Is habitat suitability sex-specific? A study of the Indian Giant Squirrel (*Ratufa indica maxima*) in the Western Ghats of India

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Habitat suitability difference between sexes results in sex specific dispersal. Although sex specific dispersal behaviour is one of the key factors in understanding population dynamics, there are limited studies to evaluate it in arboreal species. We studied distribution of the Indian Giant Squirrel (IGS; *Ratufa indica maxima*) from a sex perspective. We also evaluated potential suitable habitat types for the species in the Nelliyampathy Reserve Forest in the Western Ghats in Kerala, India. We used the sweep survey method to record the distribution pattern of squirrels, and analyzed the influence of climatic layers and other variables on distribution using MaxEnt. The study revealed that there was a difference between the sexes in habitat selections. Males tended to prefer more landuse types than females, which were restricted to only certain landuse types. Some of
the major factors which determined the distribution of species were distance from urban
settlement (50.1%), distance from shade plantation (23.2%), distance from rocky outcrop
(9.2%), minimum temperature of coldest month (9%), and precipitation of wettest quarter
(8.5%). The final MaxEnt model output predicted 10.46% to be suitable habitat for IGS, of
which 9.70% and 7.34% was suitable for males and females respectively with an overlap of
6.57% between the sexes. We suggest that it would be important to include a sex perspective
in species habitat suitability studies in order to gain insights into the sex related habitat
specificity and its role in dispersal.

**Keywords:** Indian giant squirrel, distribution modeling, habitat loss, sex-specific dispersal,
Western Ghats,

Males and females of a species may exhibit different spatial distribution patterns from each
other. The factors related to physical, physiological and behavioral variations may lead to
varied use of different habitat types leading to differences in habitat preferences between the
sexes. Since males and females of a certain species have evolved different strategies in choosing
their habitats, it is critical to evaluate their habitats separately, and include this while devising
conservation and habitat management policies.

There could be several reasons for choice of different habitats by male and female
individuals of the same species. Among them, sex biased dispersion is one of the major factors
for differential habitat selection between sexes, especially in vertebrates. Sex-Biased Dispersion
(SBD) results when individuals of one sex disperse more than that of the other. The "Resource
Competition Theory" (RCT), the "Local Mate Competition Hypothesis" (LMC), and the
"Inbreeding Avoidance Hypothesis" (IAH) are some of the hypotheses that have been put
forward to explain SBD behaviour. The RCT, which describes how competition for local
resources and for mate choice can cause population dispersion, is the most well acknowledged
hypothesis to explain SBD. As dispersion bias influences population dynamics, understanding the dispersal bias in a species
and between the sexes can help to predict how vulnerable a population would be. The response
to change in environmental factors such as habitat fragmentation, degradation and change in the
vegetation pattern act as selective pressures and may lead to dispersal behavior. Males can help save populations genetically, but not demographically. Male-biased dispersal can help to maintain genetic diversity within a population by reducing the risk of inbreeding and the negative effects that can result from mating with close relatives but in some cases, male dispersal may actually lead to a decline in population size or even extinction. For example, if male dispersal leads to a reduction in the number of males within a population, this can result in decreased reproductive output and reduced genetic diversity in future generations. Similarly, if males are more vulnerable to predation or hunting, their increased mobility and dispersal may increase their exposure to these threats. The potential of extinction may therefore be higher for populations with male-biased dispersal than for those with a female bias. For better comprehension of the ecological and evolutionary causes of distinct spatial patterns of biodiversity and for conservation planning and forecasting, extensive research regarding the species' habitat suitability is required. Here, we assessed the potential suitable habitats of males and females of an arboreal mammal, the Indian Giant Squirrel (IGS; Ratufa indica maxima) in highly fragmented forests of the Western Ghats. Since in mammals, it has been found that male dispersal is more common than female dispersal, we expected males to disperse between female ranges and females to stay in their smaller ranges. If so, we expect a difference in the habitat use of males and females. Our study also explored the impact of climatic factors, land use, slope, elevation, distance from rainforest and distance from urban settlement, on habitat suitability among male and female Indian giant squirrels. We suggest that mapping the habitat suitability of male and female Indian Giant Squirrel may have an impact on its conservation and population management.

Study area

The study was conducted in the Nelliyampathy Reserve Forest (Figure 1) situated at 76° 30’ to 76° 50’ E and 10° 20’ to 10° 35’ N in the Palakkad district of Kerala. It is located near the confluence of the Karapara and Parambikulam rivers, close to the south and west borders. It covers a region of around 736 sq. km. The altitude ranges between 500 and 1633 meters. The average annual rain fall is 3378mm. Average temperature ranges from 15°C in winter to 30°C in summer. The major landuse types are coffee, tea, cardamom, orange, and rubber plantations that are maintained by private/government parties either on their own property or on leased lands.
from the government. These plantations, which are scattered throughout the evergreen and
deciduous forest patches and grasslands, serve as corridors for numerous species, as well as
habitats for a variety of faunal and floral species.

**Study species**

One of the four subspecies of Indian giant squirrels, *Ratufa indica maxima* can be found only in
the southern part of the Western Ghats, south of the Palakkad gap\(^{11,12}\). The species is completely
arboreal in nature and occasionally comes to the ground only if there is a break in canopy
continuity\(^{14}\). This species is found in both moist deciduous and evergreen forests\(^{11,15}\). These are
solitary creatures that are facultative frugivores and generalist herbivores\(^{16}\). They construct
several nests, also known as dreys, within their home ranges for resting, caring for young and for
food hoarding\(^{17,18}\). The Wildlife (Protection) Act of India, 1972 classifies it as a Schedule I
species, while the IUCN Red List rates it as Least Concern though the population is continuously
declining\(^{19}\). Some of the major reasons for this species decline are deforestation and habitat
fragmentation\(^{20}\). Hunting is also adding up to the severe decline of local population densities\(^{21}\).
Agencies such as the IUCN and CITES have acted to reduce their chance of extinction and
habitat from further fragmentation\(^{22}\).
Figure 1. Map of the study area and the occurrence locations of Indian Giant Squirrels in the Nelliyampathy Reserve Forest, Kerala (inset: The Western Ghats range in the southern part of India).

Methods

Data collection

Sweep surveys

The study area was thoroughly surveyed for IGS by systematic sweep sampling method during which two or more observers walked simultaneously along the pathways keeping 100m apart.
We walked slowly at the rate of 1km/hr using the pre-existing forest tracks and trails only once, and covered a total distance of 296 Km. Observers started the transects simultaneously, and paused at the midpoint to resynchronize the movement. During the sweep survey, data on the distribution, through direct sighting of an individual in a given place, and ecological conditions of the study species' habitats, were recorded using GPS coordinates (Montana 650) from November 2017 to January 2018. We made sure that all the represented landuse types were sampled. Additional data on the species' presence or absence was acquired from local residents, forest department employees, fecal deposits, calls, and foraging and roosting signs in the study area but not at the level of sex identification. The information obtained in this manner was considered and re-evaluated by surveying in those areas to determine the accuracy of the information only through direct sighting of the IGS by the observers. Hence these are also considered as primary information during the later stage. Altogether, we had 108 points of species occurrence locations in which 25 were males, 72 were females and 11 were unidentified individuals. Unidentified individuals were not included in the analysis.

Data analysis

Environmental layers and modeling

The habitat suitability of the IGS was assessed using bioclimatic factors since these provided information which was biologically more meaningful than sampling temperature and precipitation data. From the WorldClim database, which has a spatial resolution of 30 arc seconds (about 1 km), 19 bioclimatic variables were derived. Along with this, we derived continuous layers of rainforest, shade plantation, dry-deciduous forest, water bodies, open plantation, pattern plantation and rocky outcrop land-use type by calculating Euclidean distance using ArcGIS 10.2 at 10m resolution and were resampled to 1km to achieve the uniformity in the resolution (Figure 2). The Digital Elevation Model (DEM) was obtained from the Indian Cartosat-1 remote sensing satellite, at a resolution of ~30 meters (bhuvan.nrsc.gov.in). The environmental layers were extracted using ArcGIS 10.2, and SDM toolbox 2.0 was used to analyze the highly correlated variables (>0.75) among the bioclimatic variables such as distance from rain forest and distance from urban settlement. To improve predictability and decrease the masking effect, twelve highly correlated bioclimatic variables with little impact on the model were eliminated. Spatial thinning was done for the occurrence points by grid based thinning
with 1sq. km. and one occurrence point was selected from each grid cell to reduce spatial autocorrelation. Aspect ratio and Slope were calculated as compass direction of the downslope direction and degrees respectively.

**Habitat suitability modeling:** We used MaxEnt version 3.3.3 k\textsuperscript{27-29} for the habitat suitability modeling because it offers high accuracies even for limited presence-only data\textsuperscript{30-32}.

**Model evaluation and validation:** A user-defined model was adopted as the default MaxEnt model which could make models complex and may overfit the data\textsuperscript{33}.

In this study, only presence data were used which was divided into 75\% random samples for the model calibration and 25\% as test samples to assess the model's performance. Since our sample sizes were low, we ran models with different feature classes and regularization multipliers. The feature classes used were linear (L), quadratic (Q), hinge (H), product (P) and threshold (T) and the combination of feature classes used included L, P, T, H, LQ, HQ, LQH, LQP, LQT, QHP, QHT, QHPT and AUTO features. 1, 2, and 5 were the regularization multipliers used to prevent the predicted values from being overfitted and to balance the model fit\textsuperscript{34,35}. To choose the best fit model, 195 models in total were created using various settings. The adjusted Akaike information criterion (AICc) values from ENMTools version 1.4.4 were then used to determine the best model\textsuperscript{36}. For selecting the best models, AICc values outperform BIC (Bayesian Information Criterion) and AUC (Area Under the Curve) values when the presence sample size is low\textsuperscript{35,36}.

The findings of the model, which indicate habitat suitability (probability of presence) of the target species, were presented in the logistic output format, which ranges from 0 (unsuitable) to 1 (maximum suitable)\textsuperscript{27}. A minimum presence thresholds was used to delineate suitable areas from non-suitable areas keeping in view the availability of presence only data. To calculate the response of each environmental variable in contributing to habitat suitability, receiver operating curves (ROC) were utilized \textsuperscript{27}. Environmental layers that made up less than 1\% of the total model were eliminated because of the less attribution to the distribution of the species.

**Results**

**Model accuracy**
The best fit models based on AICc scores were QHP2, LQT1 and LQ1 for the Overall distribution, Males and Females respectively (Table 1). The test AUC and training AUC values obtained from final model were 0.84 and 0.86 for overall distribution, 0.82 and 0.80 for male distribution and 0.84 and 0.85 for female distribution.

*Important environmental variables:* Of the 25 variables (Supplementary Table 1) used for modeling, the significant factors affecting the spatial distribution of Indian giant squirrels (Figure 3) were distance from urban settlements (50.1%), shade plantation (23.2%), rocky outcrops (9.2%), minimum temperature of coldest month (9%) and precipitation of wettest quarter (8.5%). For males (Figure 4), the factors which affected their spatial distribution were shade plantation (62.6%) and distance from urban settlements (37.4%). The response curves showed that the males preferred shade plantations and areas closer to human settlements. For females (Figure 5), the factors contributing to the model were distance from urban (67.1%), shade plantations (17%), distance from rainforest (10.4%) and minimum temperature of coldest quarter (5.5%). The females preferred areas closer to the human settlements, shade plantations, rainforests, and areas with low minimum temperature in the coldest quarter.

**Figure 2.** Land use pattern in Nelliyampathy reserve forest
Figure 3. Current distribution of the Indian giant squirrel

Figure 4. Predicted potential distribution of the male Indian giant squirrels
Habitat suitability and conservation implications: Overall, 10.46% (77.05 sq. km.) was found to be suitable for IGS in Nelliyampathy. Male IGS with 9.70% (71.40 sq. km.) was found to have more potential suitable area than female with only 7.34% (54.05 sq. km.) (Table 1). Rainforest was found to be the most suitable habitat for male and female Indian giant squirrel, wherein females preferring it more than males. Following rainforest, males preferred shade plantation (31.43%), open plantation (19.68%), pattern plantation (8.75%), rocky outcrop (3.40%) and dry-deciduous (1.83%) habitats. Females preferred shade plantation, open plantation, pattern plantation, rocky outcrop, dry-deciduous habitats with 29.49%, 18.87%, 5.47%, 1.89% and 1.77% respectively (Table 2). Although, there was a high overlap between male and female potential habitats, males were shown to have a broader suitable habitat than females. The preferred habitats for males were highly dispersed in the whole landscape, when compared to female preferred habitats which were concentrated in a particular area (Figures 4, 5).
Table 1. Total predicted potential habitat suitability area in Nelliyampathy reserve forest.

<table>
<thead>
<tr>
<th></th>
<th>Total area (sq. km.)</th>
<th>Percentage (%)</th>
</tr>
</thead>
<tbody>
<tr>
<td>Overall distribution</td>
<td>77.05</td>
<td>10.46</td>
</tr>
<tr>
<td>Males</td>
<td>71.40</td>
<td>9.70</td>
</tr>
<tr>
<td>Females</td>
<td>54.05</td>
<td>7.34</td>
</tr>
<tr>
<td>Overlap</td>
<td>48.40</td>
<td>6.57</td>
</tr>
</tbody>
</table>

Table 2. The predicted potential suitable landuse available for Indian giant squirrel in the Nelliyampathy Reserve forest.

<table>
<thead>
<tr>
<th>Landuse Type</th>
<th>Males</th>
<th>Females</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>sq. km.</td>
<td>Percentage</td>
</tr>
<tr>
<td>Rocky outcrop</td>
<td>2.43</td>
<td>3.40</td>
</tr>
<tr>
<td>Pattern plantation</td>
<td>6.25</td>
<td>8.75</td>
</tr>
<tr>
<td>Rainforest</td>
<td>24.90</td>
<td>34.91</td>
</tr>
<tr>
<td>Shade plantation</td>
<td>22.44</td>
<td>31.43</td>
</tr>
<tr>
<td>Open plantation</td>
<td>14.05</td>
<td>19.68</td>
</tr>
<tr>
<td>Dry-deciduous</td>
<td>1.31</td>
<td>1.83</td>
</tr>
</tbody>
</table>

Table 3. Maxent output values for test AUC and training AUC for the males and females Indian giant squirrel.

<table>
<thead>
<tr>
<th></th>
<th>Best Model</th>
<th>AUC (test)</th>
<th>AUC (training)</th>
</tr>
</thead>
<tbody>
<tr>
<td>Overall distribution</td>
<td>QHP2</td>
<td>0.84</td>
<td>0.86</td>
</tr>
<tr>
<td>Males</td>
<td>LQT1</td>
<td>0.82</td>
<td>0.80</td>
</tr>
<tr>
<td>Females</td>
<td>LQ1</td>
<td>0.84</td>
<td>0.85</td>
</tr>
</tbody>
</table>

Discussion

Our findings demonstrated that the inclusion of a sex perspective in mammal dispersal studies could aid in detecting habitat preferences between sexes (key to population dynamics) and its
potential causes, as well as better understanding of the dispersal behaviour of a solitary species inhabiting different habitat structures. The Nelliyampathy area contains potentially appropriate habitats for IGS, according to our models. Our models show that distance from the urban settlement is one of the major factors which is affecting the distribution of both male and female IGS. This may be due to the availability of a variety of food resources abundantly in and around human habitation throughout the year, and also the lesser chances of the potential predators due to the human presence. However rainforest is the most preferred habitat type for both males and females which maybe due to the high percentage of canopy connectivity which helps the movement in this habitat structure and also due to the presence of trees preferred for nesting.

Our models demonstrate that shade plantations, which include coffee and cardamom plantations with natural rain-forest shade trees, were the second highly preferred habitat of both male and female IGS. Agro-ecosystems, such as shade plantations with coffee and cardamom trees, offer many species with ideal habitats and dispersal routes and our results are consistent with other studies that demonstrate the value of fragmented habitats and forest edges for arboreal species. Using this information, we observe that male IGS preferred and occupied diverse types of land use such as pattern plantation, rocky outcrop and dry deciduous compared to female IGS who were largely restricted to rain forests, shade plantations and open plantations. In populations with a strong sex ratio bias, sex-biased dispersal is anticipated. According to theoretical predictions, the most dispersive sex would be the most abundant sex in natal patches that are experiencing high competition. Low female dispersal ability, however, could be caused by any of the following: (1) females may incur higher dispersal costs than costs associated with competition; (2) intrasexual competition is not a significant factor to induce dispersal bias; or (3) intrasexual competition for feeding resources may not exist within females. To test these theoretical hypotheses, additional variables should be considered because the potential benefits of dispersal might outweigh the physiological costs, which might lead to an actual bias in dispersal between sexes. Some of the lacunae in the present study was that, we used presence only data (direct observation) for the analysis. Direct observation depends on the observer’s identification skills, detectability of a species, and duration of spatial and temporal coverage of the study area. Furthermore, we only used the variables related to climate, topography and vegetation other environmental factors that may also affect the species distribution include fruit tree distribution, tree species preferred for nesting etc. could not be included in this study. The seasonal occurrence data were not incorporated into the models we used, despite the fact that
they might increase the accuracy of habitat appropriateness. We used complete occurrence data for the final models of the overall distribution even though we ran models with bootstrapped data for cross-validation (with 25% of occurrence data) of males and females separately this was done to boost prediction probabilities. For males and females, the test AUCs for the models with cross-validation were 0.82 and 0.84 respectively (Table 3). When sample numbers are low, such cross-validation with bootstrapping can be used for additional investigations. The presence records mostly come from the dispersal events and do not represent the actual habitat space occupied by the species, which can lead to inaccurate predictions, specifically when the dispersal distance is more than the spatial resolution of the data used. But when a species is found to be in a certain habitat, it represents the spatial and temporal plasticity of behaviour in that species. Hence, species-specific microclimatic studies are needed to standardize the variables necessary for species distribution modeling.

**Conclusion**

Though the Indian giant squirrel is a habitat generalist species, it prefers to live in forested areas. Forest fragmentation and change in landuse type are expected to have an impact on their distribution, use of available space, and dispersal. Because of the disappearance of large forests, local population extinction in remote regions may be possible due to forest fragmentation and isolation of woodlands. In our study population, males tend to disperse in wider habitat types compared to females. Our findings highlight the need for including sex as a factor that influences the distribution of species. In addition, investigating the potential causes of sex bias dispersal might help forecast how vulnerable a species is for extinction, as populations of species with poorly dispersing females are more susceptible because of their role in population dynamics. These endemic species require more targeted conservation prescriptions, for which detailed sex perspective studies must be undertaken.

*Conflicts of interest:* The authors declare that there is no conflict of interest.


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thanks SERB- Distinguished Fellowship (SB/S9/YSRP/SERB-DF/2018(1)) and JJ thanks SERB
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**Supplementary Table 1**

<table>
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<tr>
<th>Sl.no</th>
<th>Parameter layer</th>
<th>Variables</th>
</tr>
</thead>
<tbody>
<tr>
<td>1</td>
<td>BIO1</td>
<td>Annual mean temperature</td>
</tr>
<tr>
<td>2</td>
<td>BIO2</td>
<td>Mean diurnal range [mean of monthly(max.-min.)]</td>
</tr>
<tr>
<td>3</td>
<td>BIO3</td>
<td>Isothermality (BIO2/BIO7)</td>
</tr>
<tr>
<td>4</td>
<td>BIO4</td>
<td>Temperature seasonality (Standard Deviation)</td>
</tr>
<tr>
<td>5</td>
<td>BIO5</td>
<td>Max temperature of warmest month</td>
</tr>
<tr>
<td>6</td>
<td>BIO6</td>
<td>Min temperature of coldest month</td>
</tr>
<tr>
<td>7</td>
<td>BIO7</td>
<td>Temperature annual range (BIOS-BIO6)</td>
</tr>
<tr>
<td>8</td>
<td>BIO8</td>
<td>Mean temperature of wettest quarter</td>
</tr>
<tr>
<td>9</td>
<td>BIO9</td>
<td>Mean temperature of driest quarter</td>
</tr>
<tr>
<td>10</td>
<td>BIO10</td>
<td>Mean temperature of warmest quarter</td>
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<tr>
<td>11</td>
<td>BIO11</td>
<td>Mean temperature of coldest quarter</td>
</tr>
<tr>
<td>12</td>
<td>BIO12</td>
<td>Annual precipitation</td>
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<td>BIO13</td>
<td>Precipitation of wettest month</td>
</tr>
<tr>
<td>14</td>
<td>BIO14</td>
<td>Precipitation of driest month</td>
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<tr>
<td>15</td>
<td>BIO15</td>
<td>Precipitation seasonality (coefficient of variation)</td>
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<tr>
<td>16</td>
<td>BIO16</td>
<td>Precipitation of wettest quarter</td>
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<tr>
<td>17</td>
<td>BIO17</td>
<td>Precipitation of driest quarter</td>
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<tr>
<td>18</td>
<td>BIO18</td>
<td>Precipitation of warmest quarter</td>
</tr>
<tr>
<td>19</td>
<td>BIO19</td>
<td>Precipitation of coldest quarter</td>
</tr>
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</table>
| 20    | Land use        | High-resolution vegetation type and land-use map (10x10m cell size) with accuracy >85% developed from Sentinel-2 MSI 10m spectral bands and Sentinel-1 SAR band, NDVI and textural layers. The different land-use types were rainforest (>60% canopy cover, dominated by evergreen and moist deciduous trees), dry deciduous (>60% canopy cover,
dominated by dry deciduous trees), water bodies, shade plantation (30-60% canopy cover, mainly included coffee and cardamom plantations with native trees), pattern plantation (>30% canopy connectivity, dominated by monoculture teak and silver oak), open plantation (<30% canopy cover, dominated by tea and coffee plantations with few trees, degraded forests) and rocky outcrop (dominated by built-up areas and exposed land with little or no vegetation, including rocky areas). An eight cell neighbourhood majority filter was applied for avoiding inconsistencies (salt and pepper pattern) for modelling. The water bodies land-use type was masked for the present study after modelling.

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<td>21</td>
<td>Elevation</td>
<td>Digital Elevation Model (DEM) generated from stereo images of Indian remote sensing satellite Cartosat-I with ~30m resolution downloaded from bhuvan.nrsc.gov.in</td>
</tr>
<tr>
<td>22</td>
<td>Distance from rain forest</td>
<td>Derived continuous layer created by calculating Euclidean distance from rainforest land-use type using ArcGIS 10.2 at 10m resolution</td>
</tr>
<tr>
<td>23</td>
<td>Distance from urban settlement</td>
<td>Derived continuous layer created by calculating Euclidean distance from urban land-use type using ArcGIS 10.2 at 10m resolution</td>
</tr>
<tr>
<td>24</td>
<td>Slope</td>
<td>Derived continuous layer from DEM. Calculated as degrees using spatial analyst extension of ArcGIS 10.2</td>
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<tr>
<td>25</td>
<td>Aspect</td>
<td>Derived continuous layer from DEM. Calculated as compass direction of the downslope direction using spatial analyst of ArcGIC 10.2</td>
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