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14 **Short title:** Use of AODs in line transect sampling

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Line Transect Sampling of Primates: Can Animal-to-Observer Distance Methods Work?

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Abstract Line transect sampling is widely used for estimating abundance of primate populations. Animal-to-observer distances (AODs) are commonly used in analysis, in preference to perpendicular distances from the line. This is in marked contrast with standard practice for other applications of line transect sampling. We formalize the mathematical shortcomings of approaches based on AODs, and show that they are likely to give strongly biased estimates of density. We review papers that claim good performance for the method, and explore this performance through simulations. These confirm strong bias in estimates of density using AODs. We conclude that AOD methods are conceptually flawed, and that they cannot in general provide valid estimates of density.

Introduction

Line transect sampling is a 'distance sampling' method (Buckland *et al*., 2001, 2004), widely used for estimating the abundance of wild animal populations. In most areas of application, disciplines have standardized their methods and use the software package

44   Distance (Thomas *et al*., in press). However, methods that in other disciplines are

45   generally considered to be obsolete are still often used and recommended in primatology:

46   the Kelker strip (Kelker, 1945) and the 'modified Kelker method' (Struhsaker, 1981),

47   which covers a range of methods based on assessing the effective width of the searched

48   strip from animal-to-observer distances or AODs. In addition, survey design issues are

49   often ignored, and the precision of abundance estimates is often not quantified,

50   compromising studies designed to compare the performance of different methods.

51   In this paper, we first consider strip transect sampling, and the assumptions under

52   which it is effective. We then explore AOD methods that are conceptually related to strip

53   transect sampling. Plumptre and Cox (2006) noted that such methods have no

54   mathematical basis; here we show that they are based on an erroneous interpretation of

55   the AOD distribution. We review studies that claim good performance of the approach,

56   and assess its performance using simulation.

57

58   **Strip Transect and Related Methods**

59   Standard Strip Transect Sampling

60   In standard strip transect sampling (Buckland *et al*., 2001), we place lines at random in

61   the survey region, or more commonly, we randomly superimpose a set of equally-spaced

62   lines on the survey region. An observer walks along each line, recording all animals

63   within a distance w of the line, where w is the strip half-width. Given random placement

64   of an adequate number of lines through the survey region, this density estimate is

65   representative of the whole survey region, allowing abundance within that region to be

66   estimated.

67   Many animals, including primates, tend to occur in groups, termed 'clusters' in

68   the distance sampling literature. In strip transect sampling, we have two main options for

69   dealing with groups. The first is to ignore them; all animals within a sampled strip are

70   counted, without regard to the groups. Thus for groups that extend beyond the survey

71   strip, some animals are counted and some not. The second option is to count the whole

72   group if its centre is within the sampled strip, and not if its centre is beyond the strip.

73

74   *Assumptions*

75   If groups are ignored, the key assumptions are:

76   1. Animals that are located within a sampled strip prior to any response to the observers

77   are certain to be detected and counted.

78   2. Animals that are located outside the sampled strips are not counted.

79

80   If groups are the recording unit, the key assumptions are:

81   1. Groups whose centres are within a sampled strip prior to any response to the observers

82   are certain to be detected and counted.

83   2. The size of each of these groups is recorded without error.

84   3. Groups whose centres are outside of the sampled strip are not recorded.

85

86   In either case, we also assume that there is an adequate sample of randomly-

87   distributed strips, or a grid of strips randomly positioned, in the survey region. This

88   assumption is not usually listed, because it is an aspect of survey design, and survey

89   design is under our control: if we use an appropriate design, we guarantee that the

90   assumption is met. However, non-randomized designs (e.g. transects along pre-existing

91   trails) with inadequate replication (fewer than 10 lines; Buckland *et al*. (2001:232)

92   recommend at least 10-20 lines) are frequent in primate surveys, so we state the

93   assumption explicitly here. In practice, we usually prefer systematic random designs to

94   designs in which each transect is independently randomized.

95

96   *Problems*

97   If individual animals are counted, we can seldom be sure of detecting all animals within

98   the sampled strips. Even if this is possible, it can be very difficult to determine whether a

99   detected animal is within the strip, especially for animals close to the edge of the strip. If

100 groups are recorded, it is generally difficult to estimate the location of the group centre.

101 For these reasons, it has become standard practice amongst some survey teams to record

102 the position of the group as being at the location of the first-detected animal (Struhsaker,

103 1981; Hassel-Finnegan *et al*., 2008). This animal is more likely to be within the sampled

104 strip than a randomly selected animal, and consequently, the strategy leads to positive

105 bias in density estimates. This bias is substantial if average group spread is of similar

106 magnitude to the strip half-width *w*.

107   Line transect sampling (Buckland *et al*., 2001) relaxes the assumption that all

108 groups in the strip are detected, but generates similar bias in density estimates if the

109 location of the group is taken as the location of the first-detected animal. This source of

110 bias is well-known (e.g. Whitesides *et al*., 1988), yet the practice persists, and as a

111 consequence, standard line transect sampling is often considered to overestimate density

112 in the primate literature (Hassel-Finnegan *et al*., 2008). Buckland *et al*. (in review)

113 discuss how to implement standard line transect methods for primates.

114

115 The Kelker Strip

116 The Kelker strip (Kelker, 1945) is a variation on strip transect sampling. Shortest

117 distances of detected animals from the line (so-called perpendicular distances) are

118 recorded, as for line transect sampling. These distances are placed into intervals, and

119 plotted in a histogram, from which the distance out to which all animals are detected is

120 assessed. When used for primate surveys, groups are recorded, together with the distance

121 of each group from the line.

122

Assumptions

The assumptions of this approach are essentially the same as for strip transect sampling, although we now estimate the strip half-width from the distribution of distances from the line, which requires accurate estimation of distances to the centres of detected groups, including those groups that are detected beyond the strip.

128

Problems

The method shares with strip and line transect sampling the difficulty of identifying the location of group centres. For strip transect sampling, this problem can be avoided if it is possible to record all individuals in the strip, and accurately determine that they are in the strip. However, because the Kelker strip requires distances from the line to be recorded, the distance of each detected animal from the line must be recorded to implement this approach. When groups are recorded, and distances from the line are taken as the distance of the first animal detected from the line, the method is prone to exactly the same upward bias as strip and line transect sampling.

The method also has problems that line transect sampling does not. First, it is subjective. Identification of the distance up to which all groups are detected can vary between analysts and between different choices of interval cutpoints for the histogram. Second, variance estimates ignore the uncertainty in estimating this distance, and so tend to be underestimates. Third, many observations are discarded because many animals are detected beyond the distance at which detection can be assumed certain, reducing precision. Fourth, for small sample sizes, the method tends to give biased estimates of abundance. When sample size is small, sampling variation tends to be large, and the choice of cutpoint can be influenced by chance variation in the proportion of detections close to the line. If by chance several groups are detected close to the line, there is a

148 tendency to set the cutpoint too small, which can lead to positive bias (Fig. 1). However,

149 if groups are missed whose centres are inside the selected cutpoint, negative bias will

150 occur. It is difficult to ensure a balance between these biases.

151

152 AOD Methods

153 AODs (called 'radial distances' in the line transect literature) are often easier to measure

154 than perpendicular distances from the line. In this case, observers generally also record

155 the sighting angle, allowing the perpendicular distance to be calculated (Buckland *et al*.,

156 2001:5). However, line transect methods that model the AOD rather than the

157 perpendicular distance have a long history (e.g. Hayne, 1949). They are now seldom

158 used, as the models are not plausible representations of the detection process (Hayes and

159 Buckland, 1983). Despite this failing, they were mathematically coherent models.

160 Unfortunately, this is not true of the AOD models used by primatologists. These have

161 their origins in surveys conducted in Kibale Forest, Uganda by Struhsaker (1975).

162 Initially during surveys carried out between 1970-1972, he plotted positions of monkey

163 groups on maps and from these he calculated the perpendicular distance of each group

164 from the line. It is not stated what he plotted on the maps: nearest animal, first animal

165 detected, or group centre. In later surveys in 1974-76, he estimated the AOD by eye.

166 The density estimates obtained using the perpendicular distances tended to overestimate

167 the 'known' primate density based on knowledge of group sizes and home range of

168 habituated groups (Struhsaker, 1975). This appears to be because perpendicular distance

169 from the line to the nearest animal of the group was recorded, as nearly 40% of groups

170 were recorded at zero distance (suggesting that nearly 40% of detected groups straddled

171 the line). He then arbitrarily chose to calculate the mean and maximum AOD across

172 detected groups, where AOD for a group was the distance to the first detected animal,

173 and used these as estimates of the strip half-width for a Kelker strip analysis. The mean

7

174   AOD tended to overestimate density of primates while the maximum AOD tended to

175   underestimate density. He then defined a 'maximum reliable AOD' – the distance at

176   which the frequency of sightings falls when plotting AOD against number of sightings.

177   This too was used as an estimate of the strip half-width. In each case, only AODs less

178   than the estimated half-width were included in the density estimate (Struhsaker, 1981).

179   We can find no published results that show that he compared methods based on

180   perpendicular distances and AODs measured in the field.

181

182   *Assumptions*

183   Beyond the assumption that the selected truncation distance results in a complete count of

184   primate groups within that same distance of the line, assumptions are never explicitly

185   stated for the modified Kelker method and its AOD variants. In fact, there is no coherent

186   framework under which the methods can be justified, so that it is not possible to specify a

187   full set of assumptions, as will be seen below.

188

189   *Problems*

190   The method, like the Kelker strip, is subjective when the 'maximum reliable AOD' is

191   used, so that different analysts may select different truncation distances, and estimation is

192   sensitive to the choice. When there is a subjective element in the analysis, and estimation

193   is sensitive to the subjective choice, it is good practice for assessments of the

194   performance of the method based on populations with known density to be performed

195   blind – that is, the analyst should be unaware of the true density when generating

196   estimates.

197   Authors who use AOD methods appear not to estimate the precision of their

198   estimates. Of the papers reviewed below that use the method, only Fashing and Cords

199   (2000) quoted standard errors, and those were based on repeat surveys of a single line, so

200 do not reflect spatial variation (so-called pseudo-replication, Hurlbert, 1984). Variance

201 could be estimated as for strip transect sampling, although this fails to incorporate

202 uncertainty in estimating the strip width.

203 However, there is a more serious problem with these methods, in that their

204 conceptual framework is erroneous. The methods confuse a probability density function

205 with a detection function. When a histogram is plotted, showing frequencies of

206 detections by distance intervals, then the histogram, if rescaled so that the total area of the

207 histogram bars is unity, provides an empirical estimate of a probability density function:

208 it shows the relative frequencies of detections by distance. By contrast, the detection

209 function is the probability of detecting a group, as a function of distance of that group

210 from the line or, for AOD methods, from the observer. When perpendicular distances

211 from the line are used, the two functions have the same shape (Buckland *et al*., 2001:53),

212 so that the histogram may be used for example to assess the perpendicular distance at

213 which probability of detection starts to fall. However, if AODs are used, this is no longer

214 the case (see e.g. Buckland *et al*., 2001:148). The point at which frequencies start to fall

215 does not correspond with the point up to which probability of detection is certain. To

216 illustrate this, we simulated data using the hazard-rate model $g(y) = 1 - \exp\{-(y/20)^{-2}\}$

217 for the detection function (Fig. 2), where $g(y)$ is the probability of detecting an animal

218 group whose centre is at perpendicular distance *y* from the line. Groups had mean size of

219 three, and half the group spread was 10m. (Full details are given in the simulation study

220 section below.) We show a histogram of simulated AODs (Fig. 3). The 'maximum

221 reliable AOD' might be taken as 30m or 40m, depending on the judgement of the analyst,

222 but detectability starts to fall away at around 10m (Fig. 2). The effect is substantial; over

223 60% of groups are undetected at 30m, and nearly 80% at 40m. In other words, for these

224   values of the maximum reliable distance, we can expect underestimation of density by

225   over 60% (30m) or nearly 80% (40m).

226   This flaw in the method is self-evident if you consider what is being done. For

227   example, Hassel-Finnegan (2008) report in their Fig. 2 an estimate of 55m, estimated

228   from AODs, up to which detection is considered to be certain for white-handed gibbons

229   *Hylobates lar carpenteri*. However, of 155 detections, 141 of these were not detected

230   until they were closer to the observer than 55m. Indeed, the median AOD is under 35m.

231   If animals at 55m were certain to be detected, then AODs of less than 55m should not be

232   observed – as the observer approaches an animal, then it will be detected at the certain

233   detection distance of 55m, if not at a greater distance.

234   Marshall *et al*. (2008), while acknowledging that the method lacks a mathematical

235   basis, state erroneously: 'Because sighting distance is used rather than distance to

236   transect, the pattern of decline with distance is a true detection function.' This is not the

237   case (Fig. 3). Hence their belief that the method should be used when other methods fail

238   lacks credibility.

239   There is a further inconsistency in the method, when the histogram is used to

240   identify the distance up to which detection is certain. AODs are used to estimate

241   (erroneously) this distance. However, this is then assumed to be the half-width of a strip

242   centred on the line, rather than the radius of a circle centred on the observer. It is also

243   used to truncate detections whose AODs are larger. Suppose we use 55m as the

244   truncation AOD as in Hassel-Finnegan *et al*. (2008). A group that is detected when still

245   80m away, but which is located on the line, is therefore excluded from the count – but its

246   location is right at the centre of the strip to which the count supposedly relates.

247   If data quality were otherwise good, each variation of the method would clearly

248   undercount groups within the sampled strip. If by chance the method does produce a

249   good estimate, it may be a consequence of defining group location with respect to the

250   observer to be the location of the first detected animal of a group: the upward bias

251   generated by this strategy might cancel with the downward bias of the modified Kelker

252   method. There is no assurance that the biases will cancel in general.

253

254   **Review of Papers that have Assessed AOD Methods**

255   Struhsaker (1981) proposed use of the modified Kelker method on the basis that it gave

256   rise to the least biased estimates of density of red colobus monkeys *Piliocolobus*

257   *oustaleti*. However, the reason for overestimation of density in his study is evident from

258   the following quote: '… nearly 40% of the 166 sightings of red colobus were over the

259   census transect and were scored as zero meters from the trail …' He does not clarify how

260   distances were measured in the field, but as all groups 'over the census transect' were

261   recorded as being at zero distance, we can infer that distance of the nearest animal to the

262   transect was recorded, with predictable overestimation of density; any attempt to salvage

263   density estimates from such poor distance data will inevitably be subjective and *ad hoc*.

264   (Another possibility is that the position of the line was not well-defined, so that any

265   animal or animal group that was close to the line was simply recorded as on the line.)

266   Defler and Pintor (1985) assessed the performance of the three modified Kelker

267   methods based on mean AOD, maximum reliable AOD and maximum AOD, against

268   known densities of three species (red howler monkey *Alouatta seniculus*, collared titi

269   monkey *Callicebus torquatus* and brown capuchin *Cebus apella*) in Colombia. Their

270   design comprised a single, non-random transect; lack of randomization means that we

271   cannot be confident that the density along the line is representative, and lack of

272   replication means that there is no basis for assessing precision of estimates. Their results

273   were very mixed. Mean AOD led to estimated biases of +12%, -30% and +538% for the

274   three species. Maximum reliable AOD gave estimated biases of +12%, -12% and

275   +668%. Maximum AOD resulted in estimated biases of -25%, -56% and +226%.

276   Chapman *et al*. (1988) used just 5 transects, subjectively placed. Their known

277 populations comprised just a single group of each of two species (white-headed capuchin

278 *Cebus capucinus* and mantled howler monkey *Alouatta palliata*) in Costa Rica. They

279 used six different methods of measuring distances: 'the mean, maximum and reliable

280 perpendicular distance from the transect to the animal first sighted and the mean,

281 maximum and reliable distance from the observer to the animal.' Thus all six methods

282 were prone to bias by assuming that the first animal sighted was at the centre of the

283 group. The authors did not quantify the precision of their estimates, and did not define

284 what a 'reliable' distance is (there is not a unique definition of it in the literature). Their

285 estimates show poor performance of all methods, with no clear winner, yet they come

286 down heavily in favour of methods based on AODs on the grounds that 'sightings that

287 occur directly over the transect or at a steep angle to it, are likely to cause bias.' They do

288 not clarify why. They also claim that the ability of the observer to estimate perpendicular

289 distance will be limited when the terrain is rough, which in our view is not a compelling

290 reason for using the wrong distance. Analyses presented in the paper do not in fact

291 support the use of AOD methods; rather, misunderstanding of the methods has resulted

292 in their recommendation to use it.

293   Brugiere and Fleury (2000) did not attempt standard line transect analysis because

294 they had only 23 detections, yet they considered this sample size to be adequate for ten

295 other methods of analysis. Their known population comprised just three groups of a

296 single species (black colobus *Colobus satanas*) in Gabon. Their design comprised just

297 two transects, subjectively positioned, and they did not quantify precision of estimates.

298 They used strip counts, with strip half-width pre-set at three values: 60, 80 and 100m;

299 strip counts, with half-width estimated from the data, using maximum, mean or

300 'maximum reliable' perpendicular distance; the modified Kelker method, using

301 maximum, mean or 'maximum reliable' AOD; and estimation of the effective strip half-

302 width from a histogram, coupled with adding half the group spread to this distance

303 (Whitesides *et al.*, 1988). Uncertainty over true density complicated assessment of the

304 methods, and they drew no firm conclusions on which method was best.

305   Fashing and Cords (2000) analysed data on two species (black-and-white colobus

306 *Colobus guereza* and blue monkey *Cercopithecus mitis*) in Kenya. They estimated true

307 densities based on home range data primarily on five groups and three groups

308 respectively, although data from additional groups were also used. The 'design' was of a

309 single non-random transect, placed along trails. They estimated precision from variation

310 in repeat runs along the same transect. They estimated transect width using a) the

311 maximum reliable AOD; b) the maximum reliable perpendicular distance; and c) the

312 maximum reliable perpendicular distance with the addition of half the group spread, as

313 recommended by Whitesides *et al*. (1988). They also used the shape-restricted estimator

314 of Johnson and Routledge (1985) (a type of perpendicular distance detection function

315 estimator that is seldom used). For both species, the method based on perpendicular

316 distances, together with the half-group spread correction, gave estimates closest to the

317 true density. The shape-restricted estimator performed particularly poorly.

318   Hassel-Finnegan *et al*. (2008) used just a single transect to estimate densities of

319 two species (white-handed gibbons and Phayre's leaf monkeys *Trachypithecus phayrei*

320 *crepusculus*) in Thailand. They assessed true density largely on the basis of a single

321 group for each species, and did not quantify precision of estimates. They used both the

322 Kelker strip and the modified Kelker method, with truncation distance estimated as the

323 point at which frequencies in the respective histograms of perpendicular distances and of

324 AODs started to fall. In addition, they used Distance (Thomas *et al*., in press) to perform

325 a standard line transect analysis of perpendicular distances. All detection distances,

326 whether perpendicular distances or AODs, were measured to the first animal detected of

327 the group. For both species, Distance and the Kelker strip gave rise to overestimates of

328   the true density, while the modified Kelker method gave estimates very slightly under the

329   true density. However, given the lack of replication (a single line, and a single group of

330   each species), it seems that little can be inferred from these results. Hassel-Finnegan *et*

331   *al.* (2008) quote the papers of Chapman *et al.* (1988) and Fashing and Cords (2000) to

332   support their contention that analyses based on AODs closely match true densities, while

333   those based on perpendicular distances overestimate. However, the results of neither

334   paper support this conclusion.

335   All of the above comparisons are based on studies where true density is

336   established by studying a small number of habituated groups, and estimating the size of

337   their home range. There are several reasons why there might be bias in these 'true'

338   densities. For example home ranges of groups may partially overlap, and because the

339   transects in these studies are positioned subjectively, they may sample parts of the home

340   range that are favoured or avoided by the habituated group, leading to a mismatch in the

341   densities being estimated by the two approaches. This is exacerbated when the sampled

342   strip(s) extend beyond the home range(s) of the habituated group(s), into other home

343   ranges. Further, lone males are not included in densities obtained from home range

344   studies, so that density might be expected to be lower as assessed by this method than

345   that obtained by appropriate application of line transect sampling methods. In the case of

346   a population of grey-cheeked mangabeys *Lophocebus albigena* in Uganda (Olupot and

347   Waser, 2005), Olupot (pers. comm.) estimates that around 30% of males are solitary,

348   corresponding to around 8% of the total population.

349   Mitani *et al.* (2000) compared censuses of seven species (black-and-white

350   colobus, Pennant's red colobus *Procolobus pennantii*, baboons *Papio anubis*, blue

351   monkeys, grey-cheeked mangabeys, red-tailed monkeys *Cercopithecus ascanius* and

352   chimpanzees *Pan troglodytes*) made along almost the same census route between years at

353   Ngogo in Kibale Forest. The three authors measured AOD separately for their respective

354 census periods (1975-76 and 1996 Struhsaker; 1997-98 Lwanga; and 1996 Mitani).

355 They also used a single transect, which formed the shape of a square route. The authors

356 found great variation in the estimation of AOD between the three of them, showing that

357 each observer would estimate a very different maximum reliable sighting distance and

358 that the shape of the sighting distributions differed significantly. They therefore could

359 not use the modified Kelker method to compare densities between years and resorted to

360 comparing encounter rates of primate groups per kilometre walked. Variation between

361 observers with the modified Kelker method eliminates any possibility of comparison

362 unlike standard perpendicular distance methods where a probability of detection can be

363 computed for each observer to allow comparisons to be made (Marques *et al*., 2007).

364   Marshall *et al*. (2008) review four methods: strip transects, the modified Kelker

365 method, and two methods based on perpendicular distances – distance from the line of

366 the group centre, and distance from the line of the centre of measurable individuals.

367 They note that methods based on truncating a substantial proportion of data need larger

368 sample sizes for comparable precision than methods that do not. They also note that the

369 assumptions of the modified Kelker method are 'unknown'. However, they still advocate

370 its use for when expertise is unavailable to apply other methods, or when the data

371 (location of group centres, or reliable estimates of mean group spread) or assumptions

372 (certain detection on the line, accurate measurement to individuals) required by other

373 methods are unachievable. They justify this recommendation on the grounds that the

374 method consistently performs well in field trials, a claim that does not stand up to close

375 scrutiny, as noted above. The recommendation presupposes that the *ad hoc* method will

376 produce useful estimates when the other methods do not. The observer effects found by

377 Mitani *et al*. (2000) for example suggest that this is unlikely.

378

379   **Simulation Study**

380   Simulating Populations and Samples

381   To assess how different methods perform, we simulated data from populations of known

382   density.   This is intentionally an idealized study, with a large sample of lines

383   systematically spaced with a random start, with certain detection of animals on the line,

384   no responsive movement, and no measurement error in distances.   If methods perform

385   poorly here, they can certainly be expected to in real studies. For simplicity, we assumed

386   a rectangular survey region, 20km long and 5km wide. We placed 25 transects in the

387   region, each 5km long, spaced 800m apart.

388   True number of groups in the survey region was 500, randomly spread through

389   the region with a uniform density. Mean group size was 3, 10 or 30 animals, so that total

390   population size was 1500, 5000 or 15000, corresponding to 15, 50 or 150 animals per

391   square kilometre. We assigned the animals to the 500 groups by first assigning a single

392   animal to each group. We then generated a random number for each remaining animal

393   from a continuous uniform distribution on $(0,500^p)$, with $p = 0.75$. We raised this

394   number to the power $1/p$, and rounded up to the next integer; the resulting value defined

395   the group to which the animal was assigned. This ensures greater variation in group size

396   than would occur if all groups had the same expected size (corresponding to $p = 1$), but

397   the expectation of mean group size was 3, 10 or 30, as required. We assigned the

398   position of each animal in a group at random within a circle of radius ρ, centred at the

399   assigned group location, with $\rho =$ 10, 25 and 50m. All group centres fell within the

400   survey region, but individual animals could be assigned a location outside the survey

401   region. To avoid the complication of partial sampling of groups straddling the boundary,

402   we extended sampling into a bufferzone, to allow the whole group to be sampled. We did

403   not count effort (i.e. length of transect) in the bufferzone; this does not create bias

404 because the additional sightings compensate for the 'missing' sightings that would have

405 occurred had groups been simulated whose centres were outside the study region, but

406 which straddled the boundary.

407 Hayes and Buckland (1983) developed a hazard-rate model of the detection

408 process. Their model is useful here to simulate the detection process as the observer

409 approaches a group of animals. In this study, we initially simulated whether or not an

410 animal was detected independently of other animals in a group. We assumed a hazard

411 function of the form $k(r) = ar^{-b}$, with $b = 3$ and $b = 5$, where r is distance between the

412 animal and the observer. If the observer has not yet detected an animal at distance r, then

413 $k(r)dx$ is the probability that the animal is detected as the observer advances a small

414 distance dx along the line. Given the above form for $k(r)$, we can derive the detection

415 function $g(y)$, which is the probability that an animal at distance y from the line is

416 detected: $g(y) = 1 - \exp\{-(y/c)^{-(b-1)}\}$. We chose ($c = 20$, $b = 3$), for which $a = 400$,

417 and ($c = 30$, $b = 5$), for which $a = 1215000$. These two detection functions are shown

418 (Fig. 2). To mimic the enhanced probability of detecting animals in a group once the first

419 animal of the group has been detected, we identified all groups for which at least one

420 animal was detected, and simulated a second 'pass' to search for undetected animals in

421 the group, again using a hazard-rate detection function, but with the scale parameter c

422 increased by 50% ($c = 30$ for scenarios with $b = 3$, and $c = 45$ when $b = 5$).

423 For a detected animal, we recorded both the AOD at the time of first detection and

424 the perpendicular distance from the line. We did not record animals further than 150m

425 from the line. Sample sizes were typically in the range 60-120.

426

427 Estimating Densities

428 For each combination of mean group size, group spread, true density and detection

429 function, we simulated 100 populations, and surveyed each once. We applied the

430 following analysis methods.

431

432 1. The modified Kelker method, based on mean AOD, where AOD for each detected

433 group is the distance of the first detected animal from the group. We took the mean AOD

434 as an estimate of the strip half-width, and the mean of recorded sizes of detected groups

435 as an estimate of mean group size in the population.

436 2. The modified Kelker method, based on maximum AOD, where AOD for each

437 detected group is the distance of the first detected animal from the group. We took the

438 maximum AOD as an estimate of the strip half-width, and the mean of recorded sizes of

439 detected groups as an estimate of mean group size in the population.

440 3. The modified Kelker method, based on maximum reliable AOD, where AOD for each

441 detected group is the distance of the first detected animal from the group. We grouped

442 AODs into 10m bins, and estimated the half-width of the strip by starting at the bin

443 closest to the line (0-10m), and identifying the first bin for which the count was at most

444 one half of the mean count for preceding bins. If for example the mean count in the first

445 four bins was 10.5, and the count for bin 5 (40-50m) was 5, then the strip half-width was

446 taken to be 40m, and detections at a greater distance were excluded from the analysis.

447 We estimated mean group size in the population by the mean of recorded sizes of

448 detected groups.

449

450 Results

451 All three modified Kelker methods have strong negative bias for all scenarios (Table 1).

452 The bias is consistent across different group sizes and spreads, but differs markedly by

18

453   detection function. This finding is consistent with the finding by Mitani *et al*. (2000),

454   that density estimates were not comparable across observers. The bias is especially large

455   for method 1, the maximum AOD method (-90.7% and -75.7% for the two detection

456   functions). For method 2, bias was -42.3% for the first detection function and -25.1% for

457   the second. The corresponding values for method 3 were -43.9% and -28.2%.

458   These biases are not fully explained by bias in recorded group sizes (Table 2).

459   Interestingly, although bias in recorded group size increases both with mean group size

460   and with group spread, for methods 2 and 3, bias in density estimates within a method

461   and detection function is largely independent of mean group size and group spread.

462   However, as the bias is not consistent across different detection functions, it suggests that

463   neither method gives a reliable estimate of relative density.

464   The bias is also not attributable to recording distances to the first detected animal,

465   rather than to the group centre. Using measurements to group centres, AODs would

466   increase, resulting in larger estimated strip widths, and reduced densities, so that bias

467   would be even larger.

468   Because the methods have no coherent mathematical framework, it is not possible

469   to identify the causes of bias, as there are no coherent assumptions that we can assess.

470

471   **Discussion**

472   In our simulation study, we found serious biases with estimators based upon AODs.

473   Hassel-Finnegan *et al*. (2008) criticize conventional line transect sampling as

474   implemented in Distance because a large number of detections is needed for reliable

475   analysis. They fail to note that this is even more true of the Kelker strip, for which many

476   of the observations are discarded (Marshall *et al*., 2008). With inadequate sample sizes,

477   choice of truncation distance is more subjective, uncertain and influential.

478   For methods based on selecting a single animal, and using the distance to it as the

479   distance to the group centre, there is some ambiguity in the literature about whether the

480   selected animal is the first animal detected or the closest animal. In general, the two are

481   not the same individual. In our simulations, we assumed that it is the first animal

482   detected. Struhsaker (1981) recorded 40% of detected groups as being on the line, which

483   suggests that he used the distance of the closest animal to the line. Alternatively, if his

484   transect was along trails, it may be that animals directly above the line were the first to be

485   detected, because they were more visible.

486   We conclude that AOD methods as used by primatologists are conceptually

487   flawed; the resulting estimates should not be treated as estimates of absolute density.

488   Whether they are acceptable estimates of relative density depends on many factors.

489   Estimates are unlikely to be comparable across different observers (Mitani *et al*., 2000) or

490   habitats for example. Estimating primate abundance is often difficult compared with

491   many other taxa, as the animals often reside in hard-to-access, low-visibility areas and are

492   often clustered, cryptic and highly mobile. Nevertheless, more reliable estimates of

493   abundance are potentially possible by combining good survey design with better field and

494   analytic methods (Buckland *et al*., in review).

495

498

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555

Figure legends

Fig. 1. Shown here are two datasets, both generated from a detection function with certain detection out to 40m, and rapidly declining detection probability at larger distances. When by chance there are more detections close to the line, visual inspection of the data leads to selection of a smaller cutpoint for the Kelker method; 20m in this example. When there are more detections close to 40m, the cutpoint is likely to be set at 40m. If we fix the cutpoint in advance, at either 20m for both analyses or 40m, we expect unbiased estimates of density, but if we use 20m for the first analysis and 40m for the second analysis, we overestimate density on average. Dashed lines: mean count with truncation at 40m. Dotted lines: mean count with truncation at 20m.

Fig. 2. The detection functions used in the simulation study. Note that these detection functions apply to each individual animal; the probability that at least one animal of a group will be detected will be larger than shown here – substantially so for large groups. The solid line is $g(y) = 1 - \exp\{-(y/20)^{-2}\}$ and the dashed line $g(y) = 1 - \exp\{-(y/30)^{-4}\}$.

Fig. 3. Histogram of AODs simulated from the hazard-rate model of the detection process, $g(y) = 1 - \exp\{-(y/20)^{-2}\}$.

1

Table 1. Mean (standard deviation in parentheses) of density estimates for the three methods of estimation.

Mean group size	3			10			30		
Half-group spread	10m	25m	50m	10m	25m	50m	10m	25m	50m
True density	15	15	15	50	50	50	150	150	150
$g(y) = 1 - \exp\{-(y/20)^{-2}\}$:									
Maximum AOD	1.6	1.6	1.6	4.2	4.2	4.3	12.8	13.2	13.1
	(0.7)	(0.7)	(0.6)	(0.6)	(0.6)	(0.7)	(1.3)	(1.3)	(1.1)
Mean AOD	8.6	8.5	8.3	29.6	29.2	29.0	85.5	88.2	87.4
	(1.9)	(1.7)	(1.5)	(5.2)	(4.0)	(4.0)	(13.4)	(12.7)	(11.9)
Max reliable AOD	8.8	8.4	8.4	28.7	28.2	27.6	80.9	83.4	83.7
	(2.1)	(1.7)	(1.6)	(5.3)	(4.3)	(4.2)	(14.0)	(12.9)	(11.2)
$g(y) = 1 - \exp\{-(y/30)^{-4}\}$:									
Maximum AOD	4.5	4.5	4.7	12.2	11.7	11.8	28.4	28.7	26.4
	(1.3)	(1.5)	(1.2)	(3.5)	(3.4)	(4.0)	(7.1)	(7.6)	(7.4)
Mean AOD	10.7	10.8	11.0	39.2	38.3	38.4	113.6	114.1	110.5
	(2.1)	(1.7)	(1.9)	(6.4)	(5.3)	(6.0)	(18.1)	(17.7)	(15.1)
Max reliable AOD	10.5	10.3	10.5	37.4	36.4	36.9	108.7	109.2	106.1
	(1.9)	(1.6)	(1.7)	(5.2)	(4.4)	(4.9)	(15.3)	(15.1)	(14.2)

Table 2. Estimates of mean group size: sample mean (standard error in parentheses) of recorded group sizes within w of the line.

Mean group size	3			10			30		
Half-group spread	10m	25m	50m	10m	25m	50m	10m	25m	50m

$g(y) = 1 - \exp\{-(y/20)^{-2}\}$:

```
         2.65   2.56   2.33   6.46   6.27   5.68  14.28  14.31  13.29
        (0.20)(0.19)(0.14)(0.39)(0.36)(0.33)(0.89)(0.97)(0.82)
```

$g(y) = 1 - \exp\{-(y/30)^{-4}\}$:

```
         2.89   2.79   2.52   8.14   7.67   6.66  19.77  19.08  16.60
        (0.22)(0.20)(0.16)(0.44)(0.45)(0.42)(1.55)(1.19)(0.92)
```

Fig. 1. Shown here are two datasets, both generated from a detection function with certain detection out to 40m, and rapidly declining detection probability at larger distances. When by chance there are more detections close to the line, visual inspection of the data leads to selection of a smaller cutpoint for the Kelker method; 20m in this example. When there are more detections close to 40m, the cutpoint is likely to be set at 40m. If we fix the cutpoint in advance, at either 20m for both analyses or 40m, we expect unbiased estimates of density, but if we use 20m for the first analysis and 40m for the second analysis, we overestimate density on average. Dashed lines: mean count with truncation at 40m. Dotted lines: mean count with truncation at 20m.
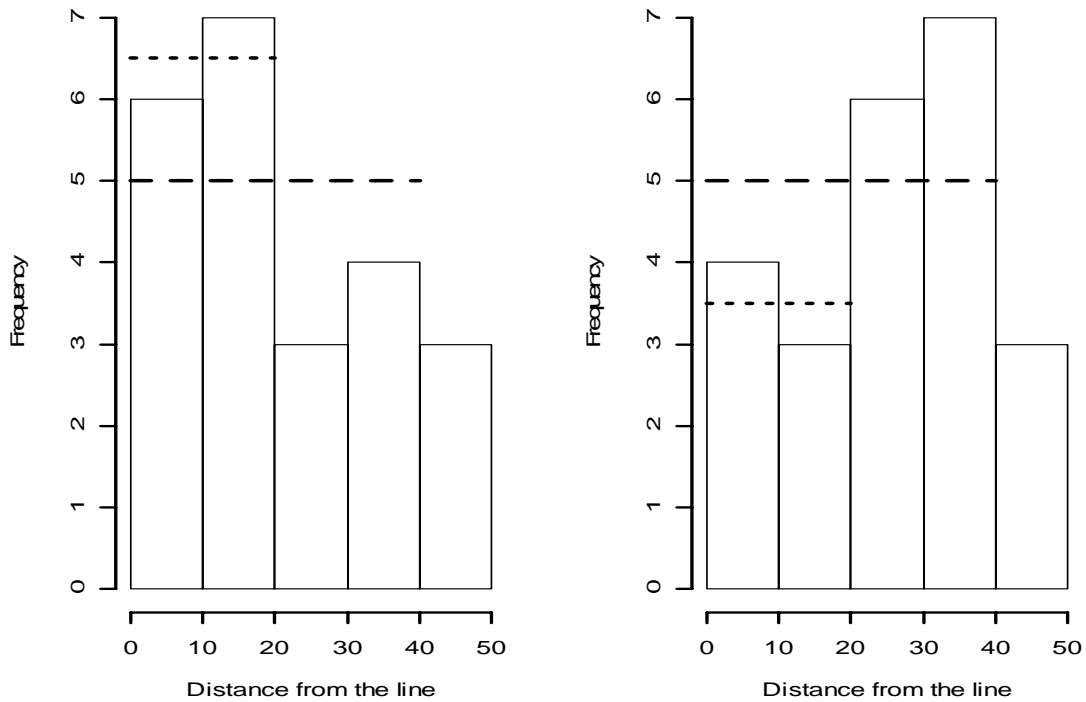
Fig. 2. The detection functions used in the simulation study. Note that these detection functions apply to each individual animal; the probability that at least one animal of a group will be detected will be larger than shown here – substantially so for large groups. The solid line is $g(y) = 1 - \exp\{-(y/20)^{-2}\}$ and the dashed line $g(y) = 1 - \exp\{-(y/30)^{-4}\}$.
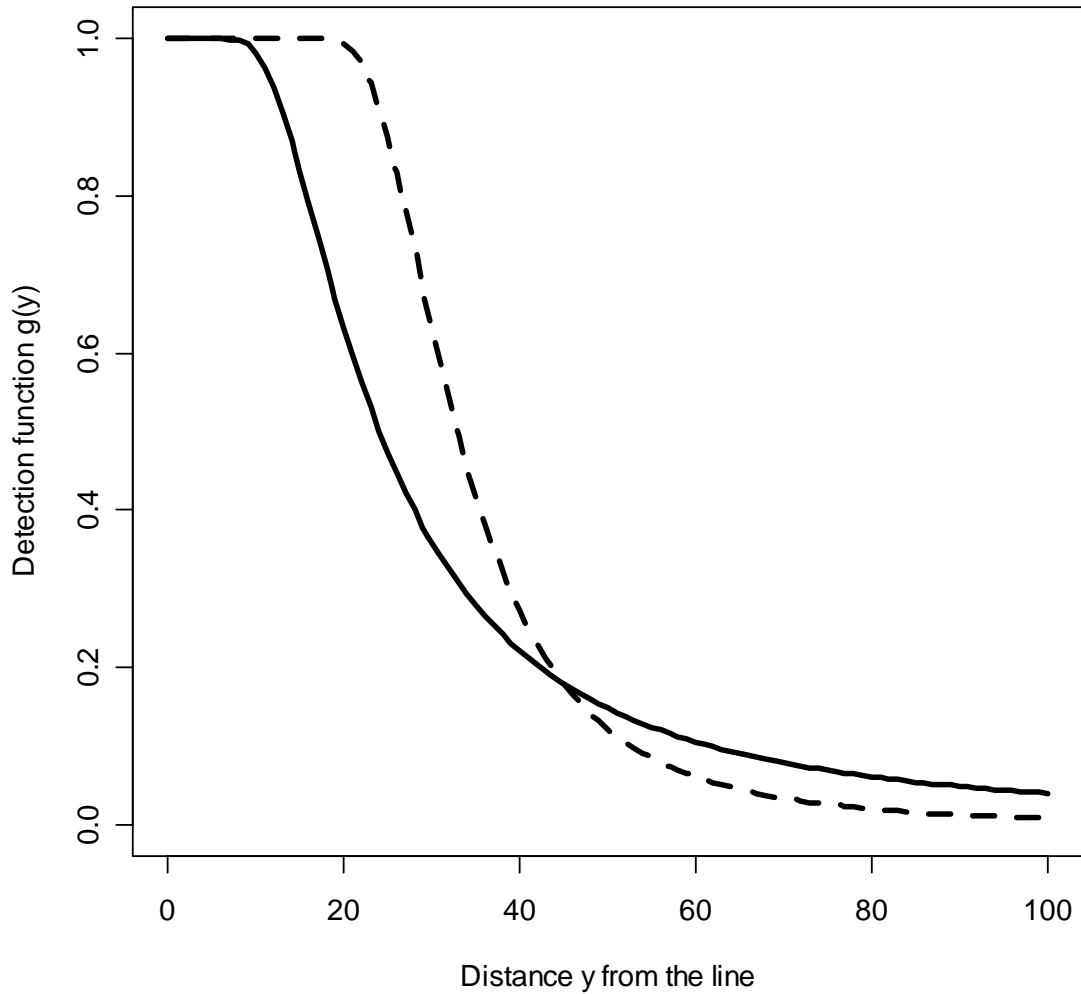
Fig. 3. Histogram of AODs simulated from the hazard-rate model of the detection process, $g(y) = 1 - \exp\{-(y/20)^{-2}\}$.