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3 **Estimating Key Largo woodrat (*Neotoma floridana smalli*) abundance using**
4 **spatially-explicit capture recapture and trapping points transects**

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6 RH: Estimating Key Largo woodrat abundance

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23 **KEY WORDS** abundance, distance sampling, small mammals, spatially explicit
24 capture-recapture, trapping point transects.

25

26 **ABSTRACT**

27 The Key Largo woodrat (*Neotoma floridana smalli*) is an endangered rodent with a
28 restricted geographic range and small population size. Establishing an efficient
29 monitoring program of its abundance has been problematic, as previous trapping
30 designs have not worked well because the species is sparsely distributed. We
31 compared Key Largo woodrat abundance estimates obtained using trapping point
32 transects (TPT) and spatially explicit capture-recapture (SECR) based on statistical
33 properties, survey effort, practicality and cost. Both methods combine aspects of
34 distance sampling with capture-recapture, but TPT relies on radio-tracking individuals
35 to estimate detectability, and SECR relies on repeat capture information to estimate
36 densities of home ranges. Abundance estimates using TPT in the spring of 2007 and
37 2008 were 333 woodrats (CV=0.46) and 696 (CV=0.43), respectively. Abundance
38 estimates using SECR in the spring, summer and winter of 2007, were 97 (CV=0.31),
39 334 (CV=0.26), 433 (CV=0.20) animals, respectively. TPT used approximately 960
40 person-hours and 1,010 trap nights per season. SECR used approximately 500 person-
41 hours and 6,468 trap nights per season. Significant time was saved in the SECR
42 survey by setting large numbers of traps close together, minimizing time walking
43 between traps. TPT was practical to implement in the field, and valuable auxiliary
44 information on Key Largo woodrat behavior was obtained via radio collaring. In this
45 particular study, detectability of the woodrat using TPT was very low and
46 consequently the SECR method was more efficient. Due to large uncertainty in
47 estimates, both methods require a substantial investment in survey effort to detect any
48 change in abundance.

49 The Key Largo woodrat (*Neotoma floridana smalli*) is one of six recognized
50 subspecies of the eastern woodrat (*Neotoma floridana*). It has a highly restricted
51 geographic range, occupying extant, tropical hardwood hammock on northern Key
52 Largo, Florida, USA. In 1984, the Key Largo woodrat was listed as a federally
53 endangered subspecies, and is subject to a recovery plan that identifies potential
54 threats and describes management actions to be undertaken (US DOI 1984; US FWS
55 1999). Management actions have included public land acquisition on north Key
56 Largo, through the establishment of two wildlife reserves that have restricted public
57 access; programs governing relocation, captive breeding and reintroduction for
58 captive bred individuals (Alligood et al. 2008, 2009, FWC unpublished data); predator
59 control (Muiznieks 2006), and enhancing habitat with supplemental nest structures
60 (Winchester et al. 2009). A reliable population abundance estimate, together with an
61 associated measure of uncertainty, is essential to evaluate the effectiveness of
62 management actions and guide decision making for the Key Largo woodrat
63 population.

64

65 Since the Key Largo woodrat is nocturnal, cryptic, and sparsely distributed, standard
66 population monitoring methods do not work well (e.g., require unrealistic investment
67 of survey effort; Winchester 2007). A review of potential methods to estimate Key
68 Largo woodrat abundance conducted by Potts et al. (2006) concluded trapping point
69 transects (TPT, Buckland et al. 2006, Potts et al. 2012) and spatially explicit capture-
70 recapture (SECR, Borchers and Efford 2008, Royle and Young 2008) were two
71 abundance estimation methods that warranted further investigation to assess whether
72 either of these methods could realistically form the basis of a long-term monitoring
73 program of Key Largo woodrat abundance.

74

75 Here, we compare abundance estimates for both methods based on statistical
76 properties, survey effort, practicality and cost for data collected on the Key Largo
77 woodrat. Due to practical limitations, the TPT and SECR surveys could not be
78 undertaken simultaneously, nor is “true” abundance of the woodrat known. Potts et al.
79 (2012) presented a detailed statistical analysis of TPT, and estimated yearly spring
80 abundance of the woodrat between 2008 and 2011 using TPT. Here, we analyze an
81 additional data set collected during a pilot study in 2007, and compare the 2007 and
82 2008 abundance estimates obtained using TPT with those from an SECR survey
83 undertaken during spring, summer and winter of 2007.

84

85 **STUDY AREA**

86 Key Largo is the first island in the Florida Keys, linking the lower keys to the
87 mainland. It is the largest island of the keys, covering approximately 21 km². Key
88 Largo has an average elevation of 2.4 m above sea level and is formed from the
89 exposed tops of ancient coral reefs (Hersh 1981). The climate of Key Largo is
90 subtropical. Mean annual rainfall is approximately 102 cm (40 inches), with the
91 majority of this precipitation occurring between June and October (US FWS 1999).
92 Average maximum daily temperature in summer is approximately 29 degC (84 degF)
93 decreasing to approximately 21 degC (70 degF) in winter (Gore and Loggins 2005).

94

95 Although tropical hardwood hammock was once the dominant vegetation type across
96 Key Largo, due to urbanization, approximately only one third remains within two
97 protected reserves that fall under different jurisdiction: the Dagny Johnson Key
98 Largo Hammock Botanical State Park, managed by the Florida Department of

99 Environment and Protection, and the Crocodile Lake National Wildlife Refuge,
100 managed by the US Fish and Wildlife Service. Despite its protected status, the
101 remaining tropical hardwood hammock is highly fragmented with roads, tracks, and
102 abandoned developments.

103

104 The age and structure of the hardwood hammock is not homogeneous throughout Key
105 Largo (Gore and Loggins 2005). Ross et al. (1992) and Ross et al. (1995) identified
106 three strata delineated by age: young (disturbed since 1971, approx. 87 ha), medium
107 (disturbed between 1940-71, approx. 327 ha), and old (disturbed before 1940, approx.
108 431 ha). A fourth stratum based urban areas located within the hammock (approx. 127
109 ha, representing approx. 13% of the total survey region) was omitted from this study
110 since it was not considered suitable habitat.

111

112 **METHODS**

113

114 **Spatially explicit capture-recapture (SECR)**

115

116 SECR uses the known locations of the traps and the spatial pattern of recapture events
117 to estimate the density of home range centers and a capture function (Borchers and
118 Efford 2008, Royle and Young 2008). The capture function is conceptually consistent
119 with a detection function in distance sampling, in that the probability of detecting an
120 individual is assumed to be a radially decreasing function of the distance between the
121 center of the animal's home range (unknown) and the distance to the trap (Buckland et
122 al. 2001). Each animal has one home range center, and it follows that the density
123 estimate of home range centers can be used to calculate abundance of all animals in

124 the survey region.

125

126 *Data collection.*— Using a stratified random design with proportional
127 allocation, 33 grids were established in the study area across three habitat strata (Fig.
128 1A). Sampling units were allocated in proportion to the area available in each habitat
129 stratum.

130

131 Each of the 33 grids was trapped during the spring (March – May), summer (July –
132 September) and winter (October – December) of 2007 for four consecutive nights.

133 Each grid was a 7 by 7 array, with one single-catch Sherman trap placed at each trap
134 station (i.e., 49 traps per grid) and 10 m spacing between traps (i.e., 19,404 trap nights
135 in total). Traps were opened and baited with whole oats in the late afternoon and
136 checked the following morning within the first two hours after sunrise. All captured
137 woodrats were double-marked with passive integrated transponders (PIT) tags (AVID,
138 Norco, California) and ear tags (#1005 Monel ear tags, National Band and Tag,
139 Newport, Kentucky). Sex was recorded. Capture and handling was conducted under
140 U.S. Fish and Wildlife endangered species permit Nos. TE139405-0, and TE137411-
141 0, and, Florida Fish and Wildlife Conservation Commission Permit Nos. WV06293,
142 Florida Department of Environmental Protection Division of Recreation and Parks
143 Research and Collecting Permit Nos. 5-07-20, and 5-08-34, and University of Georgia
144 Institutional Animal Care and Use Permit No. A2006-10206-m1.

145

146 *Capture probability model.*—The capture probability model, $p_s(\mathbf{d}_k(X))$,
147 models the probability of detecting an animal at trap k on occasion s , when the
148 animal's true but unknown home range center is X (as defined by the coordinates of a

149 point). Three forms of the capture probability model were considered: the half-
150 normal, the exponential or the hazard rate. Following Efford et al. (2009), the form of
151 the capture probability was first selected (i.e., null models were fitted whereby the
152 parameters in the capture probability models were not dependent on any covariates).
153 We used stepwise AIC to select a suitable model (but not necessarily the model with
154 minimum AIC, Akaike 1973, Buckland, Burnham and Augustin 1997, Burnham and
155 Anderson 2003). The covariates considered during model selection included time (as
156 a factor, one level for each occasion), sex (as an individual level covariate), habitat
157 (habitat strata was either young, medium or old), and two global behavioral trapping
158 responses (learned, whereby there was a step change in the parameter after the first
159 detection of an animal; or transient, where the parameter depended on detection at a
160 previous occasion, i.e., a Markovian response).

161

162 Since the data were naturally sparse (i.e., few captures across the 33 grids, despite a
163 large survey effort), “grid” could not be used as a covariate in the model, and
164 consequently the probability of capture at distance zero (g_0), and also the shape
165 parameter (σ) was assumed equal across all grids. This assumption may not hold if the
166 capture probability differs between grids (e.g., if there is a north-south gradient in
167 capture probability with grid location, or changes with habitat type) and consequently
168 the variability of abundance estimates might be biased low. A step-wise model
169 selection procedure was used (rather than testing all combinations of covariates), as
170 not all models could be fitted with all combinations of covariates, as the number of
171 recapture events was small and this caused parameter identifiability issues (as
172 observed when e.g., estimates of standard errors are unrealistically low – essentially
173 zero – or unrealistically high).

174

175 *Estimating density of home range centers.*—Density (\hat{D}) of home range
176 centers was assumed to be distributed in space by a homogeneous Poisson process. \hat{D}
177 was estimated using a Horvitz-Thompson-like estimator (Borchers and Efford 2008):
178

179
$$\hat{D} = \sum_{i=1}^n \frac{1}{\hat{a}(\hat{\theta}, z_i)}$$

180

181 where $\hat{a}(\hat{\theta}, z_i)$ was the probability of detecting an animal i (for $i= 1, \dots, n$) given the
182 parameters of the capture probability model defined in $\hat{\theta}$ (e.g., g_0 and σ for a half-
183 normal detection function) and a set of individual-based observed covariates z_i ,
184 regardless of its home range center (i.e., $\int p(X) dX$ where $p(X)$ is the probability of
185 detecting an animal at least once in any trap). The integration of $\int p(X) dX$ was
186 bound in space by specifying a habitat mask, that essentially defines a set of points in
187 the survey region where an animal's home range center may be located. Without
188 specifying a habitat mask, home range centers might be located in habitat known to be
189 unsuitable causing density to be underestimated (Efford et al. 2009). A habitat mask
190 was created using the boundary between known potential habitat (i.e., hammock) and
191 non-habitat (i.e., surrounding mangrove swamp), available as an ESRI shapefile
192 (<http://www.esri.com/>).

193

194 Density and variance were estimated by model-averaging across all fitted models
195 proportional to AIC weight. All modeling was undertaken using the “secur” package
196 (version 2.9.5, Efford 2010) in the statistical program R (v. 3.2.2, R Development
197 Core Team 2010). Density (D) was then converted to abundance (N) using the area

198 (A) contained in the survey region (as defined by the habitat mask): $N = D A$.

199

200 In addition to the classic assumptions of standard capture-recapture (i.e., the
201 population is closed within each of the 4-day secondary sampling occasions, each
202 captured individual is uniquely marked and marks were not lost, or misread), SECR
203 has the following additional assumptions (Borchers and Efford, 2008):

- 204 1. Animals occupy home ranges, and home-range centers are distributed within
205 the masked habitat region following a Poisson-distribution, and
- 206 2. Animals are detected independently of each other.

207

208 **Trapping point transects (TPT)**

209

210 TPT requires two surveys (Buckland et al. 2006, Potts et al. 2012). Data collected
211 during the *trial survey* are used to estimate a detection function, $g(r)$ (i.e., the
212 probability of catching an animal in a trap, given that the animal was at distance r
213 from the trap, when the trap was set). The distance between the animal and the trap,
214 when the trap was set might be known by visually locating the animal (e.g., Buckland
215 et al. 2006) or via radio tracking (e.g., Potts et al. 2012). Then, for each animal
216 detected during a separate *main survey*, its probability of detection can be predicted
217 using the estimated detection function. A Horvitz-Thompson-like estimator (Borchers
218 et al. 1998) can be used to estimate overall abundance. A TPT pilot survey was
219 undertaken in spring 2007, and repeated yearly each spring between 2008 and 2011
220 (Potts et al. 2012). Here, we describe data collection for the 2007 and 2008 field
221 seasons.

222

223 *Main survey data collection.*—The *main survey* comprised a randomly placed
224 systematic grid of 137 sample points with 250 m trap spacing throughout potential
225 habitat (Fig. 1B). Two traps were set at each trap location, following the same
226 procedures as the SECR survey (i.e., opened in the afternoon using whole oat bait and
227 checked the following morning), and trapped for three consecutive nights. All
228 captured woodrats were double-marked with PIT (AVID, Norco, California) and ear
229 tags (#1005 Monel ear tags, National Band and Tag, Newport, Kentucky). Sex was
230 recorded. Trapping point transect fieldwork was permitted by the US Federal Fish
231 and Wildlife Permit #TE139405-2, Florida Fish and Wildlife Conservation
232 Commission #WV08573 and Florida Department of Environmental Protection #5-11-
233 03.

234

235 *Trial survey data collection.*—Radio-transmitters were attached using a neck
236 collar (mass < 10 g, AVM Instruments, California) to a subset of captured woodrats
237 for the *trial survey*. Woodrats were selected to ensure equal sex representation in the
238 sample and all weighed over >100 g (i.e., all were adults) to ensure collar weight did
239 not exceed 10% of their body mass (as per permitting regulations). Each radio-
240 collared woodrat was located at its nest daily (the trial start point), and two trial traps
241 were set some random direction away from the trial start point. Typically, three trials
242 were performed at each 5-m interval between 5 m and 60 m, but trial distances did
243 extend beyond 60 m (up to 320 m) to ensure the tail of the distribution function was
244 estimated accurately. Trial traps were checked the following morning to determine
245 whether the radio-collared woodrat was captured at that trial distance, or not.

246

247 *Estimating the detection function.*—Using data collected during the trial

248 survey, a detection function can be fitted using e.g. generalized linear mixed modeling
 249 (GLMM, Bates and Maechler 2009). The sample size of radio-collared woodrats in
 250 the trial survey conducted in 2007 and 2008 was not large enough to estimate the
 251 detection function reliably. And so the detection function used in this analysis was
 252 fitted to trial survey data pooled over 2008-2011 (see Supporting Information). The
 253 detection function assumed that the average probability of detection depended only on
 254 sex of the woodrat, distance of the trial animal from the trap when the trap was
 255 opened and a random effect about the intercept term. The ‘glmer’ function within the
 256 “lme4” package (v 1.1-7, Bates and Maechler 2009) in R (v 3.0.3, [http://cran.r-](http://cran.r-project.org)
 257 [project.org](http://cran.r-project.org)) was used to estimate the detection function.

258

259 *Estimating abundance.*—Abundance estimation followed using a Horvitz-
 260 Thompson-like estimator:

261

$$262 \quad \hat{N} = \frac{A}{A_c} \sum_{i=1}^n \frac{1}{\int_0^w \pi_b(b) \hat{P}(b; z_{i1}, \dots, z_{ij}) db}$$

263

264 where A and A_c are the area of the survey region and covered region, respectively

265 (note, A is the same area as specified by the habitat mask used for the SECR

266 analysis); $\pi_b(b)$ is the probability density function of the random effects distribution;

267 and $\hat{P}(b; z_{i1}, \dots, z_{ij})$ is the estimated probability of detecting the i th animal captured

268 in the main survey unconditional on its distance from the trapping sample point r .

269 That is, $\hat{P}(b; z_{i1}, \dots, z_{ij}) = \int_0^w \pi_r(r) p(r, b; z_{i1}, \dots, z_{ij}) dr$, where $\pi_r(r)$ is the

270 probability density function of distances of individuals from the trapping sample

271 point. A non-parametric bootstrap with $n = 999$ resamples was used to estimate the
272 variance in abundance (Buckland et al. 2006, Potts et al. 2012).

273

274 It is assumed that the estimated detection function of animals in the trials survey is
275 reflective of all animals in the main survey, and all sources of individual variation are
276 included in the detection function.

277

278 **Comparison of survey design-cost considerations**

279

280 Survey effort (i.e., time spent), practicality and cost of data collected with both survey
281 methods are compared and discussed.

282

283 **RESULTS**

284

285 **Comparison of abundance estimation methods**

286

287 In the SECR survey, capture rates were very low despite the large survey effort,
288 ranging between 0.53 capture events per 100 trap nights in summer 2007 to 1.0
289 capture events per 100 trap nights in winter 2007. The number of total capture events
290 in the hardwood hammock varied from 1.7 capture events per 100 trap nights in
291 medium-aged hammock strata to 2.7 capture events per 100 trap nights in the old
292 hammock strata (Table 1).

293

294 The capture model with the lowest AIC suggested g_0 was dependent on sex of the
295 woodrat, and σ was dependent on session. The model-averaged abundance estimates

296 using SECR in the spring, summer and winter of 2007, were 97 (CV = 0.31), 334 (CV
297 = 0.26), 433 (CV = 0.20) animals, respectively (Table 2). See Supporting Information
298 for full model selection results.

299

300 In the main survey of the TPT method, in 2007 there were two female and four male
301 woodrats captured three and six times, respectively, giving a capture rate of 1.1
302 capture event per 100 trap nights. In 2008, six female and eight male woodrats were
303 captured six and 13 times, respectively, giving a capture rate of 2.3 capture events trap
304 100 trap nights. The detection probability of female and male woodrats, as estimated
305 using a detection function fitted to NEW ANALYSIS 645 662 trial points collected on
306 34 35 female woodrats and 552 570 trial points collected on 23 24 male woodrats
307 captured between 2008-2011, was very low (Fig. 2). The resulting estimates of
308 woodrat abundance were 333 woodrats (CV = 0.46) and 696 (CV=0.43) in 2007 and
309 2008, respectively (Table 2).

310

311 **Comparison of survey design-cost considerations**

312

313 The uncertainty in abundance estimates using both methods was disappointingly
314 large, despite the large investment in survey effort. In total, the TPT method required
315 approximately 1,000 trap nights per field season, which equated to approximately 960
316 person-hours (a 4-person field team working full-time for approximately 8 weeks).
317 The majority of this time was spent on the trials survey, and to obtain the detection
318 function used here (Fig. 2), data were pooled across multiple years (2008-2011, Potts
319 et al. 2012). It would be impractical to obtain a sample size sufficiently large within
320 one field season to estimate the detection function used here, as woodrats are rarely

321 captured, making it problematic to catch sufficient individuals to radio-collar in the
322 trials survey (i.e., the trial survey was conducted on 59 individual animals between
323 2008-2011, and it is unlikely that 59 animals could be caught in one field season to
324 allow sufficient trials).

325

326 Survey effort utilized in the SECR study was 6,468 trap nights each season, requiring
327 approximately 720 person-hours (a 2-person field team working full-time for
328 approximately 45 days). However, whilst undertaking this survey, all small mammals
329 captured (including the Key Largo cotton mouse, *Peromyscus gossypinus*
330 *allapaticola*) were processed. During 2007, there were approximately 1,700 small
331 mammal captures, of which, Key Largo woodrat captures represented less than 10%.

332 If the same survey design were to be undertaken focusing just on Key Largo
333 woodrats, we estimate that it might take less than 500 hours per survey, since time
334 would be saved by processing only the target species and not by-catch as well.

335 Significant time-efficiencies for the SECR method, calculated per trap night (i.e., less
336 person-hours required to check more traps) were gained by setting large numbers of
337 traps close together, minimizing the time taken to walk between traps.

338

339 In both methods, traps can be set simultaneously. In the SECR method, approximately
340 3-4 grids were set simultaneously, requiring 196 unique traps. In contrast, TPT
341 required approximately 60 unique traps (20 traps for the main survey and 10 trials, per
342 night), so the initial out-lay for purchasing traps prior to commencing the survey was
343 much less. Also, undertaking 6,468 trap nights in the SECR survey versus *c.* 1,000
344 trap nights in the TPT survey, required approximately six times as much bait to be
345 purchased each survey season. However, the cost of bait for this project was small

346 compared to the overall cost of each survey. These survey costs will vary when
347 implementing these surveys for other species, but typically TPT will require
348 substantially fewer traps than SECR.

349

350 **DISCUSSION**

351

352 **Statistical estimation**

353 In an ideal world, an experimenter would know the true abundance of a population,
354 and use a variety of field methods and statistical techniques to estimate it (e.g.,
355 Parmenter et al. 2003 estimated abundance via complete removal within fenced
356 enclosures). By knowing the survey effort of each field method, and the bias and
357 precision associated with each abundance estimate, the experimenter can make an
358 informed decision about which survey and statistical method provides the smallest
359 variance and least biased estimate of the true population abundance. Although such
360 studies are desirable, they are rare and perhaps impossible for many species and
361 habitats, especially the Key Largo woodrat, with its cryptic nature and low
362 detectability. By comparing population estimates obtained using data collected at
363 around the same time, the risk that differences in population estimates from each
364 method are attributable to population change is reduced.

365

366 Alternatively, simulation studies provide a means for investigating how different
367 sampling strategies and levels of survey effort influence bias and variance in estimates
368 of abundance (e.g., Potts et al. 2012). Potts et al. (2012) and Potts (2011) presented a
369 simulation study for the trapping point transect survey, and found percentage bias in
370 estimated abundance was low (*c.* 5%) with modest levels of survey effort (360 trap

371 nights in the trial survey), but only if underlying average detection probability was
372 high (probability of detecting an individual at distance zero was 0.8) and between-
373 individual heterogeneity was low. Uncertainty and relative bias in population
374 estimates increase with decreasing capture probabilities and increasing individual
375 heterogeneity (i.e., between-individual variation). Field methods in the TPT survey
376 (discussed below) could be changed to increase detectability of woodrats by e.g.,
377 changing bait type, or changing season in which the trapping survey occurs. In
378 addition, we assume the estimated detection function is representative of all woodrats
379 in the main survey and the estimated detection function models all sources of capture
380 heterogeneity.

381

382 The simulation study conducted in Potts et al. (2012) found that detectability and
383 between-individual variability comparable with this trapping point transect study
384 concluded that bias was lowest (*c.* 7%) when at least 24 trials were conducted on each
385 individual in the trial survey. Here, an average of 19 trials were conducted on 35
386 female woodrats and 24 trials on 24 male woodrats, between 2008 and 2011. Since
387 the sample sizes used here are substantially smaller than required to have minimal
388 bias, abundance estimates for the Key Largo woodrat obtained in this trapping point
389 transect study may be biased high. Additionally, simulation studies presented in Potts
390 (2011) and Potts et al. (2012) show that a tripling of effort in the main survey would
391 reduce uncertainty by half.

392

393 In the spatially explicit capture-recapture analysis, we assumed that traps could
394 capture more than one animal, but this is not true since single-catch Sherman traps
395 were used in the field. Since single-catch traps are able to catch only one animal at a

396 time, the capture probability is affected by the presence of other animals that may
397 compete for traps. Capture of an animal disables a trap and immediately reduces the
398 capture probabilities of neighboring animals. This assumption is clearly violated by
399 the method of trapping used in the spatially explicit capture-recapture study, but any
400 bias in estimated density is negligible unless trap saturation is very high ($> 86\%$,
401 Efford et al. 2009). Since the Key Largo woodrat population is at extremely low
402 densities, levels of trap saturation at which density estimates will be biased are
403 unlikely to be attained. In addition, every trap on the trapping grid will have between
404 2 and 4 adjacent traps within 10 meters, which would provide sufficient available
405 traps to any individual woodrat. Examining by-catch for this study, during 2007 there
406 were approximately 1,700 small mammal capture events across the entire survey year,
407 but this was not problematic in terms of trap saturation, as it corresponds
408 approximately to 9% of traps filled. Consequently, we assume that the effect of
409 violating this assumption in the spatially explicit capture-recapture study is minimal.

410

411 There was a large discrepancy in estimated abundance in spring 2007, when both
412 population estimation methods were applied simultaneously. Yearly-variation in the
413 detection function was not taken into consideration in the trapping point transect
414 survey as there were not enough data collected per year to determine this effect (i.e.,
415 the detection function reflects detectability of woodrats between 2008 and 2011, as
416 estimated in Potts et al. 2012). Therefore, the abundance estimate in 2007 using the
417 trapping point transect method might be biased. The discrepancy between estimates in
418 the winter of 2007 using spatially explicit capture-recapture and the spring of 2008
419 using trapping point transect was also large; and the differences might simply reflect
420 the large uncertainty in abundance estimates. Using other statistical models, for

421 example open population spatially explicit capture-recapture models such as those
422 developed by Gardner et al. (2010) may reduce uncertainty in abundance estimates.

423

424 **Field design considerations**

425 In the trapping point transect method, the large spacing (250 m) between trap
426 locations in the main survey increased time to walk between locations to check traps.
427 The benefit of this sparse array of traps was high survey coverage over the area of
428 potential habitat. Consequently, areas of habitat were trapped that had not previously
429 been surveyed. This sparse survey design also increased the encounter rate (i.e.,
430 number of captures per trap night) compared to any other study recently employed in
431 the region. For example, McCleery (2003) and Winchester (2007) obtained capture
432 rates of 0.11 and 0.29 woodrats per 100 trap nights, respectively, whereas the overall
433 encounter rate using trapping point transect was 1.7 woodrats per 100 trap nights (i.e.,
434 28 capture events across both years divided by 1,644 trap nights in the main survey),
435 and for spatially explicit capture-recapture, it was 0.7 (i.e., 40 capture events across
436 three seasons divided by 19,404 trap nights). Importantly, this does not imply that the
437 woodrat population is increasing, just that efficiencies can be gained by differing
438 survey design.

439

440 Extra time-efficiency might be gained by modifying trap configuration, for example
441 by using hollow grids for the spatially explicit capture-recapture approach (Efford et
442 al. 2005). However, hollow grids may reduce an already low encounter rate, and
443 sparse data cause imprecise estimates (Efford et al. 2009). Alternatively, the spatial
444 layout of the grid could be changed (e.g., McCleery 2003 and Winchester 2007 used
445 10 by 10 trapping grids with 25 m trap spacing), or more trapping grids could be

446 placed in the survey area.

447

448 The most expensive aspect of the trapping point transect survey implemented in this
449 study was the initial purchase of radio collars and the field time taken to locate radio-
450 collared woodrats. Key Largo woodrats tend to nest below ground in rock-crevices, or
451 in dumped rubbish including cars, washing machines and refrigerators. Such nesting-
452 substrate attenuates the radio-tracking signal, increasing the time taken to locate
453 individual woodrats (e.g., in some cases, it took 5 or more hours to locate a single
454 woodrat). Should the trapping point transect method be applied to other species that
455 nest in substrate that does not attenuate the radio-tracking signal, the time taken to
456 locate individuals would be substantially less. In future research, it might be possible
457 to avoid the radio-tracking component of the trial survey (leading to significant cost
458 savings), by using the point-of-release as the trial start point (see Potts et al. 2012 and
459 Potts 2011 for further discussion). This point-of-release approach could be viewed as
460 a combination of trapping point transect and spatially explicit capture-recapture, in
461 that the location of traps in the spatially explicit capture-recapture survey are moved
462 each night, in response to where the animal was being captured (centered on its home
463 range). This approach could be used for species that are too small to attach radio
464 collars and should be investigated further.

465

466 One benefit of radio-collaring woodrats in the trapping point transect survey was
467 gathering auxiliary information. Firstly, nest locations were identified and nesting
468 behavior observed. Secondly, in our study we observed predation events by invasive
469 species including Burmese pythons (*Python molurus bivittatus*, Greene et al. 2007)
470 and feral cats.

471

472 With sufficient sample sizes and higher detectability, the trapping point transect
473 approach can perform well with minimal bias in abundance estimates (Potts et al.
474 2012). When applied to the Key Largo woodrat, uncertainties were disappointingly
475 large for the level of survey effort invested here. However, through radio tracking of
476 individuals in the trial survey auxiliary information was obtained on movement,
477 nesting locations and predator activity. The spatially explicit capture-recapture
478 approach also had large uncertainty but was less than the trapping point transect and it
479 did use fewer resources than the trapping point transect survey in terms of man-hours
480 undertaken to complete the survey. Both monitoring approaches would require
481 significant increases in survey effort to have any reasonable confidence of detecting
482 further population declines of the Key Largo woodrat, or increases in abundance in
483 response to management actions.

484

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486

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495

496

497

498 **LITERATURE CITED**

499

500 Akaike, H. 1973. Information theory as an extension of the maximum likelihood
501 principle. Pages 267–281 in B. N. Petrov and F. Csaksi, editors. Second
502 International Symposium on Information Theory. Budapest, Hungary.

503

504 Alligood, C. A., C. J. Wheaton, H. M. Forde, K. N. Smith, A. J. Daneault, R. C.
505 Carlson, and A. Savage. 2008. Pup development and maternal behavior in
506 captive Key Largo woodrats (*Neotoma floridana smalli*). *Zoo Biology* 27:394–
507 405.

508

509 Alligood, C. A., C. J. Wheaton, A. J. Daneault, J. K. Carlson, and A. Savage. 2009.
510 Behavioral predictors of copulation in captive Key Largo woodrats
511 (*Neotoma floridana smalli*). *Behavioural Processes* 81:337–342.

512

513 Bates, D., and M. Maechler. 2009. *Package 'lme4': Linear mixed-effects models*
514 *using S4 classes* (v0.999375-34). <http://lme4.r-forge.r-project.org/>.

515

516 Borchers, D. L., S. T. Buckland, P. W. Goedhart, E. D. Clarke, and S. L. Hedley.
517 1998. Horvitz-Thompson estimators for double-platform line transect surveys.
518 *Biometrics* 54:1221–1237.

519

520 Borchers, D. L., and M. G. Efford. 2008. Spatially explicit maximum likelihood
521 methods for capture-recapture studies. *Biometrics* 64:377–385.

522

523 Buckland, S. T., D. R. Anderson, K. P. Burnham, J. L. Laake, D. L. Borchers, and L.
524 Thomas. 2001. Introduction to Distance Sampling. Oxford University Press,
525 Oxford.

526

527 Buckland, S. T., K. P. Burnham, and N. H. Augustin. 1997. Model selection: an
528 integral part of inference. *Biometrics* 53:603–618.

529

530 Buckland, S. T., R. W. Summers, D. L. Borchers, and L. Thomas. 2006. Point transect
531 sampling with traps or lures. *Journal of Applied Ecology* 43:377–384.

532

533 Burnham, K. P., and D. R. Anderson. 2003. Model selection and multi-model
534 inference - A practical information-theoretic approach. Springer, USA.

535

536 Efford, M.G., B. Warburton, M. C. Coleman, and R. J. Barker. 2005. A field test of
537 two methods for density estimation. *Wildlife Society Bulletin* 33:731–738.

538

539 Efford, M. G., D. L. Borchers, and A. E. Byrom. 2009. Density estimation by
540 spatially explicit capture-recapture: likelihood-based methods *in* D. L.
541 Thomson, E. G. Cooch and M. Conroy, editors, *Modeling Demographic*
542 *Processes In Marked Populations*, pages 255-269. Springer.

543

544 Efford, M. G. 2010. Package ‘secr’ (v. 2.9.5). [www.otago.ac.nz/density/pdfs/secr-](http://www.otago.ac.nz/density/pdfs/secr-manual.pdf)
545 [manual.pdf](http://www.otago.ac.nz/density/pdfs/secr-manual.pdf).

546

547 Gardner, B., J. Reppucci, M. Lucherini, and J. A. Royle. 2010. Spatially explicit
548 inference for open populations: estimating demographic parameters from
549 camera-trap studies. *Ecology* 91(11):3376–3383.
550

551 Gore, J. A. and Loggins, R. E. 2005. Long term monitoring plan for the Key Largo
552 woodrat and cotton mouse. Technical report, Florida Fish and Wildlife
553 Conservation Commission, FWRI File Code F2160-03-F.
554

555 Greene, D. U., J. M. Potts, J. G. Duquesnel, and R. W. Snow. 2007. Geographic
556 distribution: *Python molurus bivittatus* (Burmese python). *Herpetological*
557 *Review* 38:355.
558

559 Hersh, S. L. 1981. Ecology of the Key Largo woodrat (*Neotoma floridana smalli*).
560 *Journal of Mammalogy* 62(1):201–206.
561

562 McCleery, R. A. 2003. Aspects of Key Largo woodrat ecology. Thesis, Texas A & M
563 University.
564

565 Muiznieks, B. 2006. Captive propagation and the Key Largo woodrat. *Endangered*
566 *Species Bulletin* XXXI(1):32–33.
567

568 Parmenter, R. R., T. L. Yates, D. R. Anderson, K. P. Burnham, J. L. Dunnum, A. B.
569 Franklin, M. T. Friggens, B. C. Lubow, M. Miller, G. S. Olson, C. A.
570 Parmenter, J. Pollard, E. Rexstad, T. M. Shenk, T. R. Stanley, and G. C.

571 White. 2003. Small-mammal density estimation: A field comparison of grid-
572 based vs. web-based density estimators. *Ecological Monographs* 73:1–26.
573

574 Potts, J., S. Buckland, L. Thomas, and E. Rexstad. 2006. A review of abundance
575 estimation methods for the Key Largo woodrat (*Neotoma floridana smalli*).
576 Technical report, Prepared by the Centre for Research into Ecological and
577 Environmental Monitoring, The University of St Andrews submitted to the
578 Department of Interior, Fisheries and Wildlife Service, USA, under agreement
579 #401816 G087.
580

581 Potts, J. M., S. T. Buckland, L. Thomas, and A. Savage. 2012. Trapping point
582 transects: cost effective monitoring of the abundance of cryptic but trappable
583 animals. *Methods in Ecology and Evolution* 3:695–703.
584

585 Potts, J. M. 2011. *Estimating Abundance of Rare, Small Mammals: A Case Study of*
586 *the Key Largo Woodrat (Neotoma floridana smalli)*. Dissertation, University
587 of St Andrews, Scotland.
588

589 R Development Core Team. 2010. R: A language and environment for statistical
590 computing. R Foundation for Statistical Computing, Vienna, Austria. ISBN 3-
591 900051-07-0, URL <http://www.R-project.org/>.
592

593 Ross, M. S., J. F. Meeder, G. Telesnicki, and C. Weekley. 1995. Terrestrial
594 ecosystems of the Crocodile Lake National Wildlife Refuge: the effects of
595 Hurricane Andrew. Technical Report 4, Submitted by the Florida International

596 University, South east Environmental Research Program. Final report to the
597 Department of the Interior, U.S. Fish and Wildlife Service, Vero Beach,
598 Florida.
599

600 Ross, M. S., J. J. O'Brien, and L. J. Flynn. 1992. Ecological site classification of
601 Florida Keys terrestrial habitats. *Biotropica* 24(4):488–502.
602

603 Royle, J. A., and K. V. Young. 2008. A hierarchical model for spatial capture-
604 recapture data. *Ecology* 89:2281–2289.
605

606 U.S. DOI. 1984. Endangered and threatened wildlife and plants; determination of
607 endangered status for the Key Largo woodrat and the Key Largo cotton
608 mouse. *Federal Register* 49:171. Washington, D.C., USA.
609

610 US FWS. 1999. Multi-species recovery plan for South Florida – the Key Largo
611 woodrat. Technical Report, United States Fisheries and Wildlife Service.
612

613 Winchester, C. 2007. An evaluation of habitat selection and an abundance estimate for
614 the endangered Key Largo woodrat. Thesis, University of Georgia, Georgia.
615

616 Winchester, C., S. B. Castleberry, and M. T. Mengak. 2009. Evaluation of factors
617 restricting distribution of the endangered Key Largo woodrat. *Journal of*
618 *Wildlife Management* 73:374–379.
619

620 **FIGURE CAPTIONS**

621

622 **Figure 1.** A) Map showing the SECR survey design. 33 trapping grids, each
623 consisting for 49 traps laid in a 7 by 7 square with 10 m trap spacing where distributed
624 in suitable habitat, defined by a “habitat mask” and shaded grey. B) Map showing the
625 TPT main survey design. 137 survey points (each consisting of two traps) were
626 distributed throughout the suitable habitat (shaded dark grey) based on a randomly-
627 placed systematic grid with a 250 m trap spacing (black dots). Traps were not placed
628 in unsuitable habitats of water (white) and mangrove swamp (light grey).

629

630 **Figure 2.** Probability of detection and 95% confidence intervals (shown as dashed
631 lines) for female and male woodrats in the TPT trial survey.

1 **FIGURE CAPTIONS**

2

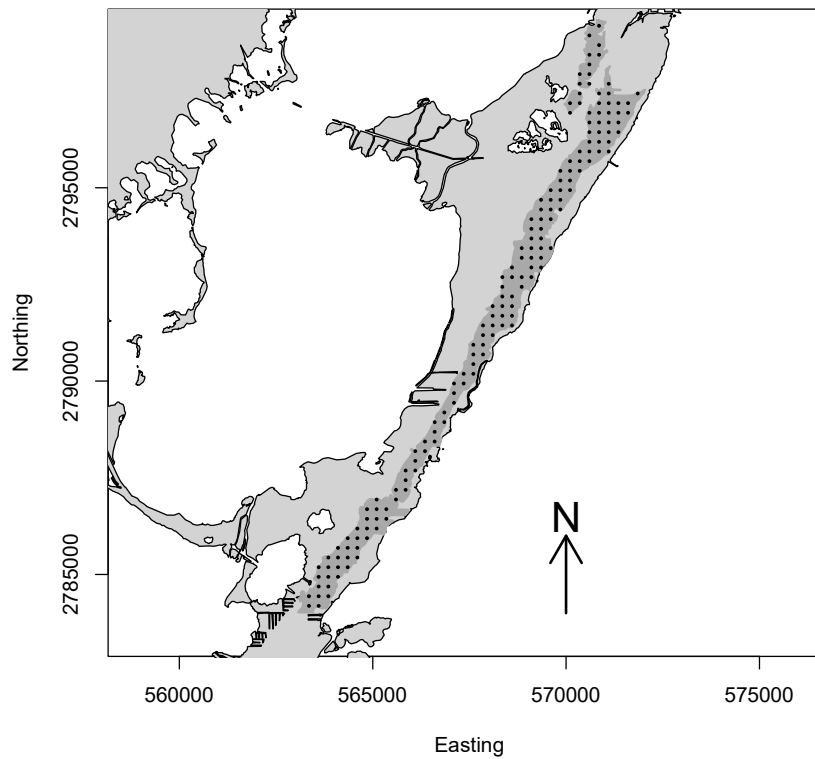
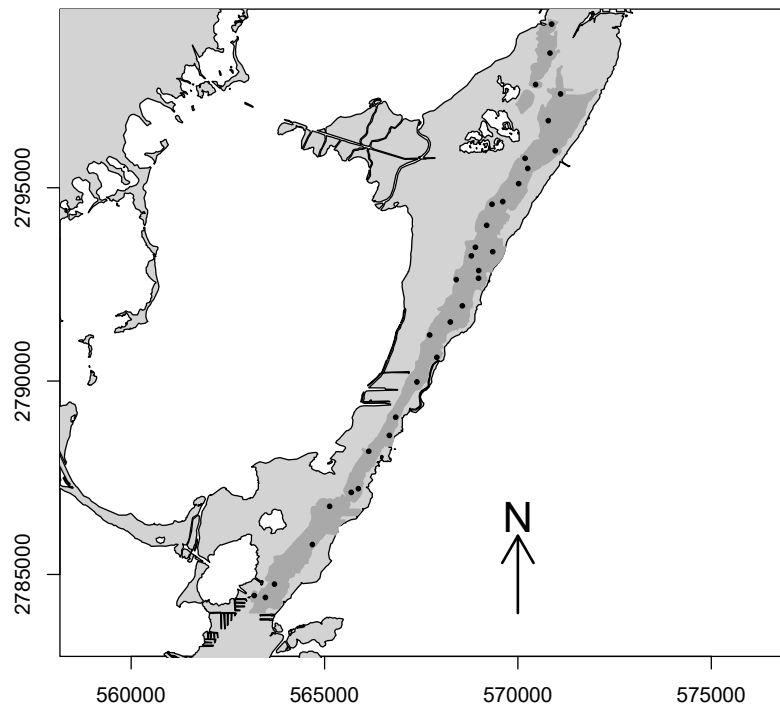
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4 consisting for 49 traps laid in a 7 by 7 square with 10 m trap spacing where distributed
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12 lines) for female and male woodrats in the TPT trial survey.

13

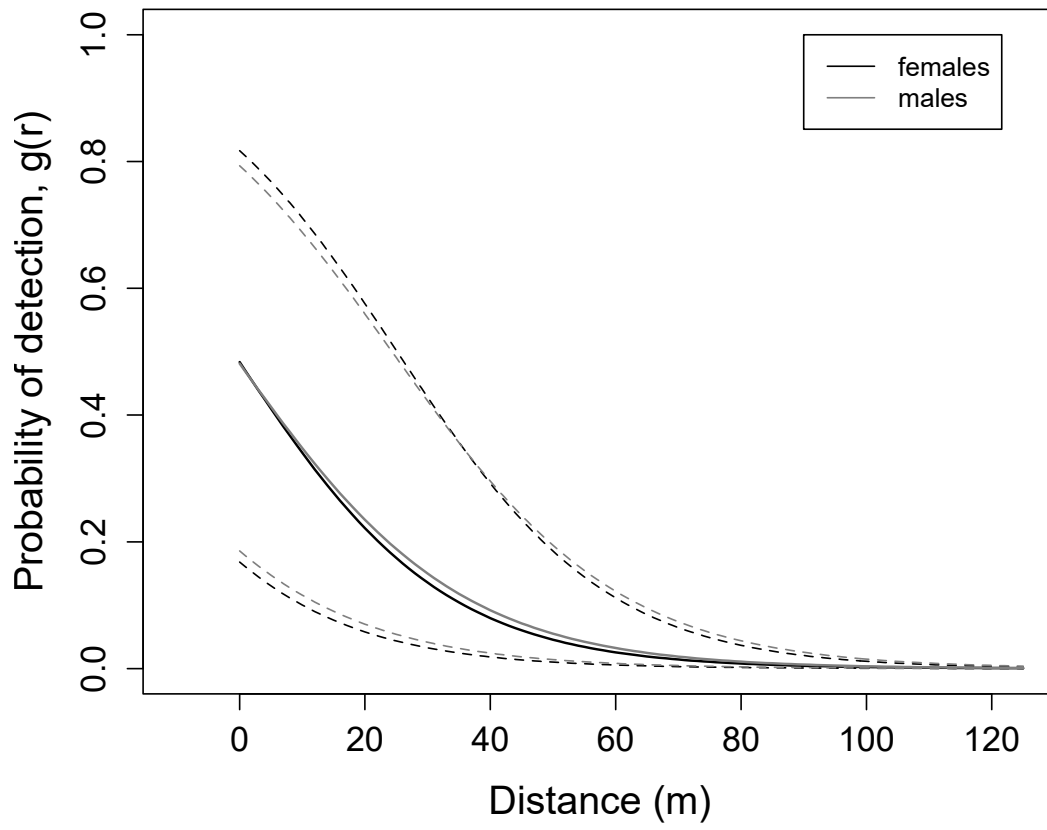
14 **Figure 1A. and Figure 1B.**



15

16

Figure 2.



TABLES

Table 1. The number of woodrat capture events, with the number of unique woodrats captured given in parentheses, and the area of habitat (in hectares) for each of three habitat strata during the spatially explicit capture-recapture survey. A total of 33 grids were set for the 3 primary sessions (spring, summer, and winter). Row totals (i.e., by strata) for the number of woodrats caught are not a direct summation of each row, as some woodrats were caught across multiple sessions.

Hardwood hammock age strata	Session			Total	No. grids	Area (ha)
	Spring	Summer	Winter			
Old	26 (9)	16 (9)	45 (21)	87 (31)	16	431
Medium	10 (4)	14 (7)	16 (7)	40 (14)	12	327
Young	4 (2)	4 (2)	9 (4)	17 (6)	5	87
Total	40 (15)	34 (18)	70 (32)	144 (51)	33	845

Table 2. Estimated woodrat abundance using spatially explicit capture-recapture (SECR) and trapping point transects (TPT) during spring, summer and winter of 2007 and 2008.

Date	Method	Estimate (CV)
Spring 2007	TPT	333 (0.46)
Spring 2007	SECR	97 (0.31)
Summer 2007	SECR	334 (0.26)
Winter 2007	SECR	433 (0.20)
Spring 2008	TPT	696 (0.43)

SUPPORTING INFORMATION

Additional supporting information may be found in the online version of this article at the publisher's web-site. Supporting information includes model selection results for the spatially explicit capture-recapture analysis, and capture information for individuals caught in the trapping point transect survey.

SUPPORTING INFORMATION

Appendix 1. The model selection results for the spatially explicit capture-recapture analysis.

Appendix 2. Capture information and analysis for individuals caught in the trapping point transect survey.

Appendix 1. AIC table of model selection results and derived abundance estimates. Capture data for the SECR analysis is available from the author upon request.

Table 1. Results of model selection for the SECR data.

model	detectfn	npar	logLik	AIC	AICc	dAICc	AICcwt
g0~sex sigma~session	halfnormal	5	-744.4703	1498.941	1499.958	0	0.7957
g0~1 sigma~session	halfnormal	4	-748.1528	1504.306	1504.972	5.014	0.0649
g0~1 sigma~session	halfnormal	4	-748.1838	1504.368	1505.034	5.076	0.0629
g0~B sigma~session	halfnormal	5	-747.1219	1504.244	1505.261	5.303	0.0561
g0~b sigma~session	halfnormal	5	-748.1354	1506.271	1507.288	7.33	0.0204
g0~t sigma~session	halfnormal	7	-747.4184	1508.837	1510.802	10.844	0
g0~session sigma~1	halfnormal	4	-754.3009	1516.602	1517.268	17.31	0
g0~1 sigma~sex	halfnormal	3	-758.2363	1522.473	1522.866	22.908	0
g0~B sigma~1	halfnormal	3	-758.796	1523.592	1523.986	24.028	0
g0~b sigma~1	halfnormal	3	-759.813	1525.626	1526.019	26.061	0
g0~sex sigma~1	halfnormal	3	-760.0062	1526.012	1526.406	26.448	0
g0~1 sigma~1	halfnormal	2	-761.1596	1526.319	1526.513	26.555	0
g0~1 sigma~b	halfnormal	3	-760.232	1526.464	1526.857	26.899	0
g0~1 sigma~B	halfnormal	3	-761.0796	1528.159	1528.553	28.595	0
g0~t sigma~1	halfnormal	5	-759.5687	1529.137	1530.154	30.196	0
g0~1 sigma~t	halfnormal	5	-760.9584	1531.917	1532.934	32.976	0

Table 2. Beta parameters of the model with the lowest AIC in Table S1 (g0~sex sigma~session).

	beta	SE.beta	lcl	ucl
g0	-0.9145916	0.3522817	-1.6050511	-0.2241321
g0.sex	-1.0659555	0.4085922	-1.8667815	-0.2651295
sigma	3.5809187	0.1269671	3.3320677	3.8297697
sigma.session2	-0.7492564	0.1403896	-1.024415	-0.4740977
sigma.session3	-0.4479637	0.1356239	-0.7137817	-0.1821458

```
> derived(gsex.ssession_norm)
```

```
# $`1`
# estimate SE.estimate      lcl      ucl      CVn      CVa      CVD
# esa 130.3455489      NA      NA      NA      NA      NA      NA
# D    0.1150787    0.03615041 0.06307651 0.2099532 0.2581989 0.1789273 0.3141363

# $`2`
# estimate SE.estimate      lcl      ucl      CVn      CVa      CVD
# esa 47.0267450      NA      NA      NA      NA      NA      NA
# D    0.3827609    0.09799164 0.2335923 0.6271864 0.2357023 0.09993458 0.2560126

# $`3`
# estimate SE.estimate      lcl      ucl      CVn      CVa      CVD
# esa 61.6313606      NA      NA      NA      NA      NA      NA
# D    0.5192162    0.1023218 0.3541582 0.7612005 0.1777641 0.08506722 0.1970698
```

Appendix 2. Capture information from the TPT main survey conducted in 2007 and 2008.

Woodrat	Sex	Year_capt	MainSurveyPoint
3603	f	2007	31
3643	f	2007	107
3643	f	2007	107
3274	f	2008	32
3297	f	2008	36
3593	f	2008	87
3803	f	2008	79
3960	f	2008	14
3961	f	2008	8
4729	m	2007	5
3635	m	2007	15
3635	m	2007	15
3646	m	2007	31
3646	m	2007	31
3634	m	2007	69
3625	m	2008	93
3832	m	2008	59
3832	m	2008	59
3912	m	2008	93
3912	m	2008	93

3927	m	2008	93
3927	m	2008	93
3935	m	2008	80
3938	m	2008	78
3962	m	2008	16
3963	m	2008	15
3963	m	2008	15
3963	m	2008	15

Capture information from the TPT trials survey conducted in 2008-2011. Trials data for the TPT analysis collected between 2008-2011 is available from the author upon request.

Full estimation details of the detection functions are provided by Potts (2011) and Potts et al. (2012). A brief description is provided here. Trials data were centered by the group mean (i.e., on individual), and then the 'glmer' function within the lme4 (v 1.1-7) package was used in R (v 3.0.3):

```
glmer(Capture~Est_distC + Est_distN -1 + (1|Woodrat),  
family=binomial("logit"), data=dat_all_years, nAGQ=5)
```

where Est_DistC was the average trial distance for each woodrat (i.e., group center), Est_distN was the distance between the group center and each trial, Woodrat was the identifier for each individual woodrat in the trials survey.