

1 TITLE: Estimating vocal repertoire size is like collecting coupons: a theoretical framework with
2 heterogeneity in signal abundance.

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15 ABSTRACT

16 Vocal repertoire size is an important behavioural measure in songbirds and mammals with
17 complex vocal communication systems, and has traditionally been used as an indicator of
18 individual fitness, cognitive ability, and social structure. Estimates of asymptotic repertoire size
19 have typically been made using curve fitting techniques. However, the exponential model usually
20 applied in these techniques has never been provided with a theoretical justification based on
21 probability theory, and the model has led to inaccurate estimates. We derived the precise
22 expression for the expected number of distinct signal types observed for a fixed sampling effort:
23 a variation of what is known in the statistical literature as the “Coupon Collector’s problem”. We
24 used empirical data from three species (northern mockingbird, Carolina chickadee, and rock
25 hyrax) to assess the performance of the Coupon Collector model compared to commonly used
26 techniques, such as exponential fitting and repertoire enumeration, and also tested the different
27 models against simulated artificial data sets with the statistical properties of the empirical data.
28 We found that when signal probabilities are dissimilar, the Coupon Collector model provides far
29 more accurate estimates of repertoire size than traditional techniques. Enumeration and
30 exponential curve fitting greatly underestimated repertoire size, despite appearing to have
31 reached saturation. Application of the Coupon Collector model can generate more accurate
32 estimates of repertoire size than the commonly used exponential model of repertoire discovery,
33 and could go a long way towards re-establishing repertoire size as a useful indicator in animal
34 communication research.

35

36 **KEYWORDS:** Animal signals, Birdsong, Communication, Repertoire size, Vocalisations

37

38 1. INTRODUCTION

39 Assessing the repertoire size of animal vocalisations has long been recognised as important
40 to understanding the development, function, and evolution of animal communication (Bradbury
41 & Vehrencamp 2011). Repertoire size is often considered to be an indicator of communicative
42 complexity (Freeberg et al. 2012), and communicative complexity has numerous implications for
43 the understanding of animal signalling and social evolution. It has been proposed that
44 communicative complexity may drive the evolution of social complexity, and vice versa
45 (McComb & Semple 2005; Pollard & Blumstein 2012). Communicative complexity may be an
46 indicator of individual fitness (Hiebert et al. 1989; Darolová et al. 2012), may influence mate
47 choice and the evolution of mating systems (Searcy 1992; Nowicki et al. 2000), and may play a
48 role in complex sender-receiver competitive games (Owren et al. 2010). Repertoire size is also
49 an important metric for assessing the tradeoff between function and variant diversity in
50 communication (Bradbury & Vehrencamp 2011), and the neurological constraints limiting the
51 use of highly complex signalling, such as syntax (Lipkind et al. 2013). Although most previous
52 research related to repertoire size has concentrated on the repertoire of birdsong, the work we
53 describe here can be generalised to consider other non-song modalities such as visual signals
54 (Peters & Ord 2003), chemical signals (delBarco-Trillo et al. 2012), and even to entire
55 behavioural repertoires (Sempo & Detrain 2004). As such, hereafter we use the term “signals”,
56 rather than “songs”, except where specifically referring to mating/territorial songs.

57 Despite the importance of repertoire size in animal species, repertoire size estimation for
58 any given species or individual is a non-trivial problem in practical situations. For species with

59 large repertoires, large sampling effort is required to enumerate all distinct vocalisations. Some
60 species of songbird, furthermore, produce much of the diversity of their song repertoire quickly
61 (immediate variety), whereas other species produce the diversity of their song repertoire over
62 much longer time frames (eventual variety; Catchpole & Slater 2003). Even if true repertoire size
63 is small, enough data need to be collected to ensure that all possible types have been recorded
64 (Hesler et al. 2012). In most cases, comprehensive sampling is impractical, and so estimation
65 techniques must be used. Most work on estimating repertoire size has been carried out with
66 songbirds, since song repertoires play such a crucial role in the social and reproductive life of
67 many species (Catchpole & Slater 2003). Songbird repertoire sizes range from a single
68 stereotyped song such as in the white-crowned sparrow *Zonotrichia leucophrys* (Soha & Marler
69 2001), through tens of distinct vocalisations, e.g. in the European blackbird *Turdus merula*, up to
70 species such as the northern mockingbird *Mimus polyglottos* and brown thrasher *Toxostoma*
71 *rufum*, which can make use of hundreds or even thousands of different songs (Kroodsma 1977;
72 Gammon & Altizer 2011). Some songbird species, furthermore, possess diverse repertoires of
73 calls, indicating that repertoire estimation is important to non-song vocal behaviour as well (e.g.,
74 call repertoires in crows and jays, chickadees and titmice, and parrots). Moreover, songbirds are
75 not the only taxon where repertoire estimation is important. Some mammal species have
76 extensive vocal repertoires, such as the rock hyrax *Procavia capensis* (Kershenbaum et al. 2012),
77 free-tailed bats *Tadarida brasiliensis* (Bohn et al. 2009), marmots *Marmota flaviventris*
78 (Blumstein 2007), and pilot whales *Globicephala macrorhynchus* (Sayigh et al. 2012), and little
79 is known about their social and evolutionary significance.

80

81 2. PREVIOUS WORK

82 Estimating the repertoire size of individuals or a group of individuals has been
83 accomplished using different methods. In one of the earliest methods (henceforth WM) ,
84 Wildenthal (1965) proposed measuring the total number of distinct signals observed as sample
85 size increases, and fitting these data to an exponential function of the form

$$86 \quad E = N\left(1 - e^{-M/N}\right) \quad (1)$$

87 where N is the true repertoire size, M is the number of observations (samples) made, and E is the
88 number of distinct signals observed. Wildenthal originally proposed this relationship based on
89 the observation that, “when the data were plotted... the curves obtained approximate exponential
90 curves” (Wildenthal 1965). Davidson & Wilkinson (2002) subsequently proposed a correction to
91 the Wildenthal model which appeared to give a better fit to the empirical data. In the Davidson &
92 Wilkinson (2002) model (henceforth, DW), the rate of increase of distinct signal types observed
93 is lower than expected by the WM, by a factor A , where $A > 1$:

$$94 \quad E = N\left(1 - e^{-M/AN}\right) \quad (2)$$

95 The DW is purely empirical, as no known probabilistic process would be expected to produce a
96 relationship as indicated in Equation 2. However, even the derivation of the WM remains
97 unexplained, and to date no examination has been made of why the number of observed signals
98 should follow this exponential relationship, or what the theoretical justification for such a model
99 might be.

100 A different approach, examined by Garamszegi et al. (2005) applied the capture-recapture
101 principle to the observation of signal types. Using the capture-recapture approach, the researcher
102 models the observation of signals in the same way as observation of marked individuals in

103 population sampling; an established technique used for the estimation of population size. This
104 technique also gives repertoire size estimates that are empirically accurate under certain
105 conditions, and is based on the theoretical similarity between sampling signals, and the sampling
106 of marked individuals.

107 Botero et al. (2008) compared these estimation techniques using artificial repertoires with
108 known repertoire sizes, and concluded that in many cases, simple enumeration of the number of
109 distinct signals observed (henceforth, EN) is the easiest and most accurate estimator of true
110 repertoire size. Since then, other researchers have proposed additional techniques that appear
111 empirically valid, such as rarefaction (Peshek & Blumstein 2011), but no bottom-up analysis of
112 the process of signal sampling has been performed to derive the precise relationship between
113 sampling effort and repertoire estimate. In practice, many researchers simply use the
114 enumeration of distinct observed signals, on the assumption that sufficient signals have been
115 sampled to represent the entire repertoire accurately (e.g. Searcy 1992; Nowicki et al. 2000; Pfaff
116 et al. 2007; Hesler et al. 2011).

117 We show that this problem of sampling signals from a repertoire is a variant of the
118 “Coupon Collector’s problem” (Erdős & Rényi 1961; Jocković & Mladenović 2011), and we use
119 probability theory to derive the precise expression for the expected number of distinct observed
120 signals, given a particular sampling effort. We show that this result closely approximates
121 Wildenthal’s and Davidson-Wilkinson’s exponential models only when each signal occurs with a
122 similar probability. When individual signals do not occur homogeneously, exponential fitting is
123 likely to underestimate total repertoire size. Although no closed-form expression exists for the
124 repertoire size estimate, non-linear least-squares fitting provides an accurate estimate, if
125 sufficient data are available to estimate the signal probabilities. Finally, we compare our method

126 to other common methods for assessing repertoire size, using examples of animal vocalisations:
127 mockingbird song, chickadee calls, and hyrax songs. Matlab scripts implementing this method
128 are available for download at [URL TO BE DETERMINED BEFORE PUBLICATION].

129

130 3. MATHEMATICAL THEORY OF THE MODEL

131 Sampling signals from a repertoire can be represented as a variant of the Coupon
132 Collector's problem, solved by Erdős & Rényi (1961) and cited in Jocković & Mladenović
133 (2011). Suppose we collect coupons (sometimes the problem is posed as collecting baseball
134 cards, or similar) of which there are N different types. We randomly select coupons with
135 replacement, i.e. the coupons are not depleted. The original problem asks for the expected
136 number of selections necessary to have collected at least one of each coupon type. We pose a
137 related question: after selecting M coupons, how many distinct different types of coupons are we
138 expected to have uncovered? This is equivalent to sampling M signals from a repertoire of true
139 size N .

140 Our problem may be posed formally as follows: Let $S = \{1, 2, \dots, N\}$ be the set of distinct
141 signals in an N -element repertoire. Each possible sample of size M from this repertoire
142 corresponds to one of the N^M sequences of the form (i_1, \dots, i_M) , where i_1, \dots, i_M are arbitrary
143 elements of S . Our sample space $\Omega(M, N)$ consists of the set of all such sequences. Equip
144 $\Omega(M, N)$ with a probability measure P defined as follows: Let $p(1), \dots, p(N)$ designate the
145 relative frequencies of the signals $1, \dots, N$, where $p(1) + \dots + p(N) = 1$. Then set
146 $P(i_1, \dots, i_M) = p(i_1) \cdots p(i_M)$, extending P to arbitrary subsets of $\Omega(M, N)$ by additivity. Note that

147 in defining P in this way, we are postulating that the signal occurring at each position in the
148 sample is *independent* of the signals occurring in earlier positions. Now consider the random
149 variable $X : \Omega(M, N) \rightarrow \{1, 2, \dots, N\}$, where $X(i_1, i_2, \dots, i_M)$ = the number of distinct signals in the
150 sequence (i_1, i_2, \dots, i_M) . Our goal is to evaluate $E(X) = \sum_{j=1}^N jP(X = j)$, the expected (or mean)
151 value of X . The evaluation of the probabilities $P(X = j) := P(\{(i_1, i_2, \dots, i_M) : j \text{ distinct}$
152 signals occur in the sequence $(i_1, i_2, \dots, i_M)\})$ is, however, a daunting task. Fortunately, we may
153 write X as the sum $X_1 + \dots + X_N$ of *indicator random variables*, where, for each $j = 1, \dots, N$,
154 $X_j(i_1, \dots, i_M) = 1$ if the number j appears in (i_1, \dots, i_M) at least once, and 0 if j never appears in
155 the sequence. For each j , $E(X_j) = P(X_j = 1) = 1 - P(X_j = 0) = 1 - (1 - p(j))^M$. By the linearity
156 of the expectation operator E (which holds, notwithstanding the fact that the random variables
157 X_j are not independent) it then follows that

$$158 \quad E(X) = \sum_{j=1}^N E(X_j) = \sum_{j=1}^N 1 - (1 - p(j))^M. \quad (3)$$

159 In the specific case where $p(1) = \dots = p(N) = 1/N$ (all signals equally likely), P is the *uniform*
160 *distribution* on $\Omega(M, N)$, and (3) reduces to

$$161 \quad E(X) = N \left[1 - \left(1 - \frac{1}{N} \right)^M \right] = \frac{N^M - (N-1)^M}{N^{M-1}} \quad (4)$$

162 Although Equation 4 is similar in shape to Equation 1, this similarity is not preserved in the more
163 general case (Equation 3) where the probabilities (relative frequencies) of each signal are not
164 homogenous. Botero et al. (2008) examined a specific case of non-homogenous probability of

165 signals, using the WM, and concluded that in this case, enumeration, or simply counting the
 166 number of distinct signal types observed, provides as good an estimate of repertoire size as
 167 curve-fitting methods. We can extend this analysis to show that the error in curve-fitting
 168 techniques depends not on the extent of “non-homogeneity” in the probability distribution, but
 169 on the number of “rare” signals. Botero et al defined half of the signals as “common”
 170 (probability P_c), and half “rare” (probability P_r), where $P_c=5P_r$. It follows therefore that
 171 $P_r=1/(3N)$, and $P_c=5/(3N)$. We can substitute these probabilities into Equation 3, which allows us
 172 to compute the expected number of distinct signal types observed (as determined by the Coupon
 173 Collector’s model):

$$174 \quad E(X) = \frac{N}{2} \left[2 - \left(1 - \frac{1}{3N}\right)^M - \left(1 - \frac{5}{3N}\right)^M \right] \quad (5)$$

175 We can extend this treatment to the case where a proportion α of the signals are
 176 “common”, and $(1-\alpha)$ “rare”, and where $P_c=\beta P_r$; $0<\alpha<1$, and $\beta>1$. In this case Equation 3
 177 becomes:

$$178 \quad E(X) = N\alpha \left[1 - (1 - \beta P_r)^M \right] + N(1-\alpha) \left[1 - (1 - P_r)^M \right] \quad (6)$$

179 Since all the signal probabilities sum to 1, $N\alpha\beta P_r + N(1-\alpha)P_r = 1$, and so solving for P_r , we
 180 have:

$$181 \quad \begin{aligned} P_r &= \frac{1}{N(\alpha\beta - \alpha + 1)} \\ P_c &= \frac{\beta}{N(\alpha\beta - \alpha + 1)} \end{aligned} \quad (7)$$

182 Substituting this into Equation 6, we can derive a general expression for the expected number of
183 distinct observed signals.

184 The Botero model is unrealistic in considering only two signal probabilities, and as a result
185 overestimates the performance of exponential curve fitting models. Before moving on to
186 consider more realistic signal probability distributions, we can perform a further simple
187 extension, by assuming that signal probabilities decline according to a simple exponential
188 probability distribution, with a single parameter μ (where $\mu > 0$) that determines how much
189 variation there is between the probabilities of different signal types..

$$190 \quad p(i) = \frac{1}{K\mu} e^{-i/\mu} \quad (8)$$

191 where K is a normalising factor, given a finite number N of signal types

$$192 \quad K = \frac{1 - e^{-N/\mu}}{\mu(1 - e^{-1/\mu})} \quad (9)$$

193

194 4. METHODS

195 We examine by simulation the performance of four techniques for estimating vocal
196 repertoire size. The WM has been extensively described above. Secondly, we test the model
197 proposed by Davidson & Wilkinson (2002), DW, which uses an additional parameter A
198 (Equation 2), and so does not lend itself to analytical scrutiny along the lines of the preceding
199 section. Thirdly, we attempt to estimate repertoire size using the model of signal occurrence as
200 determined by the Coupon Collector's model (henceforth, CC). Finally, we compare these

201 techniques to simple enumeration (EN) of distinct observed signals, as an estimate of true
202 repertoire size.

203 We applied all four repertoire estimation techniques against real data taken from three
204 species in the field. First, the northern mockingbird possesses a highly diverse repertoire of songs
205 based largely on mimicry of other species, and is an important subject for repertoire size
206 estimation. We used data gathered on nine male mockingbirds from 2010-2011 in Elon, North
207 Carolina; for details on the methods, see Gammon (2014). The songs were analysed and assigned
208 a classification according to the heterospecific mimicked species and song type, breaking song
209 sequences where the bird interspersed native mockingbird song. Our data set comprised 1184
210 sequences (i.e. $M \leq 1184$), consisting of 100 different mimicries (signals) of 41 different species.
211 Sequences varied in length between one and 16 signals (mean 2.4). Our aim here was to
212 determine the repertoire size (N) in terms of the number of different heterospecific signals the
213 birds can mimic. We estimated the repertoire size for the study population as a whole, rather than
214 for each of the nine birds individually, due to the small sample size at the individual level.

215 Our second data set is a collection of calls of Carolina chickadees, recorded from 40 flocks
216 in eastern Tennessee (Freeberg 2008) and 20 flocks in central Indiana (Freeberg 2012). Calls
217 were recorded from late fall through early spring months when chickadee flocks naturally occur.
218 Calls from a single flock were typically obtained in 45-90 minutes of recording in a 1-2 day
219 period. The observer used a naturalistic observation approach, attempting to get close enough to
220 the wild birds to obtain high quality recordings, without otherwise disrupting the birds' normal
221 behaviour. The chickadee data set consists of 8124 different calls, consisting of 7 different note
222 types, and varying in length between one and 45 notes (mean 6.1) per call. In total, there are
223 1284 distinct sequences in this corpus. Our aim here was to estimate the repertoire size of all the

224 birds together (rather than of individual chickadees) in terms of call combinations, as in the song
225 analysis above for mockingbirds. However, since call sequence length is essentially unbounded,
226 and so the potential repertoire size unlimited, we restricted ourselves to examining all observed
227 sequences of 5 successive notes in the corpus. We treated each of these “5-grams” as a distinct
228 signal type (preliminary investigation indicated that choosing 4- or 6-grams did not significantly
229 alter the results). This provides a potential signal-space of $7^5=16807$ distinct signal types,
230 although in the 18593 5-grams obtained in the data set, there were only 352 distinct signal types.

231 Our third data set used songs of a terrestrial mammal, the rock hyrax *Procavia capensis*,
232 recorded in northern Israel (Kershenbaum et al. 2012). Opportunistic recordings were made from
233 males at 18 colonies, and analysed to identify syllable types using the same classification
234 technique used in Kershenbaum et al. (2012). This data set consists of 969 sequences, consisting
235 of 5 different syllables, varying in length between one and 81 syllables (mean 45). As with the
236 chickadee corpus, we examined all 2028 5-grams in these data, in which there were 849 distinct
237 signals, out of $5^5=3125$ possible 5-grams.

238 Empirical observations suggest that the frequencies of different signal types in real bird
239 and mammal samples are not well described by a simple probability distribution, such as
240 Equation 8, but follow a heavy-tailed distribution, with a few common signals, and a large
241 number of rare ones. Although we do not have a mechanism explaining the distribution of signal
242 probabilities, we attempted fitting the probability distribution of signal types (or 5-gram types) to
243 two classes of similar heavy-tailed distribution functions: the double exponential function

$$244 \log[p(i)] = a e^{-bi} + c e^{-di} \quad (10)$$

245 and the logarithmic power function:

246 $\log[p(i)] = ai^b + c$ (11)

247 where a , b , c , and d are unknown parameters, determined by fitting Equation 10 or 11 to
248 observed data. The function with the best fit to the signal type distribution was chosen to model
249 the probabilities for that species.

250 In our first test, we used each of the four methods to estimate the repertoire size of the
251 three species, and compared the prediction of each model to the curve showing the number of
252 distinct signal types observed vs. increased sampling effort. We randomly shuffled the sequence
253 of signals, to produce 10 random ordering of the signals from each of the four species, and
254 calculated the estimated asymptotic repertoire size using each of the four methods. For
255 illustrative purposes, we additionally varied the notional "sample size", M , by taking the first M
256 signals from each of the 10 random orderings, and estimating repertoire size $E(X)$ using each of
257 the methods.

258 In our second test, we performed simulations to generate artificial signal sequences with
259 the statistical properties of the empirical data, for each of the three signal probability
260 distributions shown above, and then tested the ability of the different repertoire estimation
261 techniques to determine the true repertoire size. We simulated a repertoire size for each of the
262 three distributions, arbitrarily chosen as being at least twice as large as the number of signals
263 observed empirically for that species: mockingbird $N=200$, chickadee $N=736$, hyrax $N=1944$. We
264 generated random sequences of signals, drawn from a repertoire of N distinct signal types, where
265 the probability of the i^{th} signal is determined by Equations 12, 13, and 14 respectively. We
266 examined the performance of each algorithm as the sampling effort M is increased. This tests
267 how each algorithm performs when the number of available observations is limited. To do this,

268 we generated a single string S of length $M=2N$, and then sampled substrings $Q=S_{1\dots m}$ for
269 $m=1\dots M$. Each substring Q represents a particular sampling effort, for instance, recording
270 birdsong in the field. For each substring Q we re-estimated the signal probability distribution,
271 using only the signals in Q . This provided an important sensitivity test of the CC algorithm to
272 poor estimates of the signal probability distribution, arising from small sample sizes. Finally, the
273 experimenter will rarely know *a priori* which probability model is most appropriate for the signal
274 distribution of the study species. Once sampling of signals has begun, however, it becomes
275 possible to estimate the distribution of signals. We can do this by applying both probability
276 models given in Equations 10 and 11 to each signal substring, selecting the model with the best
277 goodness of fit. Furthermore, once string Q has been sampled, we can improve our estimate of
278 $E(X)$ by shuffling $Q\rightarrow Q'$, and then again measuring $F(r)$, the number of distinct signal types in
279 Q'_1 . We repeated this process 10 times, to determine $Q'_{1\dots r}$ for $r=1\dots m$, which provided us with
280 an averaged $F(r)$ over 10 random shufflings of Q , for each r .

281 For the WM and DW, we performed a non-linear least-squares fit of $F(r)$ to r , using the
282 Matlab function *fit*. This gave an estimate of N for the WM, and of N and A for the DW, for each
283 value of m . For the EN method, $F(r)$ measures the number of distinct observed signal types
284 directly.

285 For the CC model, we first estimated the parameters of Equations 12, 13 or 14, for each
286 substring Q of each length $m=1\dots M$, using the Matlab function *fit*, given the distribution of
287 signals in Q , and the probability density model in Equation 8. We then performed a non-linear
288 least-squares fit to the CC model (Equation 3), to find N .

289 Finally, for the purpose of comparison, we repeated the analysis of simulated empirical
290 signals using the mark-recapture technique as implemented using Schnabel's estimator
291 (Sutherland 2006), where each signal type observed was considered a new sampling event.

292

293 5. RESULTS

294 In the example given by Botero et al. (2008) using non-homogeneous signal probabilities,
295 the predictions of the WM (Equation 1) and of the CC model (Equation 5) deviate prominently
296 from each other. Figure 1 shows the expected number of distinct signals observed, if the WM
297 and CC models were driving the presentation of the repertoire, i.e. how quickly each model
298 predicts new signals to appear. The figure indicates that if signals were observed according to an
299 exponential model such as the WM, the expected number of distinct signals observed would rise
300 much faster than predicted by the CC model. However, as we have shown in the section
301 Mathematical Theory of the Model, signal selection is more precisely modelled as coupon
302 collection, rather than WM exponential growth. Thus signals will accumulate more slowly than
303 expected by WM dynamics, fewer distinct signal types will be observed in practice than
304 expected by the WM model for any particular sampling effort, and applying the WM will tend to
305 underestimate total repertoire size.

306 When the two-probability model is extended to a variable number of "common" and "rare"
307 signals (Equation 6), the divergence of the WM and CC models becomes more prominent. Figure
308 2 shows examples of these results for varying α and β . It is clear that the predictions of the WM
309 only agree with the expected number of distinct observed signal types when two conditions are
310 met: when the signal probability distribution is homogenous, and when the number of rare

311 signals is small (α is large). Thus, a large number of rare signals will typically result in the WM
312 underestimating the true signal repertoire size (many signals will be unobserved for any given
313 observation effort).

314 Examples of this distribution for different values of μ , and the predictions of the Wildenthal
315 model, are given in Figure 3. For low μ (many rare signals), in comparison with the Coupon
316 Collector model, the Wildenthal model expects many more distinct signals to occur in the first M
317 samples, and therefore greatly underestimates the total repertoire size by the conclusion of
318 sampling effort.

319 The results of fitting signal probabilities to the two probability density models (double
320 exponential, Equation 10; and logarithmic power, Equation 11) are shown in Figure 4 for each of
321 the three species. In the case of the mockingbird, the signal probabilities best fit the double
322 exponential model, with the following parameters (Figure 4a):

$$323 \quad \log[p(i)] = 3.827 e^{-0.363i} - 3.940 e^{0.007i} \quad (12)$$

324 For the chickadee data, the logarithmic power model provided the best fit to the 5-gram
325 signal probabilities, with the following parameters (Figure 4b):

$$326 \quad \log[p(i)] = -9.143i^{0.118} + 7.922 \quad (13)$$

327 The hyrax 5-gram probabilities also fit the logarithmic power distribution, with the
328 following parameters (Figure 4c):

$$329 \quad \log[p(i)] = 13.18i^{-0.07128} - 15.95 \quad (14)$$

330 Consequently, these relationships were used when determining the probabilities $p(i)$ for use
331 in the Coupon Collector's model Equation 3.

332 Figure 5 shows the result of using each of the four techniques to estimate the repertoire
333 size of the vocal signals from the three species examined. With the mockingbird and chickadee
334 data, both the WM and DW techniques saturate at a repertoire size below the maximum number
335 of distinct signal types observed (EN), and this by definition must be an underestimate of the true
336 repertoire size. However, most noticeably in the mockingbird and chickadee data sets (Figure
337 5a,b), the exponential techniques fail to capture the shape of the repertoire vs. samples curve.
338 The CC model, on the other hand, closely matches the empirical data at every point. In the case
339 of the chickadee data (Figure 5b), the WM underestimates the true repertoire size even more
340 markedly, and the DW also saturates below the enumeration result, whereas the CC model again
341 matches the observed data well. The hyrax data set has a much larger number of distinct
342 observed signal types, and the number of observations is insufficient to characterise the curve
343 accurately. However, the WM still clearly underestimates the total repertoire size, while both the
344 DW and CC methods provide higher estimates.

345 When simulating signal sequences using the statistical properties of the real signal type
346 distributions, the Coupon Collector model provides the only accurate method of those tested for
347 estimating repertoire size, at reasonable sampling efforts (Figure 6); and even when the CC
348 estimates are highly variable (Figure 6b) they are consistently more accurate than the WM, DW,
349 or EN techniques. The exponential models, as well as the enumeration technique, greatly
350 underestimate the repertoire size for all data sets. Notably, for the mockingbird and chickadee
351 data sets, the enumeration estimate is many times lower than the true repertoire size, even though
352 the enumeration "appears" to have saturated at the end of the sampling period. The mark-

353 recapture (Schnabel) method likewise performed poorly in comparison to CC, and provided no
354 benefit over any of the other approaches.

355

356 6. DISCUSSION

357 We derived a precise, powerful and accurate statistical model for predicting the number of
358 distinct signal types observed from a repertoire, given a particular sampling effort. This model is
359 based upon different assumptions than those made by researchers in the past that observed signal
360 types should follow an “exponential” model. The predictions of our “Coupon Collector” model
361 do not differ substantially from those of the exponential models when the probabilities of the
362 different signal types are similar. However, in realistic scenarios, animals vocalise with
363 numerous syllables of markedly different prior probabilities, and it is often the case that certain
364 signal types are rarely observed. In such a case, using an exponential model to predict the total
365 signal repertoire will underestimate repertoire size. We showed that when the number of rare
366 signals is large, the predictions of the exponential model can be highly inaccurate (Figure 3). Use
367 of the Coupon Collector model requires an estimate of the prior probability distribution of the
368 different signal types, which is easily estimated from the data. Once this estimate is calculated,
369 furthermore, the Coupon Collector model is the only one of the techniques tested that provides
370 an accurate indication of the true repertoire size (Figure 6). Examination of the observed
371 repertoire size vs. sampling effort curves (Figure 5) shows how inappropriate the exponential
372 models and the enumeration method are for the real data sets analysed here.

373 Repertoire size has often been cited as an indicator of ecological and neurological
374 importance in animal vocalisation studies. Repertoire size has been particularly well studied in

375 oscine birds, and has been found to correlate with age (Hesler et al. 2012), population viability
376 (Laiolo et al. 2008), physical condition (Kipper et al. 2006), territory maintenance (Hiebert et al.
377 1989), and brain structure (Pfaff et al. 2007). In mammalian studies, repertoire size is difficult to
378 assess, but a relationship between repertoire size and social complexity has been demonstrated in
379 some taxa (McComb & Semple 2005; Pollard & Blumstein 2012). Despite this, the utility of
380 repertoire size estimates is unclear, precisely because of the apparent inability of existing
381 methods to derive such an estimate from realistically sized data sets. One of the challenges to
382 estimating repertoire size is that exhaustive sampling of all signals is unrealistic, and the
383 sampling effort to capture even a large majority of all signals may be costly and time-consuming.
384 Clearly, estimation techniques that can approximate repertoire size based on a relatively small
385 sample are appealing. Although many studies (e.g. Pfaff et al. 2007; Laiolo et al. 2008; Hesler et
386 al. 2011; Boogert et al. 2011) have used simple estimates of repertoire size – particularly signal
387 type enumeration – it has been pointed out that many species continue to produce “novel” signals
388 after “exhaustive” collection has been completed (e.g. Balsby & Hansen 2010; Hesler et al.
389 2011). Our results show that using the total number of observed signals can be greatly
390 misleading, even when the curve of observed repertoire vs. collection effort appears to have
391 “flattened out”. Our model provides a more rigorous approach to estimating vocal repertoire size,
392 and should go a long way towards addressing the criticisms of previous studies.

393 Although the overwhelming majority of research into repertoire size has been in the
394 context of vocal communication, our method can be applied generally to other repertoire types,
395 most usefully if the true repertoire size is sufficiently large to make simple enumeration
396 impractical. However, most visual signalling modalities consist of a very small number of signal
397 types, e.g. the five display types of the Jacky Dragon *Amphibolurus muricatus* (Peters & Ord

398 2003), or the eight display types of the mallard *Anas platyrhynchos* (Lorenz 1971, cited in
399 Bradbury & Vehrencamp 2011), and so may benefit less from our methodology. Conversely,
400 large behavioural repertoires (~50 behavioural patterns) have been examined in *Pheidole* ants,
401 and assessment of repertoire size in this system has been recognised as being problematic
402 (Sempo & Detrain 2004). Use of the Coupon Collector model should allow more accurate
403 assessments to be made.

404 Although the Coupon Collector model is a precise theoretical formulation of the process of
405 observing signals from a repertoire, it is necessarily more complex than simple exponential
406 models. To provide an accurate model, it is necessary to specify the prior probability of each
407 signal in the repertoire, something clearly impossible when not all signals have been observed.
408 Our approach is to find a parametric approximation to the prior probability distribution for signal
409 types, and to extrapolate this to unknown signals that are rarer than those already observed. In
410 this case, the computational complexity of the Coupon Collector analysis is dependent on the
411 number of parameters in the probability distribution model. In the data presented here, we have
412 accurately modelled the signal probability distributions with just three or four parameters;
413 making non-linear least-square fitting realistic for the size of the data sets used. We have also
414 used just two separate statistical models: the double exponential (Equation 10) and the
415 logarithmic power (Equation 11). Either of these is easy to apply to empirical data gathered in
416 the field. The Wildenthal (1965) model is far simpler, using no indication of signal probability
417 heterogeneity, but suffers in performance from this unrealistic assumption. The Davidson &
418 Wilkinson (2002) model attempts to compensate for this by introducing an arbitrary rate
419 parameter A , to capture the “slowing down” of signal discovery inherent when many rare signals
420 exist. However, although it could be argued that both the Davidson-Wilkinson model and the

421 mark-recapture model have an advantage of computational simplicity over the Coupon Collector
422 model, the predictions of the Davidson-Wilkinson and the mark-recapture models can be so
423 inaccurate that they have little advantage over the Wildenthal model. In addition, the rate
424 parameter A in the Davidson-Wilkinson model has no clear biological or statistical basis,
425 whereas the parameters of the Coupon Collector model directly reflect the rarity of signals in the
426 animal's repertoire.

427 In understanding the evolution of communicative complexity, we are typically interested in
428 the repertoire sizes of populations or species (e.g., Pollard & Blumstein 2012). From
429 developmental and ecological standpoints, however, we are frequently interested in repertoire
430 sizes of individuals, rather than of groups. In this study we have made a number of assumptions
431 and simplifications, particularly by analysing the repertoire of all the signals of a species
432 together, rather than analysing individuals separately. Although the distribution of the
433 frequencies of different signal types may be different between individuals and populations, we
434 feel that this approach better assesses the accuracy of the Coupon Collector model, by providing
435 a larger data set, rather than attempting to draw direct conclusions on individual behaviour from
436 this analysis. In any case, although the repertoire sizes of individuals and populations may differ,
437 we do not believe that the methodologies for estimating these repertoires should be different in
438 these two cases. It is clear from Figure 6 that the Coupon Collector model should provide a
439 superior estimate of true repertoire size, and at smaller sample sizes.

440 The analysis that leads to Equation 3 as the precise estimate of expected observed
441 repertoire size importantly assumes that signal incidences are independent. This assumption is
442 necessarily incorrect in those species where note or call sequences are constrained by rules of
443 note or call ordering, such as the mockingbird (Gammon & Altizer 2011), hyrax (Kershenbaum

444 et al. 2012) or chickadee (Freeberg & Lucas 2012). However, incorporating inter-syllable
445 statistical dependence has never been addressed by any of the analytical techniques used to
446 assess repertoire size. We also note that, regardless of technique, the presence of ordering rules
447 will have the effect of reducing the estimated repertoire size, and the Coupon Collector model
448 performed the best at preserving a high estimated repertoire size.

449 Other authors have attempted to model the repertoire size observation pattern using other
450 approaches, such as mark-recapture (Garamszegi et al. 2005), or rarefaction (Peshek &
451 Blumstein 2011). We provide only a brief comparison of the Coupon Collector model with one
452 of these approaches, partly because they are far less commonly used in the literature than the
453 exponential models, but also because we believe that there is inherent merit in adopting the
454 model supported by theory, rather than more arbitrary models that may provide a certain level of
455 empirical correspondence with data. However, we do not dismiss the use of rarefaction or other
456 techniques where the particular requirements may make use of the Coupon Collector model
457 impractical; particularly where insufficient data exist to estimate the signal prior probability
458 distribution.

459 In summary, we present theoretical and analytical support for the Couple Collector's
460 Model to assess signal repertoire size. We have shown that realistic estimates of repertoire size
461 cannot be achieved using an inaccurate statistical model of repertoire discovery. We have
462 explicitly used the terms 'signal' and 'signal repertoire size' in instances that were not
463 specifically about song or song repertoire size *per se*. This is because our arguments here relate
464 to estimates of signal repertoire size in any signalling modality in which the system contains
465 more than one variant. There is a place for simplified or empirical models that adequately
466 describe the data despite not being theoretically grounded. However, we have shown that in

467 cases of animal vocal repertoires where a significant number of rare signals exist, such models
468 do not reflect observations accurately. Our presentation of the Coupon Collector model will
469 hopefully encourage researchers to derive more reliable estimates of repertoire size, and
470 eventually to re-evaluate the utility of this metric in ecological research.

471

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483 8. REFERENCES

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585

586

587

588 FIGURE LEGENDS

589

590 Figure 1. Examples of the number of distinct signal types observed, vs. sampling effort (M), as
591 predicted by two different models (solid line: Coupon Collector model; dashed line: Wildenthal
592 model), with total repertoire size $N=100$, and a non-homogenous song prior probability
593 distribution as described in (Botero et al. 2008). If repertoire sampling followed the assumptions
594 of the Wildenthal model, the number of observed distinct signal types would rise much faster
595 than is actually the case.

596

597 Figure 2. Expected number of distinct signal types observed with varying number of samples,
598 with total repertoire size $N=100$, and different signal prior probability distributions, following
599 (Botero et al. 2008). (a) The first column shows the prior probability $p(i)$ of the i^{th} signal, for
600 varying number of “rare” signals α , with the relative frequency of rare signals β held constant.
601 The second column shows the expected number of distinct signal types observed for the
602 corresponding probability distribution (solid line), and the Wildenthal model (dashed line). Each
603 row indicates a different value of $\alpha=\{0.2, 0.4, 0.6, 0.8\}$. (b) The estimated repertoire size, for
604 varying number of rare signals α , and relative frequency of rare signals β , as calculated by the
605 two models (upper: Coupon Collector model; lower: Wildenthal model).

606

607

608 Figure 3. Expected number of distinct signal types observed with varying sampling effort, for
609 different signal prior probability distributions according to an exponential probability density
610 function. The first column shows the prior probability of the i^{th} song; each row showing a
611 different mean of the distribution μ . The second column shows the expected number of distinct
612 signal types observed for the corresponding probability distribution (solid line: Coupon Collector
613 model; dashed line: Wildenthal model).

614

615 Figure 4. Sorted signal probabilities for (a) the mockingbird data set, (b) chickadee data set, and
616 (c) hyrax data set. Black points represent the relative probabilities on a log scale of all the signals
617 in the observed repertoire, sorted in descending order. The red line shows the fit of the modelled
618 probability function, and the parameters of the fit (a , b , c , and d) are shown next to the fitted line.

619

620 Figure 5. Best fits of the different repertoire estimation techniques, for the empirical data sets: (a)
621 mockingbird, (b) chickadee, (c) hyrax. Each model was fit to the entire data set, and the resulting
622 parameters used to predict the expected number of signal types observed for different sampling
623 efforts. The estimated repertoire size is shown for each technique in the legend, and as a dashed
624 line of corresponding colour.

625

626 Figure 6. Estimated repertoire size for the different repertoire estimation techniques, for
627 simulated data sets based on the empirical data sets: (a) mockingbird, (b) chickadee, (c) hyrax.

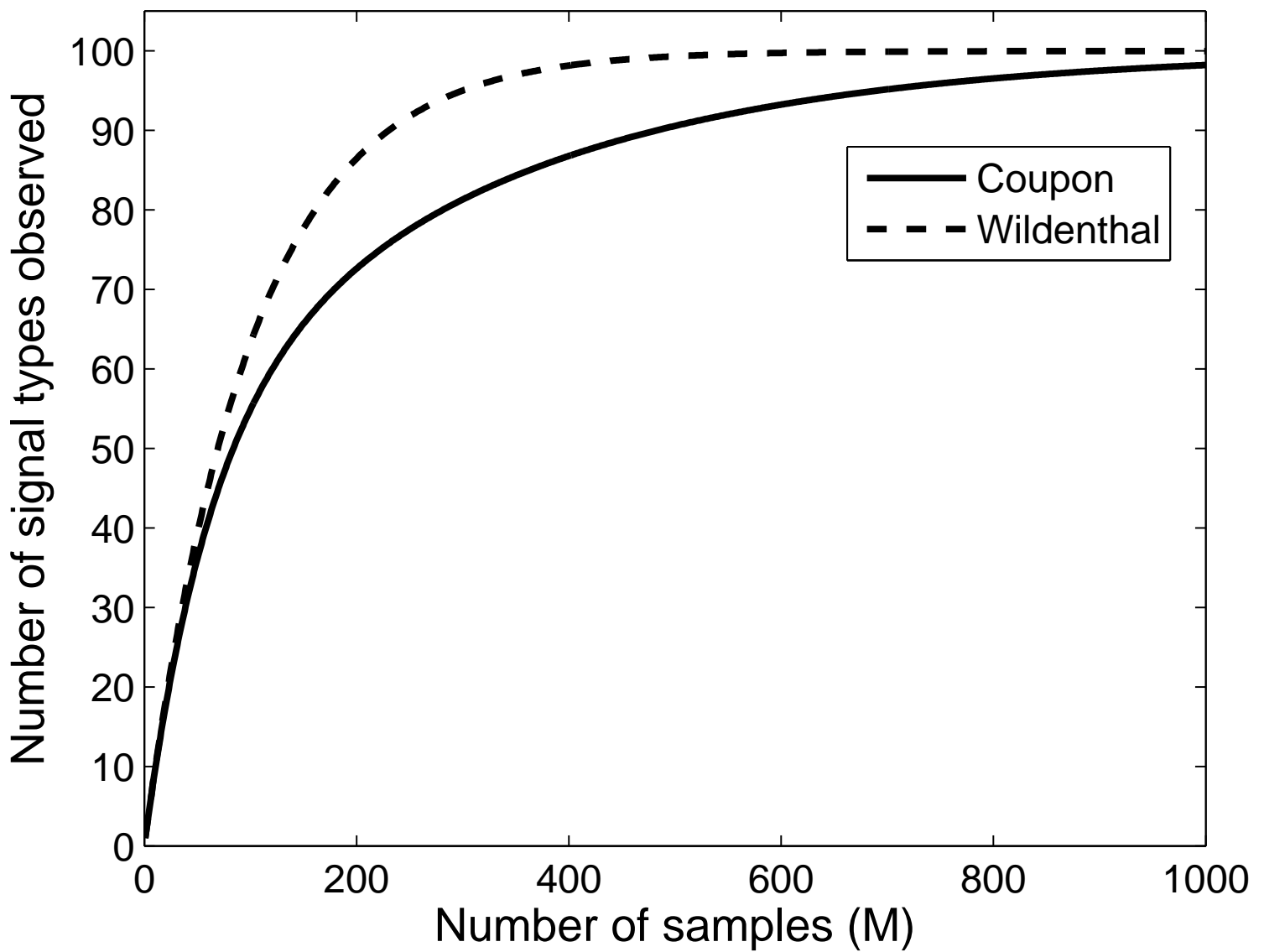
628 True repertoire size is shown as a broken line. Each curve represents the repertoire size estimate
629 for varying sampling effort, and error bars indicate standard error.

630

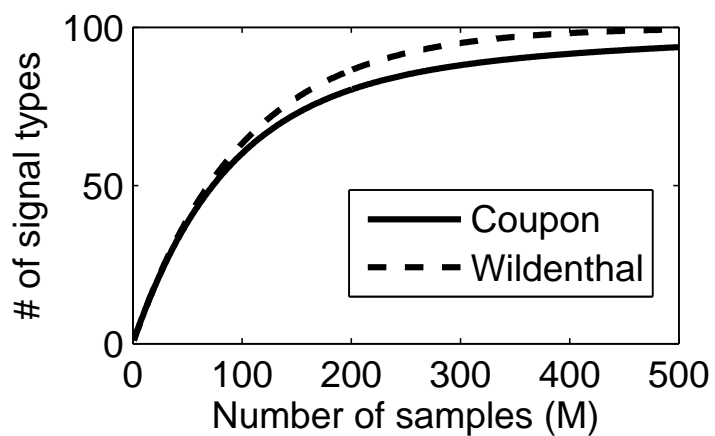
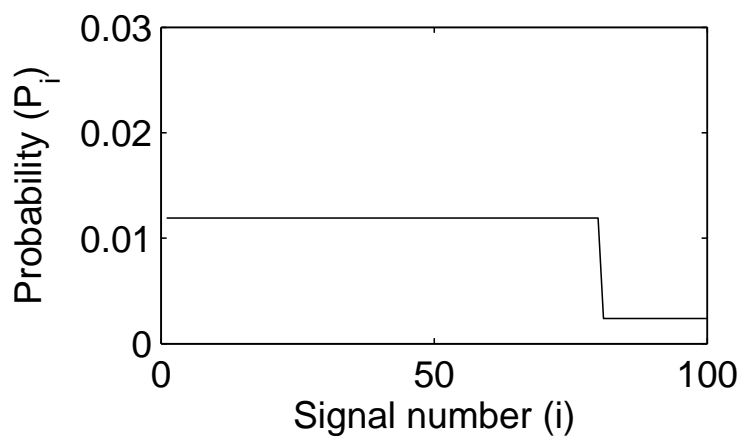
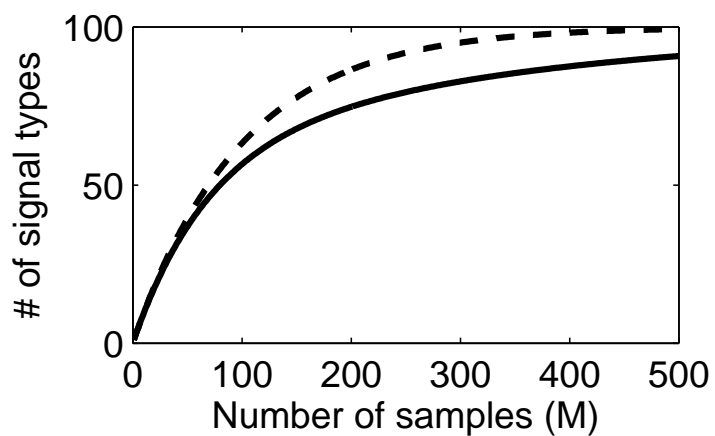
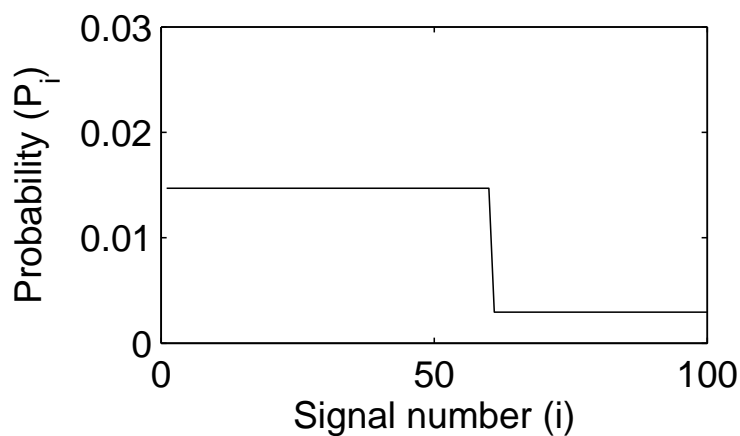
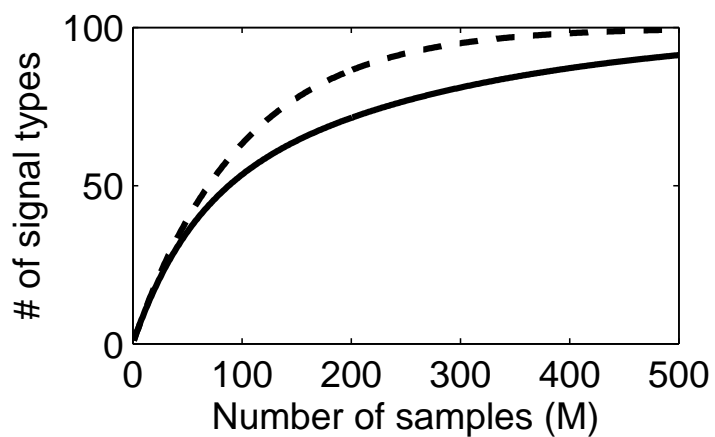
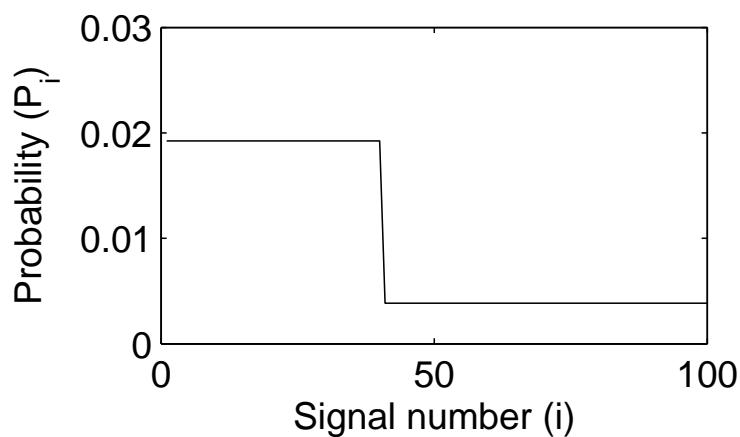
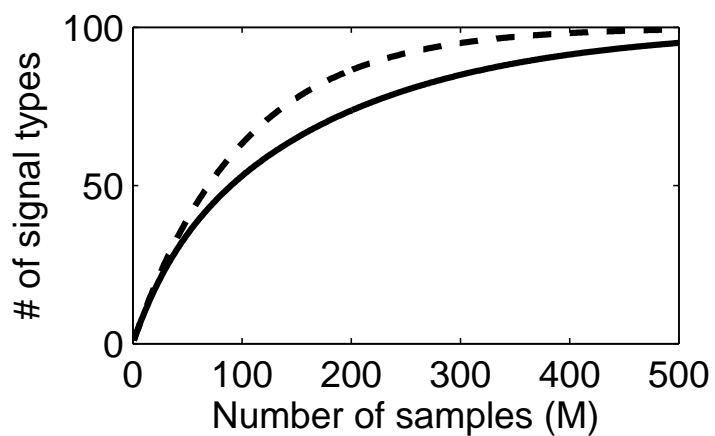
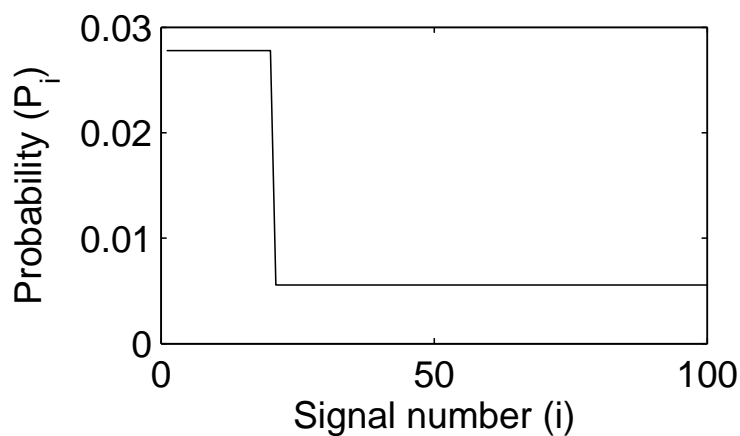
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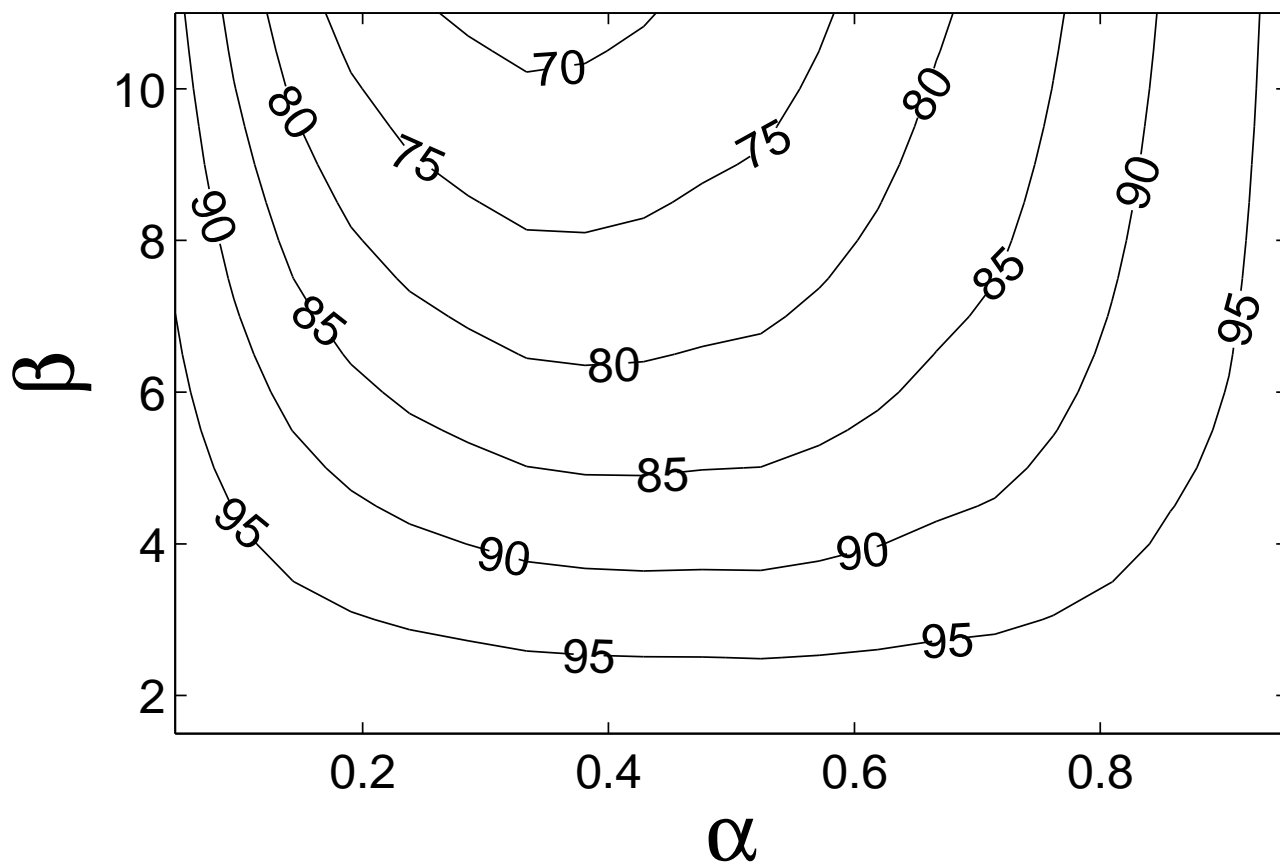
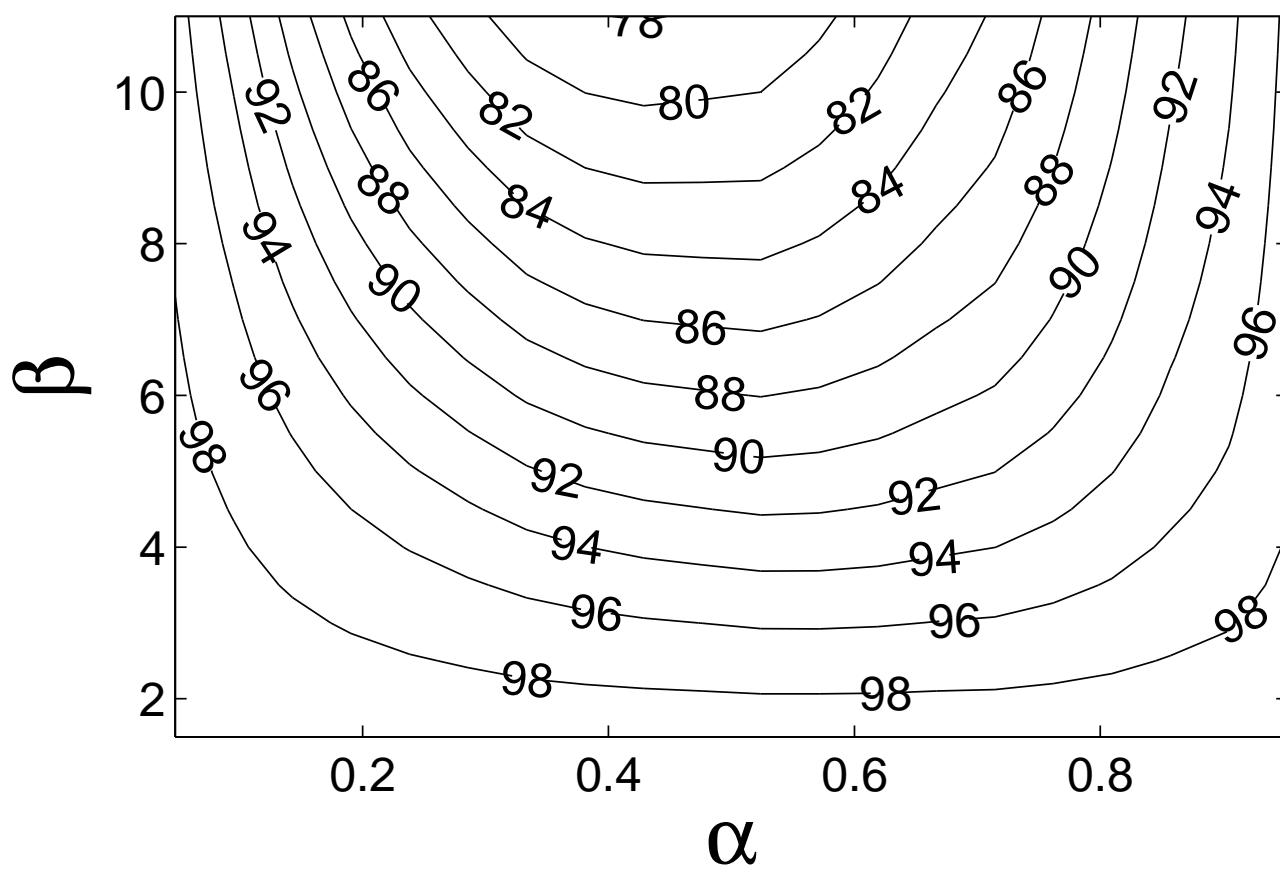
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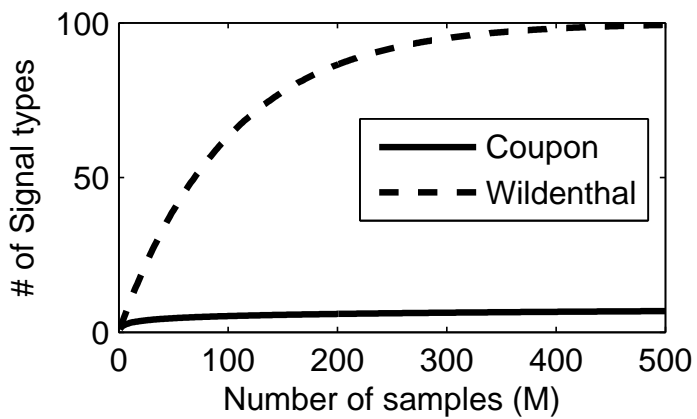
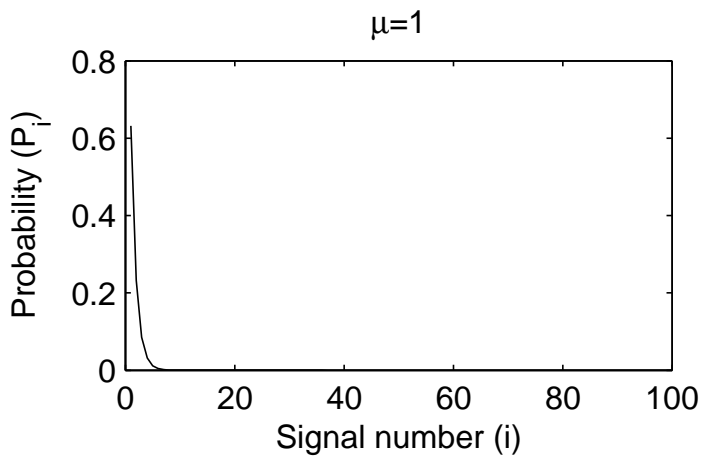
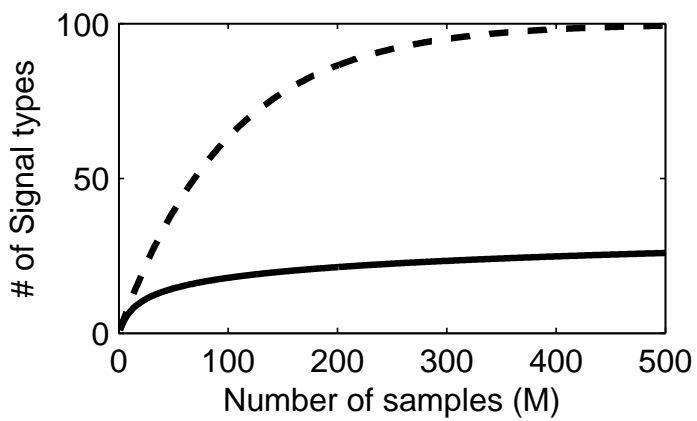
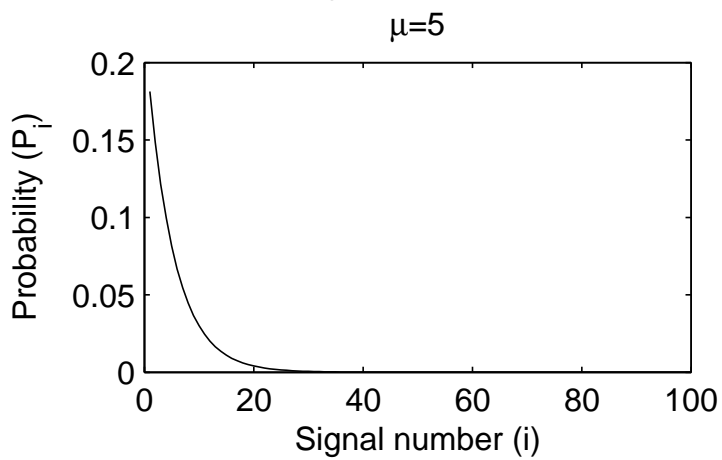
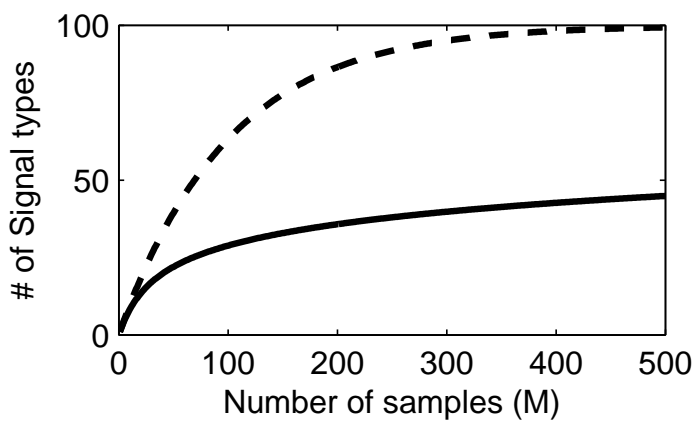
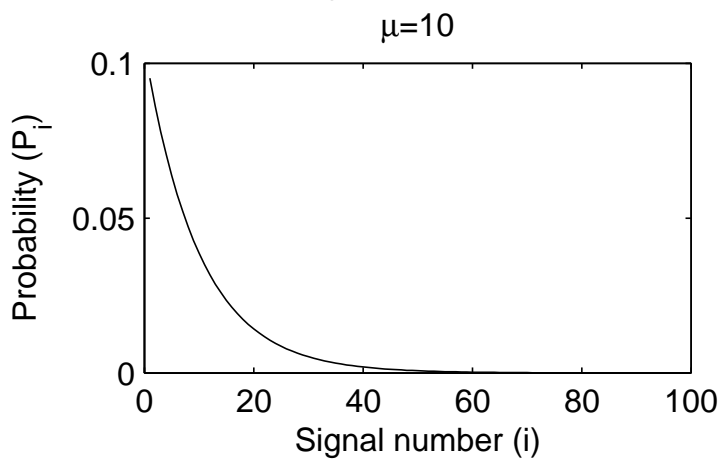
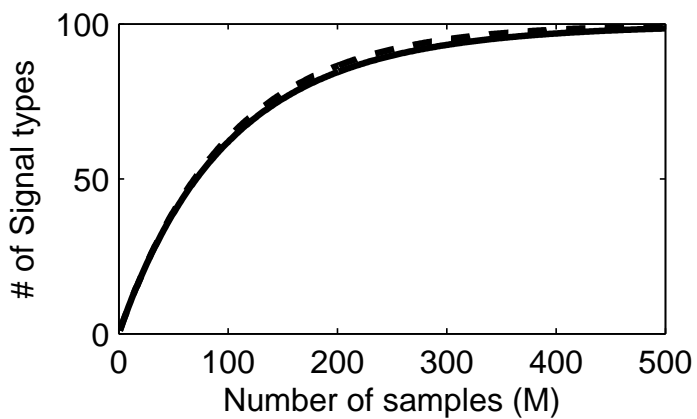
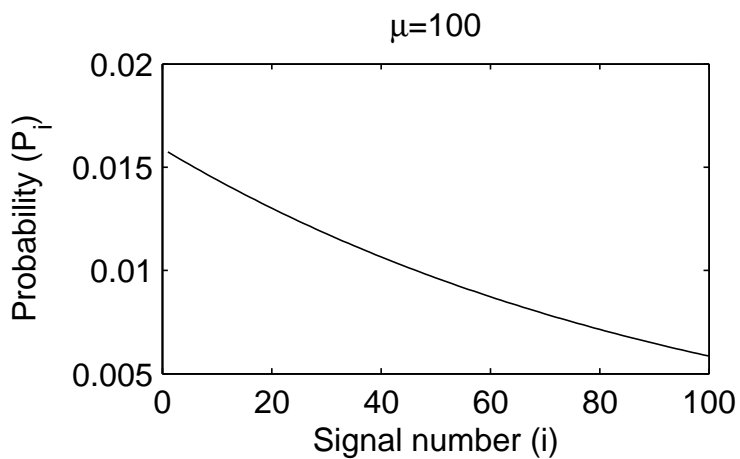
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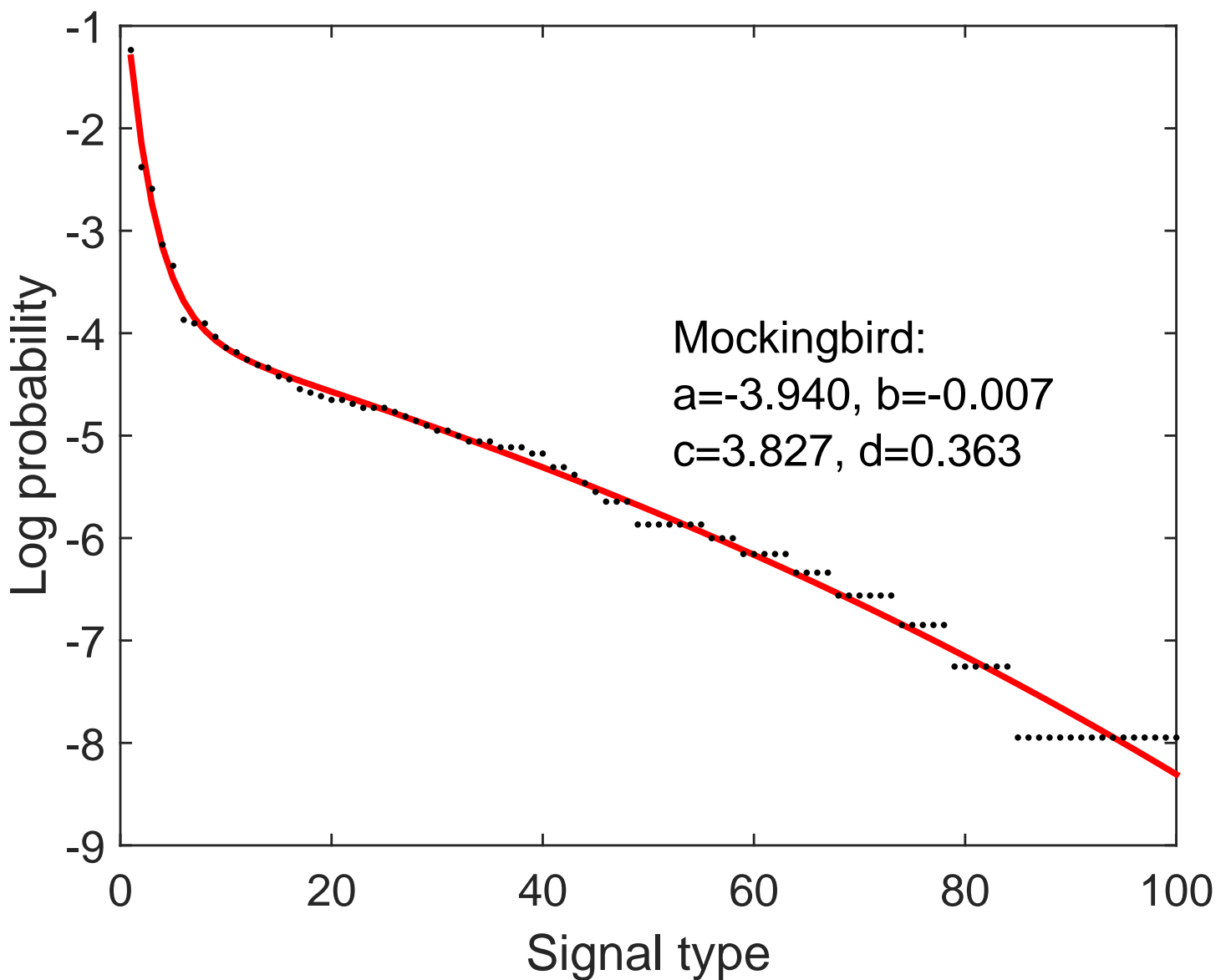


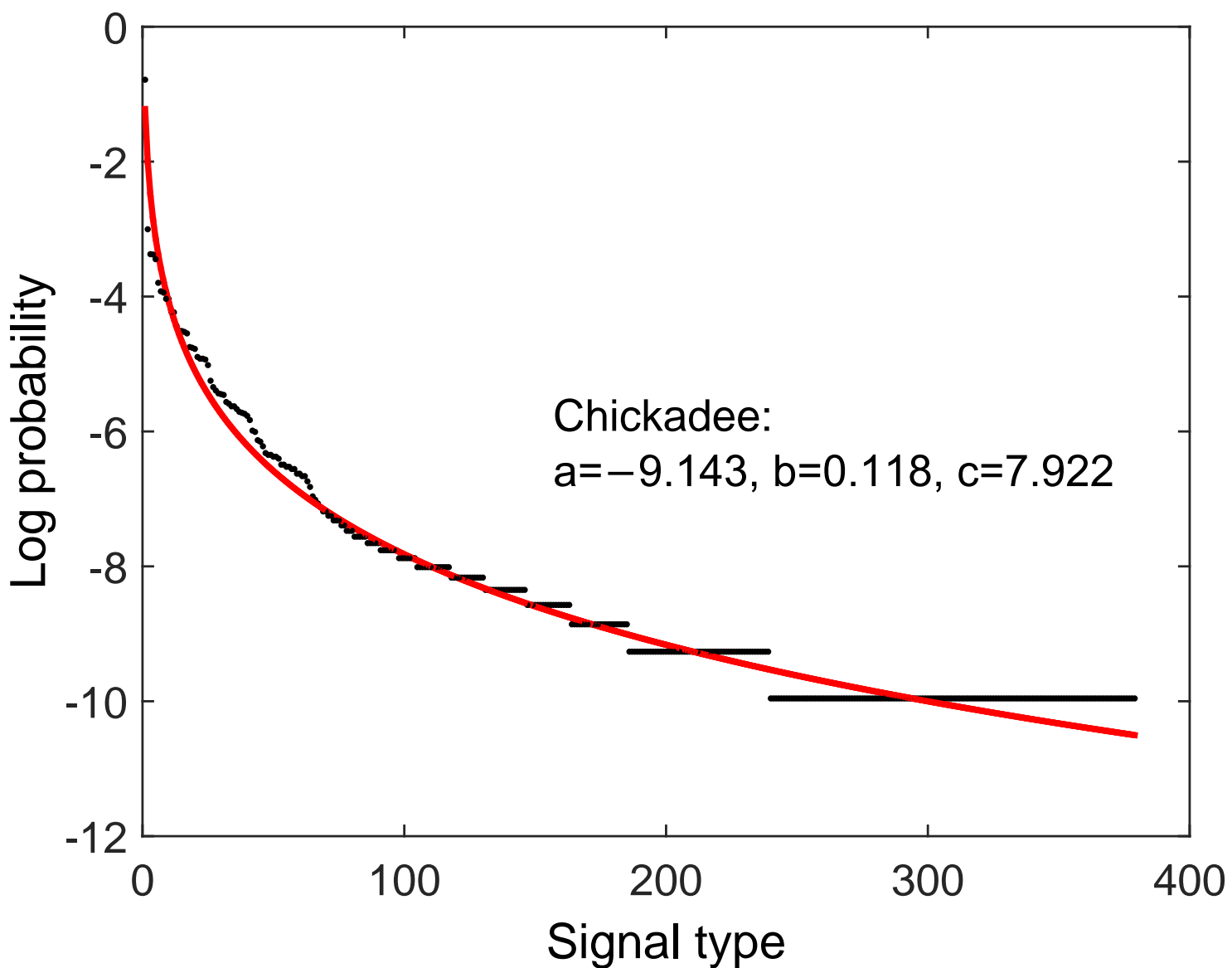
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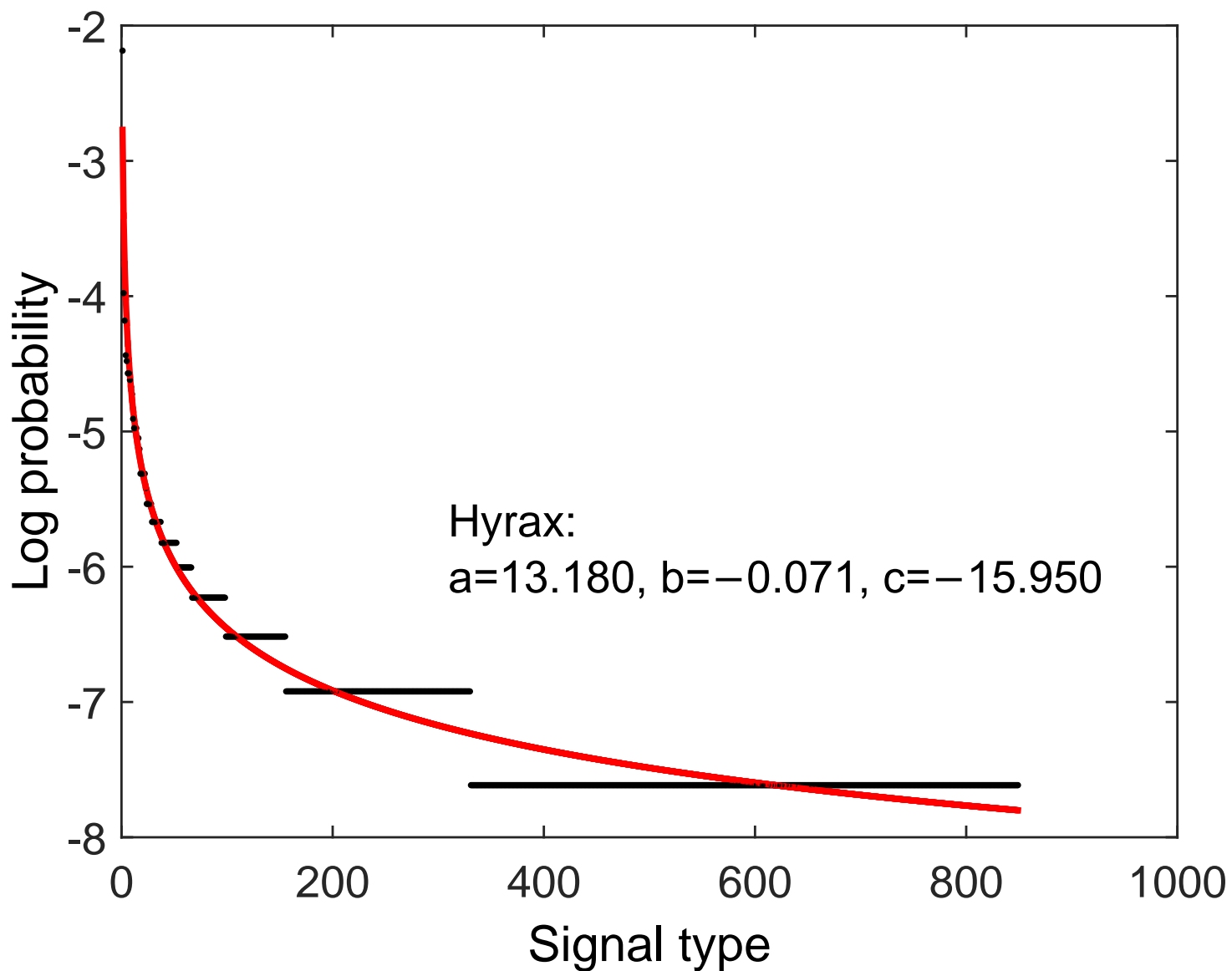


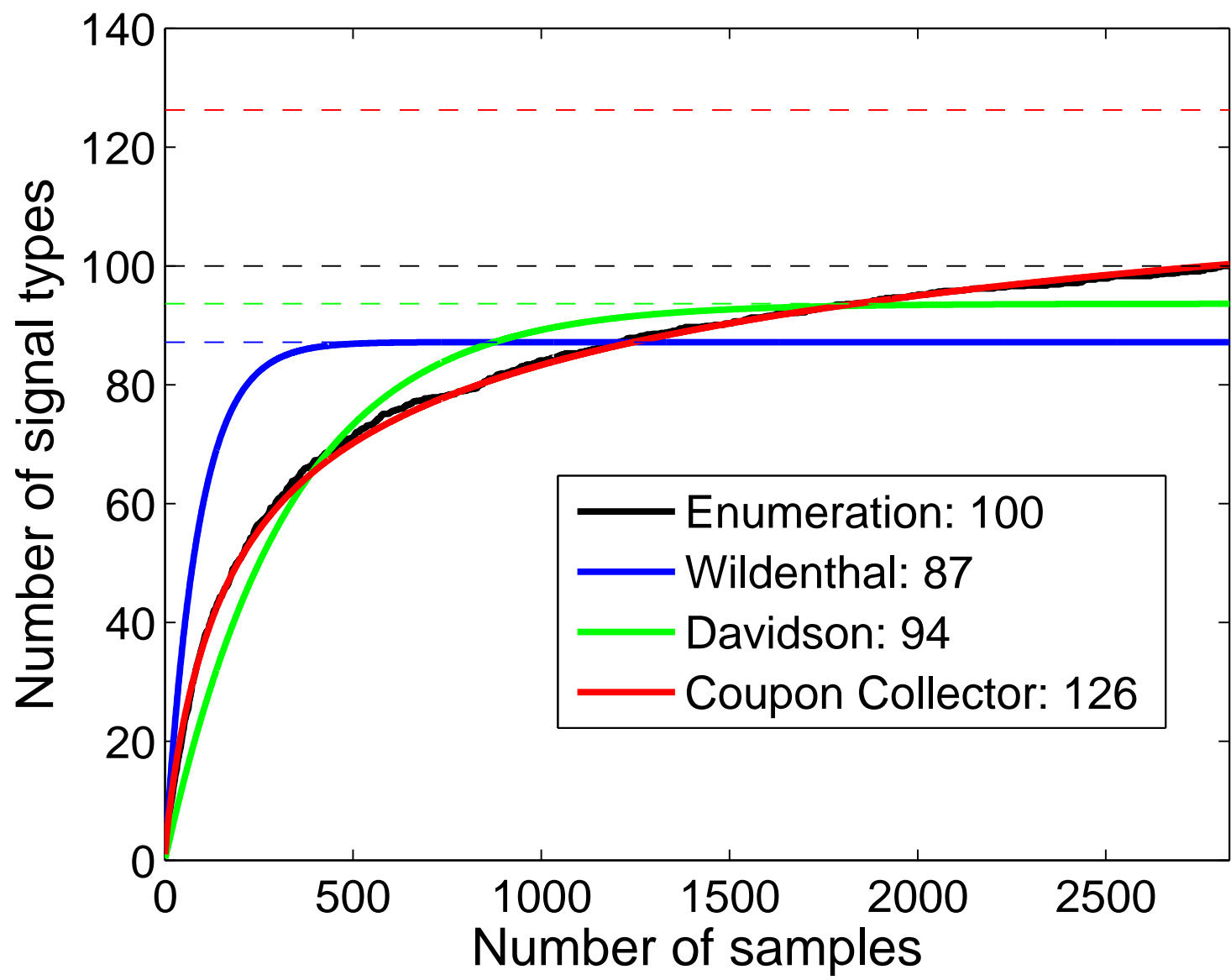
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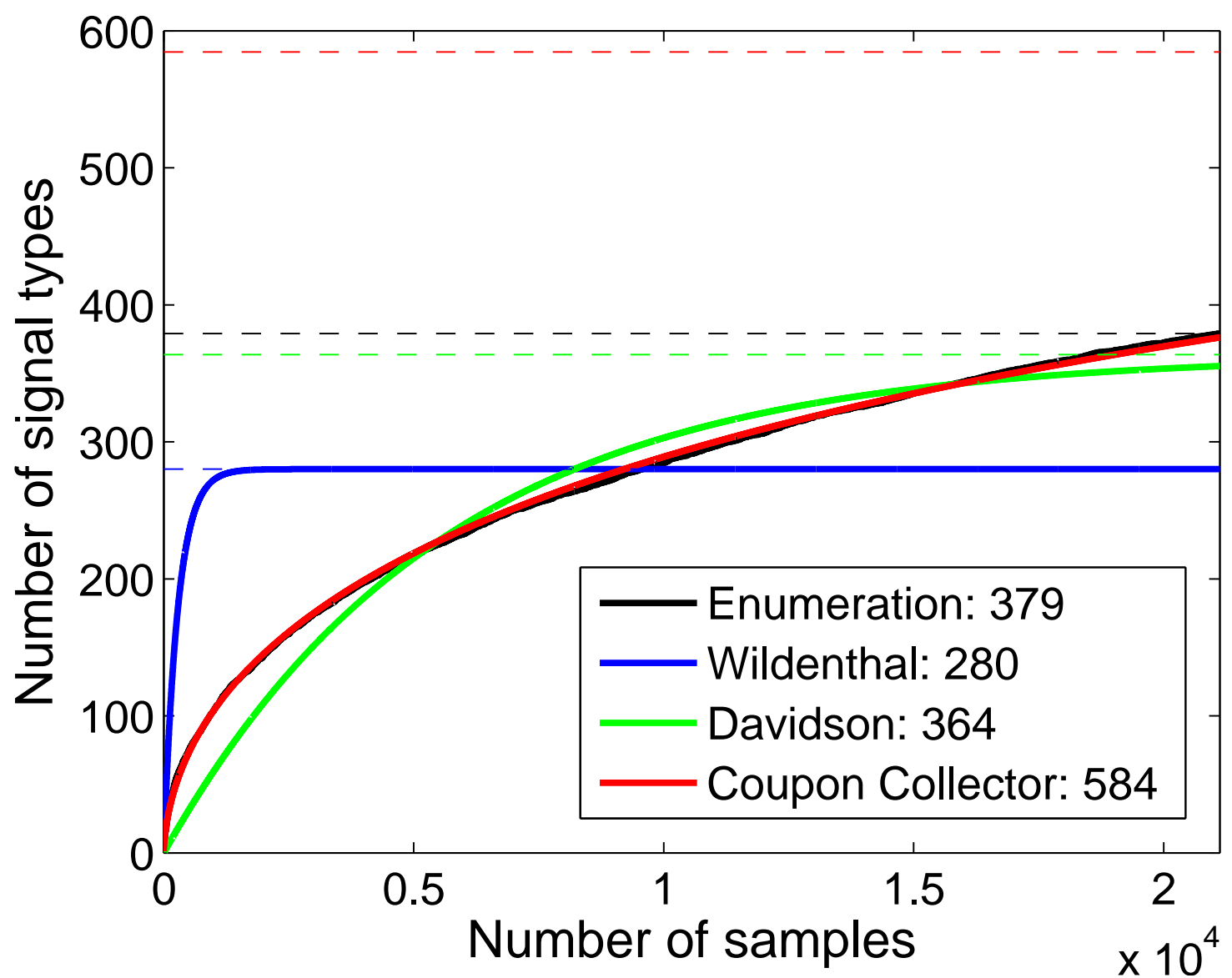


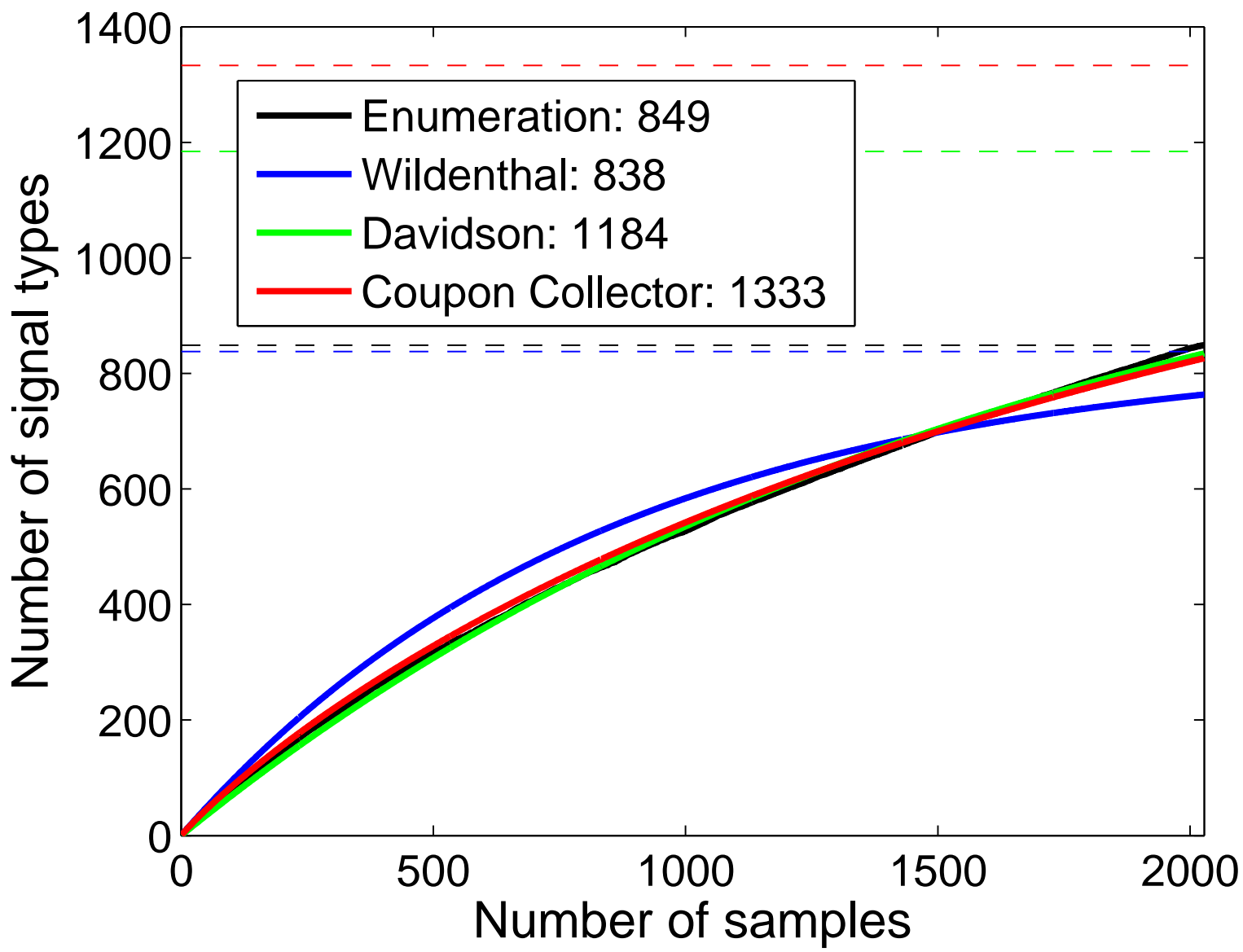




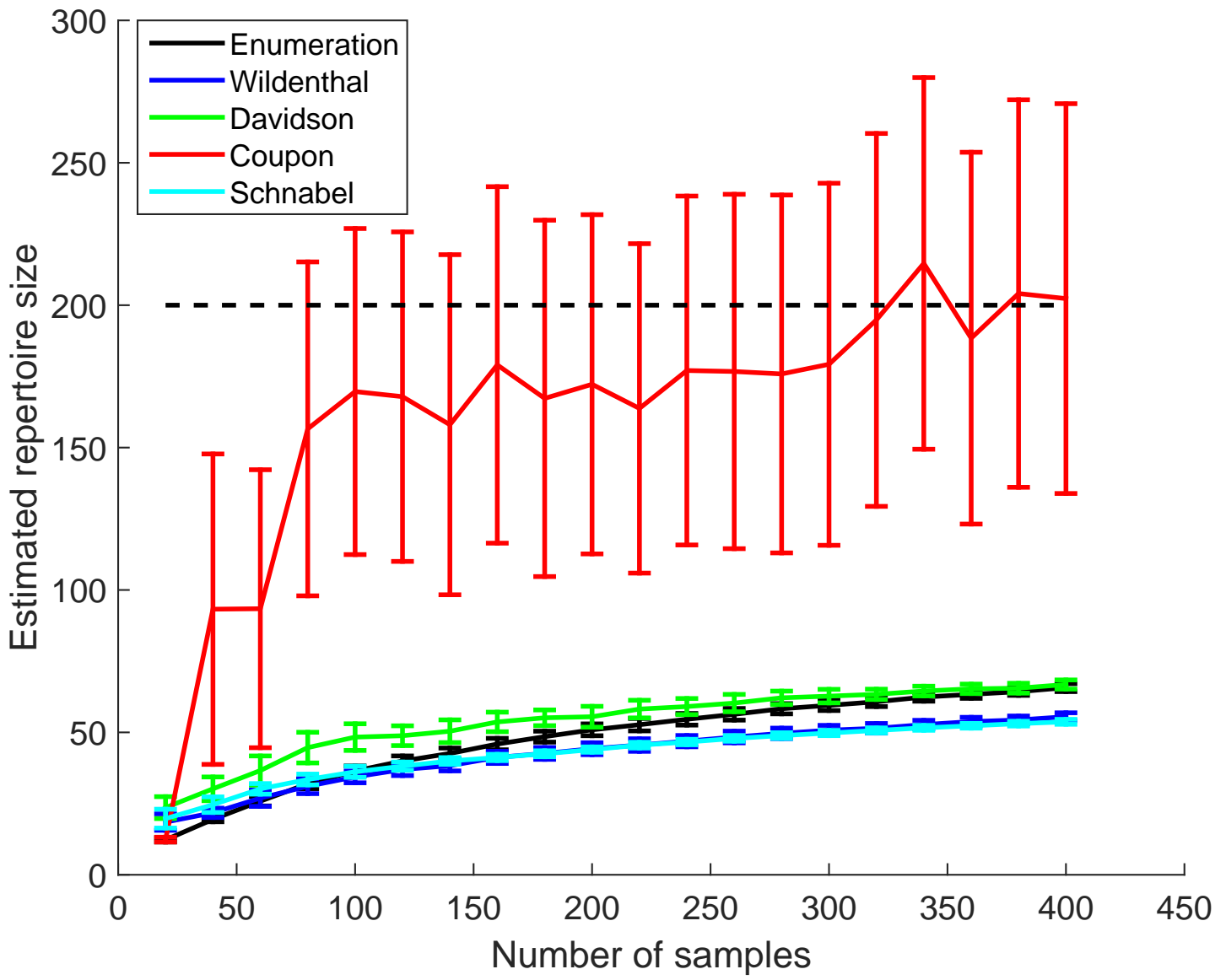




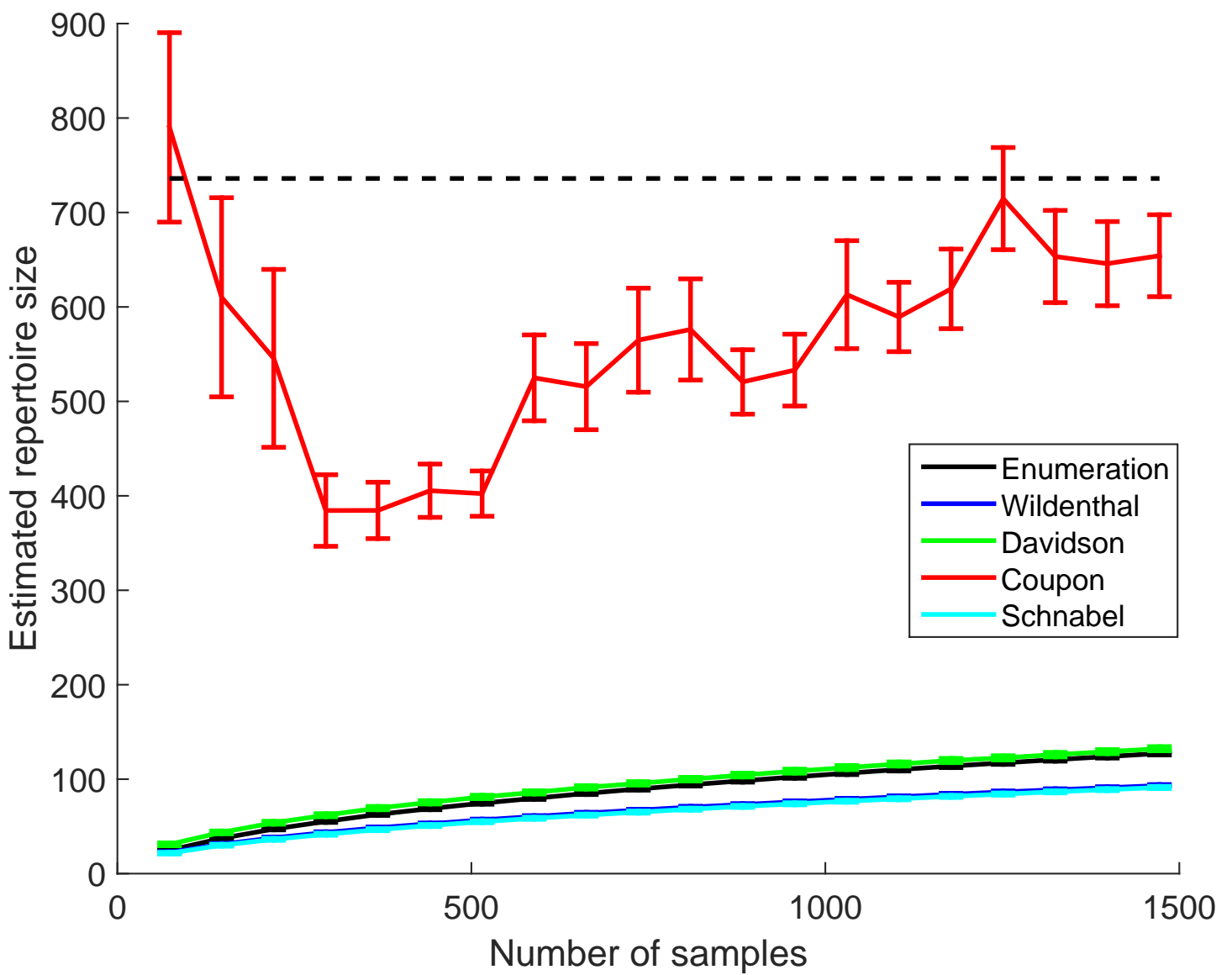




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4. Figure 6b
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4. Figure 6c
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