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On the Use of Allele Frequency Data Within A Bayesian Framework to Evaluate the Relative Probabilities of Alternative Stock Structure Hypotheses for the North Pacific Minke Whales

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ABSTRACT

Genotype frequency information for one or more loci are used within a Bayesian modelling framework to assign relative probabilities to alternative stock-structure hypotheses by means of the Bayes factor approach. This framework has advantages over maximum likelihood estimation as it provides the information needed to select amongst hypotheses. When applied to the data for the *Adh-1* and *Gpi* loci for sub-areas 6, 7 and 11 for the North Pacific minke whales, the results confirm those of previous studies that there are (at least) two stocks in these sub-areas. In contrast, applications to data for sub-areas 7, 8 and 9 support the hypothesis of a single stock in these sub-areas, unless it can be argued that, *a priori*, the allele frequencies for two stocks that are adjacent spatially are likely to be very similar.

INTRODUCTION

Punt *et al.* (1995) and Butterworth *et al.* (1996) analysed *Adh-1* and *Gpi* locus data using maximum likelihood methods to estimate mixing proportions for the J and O minke whale stocks in sub-area 7 of the North Pacific. A disadvantage of these methods is that while rejection of the null hypothesis of single stock can be used to identify the presence of multiple stocks, an inability to reject this null hypothesis does not imply necessary acceptance of the hypothesis of a single stock. There are two reasons for this. The first is the sample size effect - if the sample sizes are too low, the null hypothesis may not be rejected even if there are two stocks present and apparently marked differences between the samples (i.e. the power of the test is too low). The second reason is that the underlying allele frequencies for two stocks that are found close to each other spatially may be very similar (in part because of occasional genetic exchange between the two stocks). In such circumstances, there may be inadequate power to distinguish the difference in frequencies, even given relatively large sample sizes.

Bayesian methods can be used to calculate the relative probability of alternative hypotheses by means of the Bayes factor (Jeffreys, 1961). For example, Wade and DeMaster (1996) contrasted alternative models for the dynamics of the Eastern North Pacific stock of gray whales using this framework.

This paper develops single- and two-stock models for allele-frequency data, where these models are then fitted using a Bayesian approach. This overall framework is then used to examine stock-structure hypotheses for minke whales in sub-areas 6, 7, 8, 9 and 11 of the North Pacific.

MATERIAL AND METHODS

The allele frequency data available for the analyses are listed in Table 1. They have been aggregated over years into three bi-monthly periods (April-May, June-July, and August-September) and are presented for five of the thirteen sub-areas for the North Pacific minke whales. Allele frequency data obtained from commercial operations are available for sub-areas 6, 7 and 11, while the JARPN programme has provided such data for sub-areas 7, 8, 9 and 11. Data for alleles that constitute a very small fraction of the total (i.e. *dg*, *di*, *gg*, *gh*, and *hi* for the *Adh-1* locus) are omitted from Table 1 and the calculations of this paper.

Under the assumption of Hardy-Weinberg equilibrium, the fractions of the three major genotypes for each locus: (for example, *hh*, *dh*, and *hh* for the *Adh-1* locus) in a homogenous stock are: $f_{hh} = p^2$, $f_{dh} = 2p(1-p)$ and $f_{dd} = (1-p)^2$, where p is the $Adh\text{-}1^h$ proportion. If it can be assumed that only a single (homogeneous) stock is found in a given sub-area A, the value for p^A_{Adh}, the $Adh\text{-}1^h$ proportion for sub-area A, can be estimated by maximising the following log-likelihood (ignoring constant terms):

$$\ell nL = n^A_{hh}\ f^A_{hh}\left(p^A_{Adh}\right) + n^A_{dh}\ f^A_{dh}\left(p^A_{Adh}\right) + n^A_{dd}\ f^A_{dd}\left(p^A_{Adh}\right) \tag{1}$$

where n^A_{hh} is the number of samples from sub-area A with genotype *hh*,

n^A_{dh} is the number of samples from sub-area A with genotype *dh*, and

n^A_{dd} is the number of samples from sub-area A with genotype *dd*.

If then similar data become available for another sub-area B, a straightforward extension of this maximum likelihood approach can be used to reject the assumption that there is only one stock in the two sub-areas. However, for the reasons given above, failure to show a significant lack of fit for a single-stock model to such data does not provide conclusive evidence of a single stock only in both sub-areas.

Even so, it is not acceptance/rejection of various stock structure hypotheses that is essential for the interpretation of the results of the *Implementation Simulation Trials* for the North Pacific minke whales (IWC, 1999), but rather the assignment of relative probabilities to such hypotheses. This necessitates changing from maximum likelihood to Bayesian methods. Under the latter paradigm, comparison of two models (1 and 2) by means of the Bayes factor involves the determination of the ratio:

$$P_1/P_2 = \iint_1 L(D\,|\,\underline{\phi}_1)\,p_1(\underline{\phi}_1)\,d\underline{\phi}_1 \Big/ \iint_2 L(D\,|\,\underline{\phi}_2)\,p_2(\underline{\phi}_2)\,d\underline{\phi}_2 \tag{2}$$

where P_1 is the probability of model 1,

P_2 is the probability of model 2,

$L(D\,|\,\phi)$ is the likelihood of the data given the vector of parameters $\underline{\phi}$,

$\underline{\phi}_1$	is the parameter vector for model 1,
$\underline{\phi}_2$	is the parameter vector for model 2,
$p_1(\underline{\phi}_1)$	is the prior probability distribution for model 1, and
$p_2(\underline{\phi}_2)$	is the prior probability distribution for model 2.

The value of the Bayes factor provides a quantitative measure of the relative weight of evidence in favour of models 1 and 2. For example, the value of Equation (2) in the limit of no informative data is 1, which indicates no preference for either model. Jeffreys (1961) and Kass and Raftery (1995) provide the following guidelines for the interpretation of values for the Bayes factor:

(a) Jeffreys (1961)

Bayes Factor	Interpretation
1 to 3.2	Not worth more than a bare mention
3.2 to 10	Substantial
10 to 100	Strong
>100	Decisive

(b) Kass and Raftery (1995)

Bayes Factor	Interpretation
1 to 3	Not worth more than a bare mention
3 to 20	Positive
20 to 150	Strong
>150	Very strong

Consider a situation where the Bayes factor is to be used to compare a single-stock model (model 1) with a two-stock model (model 2), where data are available for two sub-areas A and B based on the *Adh-1* locus. Model 1 has a single parameter $p^A_{Adh} = p^B_{Adh}$, while model 2 has two parameters p^A_{Adh} and p^B_{Adh} which may (or may not) be the same. A reasonable prior for p^A_{Adh} (and hence also p^B_{Adh} for model 1) is U[0, 1], because *a priori* there is no reason to favour any one value over another for this proportion. However, this is not a reasonable prior for p^B_{Adh} for model 2, as there is some *a priori* chance that p^B_{Adh} is positively correlated to p^A_{Adh}. This is because the *Adh-1* proportion for stocks that are adjacent in space may be similar as a result of limited genetic interchange (and/or common ancestry). The particular formalism chosen in this paper to model this *a priori* correlation is to assume a mixture distribution for the prior for p^B_{Adh}. This prior is U[0,1] with probability x and a distribution proportional to a symmetric triangular function centred on p^A_{Adh} of width $2e$ with probability 1-x. This shape is illustrated in Fig. 1 - in cases where one or both sides of the triangle intersect the possibilities of 0 and/or 1 for p^B_{Adh}, the normalisation of the prior is adjusted appropriately. Other forms for the distribution centred at p^A_{Adh} could have been considered (e.g. normal), but this simple function is sufficient for the purposes of this paper which considers wide ranges of possible values for x and e. This mixture distribution therefore captures the range from a pure uniform prior

(x=1) to a delta-function prior at p^A_{Adh} (x=0;e=0). Naturally, the Bayes factor for an analysis based on this last prior would be 1.

Either genetic mutation rate models, empirical evidence from adjacent stocks of the same species, or some combination of the two could form the basis for developing a prior for p^B_{Adh}, i.e. choosing values for e and x for the context considered here. Such considerations are beyond the scope of this paper, which is why the results of computations of Bayes factors are shown across wide ranges of values for these parameters. These computations were effected by integrating Equation (2) numerically using a simple (and therefore somewhat inefficient) variant of the Sample-Importance-Resample algorithm (Rubin, 1987).

RESULTS AND DISCUSSION

J vs O stock comparisons

There is substantial evidence from allele frequency (Wada, 1984, 1991; Punt *et al.*, 1995; Butterworth *et al.*, 1996), conception date (Best and Kato, 1992), mtDNA (Goto and Pastene, 1997) and morphological (Kato *et al.*, 1992) information, that two minke whale stocks (J and O) are present in North Pacific sub-areas 6 (J stock) and 7+11 (primarily O). There is certainly mixing in sub-area 11 in April-May, and there may also be some J animals present in this sub-area in other months, and in sub-area 7 in August-September. A first test of the framework described above is therefore to apply it to the data for sub-areas 6, 7 and 11 to determine whether it provides a result that is consistent with those of previous investigations.

Table 2 lists the value of the Bayes factor (i.e. P_1/P_2) and the fraction of the total percentage probability assigned to the single-stock model, model 1 (i.e. $100P_1/(P_1+P_2)$) for a range of values for e and x. Results are shown in this Table for analyses based on each of the *Adh-1* and *Gpi* loci. The analyses in question compare the allele frequencies for sub-area 6 with those for sub-areas 7, and also with those for sub-areas 7 and 11 combined. For this last data set, the samples for the April-May period are omitted as it is known that substantial mixing between J and O stock animals occurs in sub-area 11 during this period (Punt *et al.*, 1995; Butterworth *et al.*, 1996).

The results in Table 2 conform exactly to expectations. Except for the case in which the prior for p^B_{Adh} is virtually perfectly correlated with p^A_{Adh} (e=0.01, x=0.00), the single stock model is accorded virtually no probability relative to that of the single stock model. In all but this case, use of the Jeffreys/Kass and Raftery guidelines would lead to the conclusion that evidence in favour of two stocks is "decisive" / "very strong".

O vs W stock comparisons

For the purposes of these comparisons, it is assumed that the O stock is restricted to sub-areas 7 and 11 (the data for sub-area 11 in April-May are ignored for the reason given above), and consideration is given to the possibility that sub-areas 8 and 9 may contain a separate (W) stock. Table 3 lists the values for the Bayes factor and the fraction of the total probability assigned to the single-stock model for the *Adh-1* and *Gpi* loci separately, while Table 4 lists these values when the data for the two loci are analysed together (the Scientific Committee has previously accepted that it is legitimate to treat these two sources of data as independent (IWC, 1997)). Results are shown in Tables 3 and 4 for the same factors as Table 2, except that, additionally, the sensitivity to excluding the data collected from commercial operations is examined.

Considering the results for each locus separately first, the Bayes factor indicates a preference for a single stock hypothesis (i.e. $P_1 / P_2 > 1$) for all choices for the factors examined, except when the analysis is based on the JARPN data for the *Adh-1* locus. The extent of preference for the single stock hypothesis (i.e. no W stock) increases (as expected) with sample size (i.e. using both the JARPN and the commercial data) and with the values chosen for e and x. The support for the single stock hypothesis for the analyses based on *Adh-1* locus increases if the data for sub-area 11 are omitted, despite the consequent lower sample sizes. The possibility of preference for the two-stock model when only JARPN *Adh-1* data are considered disappears in such circumstances. The likely reason for this result is the presence of J stock animals in sub-area 11 during June-July - note the non-zero point estimate for the pertinent proportion in Table 1 of IWC (1997).

When x is 0.01, or when $x = 0.1$ and $e = 0.1$ or lower, the bulk of the values for the Bayes factor would rate as "barely worth a mention" indicating that the data cannot conclusively select between the single- and two-stock models in those circumstances. However, these values for x and e correspond to giving the assumption that the two stocks may have similar allele frequencies very high weight *a priori*. When the data for the two loci are analysed together (Table 4), discriminatory power is greatly enhanced and the preference for the single-stock hypothesis is considerably increased. A rating of positive (75% or more of the total probability) is assigned to the single-stock model for most of the values for e and x when all of the data (commercial and JARPN, sub-areas 7, 8, 9, and 11) are analysed simultaneously.

Discussion

The framework developed in this paper provides a basis to discriminate between single-stock and two-stock hypotheses. The results confirm the expectation from previous analyses that there is more than one stock of minke whales in sub-areas 6 and 7 of the North Pacific, but there is strong support for a single stock only in sub-areas 7, 8, and 9 for most choices for the parameters that define the prior for the two-stock model. However, for some choices for this prior (those that imply a high *a priori* correlation between the allele proportions for the two stocks), there is little basis to choose between a single-stock and a two-stock hypothesis. The appropriate choice of parameter values for a prior distribution for p, based on information for other adjacent whale stocks and on genetic mutation theory, merits discussion.

The analyses of this paper are restricted to the use of isozyme data and the assumption that each sub-area included in the analysis contains a single homogeneous stock. In principle, it is possible to extend the methodology for other sources of data (e.g. mtDNA information) and for cases where there is mixing. However, this would increase the number of estimable parameters substantially, complicating both the design of the prior and the evaluation of the Bayes factor through Equation (2).

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Table 1

Genotype frequencies for the *Adh-1* and *Gpi* loci for the North Pacific minke whales (but omitting very rare *Adh-1* alleles). Due to the well-established fact of mixing of J and O stock animals in sub-area 11 during April-May, the data indicated by the asterisk are ignored in the calculations of this paper. The JARPN data include animals sampled between 1994 and 1999.

Sub-area	Period	Data source	*Adh-1* locus			*Gpi* locus		
			hh	*dh*	*dd*	*bb*	*ab*	*aa*
6	Sept-Oct	Commercial	1	4	40	19	19	4
7	Apr-May	JARPN	29	19	8	52	4	0
7	June-July	JARPN	23	24	5	52	1	0
7	Aug-Sept	JARPN	15	12	3	29	1	0
7	Apr-May	Commercial	142	127	25	174	5	0
7	June-July	Commercial	93	90	18	132	7	0
7	Aug-Sept	Commercial	38	54	13	99	4	0
8	Apr-May	JARPN	2	4	2	8	0	0
8	June-July	JARPN	31	35	10	73	5	0
8	Aug-Sept	JARPN	3	2	0	5	0	0
9	Apr-May	JARPN	15	7	2	27	0	0
9	June-July	JARPN	55	55	7	117	6	0
9	Aug-Sept	JARPN	17	17	5	34	4	0
11	June-July	JARPN	8	27	12	45	4	0
11	Aug-Sept	JARPN	10	10	9	27	3	0
11*	Apr-May	Commercial	64	72	64	112	13	2
11	Jun-July	Commercial	35	25	9	59	5	1
11	Aug-Sept	Commercial	11	7	1	14	0	0

Table 2

Use of the Bayes factor to compare a single-stock with a two-stock hypothesis for North Pacific minke whales (models 1 and 2 respectively) for sub-areas 6, 7 and 11. P_1 is the probability of model 1 and P_2 is the probability of model 2. Results are shown for the *Adh-1* and *Gpi* loci separately, for analyses that either use or ignore the data for sub-area 11.

e	x	*Adh-1* locus				*Gpi* locus			
		Sub-areas 6, 7, 11		Sub-areas 6, 7		Sub-areas 6, 7, 11		Sub-areas 6, 7	
		P_1 / P_2	$\frac{100P_1}{P_1+P_2}$	P_1 / P_2	$\frac{100P_1}{P_1+P_2}$	P_1 / P_2	$\frac{100P_1}{P_1+P_2}$	P_1 / P_2	$\frac{100P_1}{P_1+P_2}$
0.01	0	0.68	40.48	0.67	40.04	0.12	10.74	0.11	9.76
0.01	0.01	10^{-26}	10^{-24}	10^{-28}	10^{-26}	10^{-14}	10^{-12}	10^{-15}	10^{-13}
0.05	0.01	0	0	0	0	0	0	0	0
0.10	0.01	0	0	0	0	0	0	0	0
0.20	0.01	0	0	0	0	0	0	0	0
0.01	0.1	0	0	0	0	0	0	0	0
0.05	0.1	0	0	0	0	0	0	0	0
0.10	0.1	0	0	0	0	0	0	0	0
0.20	0.1	0	0	0	0	0	0	0	0
0.01	0.5	0	0	0	0	0	0	0	0
0.05	0.5	0	0	0	0	0	0	0	0
0.10	0.5	0	0	0	0	0	0	0	0
0.20	0.5	0	0	0	0	0	0	0	0
N/A	1	0	0	0	0	0	0	0	0

Table 3

Use of the Bayes factor to compare a single-stock with a two-stock hypothesis (models 1 and 2 respectively) for sub-areas 7, 8, 9 and 11. P_1 is the probability of model 1 and P_2 is the probability of model 2. Results are shown for data for the *Adh-1* and *Gpi* loci separately for analyses that either use or ignore the data for sub-area 11. An asterisk denotes a value for the Bayes factor that is "positive", two asterisks a value that is "strong", and three one that is "very strong", based on the Kass and Raftery (1995) guidelines.

(a) JARPN and Commercial data

e	*x*	*Adh-1* locus				*Gpi* locus			
		Sub-areas 7, 8, 9, 11		Sub-areas 7, 8, 9		Sub-areas 7, 8, 9, 11		Sub-areas 7, 8, 9	
		P_1/P_2	$\frac{100P_1}{P_1+P_2}$	P_1/P_2	$\frac{100P_1}{P_1+P_2}$	P_1/P_2	$\frac{100P_1}{P_1+P_2}$	P_1/P_2	$\frac{100P_1}{P_1+P_2}$
0.01	0	1.02	50.4	1.02	50.6	1.14	53.2	1.05	51.1
0.01	0.01	1.02	50.6	1.02	50.6	1.14	53.2	1.04	50.9
0.05	0.01	1.30	56.4	1.35	57.5	2.54	71.7	1.78	64.0
0.10	0.01	1.96	66.2	2.11	67.8	3.83*	79.3	2.67	72.8
0.20	0.01	3.45*	77.5	3.75*	78.9	6.21*	86.2	4.37*	81.4
0.01	0.1	1.13	52.9	1.13	53.0	1.25	55.6	1.16	53.7
0.05	0.1	1.42	58.7	1.48	59.6	2.77	73.5	1.97	66.3
0.10	0.1	2.14	68.1	2.27	69.4	4.18*	80.7	2.89	74.3
0.20	0.1	3.73*	78.9	4.03*	80.1	6.90*	87.4	4.76*	82.6
0.01	0.5	1.90	65.5	1.91	65.6	2.22	68.9	2.02	66.9
0.05	0.5	2.39	70.5	2.47	71.2	4.83*	82.8	3.37*	77.1
0.10	0.5	3.46*	77.6	3.70*	78.7	7.09*	87.6	4.76*	82.6
0.20	0.5	5.65*	85.0	6.1.0*	85.9	11.36*	91.9	7.63*	88.5
N/A	1	15.15*	93.8	16.67*	94.3	47.62**	98.0	34.48**	97.2

(Table 3 Continued)

(b) JARPN data only

e	x	*Adh-1* locus				*Gpi* locus			
		Sub-areas 7, 8, 9, 11		Sub-areas 7, 8, 9		Sub-areas 7, 8, 9, 11		Sub-areas 7, 8, 9	
		P_1 / P_2	$\frac{100P_1}{P_1+P_2}$	P_1 / P_2	$\frac{100P_1}{P_1+P_2}$	P_1 / P_2	$\frac{100P_1}{P_1+P_2}$	P_1 / P_2	$\frac{100P_1}{P_1+P_2}$
0.01	0	0.98	49.4	1.01	50.3	1.08	51.9	1.06	51.4
0.01	0.01	0.98	49.4	1.02	50.4	1.09	52.1	1.06	51.4
0.05	0.01	0.60	37.6	1.17	54.0	1.99	66.6	1.79	64.2
0.10	0.01	0.38	27.6	1.60	61.5	2.94	74.6	2.64	72.5
0.20	0.01	0.41	28.9	2.67	72.8	4.70*	82.4	4.26*	81.0
0.01	0.1	1.01	50.1	1.12	52.7	1.19	54.3	1.17	53.9
0.05	0.1	0.64	39.0	1.28	56.2	2.18	68.6	1.98	66.4
0.10	0.1	0.42	29.3	1.73	63.4	3.23	76.3	2.90	74.4
0.20	0.1	0.44	30.7	2.87	74.2	5.18*	83.8	4.67*	82.4
0.01	0.5	1.15	53.6	1.85	64.9	2.09	67.7	2.04	67.1
0.05	0.5	0.84	45.6	2.11	67.8	3.79*	79.1	3.40*	77.3
0.10	0.5	0.60	37.3	2.77	73.5	5.46*	84.5	4.85*	82.9
0.20	0.5	0.63	38.7	4.33*	81.2	8.40*	89.4	7.52*	88.3
N/A	1	1.38	58.0	11.36*	91.9	37.04**	97.3	33.33**	97.1

Table 4
Use of the Bayes factor based on information for data for both the *Adh-1* and *Gpi* loci to compare a single-stock with a two-stock hypothesis (models 1 and 2 respectively) for sub-areas 7, 8, 9 and 11. P_1 is the probability of model 1 and P_2 is the probability of model 2. Results are shown for analyses that either use or ignore the data for sub-area 11. An asterisk denotes a value for the Bayes factor that is "positive", two asterisks a value that is "strong", and three one that is "very strong", based on the Kass and Raftery (1995) guidelines.

e	x	JARPN and Commercial data				JARPN data only			
		Sub-areas 7, 8, 9, 11		Sub-areas 7, 8, 9		Sub-areas 7, 8, 9, 11		Sub-areas 7, 8, 9	
		P_1/P_2	$\frac{100P_1}{P_1+P_2}$	P_1/P_2	$\frac{100P_1}{P_1+P_2}$	P_1/P_2	$\frac{100P_1}{P_1+P_2}$	P_1/P_2	$\frac{100P_1}{P_1+P_2}$
0.01	0	1.16	53.6	1.07	51.7	1.05	51.3	1.07	51.7
0.01	0.01	1.17	53.8	1.06	51.5	1.06	51.4	1.07	51.8
0.05	0.01	3.29*	76.7	2.40	70.6	1.20	54.5	2.10	67.8
0.10	0.01	7.51*	88.3	5.63*	84.9	1.12	52.9	4.21*	80.8
0.20	0.01	21.42**	95.5	16.36*	94.2	1.91	65.6	11.38*	91.9
0.01	0.1	1.41	58.5	1.31	56.7	1.19	54.4	1.30	56.6
0.05	0.1	3.94*	79.8	2.90	74.4	1.39	58.2	2.53	71.7
0.10	0.1	8.94*	89.9	6.57*	86.8	1.34	57.2	5.02*	83.4
0.20	0.1	25.73**	96.3	19.20*	95.1	2.29	69.6	13.43*	93.1
0.01	0.5	4.22*	80.8	3.86*	79.4	2.41	70.7	3.77*	79.1
0.05	0.5	11.56*	92.0	8.31*	89.3	3.18*	76.1	7.16*	87.8
0.10	0.5	24.54**	96.1	17.64*	94.6	3.26*	76.5	13.45*	93.1
0.20	0.5	64.20**	98.5	46.55**	97.9	5.30*	84.1	32.55**	97.0
N/A	1	721.50***	99.9	574.71***	99.8	51.02**	98.1	378.79***	99.7

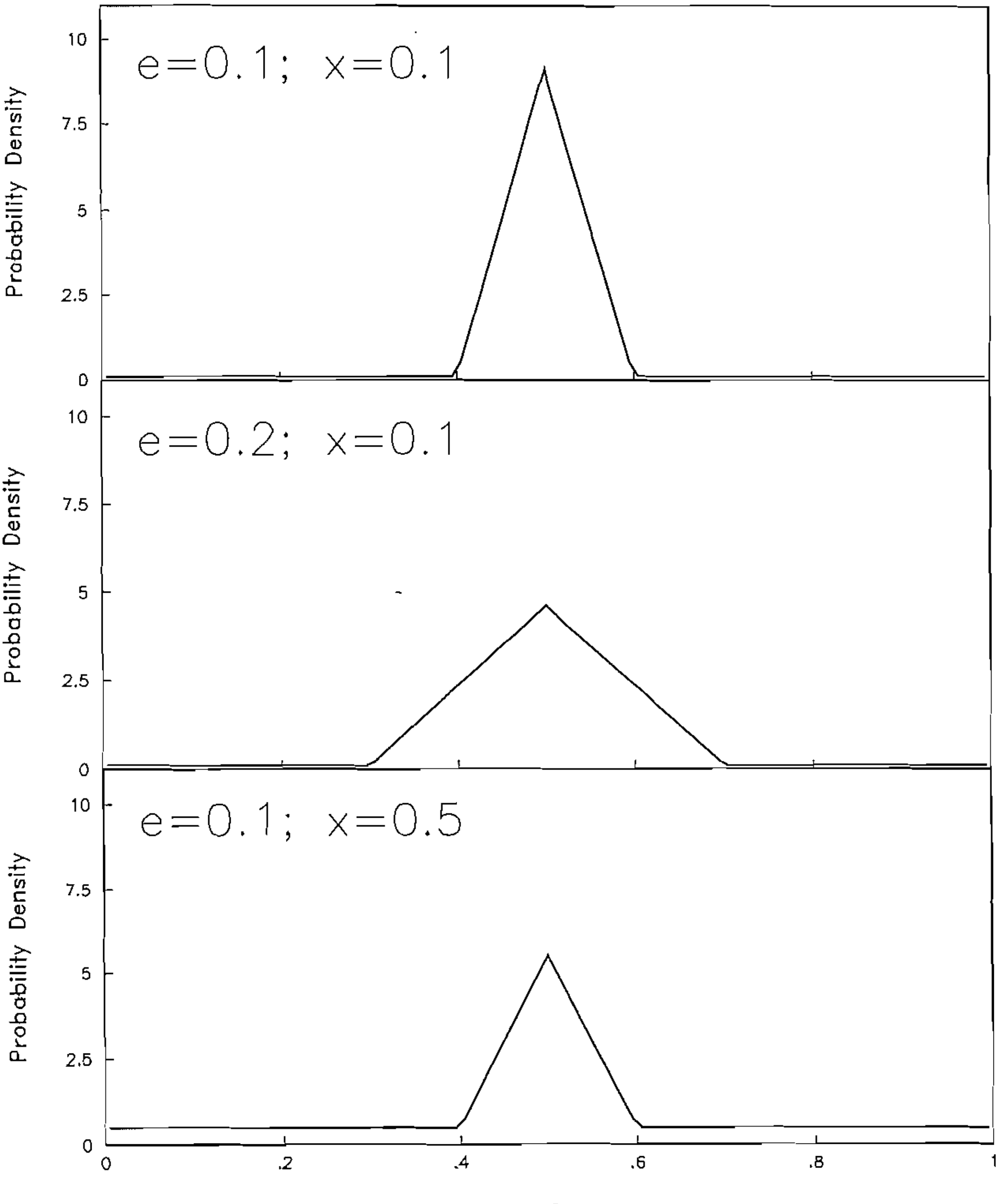
e=0.1; x=0.1
e=0.2; x=0.1
e=0.1; x=0.5
Probability Density
10
7.5
5
2.5
0
.2
.4
.6
.8
1
P^B

Figure 1