabitats and resource selection**

Of the 13 species sampled, six belonged to the superfamily Grylloidea, six to the superfamily Tettigonioidae and one to the superfamily Gryllacridoidea (Diwakar & Balakrishnan, 2007a). Acoustic sampling revealed a disproportionate use of microhabitats by the 13 species of crickets (Fig. 2). The understorey harboured the highest number of species (seven) followed by the ground (four). Both canopy and dead logs were used by two species each, whereas tree trunks and brambles were occupied by one species each (Fig. 2). Although most species were consistently found calling in only a particular microhabitat, in a few species, individuals were found calling in more than one microhabitat type.

To examine patterns of differential use of calling sites across the six microhabitats, RSF values were examined. The RSF values revealed 100% selection for particular microhabitats in 10 of the 13 species (Fig. 2). Of the six gryllids, three species (Callogryllus sp., Scleropterus sp. and Gryllitara sp.) showed strong selection for the ground as a calling site. One gryllid species, Landrew sp., showed 100% selection for dead logs, a rare microhabitat. The remaining two gryllids (Phaloria sp. and Whiner) showed 100% selection for the understorey (Fig. 2). Of the six tettigoniids, three (Brochopeplus sp., Pirmesa rosetta and 15 kHz) were found to have 100% selection for the understorey, whereas Mecopoda 'Two part' moved between three microhabitats. The remaining two tettigoniids (Onomarchus sp. and Phyllophorus sp.) called exclusively from the canopy. The gryllacridoid (weta) Gryllacropsis sp. called solely from tree trunks (mean GBH 1.12 m ± 0.46 SD). Overall, of the 13 species sampled, only three species (Callogryllus sp., Mecopoda 'Two part' and Gryllitara sp.) moved between microhabitats (Fig. 2). Although Mecopoda 'Two part' used three different microhabitats (ground, brambles and understorey), it showed fairly high selection for brambles.

**Effect of estimation errors**

Accurate quantification of availability and use is important in studies on selection. Owing to the complexity and structural heterogeneity of forest architecture, the quantification of microhabitat availability provides a challenge. Estimation of foliage density in particular is prone to error, with most indirect methods underestimating foliage density by 20–40% (Chanson et al., 1991; Dufrene & Breda, 1995). A previous study (Jain et al., 2010) compared different methods of estimating foliage density in this forest and found that the photographic method used in this study can result in 20–40% underestimation of foliage density. This would directly affect the estimates of total surface area of the understorey and canopy. Hence, as an exercise, the foliage density values and total surface area estimates of the understorey and canopy were corrected for the maximum possible underestimation by the method. The corrected proportions (canopy 0.44, understory 0.32, ground 0.12, tree trunk 0.1, bramble and dead log 0.01 each) were not far from the uncorrected values used for the analyses and hence would not significantly affect our results. Thus, for the purpose of this study, the original values were retained. Visual estimation of canopy height could result in estimation errors of the order of 25–30%, corresponding to under- or overestimation of foliage density. Our calculations revealed, however, that these estimation errors had only a small effect on the value of the resource selection function, in large part because of the dominance of foliage in proportion to all other microhabitats.

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**Table 1. Availability of the six different microhabitats (in m³).**

<table>
<thead>
<tr>
<th>Quadrat</th>
<th>Ground</th>
<th>Brambles</th>
<th>Dead logs</th>
<th>Tree trunks</th>
<th>Understorey</th>
<th>Canopy</th>
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<tr>
<td>Q1</td>
<td>549.26</td>
<td>39.83</td>
<td>45.01</td>
<td>459.61</td>
<td>895.25</td>
<td>1611.45</td>
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<tr>
<td>Q2</td>
<td>569.02</td>
<td>38.28</td>
<td>65.40</td>
<td>657.13</td>
<td>863.68</td>
<td>1809.05</td>
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<tr>
<td>Q3</td>
<td>559.86</td>
<td>44.02</td>
<td>50.31</td>
<td>392.35</td>
<td>1242.20</td>
<td>1379.93</td>
</tr>
<tr>
<td>Q4</td>
<td>559.07</td>
<td>79.43</td>
<td>39.54</td>
<td>302.81</td>
<td>1163.25</td>
<td>1358.58</td>
</tr>
<tr>
<td>Q5</td>
<td>560.48</td>
<td>12.66</td>
<td>24.76</td>
<td>389.27</td>
<td>1110.25</td>
<td>1164.98</td>
</tr>
<tr>
<td>Q6</td>
<td>549.51</td>
<td>6.77</td>
<td>25.98</td>
<td>596.95</td>
<td>1104.57</td>
<td>1419.45</td>
</tr>
<tr>
<td>Mean</td>
<td>557.87</td>
<td>36.83</td>
<td>41.84</td>
<td>466.35</td>
<td>1063.19</td>
<td>1457.24</td>
</tr>
<tr>
<td>SE</td>
<td>3.06</td>
<td>10.59</td>
<td>6.29</td>
<td>55.27</td>
<td>61.64</td>
<td>91.31</td>
</tr>
</tbody>
</table>

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Discussion

Quantifying microhabitat selection

We have provided for the first time a quantitative demonstration of microhabitat selection in a natural assemblage of cricket species, using resource selection functions based on proportional use and availability. There are several ways to quantify selection (Manly et al., 1993) and many studies on vertebrates have attempted to do so (McLoughlin et al., 2002; Ciarniello et al., 2007; Morales et al., 2008). In the case of insects, however, studies that demonstrate microhabitat selection in a quantitative manner are few. Moreover, most studies on habitat selection in invertebrates have focused on oviposition site preference (Rausher, 1979; Foglemann et al., 1981) or photo preference (Kawanishi & Watanabe, 1978). Calver and Bradley (1991) examined background colour matching in grasshoppers and found a significant sex-morph association that was attributed to differences in microhabitat selection by the two sexes. Frey and Leong (1993) studied monarch butterflies to examine if microhabitat selection has any effect on their sex ratio, but they examined only the roosting patterns of these butterflies and selection per se was not studied. In a classic study on aphids by Whitham (1978), detailed measurements of availability and use of leaves of different size classes were made and the fitness effect of colonisation of a particular leaf size was clearly demonstrated. It was clear that the aphids select large leaves disproportionately more than the actual availability of such large leaves. This study provided a rigorous examination of microhabitat use versus availability. Joern (1982) carried out a detailed examination of vegetation structure and microhabitat selection in an assemblage of grasshoppers and found a non-random occupancy of microhabitats. In this study, the proportional use of a microhabitat type was measured but the selection value was not calculated, which makes it difficult to make comparisons across species. In the case of crickets, Diwakar and Balakrishnan (2007b) examined the vertical stratification of species in terms of their calling heights in the Kudremukh cricket assemblage. Selection for calling sites, however, was not examined. This study is the first description of microhabitat selection in an insect assemblage where rigorous quantification of proportional use versus availability of microhabitats has been attempted.

Potential factors driving microhabitat selection

The forest harboured different microhabitats ranging from the abundant canopy and understory (together contributing approximately 70% of available area) to the tree trunks and leaf litter-covered ground (accounting for approximately 15% of total area) and the rare dead logs and brambles (each providing only 1% of the total area).

Using RSF, we found 100% selection for specific microhabitats in 10 of 13 cricket species. Individuals of the remaining three cricket species showed movement between habitats, nonetheless selection for microhabitats was fairly strong in these species as well. Landreva sp. is interesting because it shows 100% selection for dead logs, which is a rare microhabitat (contributing only 1% of available area) in these forests. Why the animal chooses to call from such a rare microhabitat is worth exploring. The animal hides under the bark of the log while calling. One possible explanation, apart from predator avoidance is that it uses the empty space between the bark and the log to amplify its calls. The unidentified gryllid species Whiner (subfamily Podoscritinae) calls from the understory from about 4-5 m height. In these forests, the foliage density decreases as a function of height.

Fig. 2. Proportional use of microhabitats by 13 cricket species. Resource selection functions (RSF): Callogryllus sp. (ground: 0.643; dead logs: 0.357); Gryllitara sp. (ground: 0.763; understory: 0.237); Mecopoda ‘Two Part’ (ground: 0.006; brambles: 0.985; understory: 0.009). RSF values for all other species = 1 for the microhabitat they specialised in. Numbers above bars indicate sample sizes.
in the understorey and, around this height, vegetation is quite sparse. Here again, there could be a possible benefit in terms of maximising broadcast area of the calling individual. Calling site selection for transmission benefits has been tested in several taxa, including birds (Mathevon et al., 1996; Blumenrath & Dabelsteen, 2004), frogs (Kime et al., 2000) and insects (Sueur & Aubin, 2003). It would be interesting to examine if the cricket species in this assemblage select calling sites to derive sound transmission benefits.

Brambles were utilised by only 1 of the 13 cricket species, *Mecopoda ‘Two part’*. The RSF value for this rare habitat was 0.985 in case of *Mecopoda ‘Two part’*. Brambles are clutters of dead twigs and dried leaves, sometimes containing thorny branches. *Mecopoda ‘Two part’* is a broadband caller and the frequency spectrum of its call spans up to 80 kHz (Nityananda & Balakrishnan, 2006). This high call bandwidth makes it susceptible to predation by gleaning insectivorous bats (H. Raghuram & R. Balakrishnan, pers. obs.). Calling from cluttered sites such as brambles could be a possible mechanism of predator avoidance.

Overall, there could be several factors driving differential microhabitat utilisation in this cricket assemblage, including predator avoidance and selection of calling sites for maximum call transmission. The possibility of such patterns of selection being driven by phylogenetic constraints is unlikely because members of the same family occupied different microhabitat types. This was true for both Gryllidae and Tettigoniidae.

**Use of RSF in habitat and community ecology**

This article demonstrates how RSF can be used to quantify community-level selection of microhabitat in addition to its traditional application in examining species-level habitat selection. This work also highlights the implications of using RSF in two different scenarios: when animals are restricted to a single microhabitat and when they move between microhabitats. In the current data set, 10 of the 13 species were restricted to a single microhabitat. When animals are restricted to a particular microhabitat, data on proportional use can be used to indicate selection and the potential of RSF is not fully realised. However, if the proportional use of a habitat deviates from 100% (as in case of 3 of 13 species presented here), it would be obligatory to quantify selection using RSF.

**Conservation implications**

We found strong associations of cricket species with different microhabitats. For instance, *Gryllacropsis* sp. calls only from tree trunks of large trees with a mean GBH > 1 m, *Landreva* sp. specifically selects for a rare habitat element, dead logs, and *Mecopoda ‘Two part’* selected for the other rare microhabitat: brambles. This study highlights the importance of preserving the structural heterogeneity of forests and the diversity of microhabitats, including rare ones, which can be of critical survival value, especially to invertebrate species. This is of particular relevance in paleotropical forests, which are often islands in a matrix of degraded landscapes and are susceptible to human exploitation in the form of dead wood and leaf litter collection and felling of large trees.

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