

1 Running Head: Demography of a tropical Indian bird

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4 Title: Demographic changes of a tropical understory bird in naturally patchy montane habitats in
5 southern India.

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14 **ABSTRACT**

15 The occurrence, density and survival of a species often depend on various aspects of the habitat
16 that it occupies including patch size and disturbance. The demography of most threatened
17 tropical species largely remain unstudied but could provide valuable information about their
18 biology and insights for their conservation. Our study examined the effect of patch size and
19 disturbance on different demographic parameters of an understory, threatened, endemic bird, the
20 white-bellied shortwing in the tropical biodiversity hotspot of the Western Ghats in India. We
21 sampled eight plots on a sky-island using mist-nets for four years in a ‘Robust design’ mark-
22 recapture framework. Based on model selection using AIC values, the model with survival as a
23 function of disturbance fits the data better than models with abundance or with these parameters
24 modeled as functions of forest patch size. Shortwing density and sex ratio were not different
25 across forest patch sizes or differing disturbance regimes. However, the survival rate of the
26 species significantly decreased with increasing disturbance but was not related to forest patch
27 size. Our study is possibly the first to provide critical baseline information on the demography of
28 a tropical understory species from this region.

29 **KEYWORDS**

30 Shortwing, Western Ghats, demography, survival rate, disturbance, birds, sky island, mark-
31 recapture, Robust design, India, Shola forest

32 **INTRODUCTION**

33 One of the most important conservation challenges of our times is the anthropogenic
34 fragmentation of contiguous habitat to form disjunct patches. In this scenario, it has often been
35 argued that preserving large tracts of habitats is essential for the long-term survival of species

36 (Diamond et al. 1987, Beier et al. 2002) though smaller patches could also contribute in this
37 regard (e.g., Githiru and Lens 2006a). In contrast to habitat loss, disturbance unobtrusively
38 affects the demography of different species, especially understory insectivorous birds that are
39 extremely sensitive to disturbances in forest structure (Thiollay 1999, Sekercioglu et al. 2002).

40 The quality of the habitat can affect critical demographic parameters of a population in various
41 ways. Better-quality areas, for example, can support higher densities of a species due to the
42 greater availability of resources leading to smaller territories (e.g., Githiru and Lens 2006b).
43 Species that are sensitive to fragmentation can also occur less commonly in sub-optimal habitats
44 such as small degraded fragments (e.g., Zanette et al. 2000). Conservation managers, in fact,
45 often use density as a surrogate for the health of a population (e.g., Irwin et al. 2005). However,
46 the rate of turnover in suboptimal habitats can be higher than that in better-quality patches (e.g.,
47 Zanette 2001).

48 Apart from survival rates and population densities, one of the important demographic factors is
49 adult sex ratio (ASR), an indicator of a population's trajectory, behavioral ecology and its
50 conservation status (reviewed in Donald 2007). ASR is often known to correlate with population
51 trends or habitat quality (Zanette 2001) and has already been used as an indicator of population
52 status in the management of some mammals (Donald 2007). Most research providing
53 information on survival rates and population densities have, however, come from temperate
54 regions.

55 Tropics, in general, are thought to be inhabited by species that have a "slow" life-history strategy,
56 where high survival rates in optimal patches generate only few openings for new recruits, leading
57 to low individual turnover rates (e.g., Morton and Stutchbury 2000). While there have been a few

58 studies estimating survival rates, particularly using mark-recapture methods, from the tropics
59 (e.g., Karr et al. 1990, Brawn et al. 1995, Brawn et al. 1999, Githiru and Lens 2006b), there have
60 been no studies from the Asian tropics, though they host several global biodiversity hotspots and
61 their endemic species.

62 The Shola forests in the high-elevation sky islands of the Western Ghats consist of naturally
63 occurring patches of forests that range from 0.1 ha to thousands of hectares, with this patchiness
64 originating from a combination of factors including the geography of the landscape, wind
65 direction and rainfall (Caner et al. 2007). Such patchiness is known to affect various aspects of
66 species demography in both naturally and artificially fragmented landscapes (e.g., Dooley Jr and
67 Bowers 1998). We investigated the effect of such patchiness and habitat disturbance or
68 degradation on the threatened (BirdLife International 2001), endemic, understory insectivorous
69 bird, the white-bellied shortwing *Brachypteryx major* (Robin et al. 2010), also known as white-
70 bellied blue robin. Specifically, we examined the effect of patch size and disturbance on (a) the
71 population density, (b) survival and (c) sex ratios of shortwing individuals in our study patches.

72 **METHODS**

73 *Study area and design*

74 This study was conducted in the Grasshills National Park, located within one of the sky-islands
75 of the Western Ghats, from 2003 to 2007. This region, lying on a high-elevation plateau, ranging
76 from 1400 m to 2400 m above mean sea level (a.s.l), has an undulating topography in a matrix of
77 natural patches of forests and grasslands (described in Shanker and Sukumar 1998).

78 We established eight study plots in the Park, at an elevation of 1450 m to 1600 m a.s.l. In one
79 large patch of forest (> 2500 ha), we laid four plots (Plots A to D) of 2.5 ha each, along a

80 disturbance gradient. Disturbance in this landscape resulted entirely from anthropogenic
81 activities, such as the collection of fuelwood. This was subjectively quantified (see below) in
82 different areas before the selection of plots. We selected Plots A to D with a gradient of
83 disturbance decreasing from Plot A to Plot C and with Plot D being an undisturbed plot. We also
84 chose four small, independent, undisturbed patches (Plots E to H; 1.6, 1.1, 0.6 and 0.6 ha in size
85 respectively), where each patch formed a separate plot. Plots E to H were selected such that they
86 would be close to one another and were also the patches closest to the large patch (Plots A to D).
87 This design was adopted to detect any metapopulation-level inter-patch movement, as well as to
88 include patches that varied in size. Note that this selection of study plots, limited by its natural
89 availability, permits some inference about relationships involving disturbance in large
90 continuous habitats, and about relationships involving patch size in relative undisturbed areas,
91 but not inferences about the potential interaction of disturbance and patch size.

92 **Trapping design**

93 Mist-nets, 12 m × 2 m, at a net density of 10 nets per hectare in each plot, were kept open from
94 the break of dawn (0550 – 0600) for five hours each day, for three consecutive days to capture
95 birds. Each captured bird was tagged with numbered metal bands. The study was designed to be
96 conducted according to Pollock's (Pollock 1982) Robust Design where primary sampling periods
97 (five) each include multiple secondary sampling periods (three). This design assumes that the
98 population is 'open' to immigration, emigration, births and mortality across the four consecutive
99 years (i.e. five primary sampling occasions) in our study while it is 'closed' across the three days
100 of secondary sampling occasions within each year. This allowed us to compute the survival rate
101 of individuals in each plot across the primary sampling periods and estimate abundance in the
102 secondary sampling periods.

103 **Density and survival analysis**

104 Two plot-specific measures, used as covariates of survival rate and abundance, were plot size (a
105 continuous variable, measured in ha) and disturbance category (a categorical variable). The plots
106 were classified into four qualitative disturbance categories, scaling from 0 (undisturbed) to 4
107 (highly disturbed), based on the number of people encountered, number of cut stems and
108 openness of the canopy.

109 From the capture data from each plot, we constructed individual capture histories with the ‘1’s
110 indicating captures and ‘0’s indicating no captures on each sampling occasion during each year.
111 Initially, we had planned to use multistate capture-recapture models in order to estimate
112 movement among patches, but the observed numbers of movements was so small (see below)
113 that we instead used single-site models. All juveniles and sub-adults were removed from the
114 analysis. Pollock’s Robust Design originally used closed population models to estimate
115 abundance and the traditional Cormack-Jolly-Seber model (CJS) to estimate survival. The closed
116 population models include estimators of capture probability and abundance that are robust to
117 heterogeneity in detection probability while the CJS model includes survival estimators that are
118 robust to this heterogeneity. Hence, Pollock’s Robust Design provides a suitable framework for
119 estimating both survival and abundance. Kendall et al. (1995) later developed a full-likelihood
120 framework that modeled within- and between-period information simultaneously, permitting the
121 use of reduced parameterizations. We used the program MARK (White and Burnham 1999) to
122 analyze the data using this integrated approach. It should be noted that here ‘survival’ is really
123 “apparent” survival, the complement consisting of mortality as well as permanent emigration,
124 which cannot be separated in this analysis. In the different models, capture and recapture
125 probabilities were modeled as either constant or variable across secondary periods and as

126 variable across primary periods. Individual heterogeneity in capture probability was included
127 using a 2-point mixture (Pledger 2000), which was allowed to vary across the years. Survival,
128 similarly, was modeled as either constant or variable across the four intervals, and/or as differing
129 between study plots. Temporary emigration was modeled as Markovian (γ' , γ''), random ($\gamma' =$
130 γ''), or absent ($\gamma' = \gamma'' = 0$) (Kendall et al. 1997). Additionally, we modeled survival probabilities
131 as functions of patch size and disturbance using the design matrix to specify linear-logistic
132 models. The effects of patch size and disturbance on survival were modeled as interacting with
133 temporal variation or as additive to temporal variation. In all, our candidate set consisted of 39
134 models. The performance of different models was assessed based on the lowest Akaike
135 Information Criterion (AIC) value. Density was estimated by calculating the effective sampling
136 area by adding a strip width equal to half the average territory diameter to the sides of a plot
137 when similar vegetation continued on that side (Wilson and Anderson 1985).

138 **Molecular sexing and sex determination**

139 The sexually monomorphic shortwing was sexed using molecular methods with standard primers,
140 P2/P8 (Griffiths et al. 1998) and using a Discriminant Function Analysis (DFA) based on
141 morphometric measurements of wing, tail and beak. Sex was assigned for 91 different
142 individuals of the total 116 captured in this study (described in Robin et al. 2011). Some
143 individuals (25) from across different plots and years remained unsexed and were not used in this
144 analysis as they were without both genetic samples and a complete set of morphological
145 measurements for the DFA to predict their sex. We calculated the sex ratio as the proportion of
146 females in the plot. We combined sex data from all small plots and denoted this combined group
147 as 'S' as the small plots E, F, G and H had very few individuals, with some years even
148 characterized by single individuals,. We then examined year- and plot-wise breakdowns of sex

149 ratios and compared them using the Kruskal-Wallis chi-square test in the statistical programming
150 language R (R Development Core Team 2011).

151 **RESULTS**

152 **Captures and movement**

153 We captured 116 individual adult Shortwings across the four years of sampling. We detected
154 only two instances of movement during the entire study period, one individual from Plot B to A,
155 the most disturbed plots, and another between two small patches (G and H). We were unable to
156 detect any regular patterns of movement across any other plots during this study period.

157 **Density and survival rate**

158 Models with survival varying as a function of disturbance received the greatest support (AICc
159 weight 0.95985) from the data of all 39 models tested, performing better than models that
160 included plot size (AICc weight 0.22108, Appendix 1). In this model, initial capture probability
161 was constant each year within a season but varied across years, while recapture probability was
162 constant within and across years (Appendix1). Parameter estimates indicated that there was
163 severe trap shyness in the birds, as the estimated recapture probability (0.21 ± 0.03 SE) was
164 much lower than the capture probabilities in different years (0.45 ± 0.04 , 0.62 ± 0.05 , 1- SE
165 not estimable). Temporary emigration was assumed to be random (Kendall et al. 1997) in the
166 highest ranked models.

167 The mean population density \pm SE across all plots was 2.8 ± 0.37 birds per ha. The abundance
168 estimates varied across years and across plots, and showed that the large patch had a higher
169 abundance of birds than did the small plots. The undisturbed plot had the highest abundance
170 estimate, while all small patches had low abundance estimates. The population density estimates

171 (Figure 1), however, did not show evidence of a difference in density between plots based either
172 on disturbance or size. The temporal variability in the density of the small patches still appeared
173 to be higher than that of the plots in the large patch. Plot C, with very little disturbance, had the
174 lowest estimated density of shortwings. The arithmetic mean survival of the population was 0.58
175 ± 0.07 , which indicated that over half the individuals from the previous year survived to the next
176 year. Survival rate was a function of disturbance in the best model (Figure 2), with disturbed
177 plots having significantly lower survival rates; Plot A, with the highest disturbance level, had the
178 lowest survival rate.

179 **Adult sex ratio**

180 The overall sex ratio (proportion females) of the entire shortwing population that was sampled
181 across different plots over all years was male-biased (0.44). However, a closer inspection of the
182 data, plot- and year-wise, showed that, barring a few years, the most disturbed plot (A) appeared
183 to be more female-biased than were less disturbed plots (Figure 3). This pattern, however, was
184 not significant over all years (Kruskal-Wallis chi-square = 2.7, $df = 2$, $p = 0.26$).

185 **DISCUSSION**

186 *Density*

187 In general, it is expected that for understory insectivorous birds, fragmented and otherwise sub-
188 optimal habitats harbor a lower density of individuals (e.g., Zanette et al. 2000) compared to the
189 largest and least disturbed fragments (e.g., Githiru and Lens 2006b). The white-bellied shortwing
190 is a species that is highly specific to this habitat and currently considered threatened due to
191 habitat loss. Our results show that there was no consistent difference in shortwing densities
192 across different patch sizes or degrees of disturbance. However, there was a marginally higher
193 estimated density (4.54 individuals/ha) and the highest estimated abundance (14 individuals) of

194 shortwings in the undisturbed plot of the large patch (Plot D). This pattern is similar to that
195 obtained in a study of the white-starred robin, another tropical passerine (Githiru and Lens
196 2006b). The failure to detect any significant effect of disturbance on shortwing density could be
197 because population density is not sensitive to the changes we are measuring. The lack of
198 baseline data on this species or data on other similar species from this region hinders any further
199 conclusions.

200 There is very little information on bird densities from the Western Ghats ., with Sridhar (e.g.,
201 Raman and Sukumar 2002, Sridhar 2005) being the only study with comparable data. This study
202 used point-counts to estimate bird densities in an area that overlapped with one of our study plots
203 (Plot B) during the same study period. The estimated shortwing density of 0.30/ha in one
204 sampling season was approximately ten-fold lower than our estimate for the same year ($3.04 \pm$
205 0.5) or that averaged over five years (2.6 ± 0.4). This could be because exclusively understory
206 species like the shortwing are inherently difficult to detect in the dense evergreen forest
207 understory, the same reason why the species may have been recorded so few times over the last
208 century (2005).

209 *Survival rates in small patches*

210 Surprisingly, forest patch size did not affect survival more than did disturbance although the
211 small forest patches were actually very small (< 1 ha). Other studies on similar species such as
212 the white-starred robin (Robin and Sukumar 2002) in Africa also failed to detect an effect of
213 forest patch size on survival although their smallest patch was three times larger (3ha) than that
214 of this study. We believe that the high survival rate in small patches may, once again, be because
215 Shola forest species such as shortwings are adapted to some level of patchiness in the landscape,
216 and individuals consistently persisted in these patches over years. Ancillary data (Robin pers.

217 obs.) indicate that shortwings were using these small patches not just for foraging but also for
218 nesting and breeding, indicating the important role that small patches of natural forest play in the
219 biology and survival of species such as the shortwing.

220 *Survival in disturbed areas*

221 We found that habitat disturbance was associated with lowered survival rates of shortwings. Our
222 most disturbed plot (A) had, in fact the lowest apparent survival rate of this bird over the entire
223 study period. This could be due to higher mortality rates from predation (Githiru and Lens
224 2006a), higher levels of permanent emigration, or because these areas are used by a larger
225 number of transients (Gibbs 1991) as has been demonstrated in other tropical regions (Perret et al.
226 2003). Other studies that have similarly demonstrated higher turnover of individuals in such
227 suboptimal habitats (Johnston et al. 1997). As our data was not sufficient to include transience in
228 our model, we are at present working towards assessing between-patch movement with genetic
229 tools.

230 *Adult sex ratios*

231 Adult sex ratios (ASR) in wild birds remain very poorly described, though skewed sex ratios are
232 common in the wild (eg. Zann 2001). Most studies have found male-biased sex ratios in birds
233 while female-skewed ASR appear to be the most common pattern in mammals. We found
234 female-biased ASR in some of our study plots, particularly the most disturbed plot, a rare pattern
235 in birds, having been recorded in only 19 studies on 14 species (9.5% of all studies) so far
236 (reviewed in Donald 2007). Given the generally balanced offspring sex ratio, a skewed ASR can
237 only be explained by higher mortality or dispersal of one of the sexes. Our limited data, with few
238 individuals in each plot, do not permit us to model the effects of transience and sex-specific
239 survival though we plan to do this in the future with additional sampling.

240 This study has provided evidence that a tropical understory insectivore is adversely affected by
241 habitat disturbance more than by habitat patchiness. Population density did not reflect
242 disturbance effects but survival rate and adult sex ratios were relatively more sensitive to
243 disturbance. Although abundance and population density continue to be used as variables that
244 inform many conservation measures, it appears from our study that other demographic
245 parameters such as survival and adult sex ratio, though less easy to measure, could be more
246 sensitive to habitat disturbance and quality. Anthropogenic habitat fragmentation is conspicuous
247 and has attracted much attention from conservation biologists for its negative effects on
248 population dynamics. In species that have evolved in patchy habitats, where fragmentation
249 predates human influence, more subtle habitat disturbance may impact the survival of such
250 species much more than would larger-scale fragmentation.

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- 340

341 **Figure legends**

342 Figure 1: Density of shortwings (number of individuals per ha) in plots across disturbance

343 categories and patch size. Error bars represent SE from yearly variation in density.

344 Figure 2: Survival rate of shortwings (expected proportion of individuals that survive and do not

345 permanently emigrate from one sampling year to the next) in plots across disturbance categories

346 and patch size. Note that the plots are aligned along a disturbance gradient, with Plot A being the

347 most disturbed and Plots D to H are undisturbed.

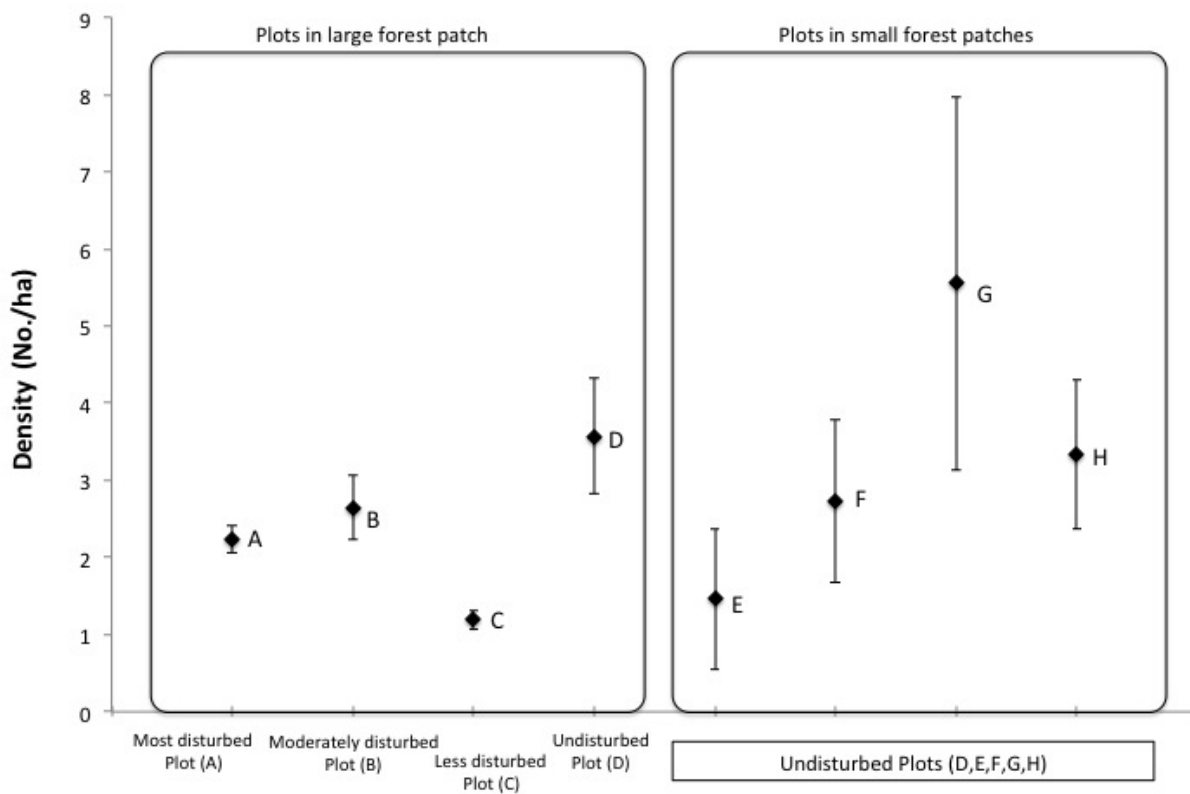
348 Figure 3: Mean Adult Sex Ratio - Proportion of females in plots. S indicates a sum of all small

349 plots (E to H). Plot A is the most disturbed plot. The error bars indicate standard error across

350 multiple years.

351

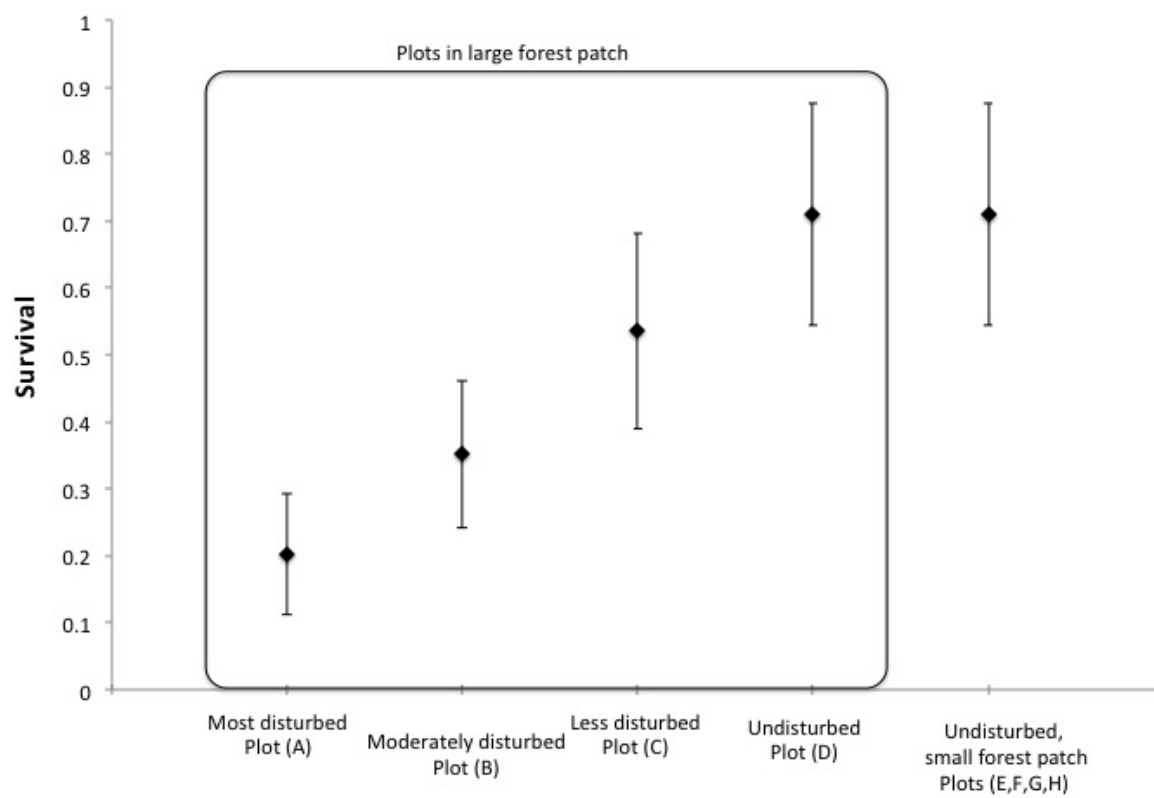
352 Figure 1:



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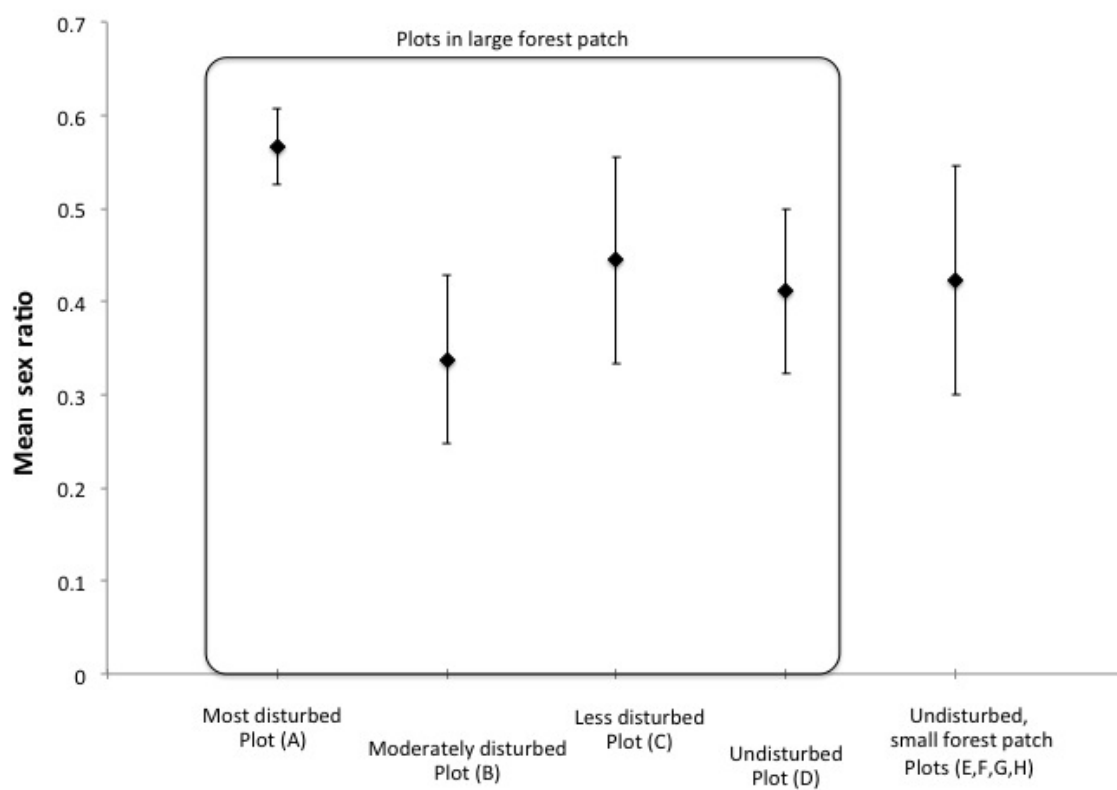
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355 Figure 2:



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358 Figure 3:



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