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 this behaviour is one of the key factors in understanding population dynamics, there are limited studies to evaluate it in arboreal species. We studied the distribution of the Indian Giant Squirrel (IGS; *Ratufa indica maxima*) from a sex perspective. We also evaluated potentially suitable habitat types for the species in the Nelliyampathy Reserve Forest, Western Ghats, Kerala, India. We used the sweep survey method to record the distribution pattern of squirrels and analysed the influence of climatic layers and other variables on the distribution using MaxEnt. The study revealed that there was a difference between the sexes in habitat selection. Males preferred more land-use types than females, which were restricted to only certain land-use types. Some of the major factors that 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 the coldest month (9%) and precipitation of the wettest quarter (8.5%). The final MaxEnt model output predicted 49.07% suitable habitat for IGS, of which 45.47% and 34.42% were suitable for males and females respectively, with an overlap of 30.82% 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 sex-related habitat specificity and its role in dispersal.

Keywords: Conservation measures, distribution modelling, habitat loss, *Ratufa indica maxima*, sex-specific dispersal.

MALES and females of a species may exhibit different spatial distribution patterns[1,2]. Factors related to physical, physiological and behavioural variations may lead to the varied use of different habitat types, resulting in differen-

ces in habitat preferences between the sexes[3]. Since males and females of a species have evolved different strategies for choosing their habitats, it is critical to evaluate their habitats separately and consider this while devising conservation and habitat management policies.

There could be several reasons for the choice of different habitats by males and females of the same species. Among them, sex-biased dispersal (SBD) is one of the major factors, especially in vertebrates. SBD occurs when individuals of one sex disperse more than those of the other[2]. The resource competition theory (RCT)[4], local mate competition hypothesis (LMC)[5] and inbreeding avoidance hypothesis (IAH)[6] have been proposed to explain SBD. RCT, which describes how competition for local resources and mate choice can cause population dispersion, is the most well-acknowledged hypothesis to explain SBD[2,4].

As dispersion bias influences population dynamics, understanding the dispersal bias in a species and between the sexes can help predict how vulnerable a population could be[2,7]. The response to changes in environmental factors such as habitat fragmentation, degradation and change in vegetation pattern acts as a selective pressure and may lead to dispersal behaviour. Males can help save populations genetically, but not demographically[8]. Male-biased dispersal can help maintain genetic diversity within a population by reducing the risk of inbreeding and the negative effects that can result from mating with close relatives. However, in some cases, male dispersal may 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 for extinction may therefore be higher for populations with male-biased dispersal than for those with a female bias[8]. 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 habitat suitability of the species is required[9,10]. In this study, we assessed the potentially suitable habitats of males and females of an arboreal mammal, the Indian Giant Squirrel (IGS; *Ratufa indica maxima*) in the highly fragmented forests of the Western Ghats, Kerala, India. Since in mammals, it has been found that male dispersal is more common than female dispersal[4], 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. This study also explored the impact of climatic factors, land use, slope, elevation, distance from the rainforest, and distance from urban settlement on habitat suitability among male and female IGS. We suggest that mapping the habitat suitability of male and female IGS may have an impact on their conservation and population management.

Study area

The study was conducted in the Nelliyampathy range of Nelliyampathy Reserve Forest situated at 76°30′–76°50′E and 10°20′–10°35′N in the Palakkad district of Kerala (Figure 1). It is located near the confluence of the Karapara and Parambikulam rivers, close to the southern and western borders. The forest covers around 157 km² of 736 km² of Nelliyampathy Reserve Forest[11,12]. The altitude ranges between 500 and 1633 m. The average annual rainfall is 3378 mm. The average temperature ranges from 15°C in winter to 30°C in summer[13]. The major land-use types are coffee, tea, cardamom, orange and rubber plantations that are maintained by private owners/government either on their own property or on lands leased 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 IGS, *R. indica maxima* can be found only in the southern part of the Western Ghats, south of the Palakkad gap[11,12]. It 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 squirrels are solitary animals that are facultative frugivores and generalist herbivores[16]. They construct several nests, also known as dreys, within their home ranges for resting, caring for their young and hoarding food[17,18]. The Wildlife (Protection) Act of India, 1972, classifies the species as a Schedule I species, while the IUCN Red List categorizes it as Least Concern though the population is continuously declining[19]. Some of the major reasons for the decline of this species are deforestation and habitat fragmentation[20].

Hunting is also resulting in a severe decline in local population densities[21]. Agencies such as the IUCN and CITES have made efforts to reduce their chance of extinction and prevent habitat fragmentation[22].

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 about 100 m apart[23]. The observers walked slowly at a rate of 1 km/h using the pre-existing forest tracks and trails only once, and covered a total distance of 296 km. They started at the transects simultaneously and paused at the midpoint to resynchronize their movement. During the sweep survey, data on the distribution, through the direct sighting of an individual at a given place, and ecological conditions of the habitat of the species were recorded using GPS coordinates (Montana 650) from November 2017 to January 2018. We made sure that all the land-use types represented were
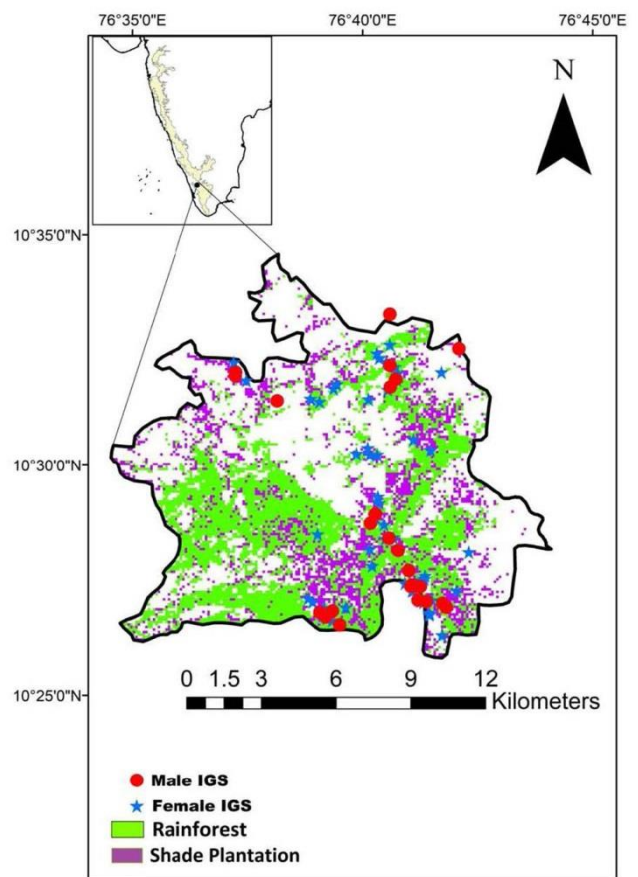

Figure 1. Map of the study area and occurrence locations of the Indian Giant Squirrel (IGS) in the Nelliyampathy Reserve Forest, Kerala, India (Inset: The Western Ghats range in the southern part of India).

sampled. Additional data on the presence or absence of the species was acquired from local residents, Forest Department employees, faecal deposits, calls, and foraging and roosting signs in the study area, but not at the level of sex identification. The information thus obtained was considered and re-evaluated by surveying those areas to determine its accuracy only through the direct sighting of IGS by the observers. Hence, these were also considered primary information during the later stage. Altogether, there were 108 points of species occurrence, of which 25 were males, 72 were females, and 11 were unidentified individuals. The unidentified individuals were not included in the analysis.

Data analysis: environmental layers and modelling

The habitat suitability of IGS was assessed using bioclimatic factors since they provide information that is biologically more meaningful than sampling temperature and precipitation data[24]. From the WorldClim database[25], which has a spatial resolution of 30 arcsec (about 1 km), 19 bioclimatic variables were derived. We also derived continuous layers of the 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 10 m resolution and resampled to 1 km to achieve uniformity in resolution (Figure 2). The digital elevation model (DEM) was obtained from the Indian Cartosat-1 remote sensing satellite, at a resolution of ~30 m (bhuvan.nrsc.gov.in). The environmental layers were extracted using ArcGIS 10.2. SDM toolbox 2.0 was used to analyse the highly correlated variables (>0.75) among the bioclimatic variables, such as distance from rainforest and from urban settlement. To improve predictability and decrease the masking effect, 12 highly correlated bioclimatic variables with little impact on the model were eliminated[25]. Spatial thinning was done for the occurrence points by grid-based thinning with 1 km^2 and one occurrence point was selected from each grid cell to reduce spatial auto-
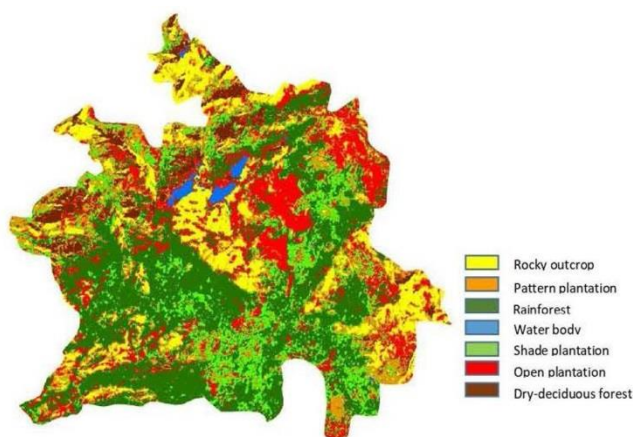
correlation[26]. The aspect ratio and slope were calculated as the compass direction of the downslope direction and degrees respectively.

Habitat suitability modelling: We used MaxEnt version 3.3.3 k (refs 27–29) for habitat suitability modelling because it offers high accuracies even for limited presence-only data[30–32].

Model evaluation and validation: A user-defined model was adopted as the default MaxEnt model, which could make the model complex and may overfit the data[33].

In this study, only presence data were used, which were divided into 75% random samples for model calibration and 25% test samples to assess the model's performance. Since the sample size was low, we used 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. 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[34,35]. To choose the best-fit model, 195 models were developed using various settings. The adjusted Akaike information criterion (AICc) values from ENMTools version 1.4.4 were then used to determine the best model[36]. For selecting the best models, AICc values must outperform BIC (Bayesian information criterion) and AUC (area under the curve) values when the sample size is low[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, ranging from 0 (unsuitable) to 1 (maximum suitable)[27]. A minimum presence threshold was used to delineate suitable areas from unsuitable 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 were utilized[27]. Environmental layers that made up less than 1% of the total model were eliminated because there was 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 overall distribution, males and females respectively (Table 1). The test AUC and training AUC values obtained from the final model were 0.84 and 0.86 for the overall distribution, 0.82 and 0.80 for male distribution and 0.84 and 0.85 for female distribution respectively.

Important environmental variables: Of the 25 variables used for modelling (Supplementary Table 1), the significant factors affecting the spatial distribution of IGS were

Figure 2. Land-use pattern in the Nelliyampathy Reserve Forest.

distance from urban settlements (50.1%), shade planta-tions (23.2%), rocky outcrops (9.2%), minimum temperature of the coldest month (9%) and precipitation of the wettest quarter (8.5%) (Figure 3). For males, the factors that affected their spatial distribution were shade plantation (62.6%) and distance from urban settlements (37.4%) (Figure 4 *a*). The response curves showed that the males preferred shade plantations and areas closer to human settlements. For females, the factors contributing to the model were a distance from urban settlements (67.1%), shade plantations (17%) distance from rainforest (10.4%) and the minimum tempera-ture of the coldest quarter (5.5%) (Figure 4 *b*). Females pre-ferred areas closer to human settlements, shade plantations, rainforests and areas with low minimum temperatures in the coldest quarter.

Habitat suitability and conservation implications: Overall, 49.07% (77.05 km^2) was found to be suitable for IGS in the Nelliyampathy Reserve Forest. Male IGS with 45.47% (71.40 km^2) was found to have more potential suitable area than females with only 34.42% (54.05 km^2) (Table 2). Rainforest was found to be the most suitable habitat for male and female IGS, with females preferring it more than males. Males preferred shade plantation (31.43%), open plantation (19.68%), pattern plantation (8.75%), rocky outcrop (3.40%) and dry-deciduous (1.83%) habitats.

Table 1. MaxEnt output values for test AUC and training AUC for male and female Indian giant squirrel (IGS)

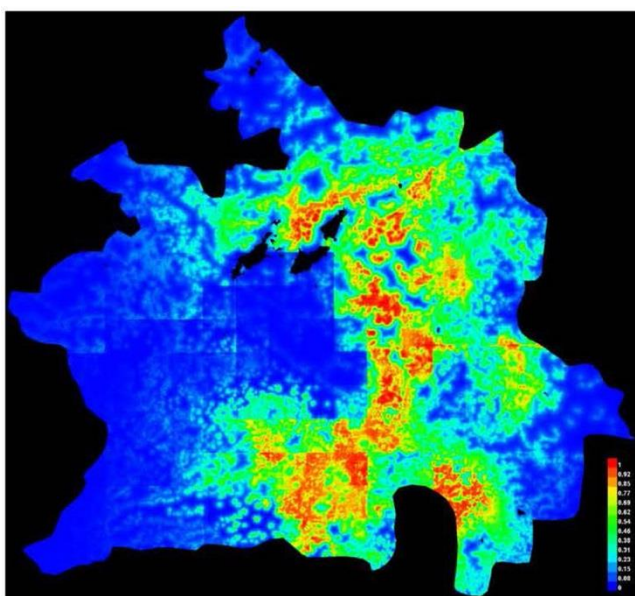| Type	Best model	AUC (test)	AUC (training)
Overall distribution	QHP2	0.84	0.86
Male	LQT1	0.82	0.80
Female	LQ1	0.84	0.85

Figure 3. Current distribution of Indian giant squirrel.

females preferred shade plantation (29.49%), open plantation (18.87%), pattern plantation (5.47%), rocky outcrop (1.89%) and dry-deciduous habitats (1.77%) (Table 3). Although there was a high overlap between male and female poten-tial habitats, males had broader suitable habitats than females. The preferred habitats for males were highly dispersed in the whole landscape compared to the female-preferred habi-tats, which were concentrated in a particular area (Figures 4 and 5).

Discussion

Our findings demonstrate that the inclusion of a sex perspec-tive in mammal dispersal studies could aid in detecting habitat preferences between sexes (key to population dynam-ics) and their potential causes, as well as a better under-standing of the dispersal behaviour of a solitary species inhabiting different habitat structures. The Nelliyampathy area contains potentially appropriate habitats for IGS, ac-cording to our models. Our models show that distance from urban settlements is one of the major factors affecting the distribution of both male and female IGS. This may be due to the abundant availability of a variety of food re-sources in and around human habitation throughout the year, as well as the lesser chances of potential predators due to human presence. However, the rainforest is the most preferred habitat type for both males and females, which could be due to the high percentage of canopy connectivity that helps in 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 rainforest shade trees are the second most 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[37–40]. Our results are consistent with other studies that demonstrate the value of fragmented habitats and for-est edges for arboreal species[41–43]. Using this information, we observed 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 rainforests, shade plantations and open plan-tations. 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[4,44–46]. Low female dispersal ability, however, could be caused by any of the following: (1) females may incur higher dispersal costs than those 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[46,47]. To test these theoretical hypotheses, additional variables should be considered be-cause the potential benefits of dispersal might outweigh the physiological costs[46], which might lead to an actual
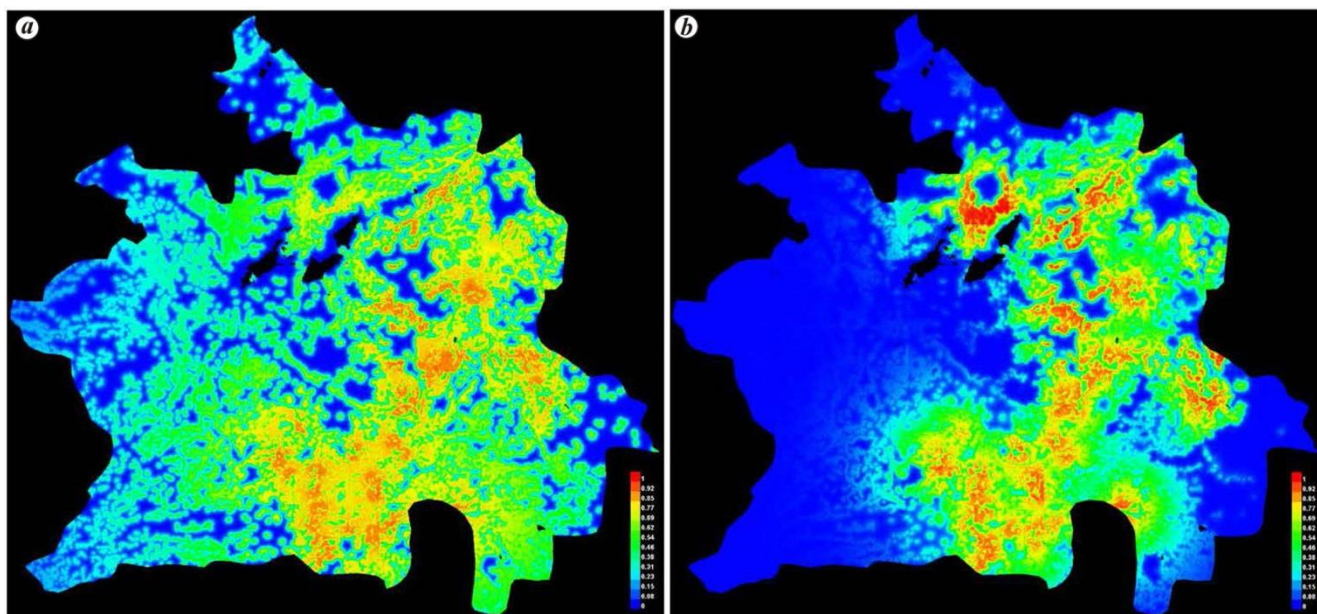
Figure 4. Predicted potential distribution of (*a*) male IGS and (*b*) female IGS.

Table 2. Total predicted potential habitat suitability area in the Nelli-yampathy Reserve Forest, Western Ghats, Kerala, India

Type	Total area (km²)	Percentage
Overall distribution	77.05	49.07
Male	71.40	45.47
Female	54.05	34.42
Overlap	48.40	30.82

Table 3. Predicted potential suitable land use available for the IGS in the Nelliyampathy Reserve Forest

Land use type	Males		Females	
	km²	Percentage	km²	Percentage
Rocky outcrop	2.43	3.40	1.02	1.89
Pattern plantation	6.25	8.75	2.95	5.47
Rainforest	24.90	34.91	22.98	42.51
Shade plantation	22.44	31.43	15.94	29.49
Open plantation	14.05	19.68	10.19	18.87
Dry-deciduous	1.31	1.83	0.95	1.77

bias in dispersal between sexes. Some of the drawbacks of the present study are the following. We used presence-only data (direct observation) for 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 variables related to climate, topography and vegetation. The other environmental factors that may affect species distribution include fruit-tree distribution, tree species preferred for nesting, etc. which could not be included in this study. The seasonal occurrence data were not incorporated into our models, 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 the prediction probabilities. For males and females, the test AUC values for the models with cross-validation were 0.82 and 0.84 respectively (Table 1). When sample numbers are low, such cross-validation with bootstrapping can be used for additional analysis[35]. The presence records mostly originate from dispersal events and do not represent the actual habitat space occupied by the species. This can lead to inaccurate predictions, specifically when the dispersal distance is greater than the spatial resolution of the data used. However, 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 modelling.

Conclusion

Though IGS is a habitat generalist species, it prefers to live in forested areas. Forest fragmentation and changes in land-use type are expected to have an impact on its distribution, use of available space and dispersal. Due to the disappearance of large forests, local population extinction in remote regions may be possible due to forest fragmentation and the isolation of woodlands. In our study population, males were found to disperse in wider habitat types compared to females. Our findings highlight the need to include sex as a factor that influences the distribution of species. In addition, evaluating the potential causes of sex-biased dispersal might help forecast how vulnerable a species is to extinction, as populations of species with poorly dispersing females are more susceptible because of their role in population dynamics[48]. These endemic species require more targeted conservation measures, 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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