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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ABSTRACT

The occurrence, density and survival of a species often depend on various aspects of the habitat

that it occupies including patch size and disturbance. The demography of most threatened

tropical species largely remain unstudied but could provide valuable information about their

biology and insights for their conservation. Our study examined the effect of patch size and

disturbance on different demographic parameters of an understory, threatened, endemic bird, the

white-bellied shortwing in the tropical biodiversity hotspot of the Western Ghats in India. We

sampled eight plots on a sky-island using mist-nets for four years in a 'Robust design' mark-

recapture framework. Based on model selection using AIC values, the model with survival as a

function of disturbance fits the data better than models with abundance or with these parameters

modeled as functions of forest patch size. Shortwing density and sex ratio were not different

across forest patch sizes or differing disturbance regimes. However, the survival rate of the

species significantly decreased with increasing disturbance but was not related to forest patch

size. Our study is possibly the first to provide critical baseline information on the demography of

a tropical understory species from this region.

KEYWORDS

Shortwing, Western Ghats, demography, survival rate, disturbance, birds, sky island, mark-

recapture, Robust design, India, Shola forest

INTRODUCTION

One of the most important conservation challenges of our times is the anthropogenic

fragmentation of contiguous habitat to form disjunct patches. In this scenario, it has often been

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 $\times$ 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.

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 (γ'=

130   γ''), or absent (γ'= γ''=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 ±

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. Zanette 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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Figure legends

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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

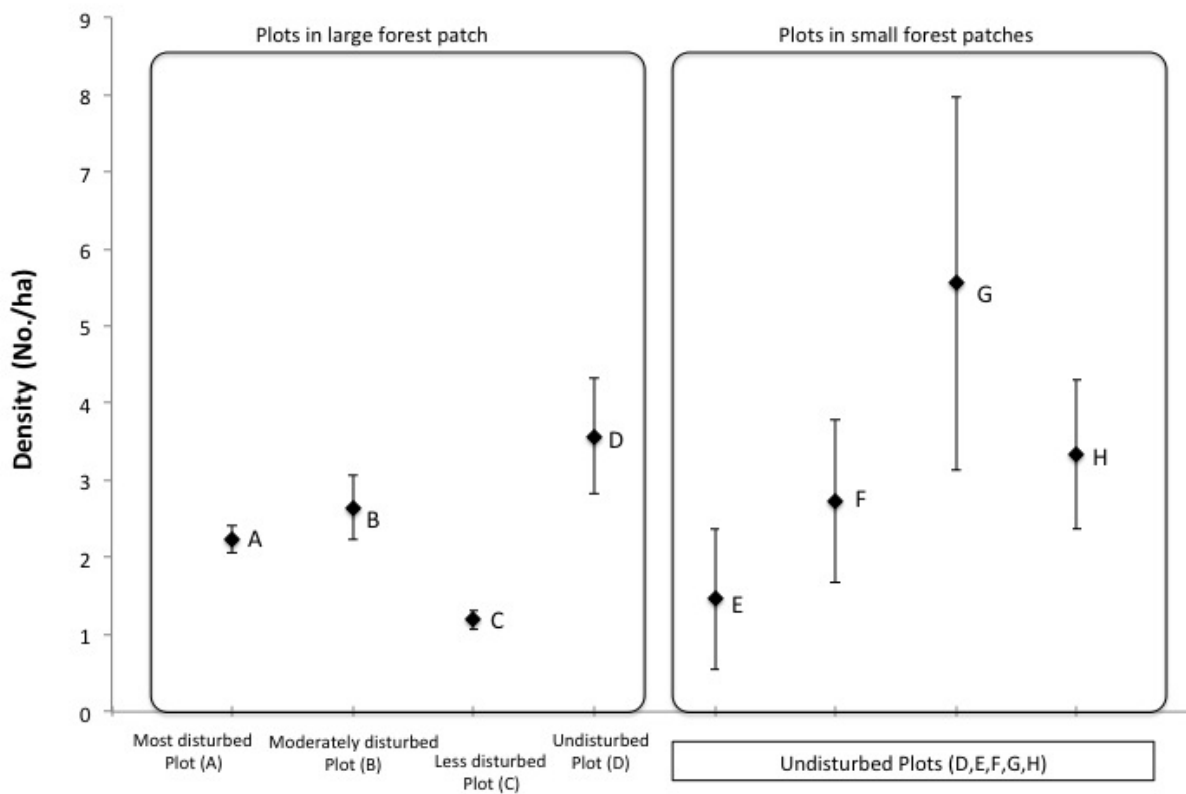347   most disturbed and Plots D to H are undisturbed.

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
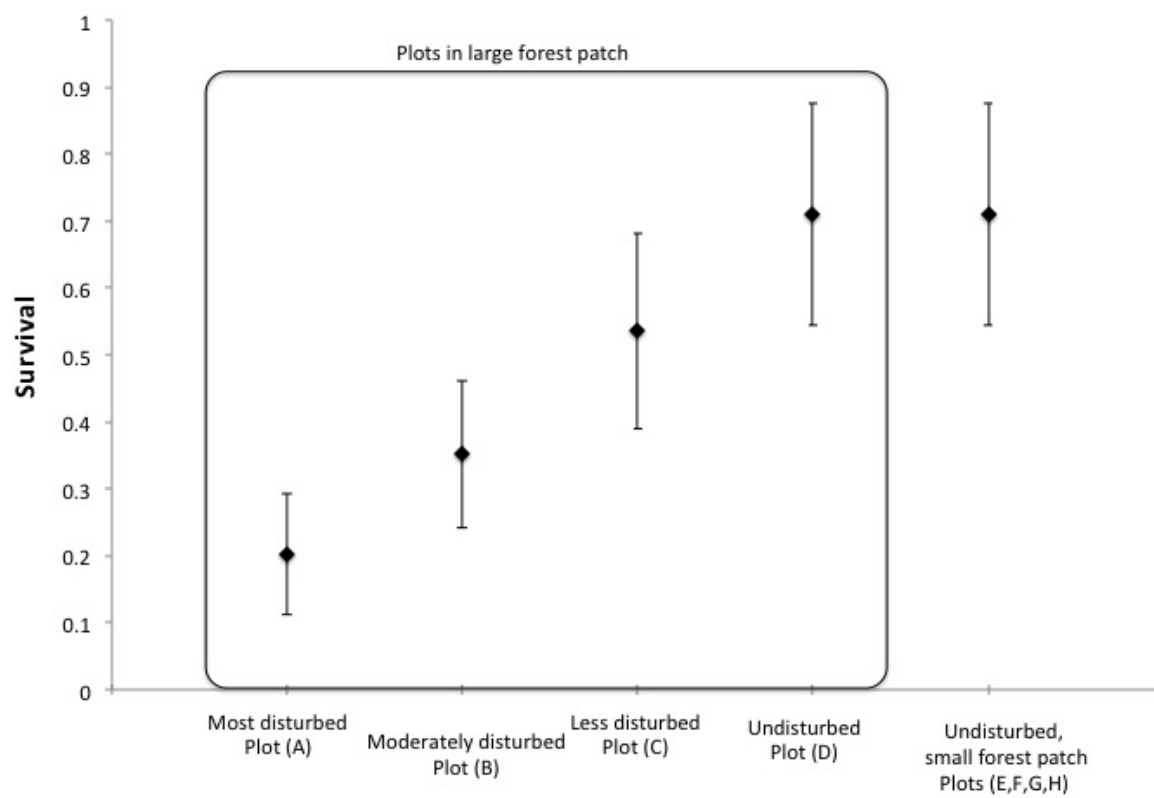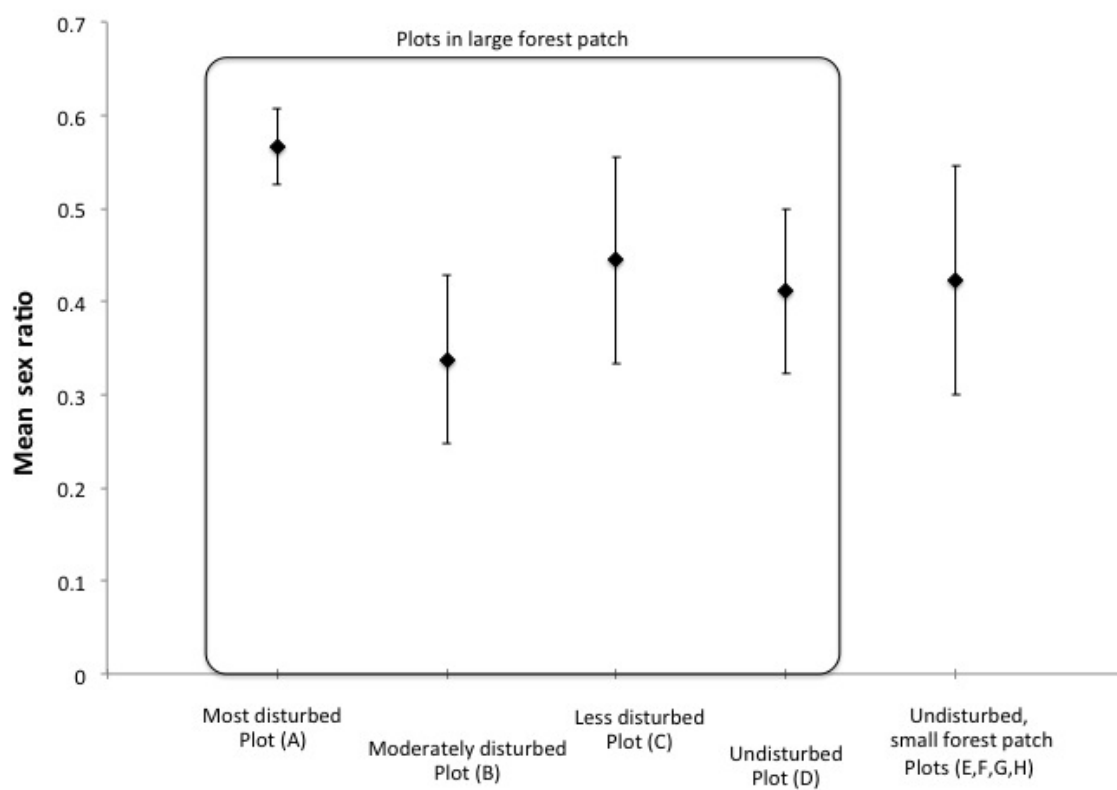
350   multiple years.

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352   Figure 1:

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