

# Quantitative Trait Loci (QTL) Mapping

CE7412: Computational and Systems Biology

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## 0.1 Preliminaries

```
library(qtl)

ls() # to view the objects in the work space

## character(0)

help(read.cross) #read from a set of files and converted into an object of class cross

# Data import
sug <- read.cross("csv", "https://rqtl.org", "sug.csv",
                   genotypes=c("CC", "CB", "BB"), alleles=c("C", "B"))

## --Read the following data:
##   163 individuals
##   93 markers
##   6 phenotypes
## --Cross type: f2
```

```
# Summaries
summary(sug)

##      F2 intercross
## 
##      No. individuals:     163
## 
##      No. phenotypes:      6
##      Percent phenotyped: 95.1 95.7 99.4 99.4 100 100
## 
##      No. chromosomes:    19
##              Autosomes:    1 2 3 4 5 6 7 8 9 10 11 12 13 14 15 16 17 18 19
## 
##      Total markers:      93
##      No. markers:        5 7 5 5 5 4 8 4 4 5 6 3 3 5 5 4 4 6 5
##      Percent genotyped:  98.3
##      Genotypes (%):     CC:23.9  CB:50.2  BB:26.0  not BB:0.0  not CC:0.0
```

```
nind(sug)
```

```
## [1] 163
```

```
nchr(sug)
```

```
## [1] 19
```

```
totmar(sug)
```

```
## [1] 93
```

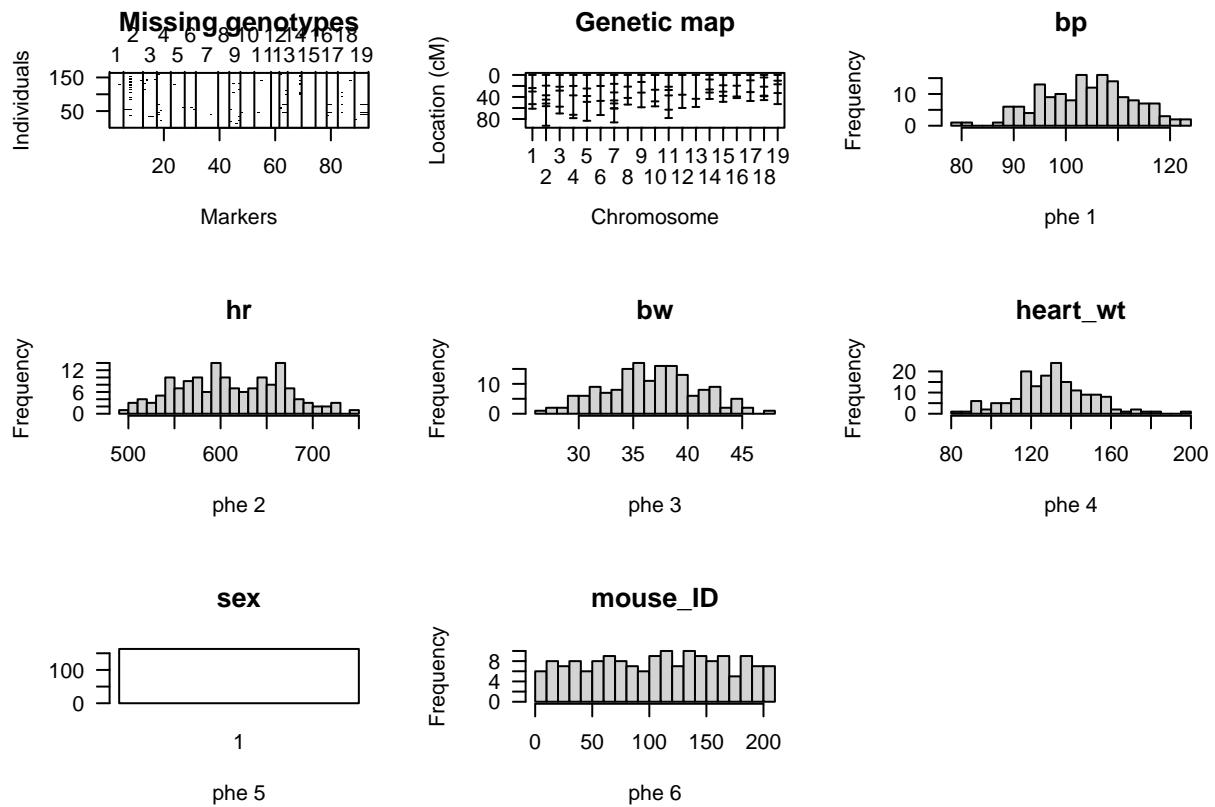
```
nmar(sug)
```

```
##  1   2   3   4   5   6   7   8   9   10  11  12  13  14  15  16  17  18  19
##  5   7   5   5   5   4   8   4   4   5   6   3   3   5   5   4   4   6   5
```

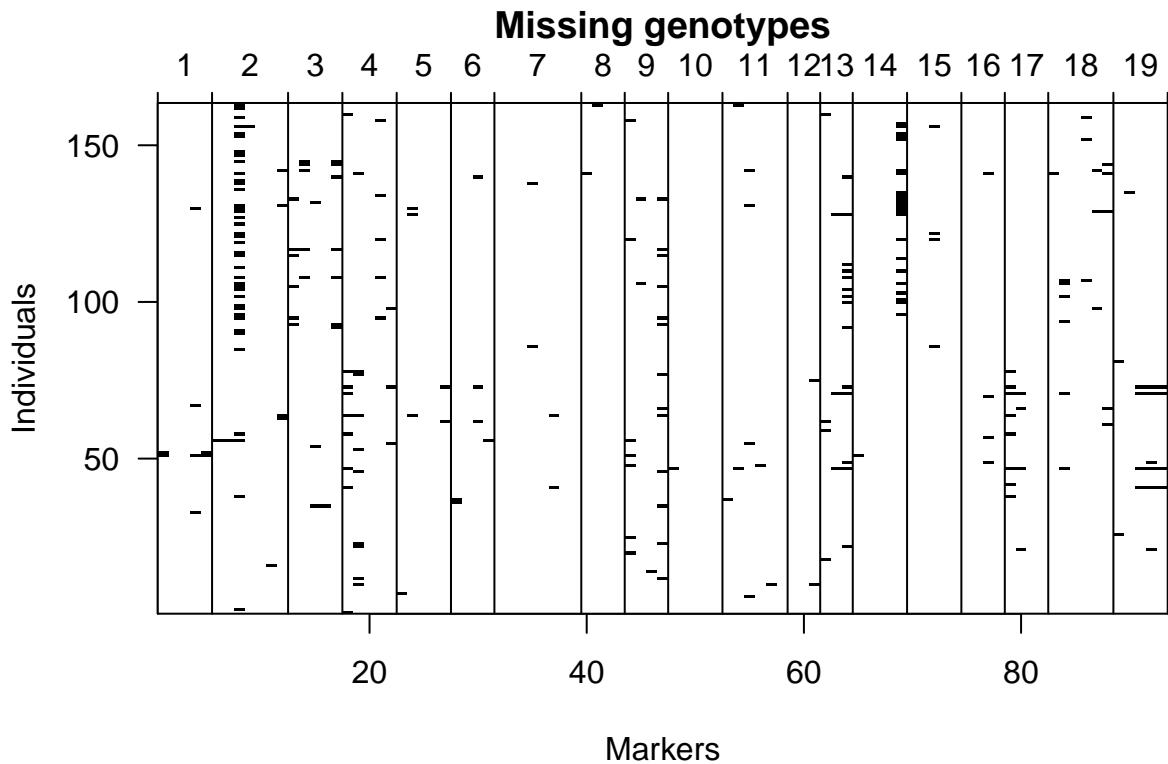
```
nphe(sug)
```

```
## [1] 6
```

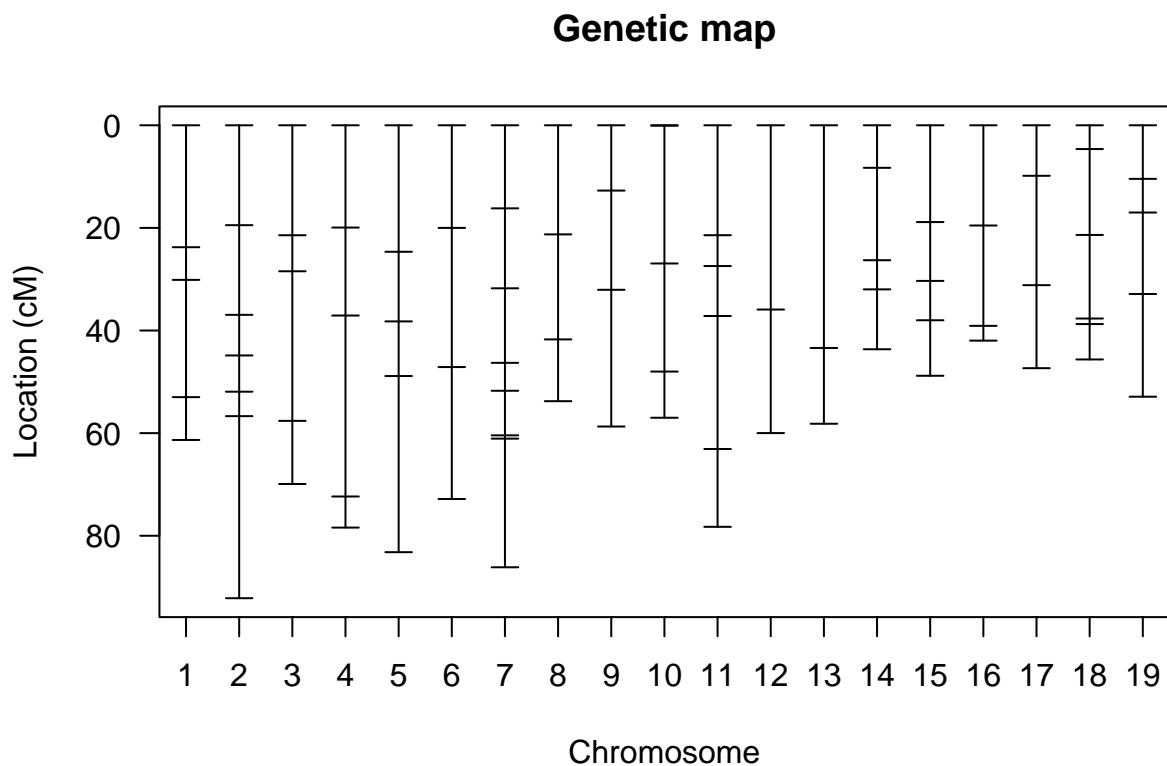
```
plot(sug)
```



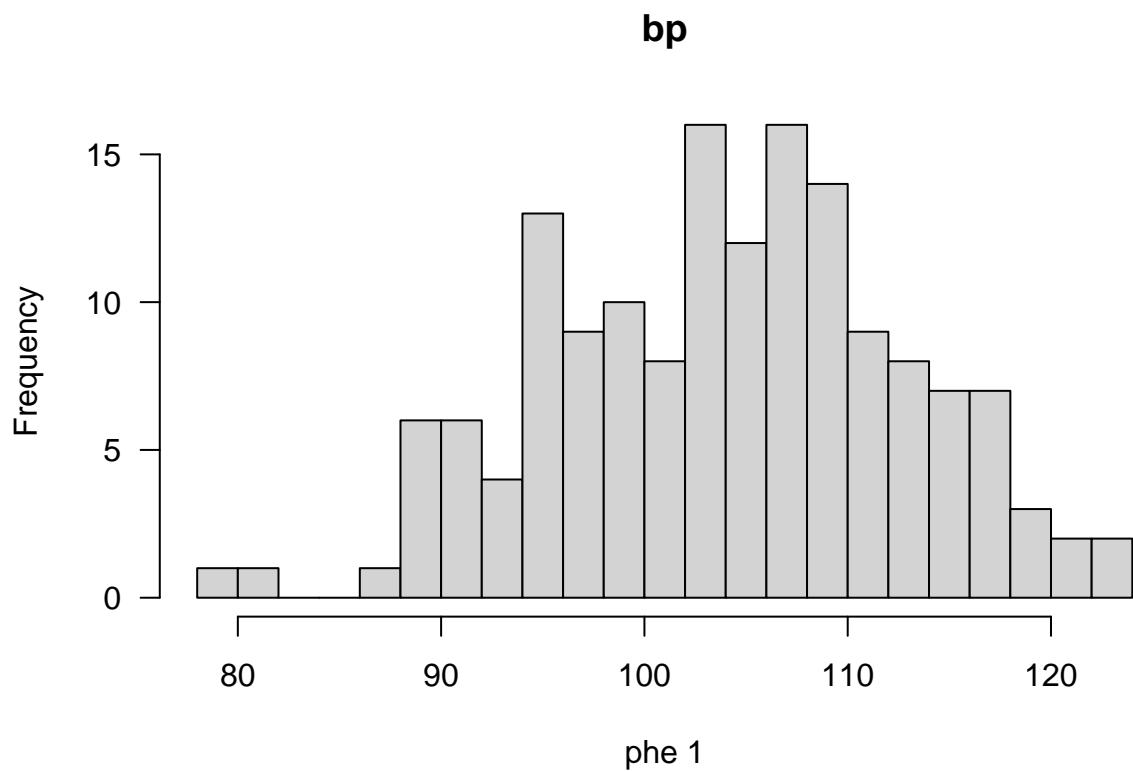
```
plotMissing(sug)
```



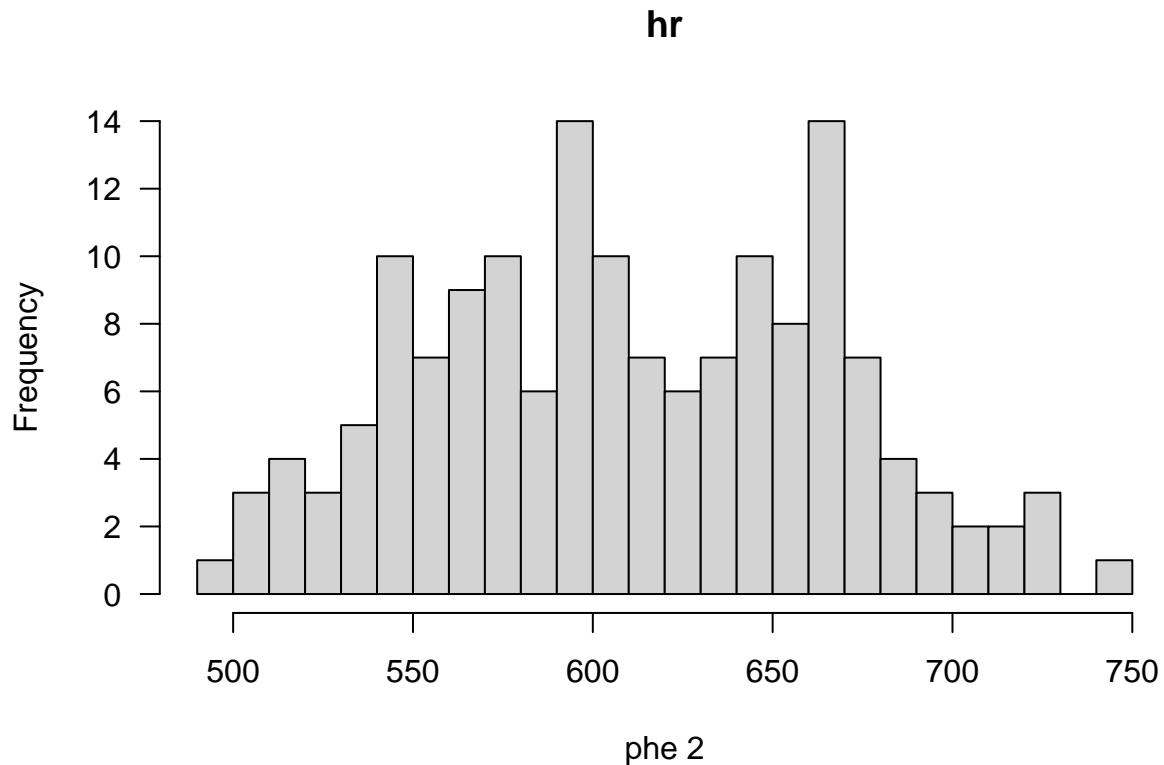
```
plotMap(sug)
```



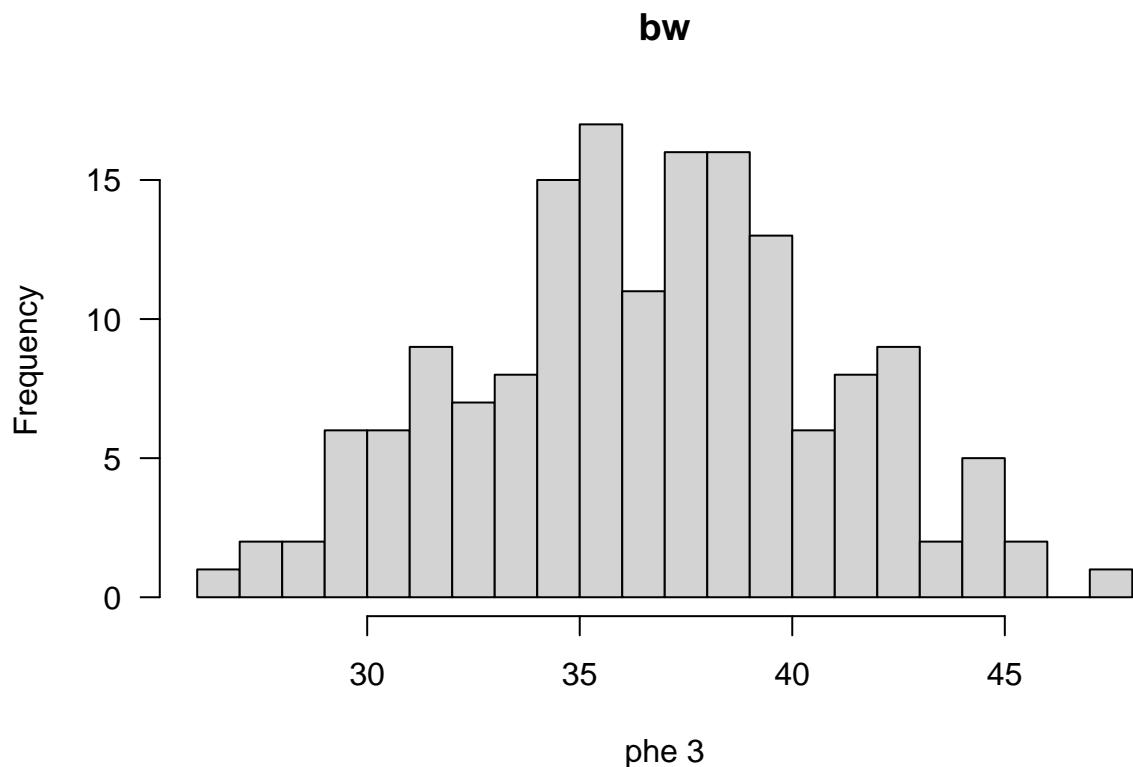
```
plotPheno(sug, pheno.col=1)
```



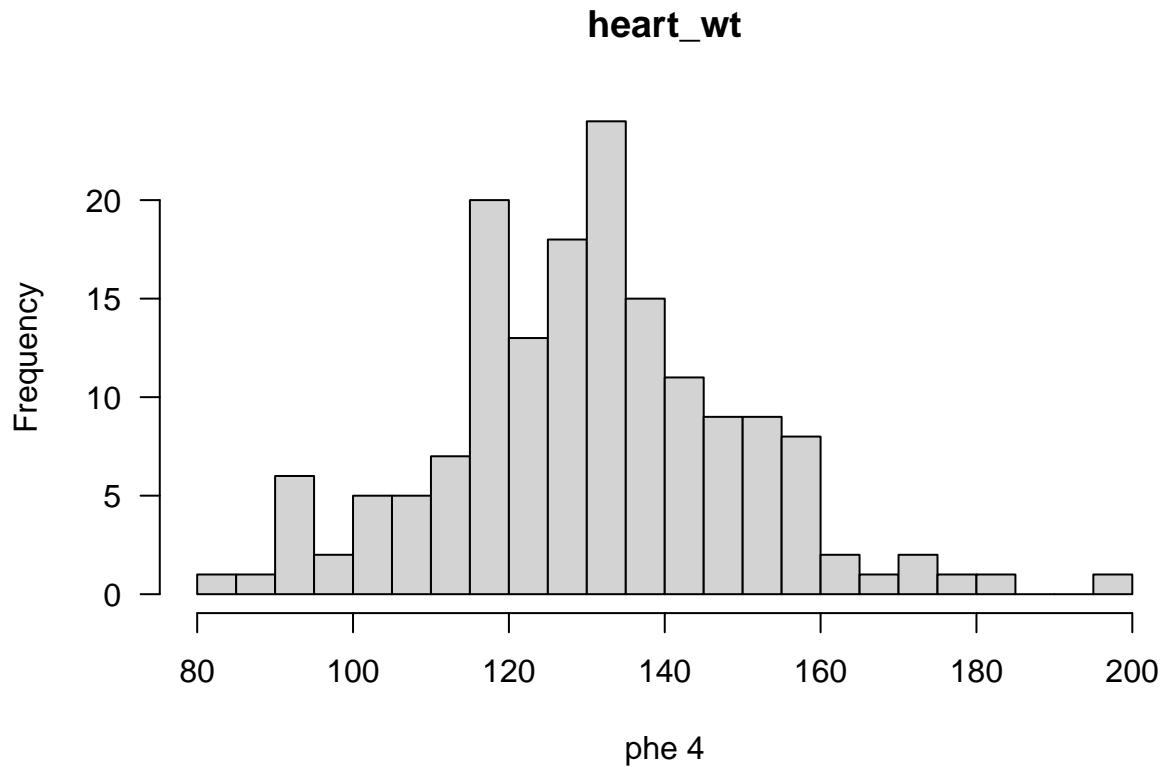
```
plotPheno(sug, pheno.col=2)
```



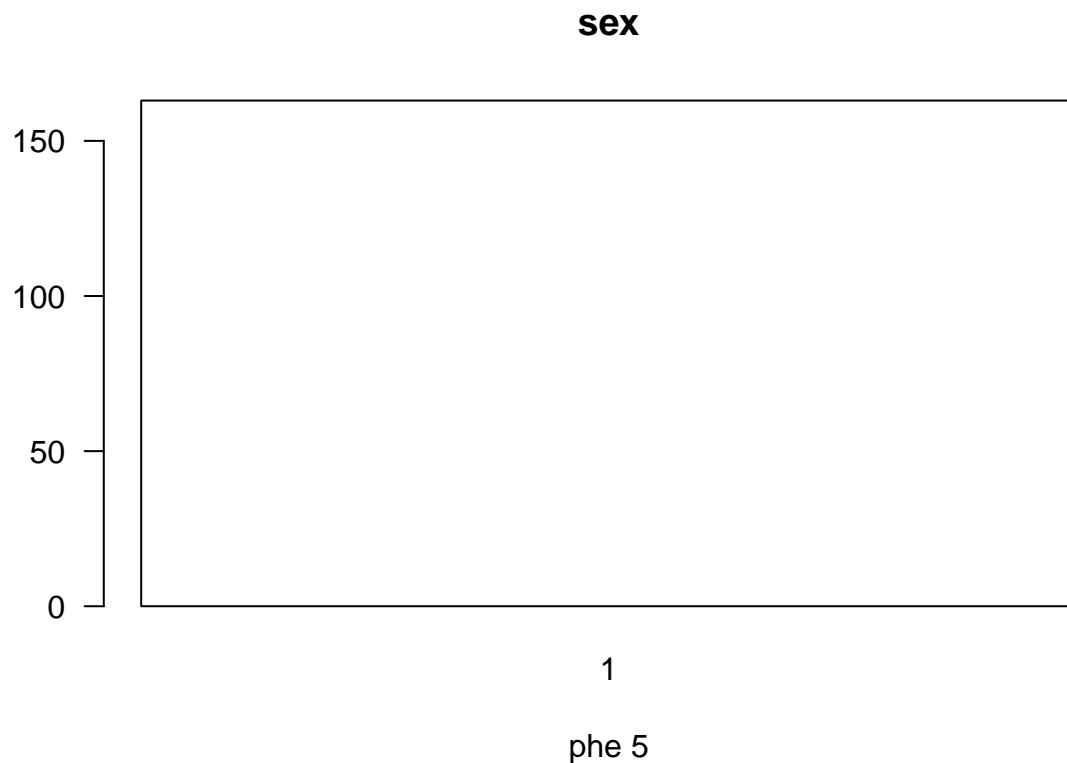
```
plotPheno(sug, pheno.col=3)
```



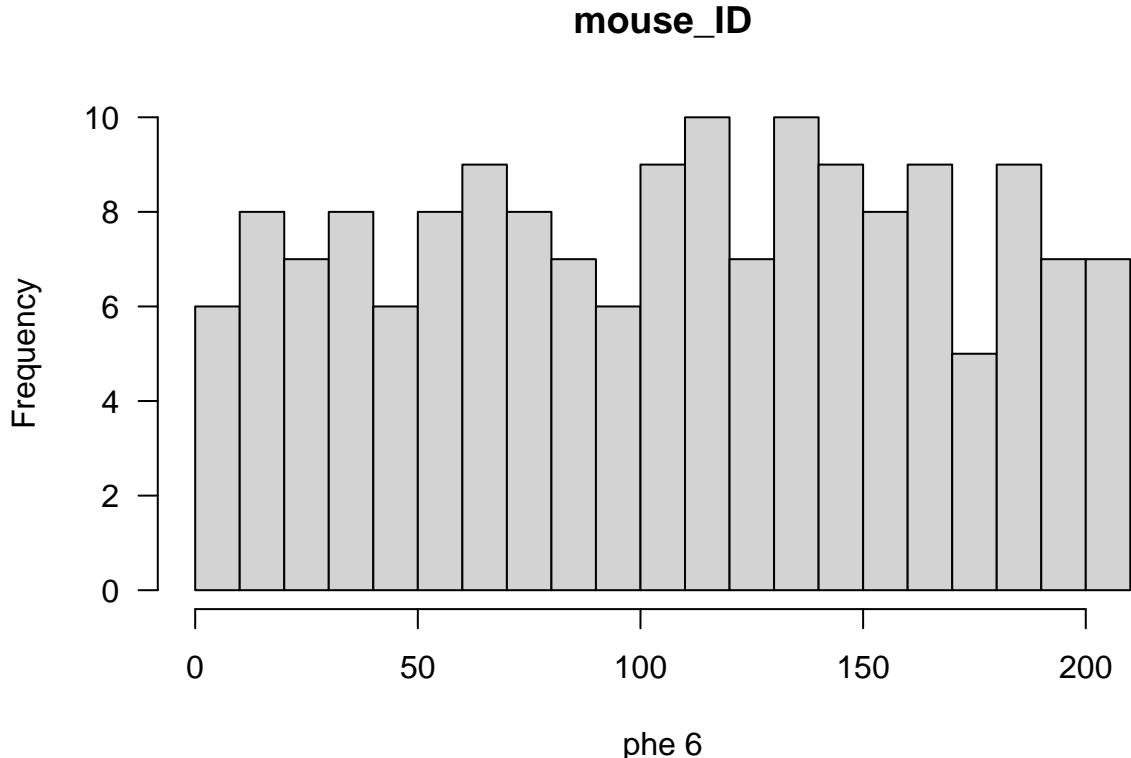
```
plotPheno(sug, pheno.col=4)
```



```
plotPheno(sug, pheno.col=5)
```



```
plotPheno(sug, pheno.col=6)
```



The output has “class” “scanone”. The summary function is passed to the function ‘summary.scanone’, and gives the maximum LOD score on each chromosome.

```
summary(out.em)
```

```

## D1MIT36      1 76.73 1.449
## c2.loc77    2 82.80 1.901
## c3.loc42    3 52.82 1.393
## c4.loc43    4 47.23 0.795
## D5MIT223   5 86.57 1.312
## c6.loc26    6 27.81 0.638
## c7.loc45    7 47.71 6.109
## c8.loc34    8 54.90 1.598
## D9MIT71     9 27.07 0.769
## c10.loc51   10 60.75 0.959
## c11.loc34   11 38.70 2.157
## D12MIT145  12 2.23 1.472
## c13.loc20   13 27.26 1.119
## D14MIT138  14 12.52 1.119
## c15.loc8    15 11.96 5.257
## c16.loc31   16 45.69 0.647
## D17MIT16   17 17.98 1.241
## D18MIT22   18 13.41 1.739
## D19MIT71   19 56.28 0.402

```

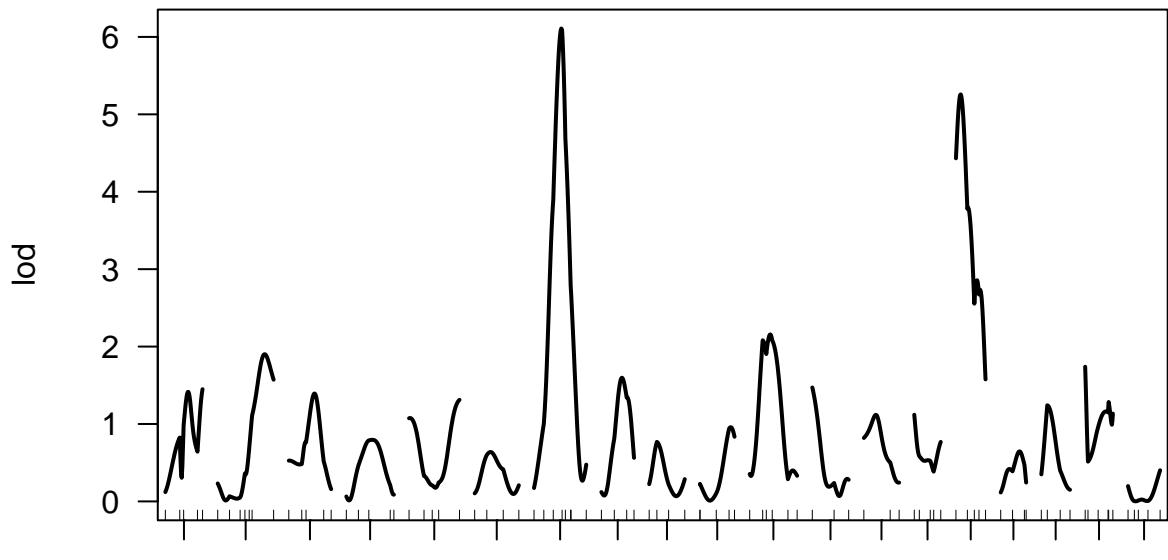
```
summary(out.em, threshold=3)
```

```

##           chr  pos  lod
## c7.loc45    7 47.7 6.11
## c15.loc8   15 12.0 5.26

```

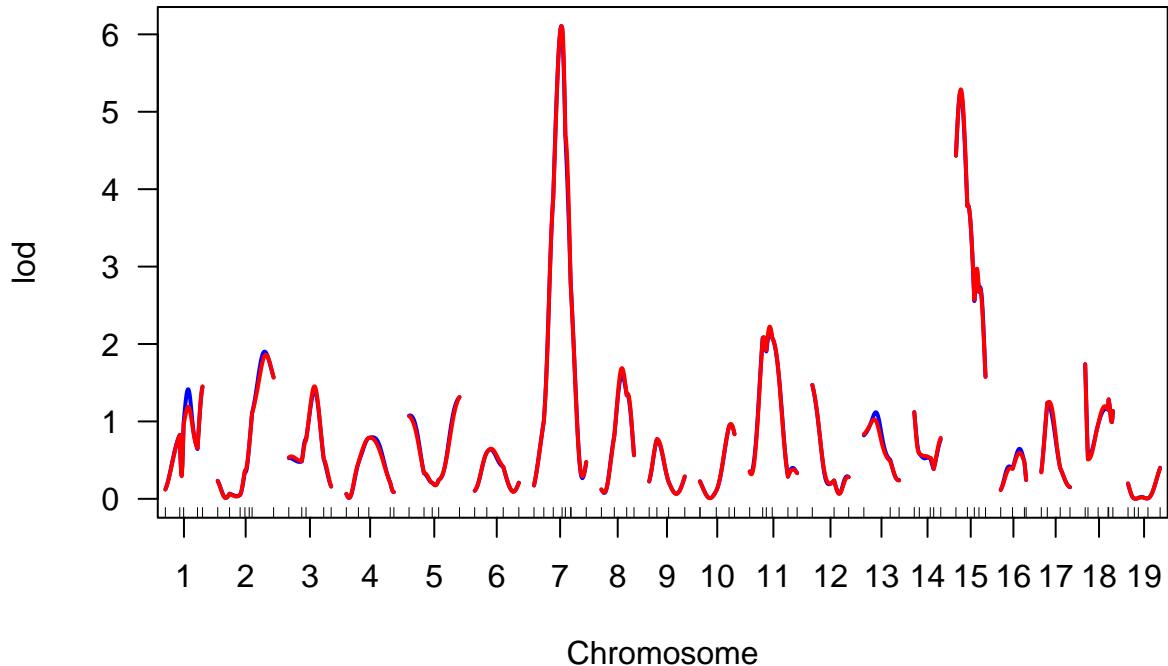
```
plot(out.em)
```



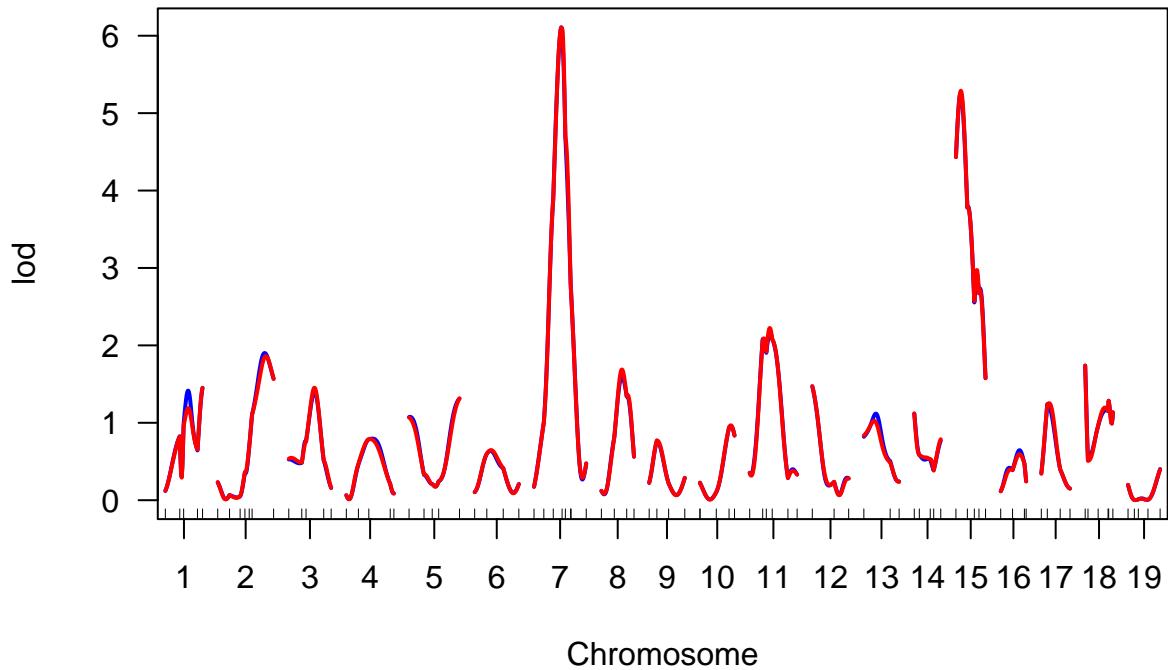
We can do the genome scan via Haley-Knott regression by calling scanone with the argument ‘method’=“hk”.

```
out.hk <- scanone(sug, method="hk")
```

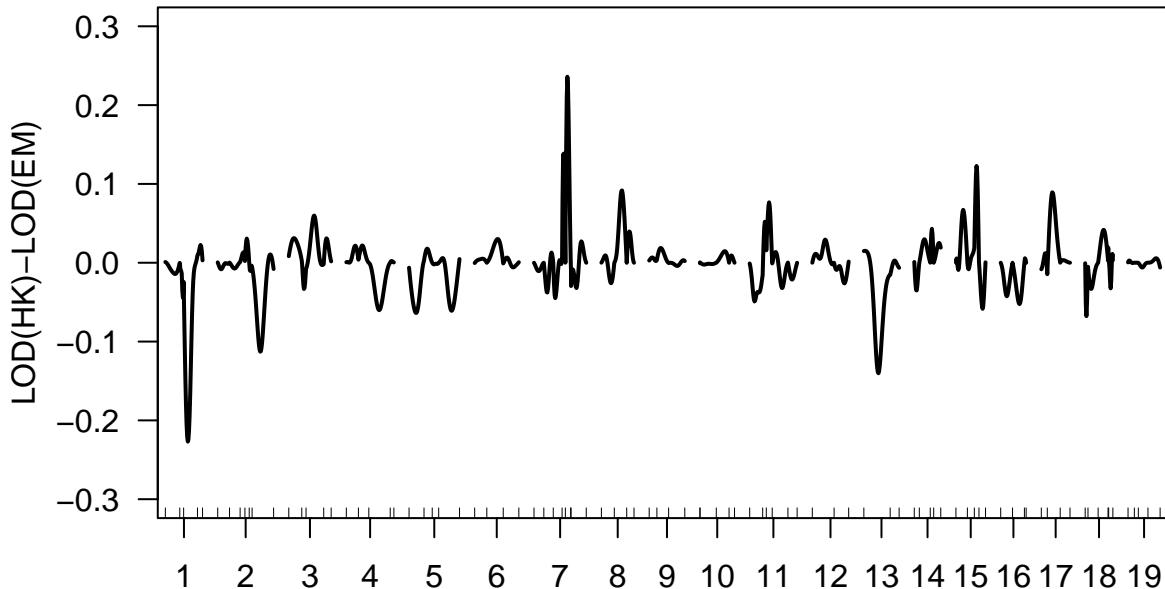
```
plot(out.em, out.hk, col=c("blue", "red"))
```



```
plot(out.em, col="blue")
plot(out.hk, col="red", add=TRUE)
```



```
plot(out.hk - out.em, ylim=c(-0.3, 0.3), ylab="LOD(HK)-LOD(EM)")
```



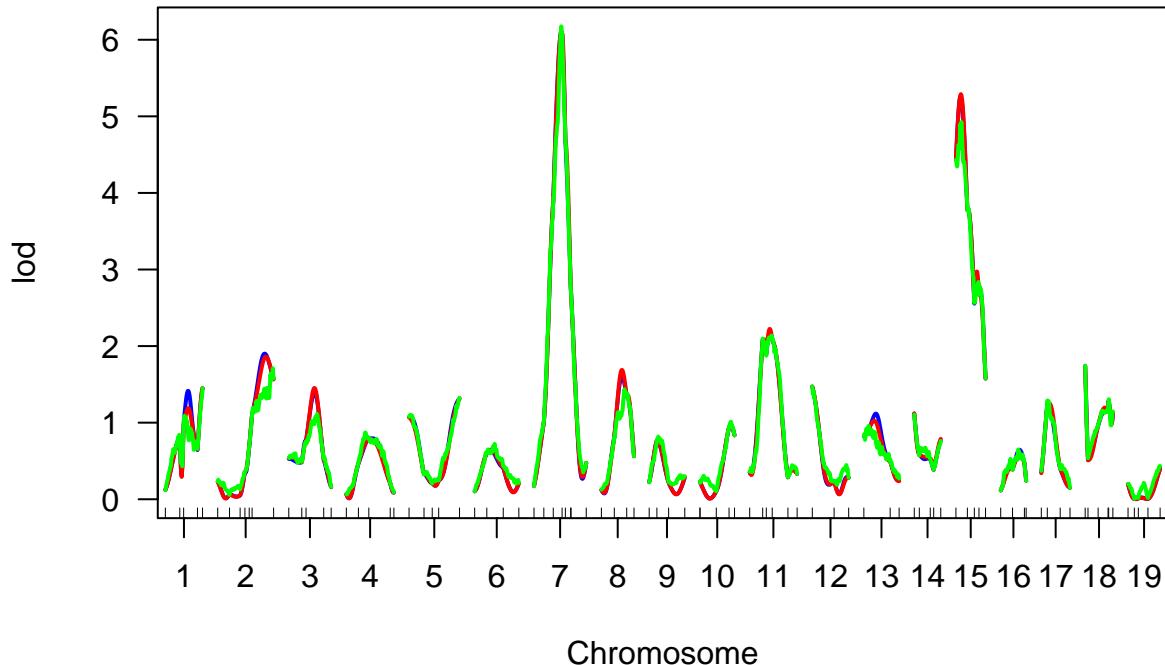
### Chromosome

To

perform a genome scan by the multiple imputation method, one must first call ‘sim.gen’ to perform the multiple imputations. This is similar to calc.genoprob, but with an additional argument, n.draws, indicating the number of imputations. We then call scanone with ‘method’=“imp”.

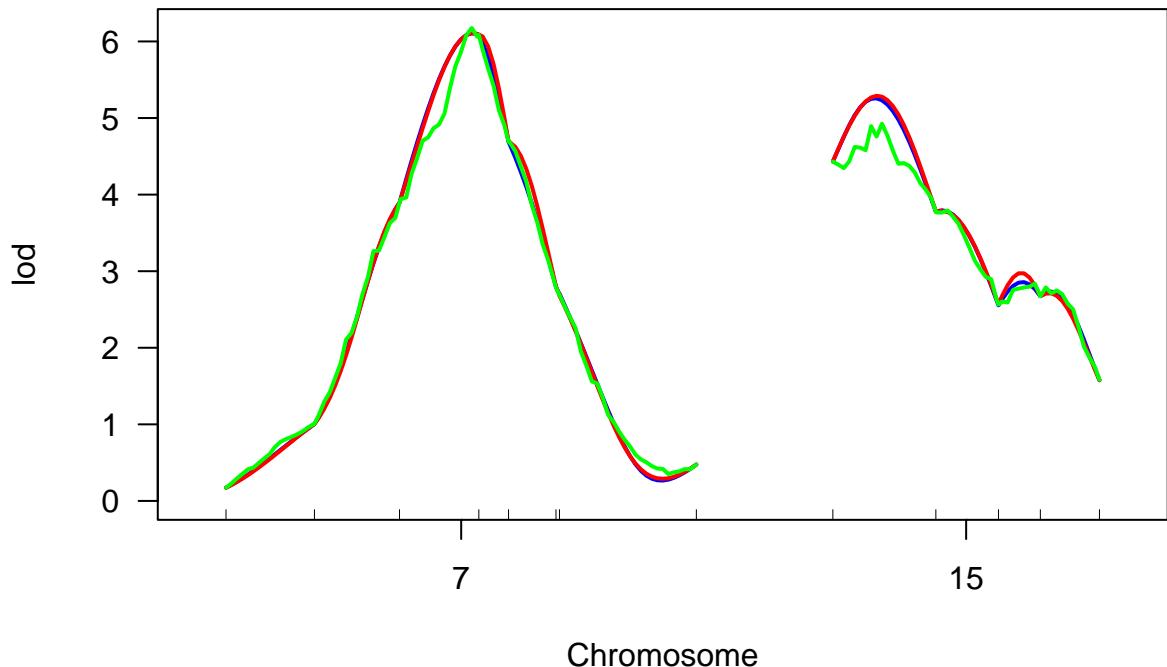
```
sug <- sim.gen(step=1, n.draws=64)
out.imp <- scanone(sug, method="imp")
```

```
plot(out.em, out.hk, out.imp, col=c("blue", "red", "green"))
```

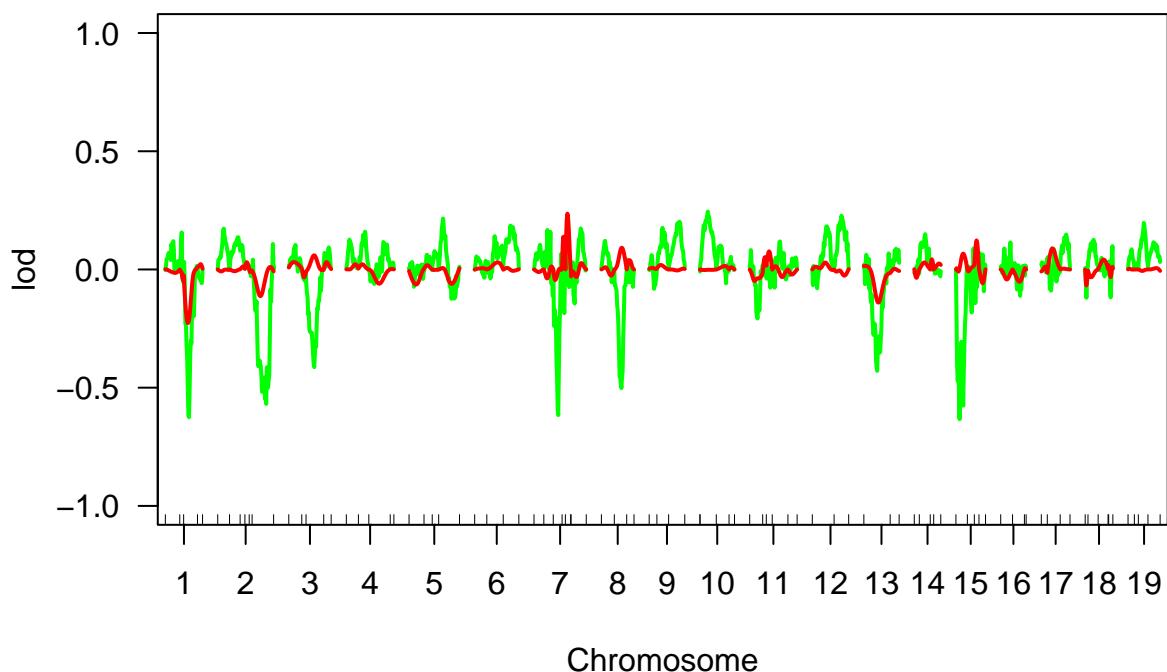


### Chromosome

```
plot(out.em, out.hk, out.imp, col=c("blue", "red", "green"), chr=c(7,15))
```



```
plot(out.imp - out.em, out.hk - out.em, col=c("green", "red"), ylim=c(-1,1))
```



### 0.3 Permutation tests

To perform a permutation test, to get a genome-wide significance threshold or genome-scan-adjusted p-values, we use ‘scanone’ just as before, but with an additional argument, ‘n.perm’, indicating the number of permutation replicates. It’s quickest to use Haley-Knott regression.

```

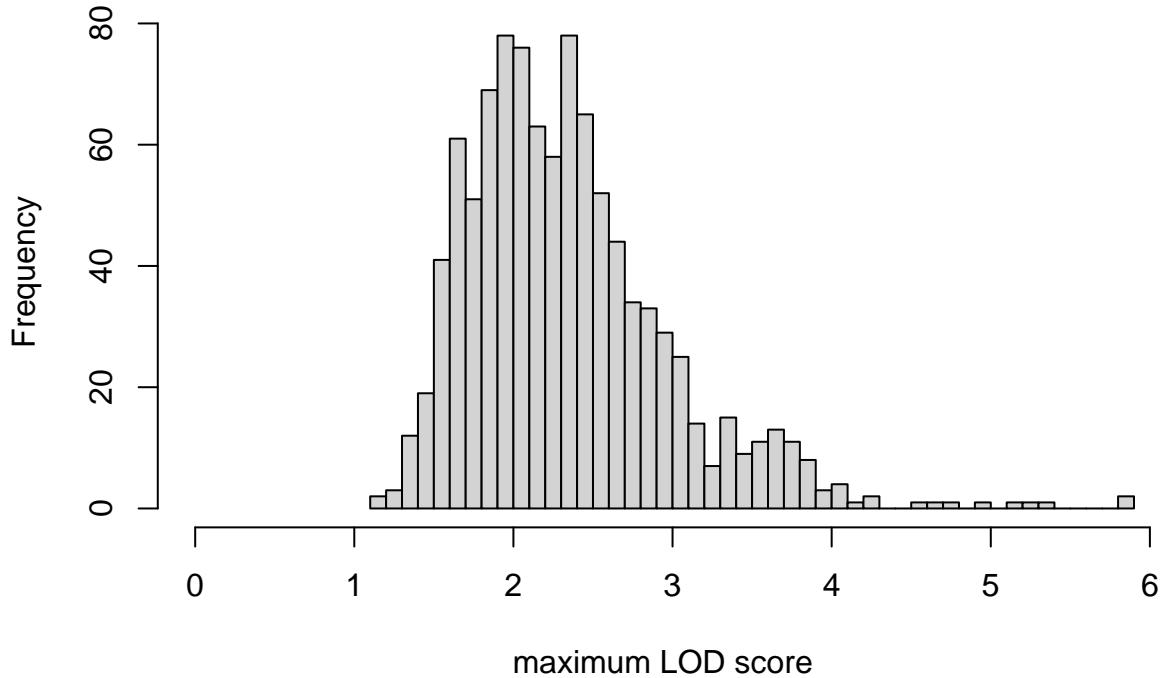
load(url("https://rqtl.org/variou.RData"))

operm <- scanone(sug, method="hk", n.perm=1000)

## Doing permutation in batch mode ...

plot(operm)

```



```

summary(operm)

## LOD thresholds (1000 permutations)
##      lod
## 5%  3.60
## 10% 3.15

summary(operm, alpha=c(0.05, 0.2))

## LOD thresholds (1000 permutations)
##      lod
## 5%  3.60
## 20% 2.78

summary(out.hk, perms=operm, alpha=0.2, pvalues=TRUE)

##           chr  pos  lod  pval
## c7.loc45    7 47.7 6.11 0.000
## c15.loc8   15 12.0 5.29 0.003

```

## 0.4 Interval estimates of QTL location

For the blood pressure phenotype, we've seen good evidence for QTL on chromosomes 7 and 15. Interval estimates of the location of QTL are commonly obtained via 1.5-LOD support intervals, which may be calculated via the function 'lodint'. Alternatively, an approximate Bayes credible interval may be obtained with 'bayesint'.

```
lodint(out.hk, chr=7)
```

```
##           chr   pos     lod
## c7.loc34    7 36.71 4.404165
## c7.loc45    7 47.71 6.107099
## c7.loc54    7 56.71 4.505278
```

```
bayesint(out.hk, chr=7)
```

```
##           chr   pos     lod
## c7.loc37    7 39.71 5.086176
## c7.loc45    7 47.71 6.107099
## c7.loc50    7 52.71 5.379287
```

It is sometimes useful to identify the closest flanking markers; use 'expandtomarkers=TRUE':

```
lodint(out.hk, chr=7, expandtomarkers=TRUE)
```

```
##           chr   pos     lod
## D7MIT176   7 34.48 3.894345
## c7.loc45    7 47.71 6.107099
## D7MIT7     7 63.14 2.800203
```

```
bayesint(out.hk, chr=7, expandtomarkers=TRUE)
```

```
##           chr   pos     lod
## D7MIT176   7 34.48 3.894345
## c7.loc45    7 47.71 6.107099
## D7MIT323   7 54.45 4.690901
```

We can calculate the 2-LOD support interval and the 99% Bayes interval as follows.

```
lodint(out.hk, chr=7, drop=2)
```

```
##           chr   pos     lod
## c7.loc32    7 34.71 3.945848
## c7.loc45    7 47.71 6.107099
## c7.loc57    7 59.71 3.849972
```

```
bayesint(out.hk, chr=7, prob=0.99)
```

```
##           chr   pos     lod
## c7.loc34    7 36.71 4.404165
## c7.loc45    7 47.71 6.107099
## c7.loc54    7 56.71 4.505278
```

The intervals for the chr 15 locus may be calculated as follows.

```
lodint(out.hk, chr=15)
```

```
##           chr   pos     lod
## D15MIT175  15 3.96 4.432504
## c15.loc8   15 11.96 5.290136
## D15MIT184  15 22.82 3.778414
```

```
bayesint(out.hk, chr=15)
```

```
##           chr   pos     lod
## D15MIT175  15 3.96 4.432504
## c15.loc8   15 11.96 5.290136
## c15.loc16  15 19.96 4.373680
```

## 0.5 QTL effects

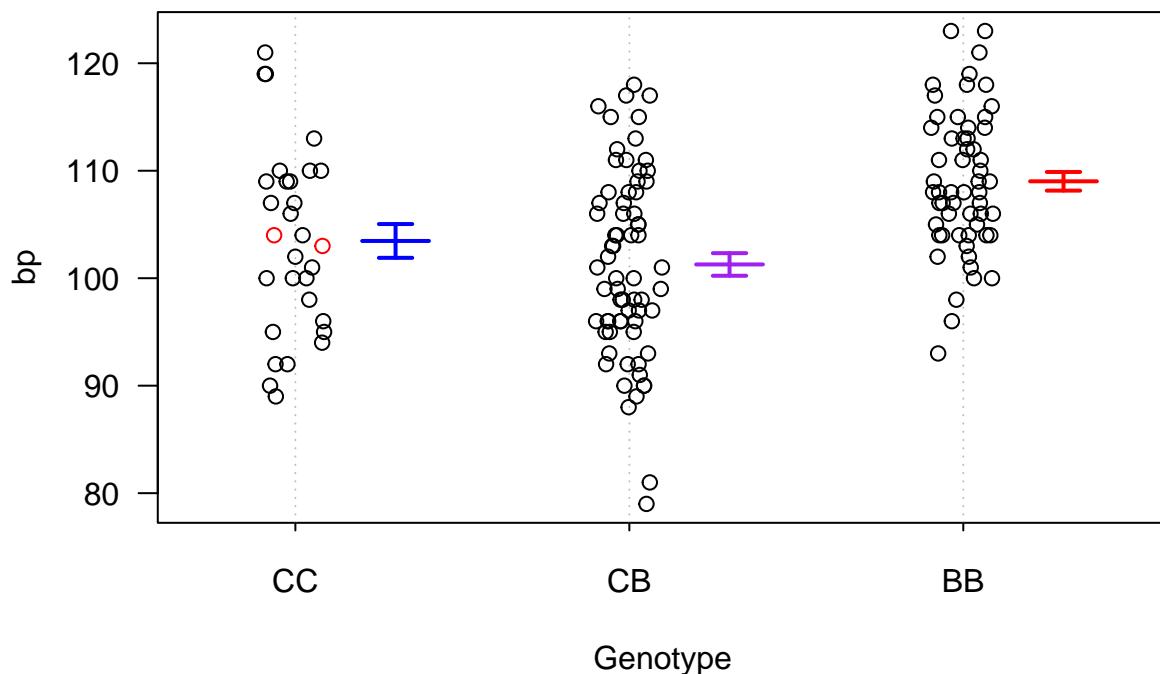
We may obtain plots indicating the estimated effects of the QTL via ‘plotPXG’, which creates a dot plot, or ‘effectplot’, which plots the average phenotype for each genotype group.

```
max(out.hk)
```

```
##           chr   pos   lod
## c7.loc45    7 47.7 6.11

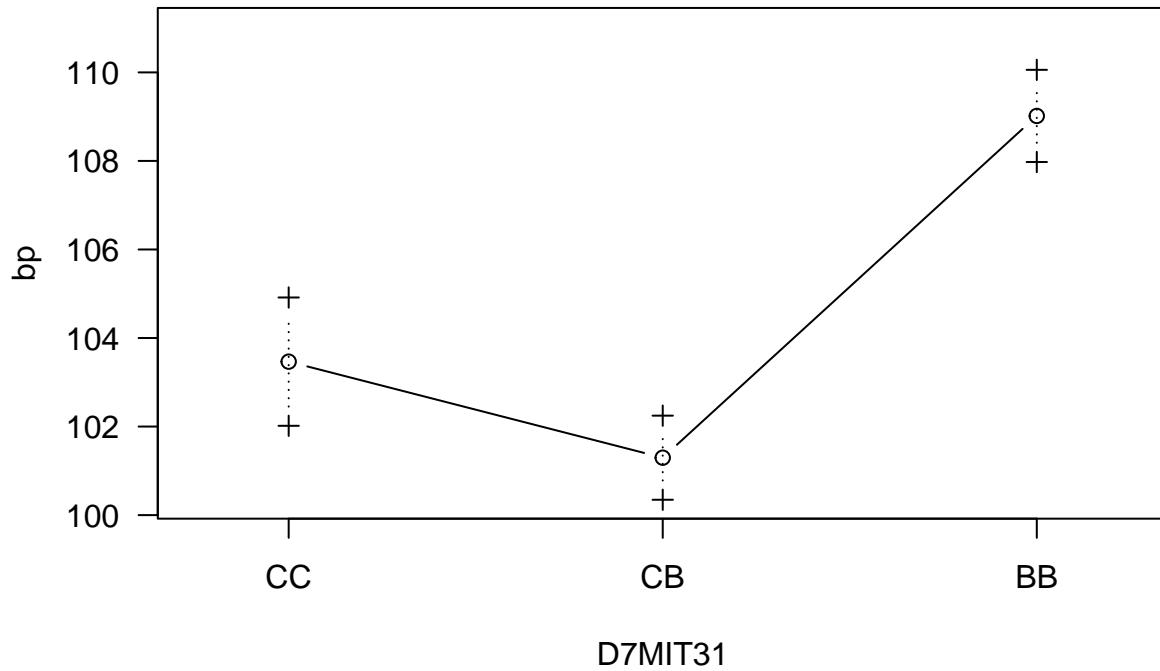
mar <- find.marker(sug, chr=7, pos=47.7)
plotPXG(sug, marker=mar)
```

D7MIT31



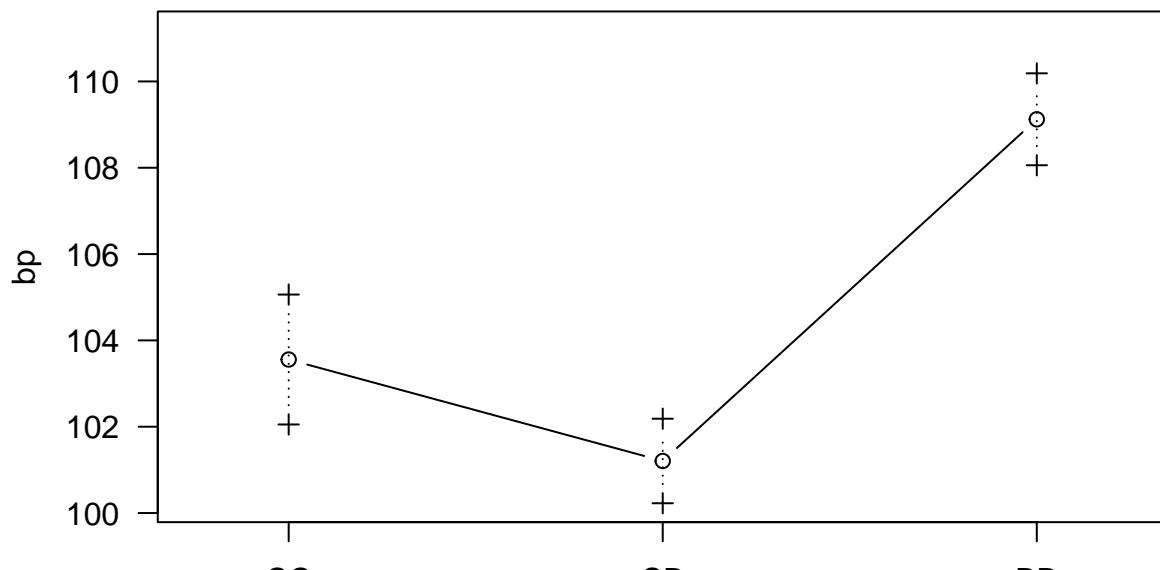
```
effectplot(sug, mname1=mar)
```

### Effect plot for D7MIT31



```
effectplot(sug, mname1="7@47.7")
```

### Effect plot for 7@47.7



7@47.7

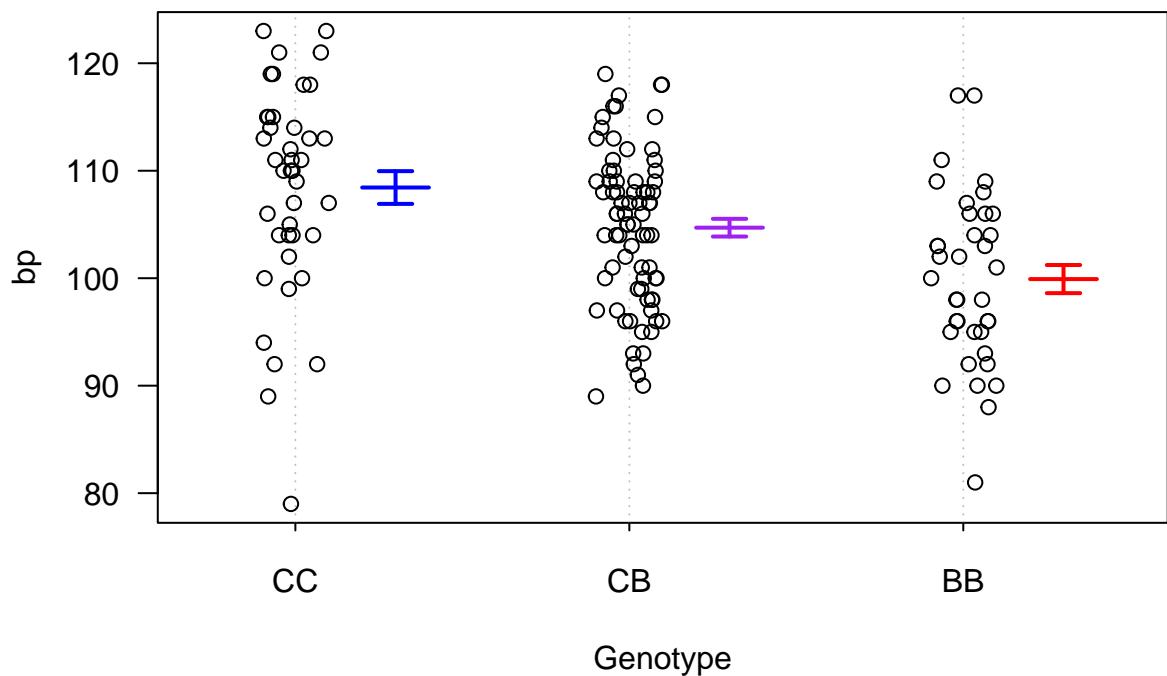
Similar plots may be obtained for the locus on chr 15.

```
max(out.hk, chr=15)

##           chr pos  lod
## c15.loc8  15   12 5.29

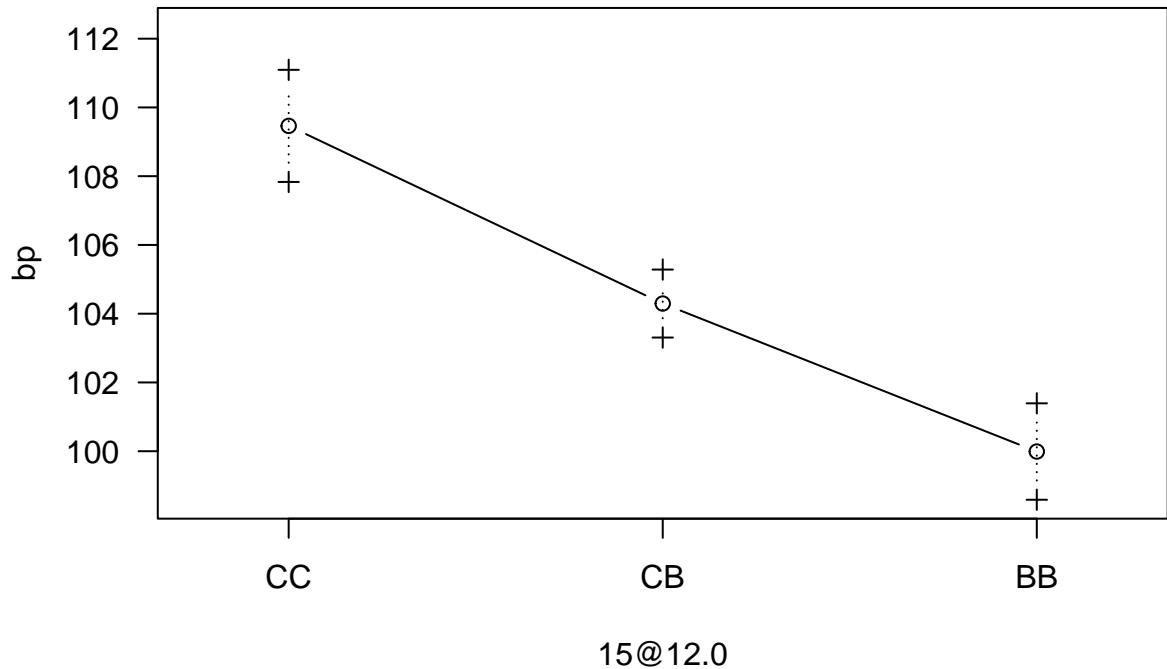
mar2 <- find.marker(sug, chr=15, pos=12)
plotPXB(sug, marker=mar2)
```

### D15MIT175

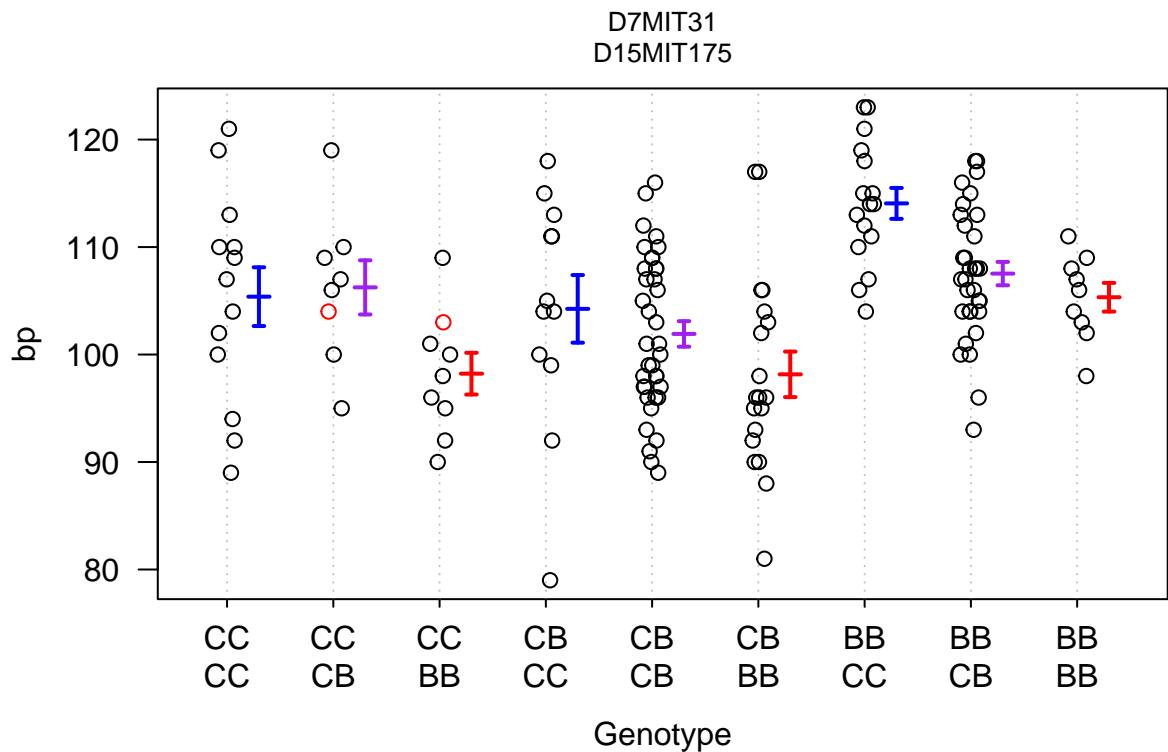


```
effectplot(sug, mname1="15@12")
```

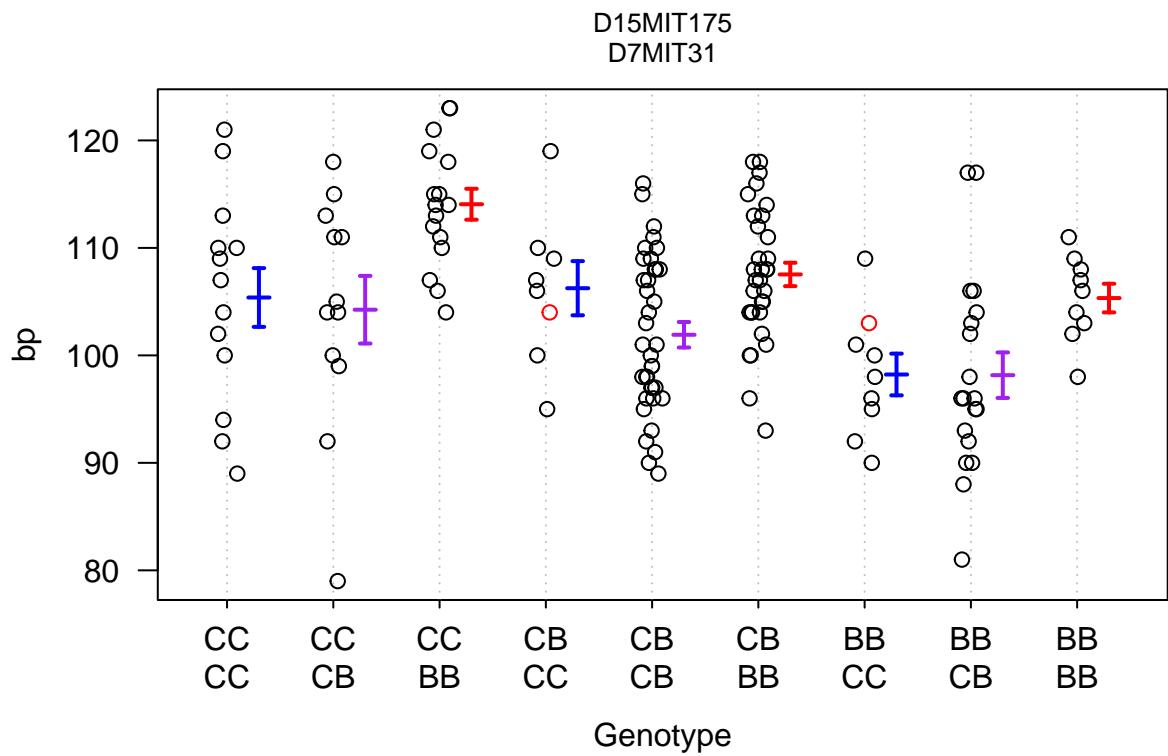
### Effect plot for 15@12.0



```
plotPXG(sug, marker=c(mar, mar2))
```

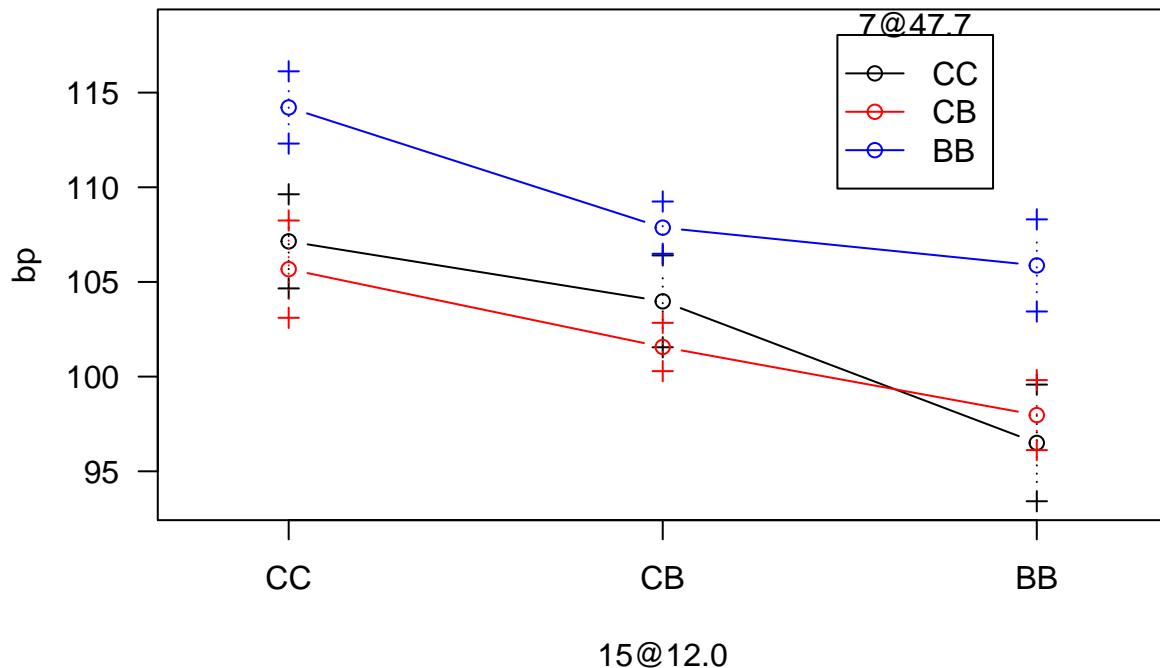


```
plotPXG(sug, marker=c(mar2, mar))
```



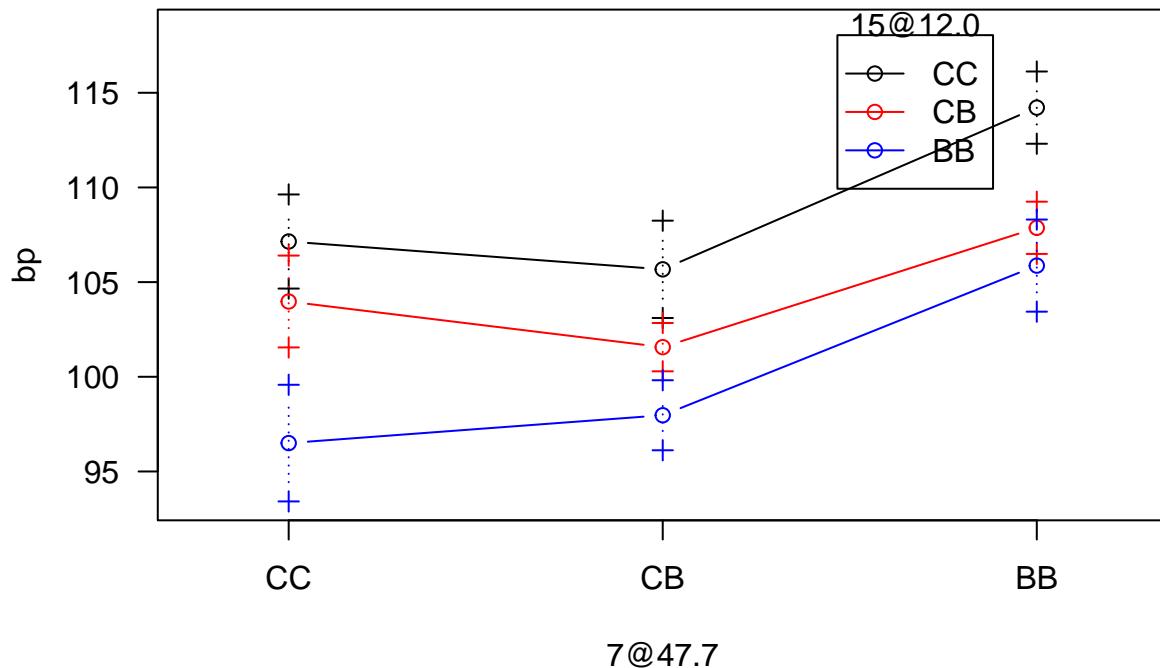
```
effectplot(sug, mname1="7@47.7", mname2="15@12")
```

### Interaction plot for 7@47.7 and 15@12.0



```
effectplot(sug, mname2="7@47.7", mname1="15@12")
```

### Interaction plot for 15@12.0 and 7@47.7



## 0.6 Other phenotypes

By default in ‘scanone’, we consider the first phenotype in the input cross object. Other phenotypes, include the parallel consideration of multiple phenotypes, can be considered via the argument ‘pheno.col’.

```
out.hr <- scanone(sug, pheno.col=2, method="hk")

out.bw <- scanone(sug, pheno.col="bw", method="hk")

out.logbw <- scanone(sug, pheno.col=log(sug$pheno$bw), method="hk")

out.all <- scanone(sug, pheno.col=1:4, method="hk")

summary(out.all, threshold=3)

##           chr   pos     bp     hr     bw heart_wt
## c7.loc45    7 47.7 6.11 0.208 0.531    0.473
## c15.loc8   15 12.0 5.29 1.616 5.423    1.216

summary(out.all, threshold=3, lodcolumn=4)

##           chr   pos     bp     hr     bw heart_wt
## c12.loc49  12 51.2 0.124 1.59 1.87      3.65

summary(out.all, threshold=3, format="allpeaks")

##   chr   pos     bp     hr   pos     bw   pos heart_wt
## 2    84.80 1.86 59.8 4.192 80.8 0.832 25.3    2.07
## 7    47.71 6.11 88.8 0.911 86.7 0.843 34.5    1.19
## 12   2.23 1.47 57.2 1.862 57.2 2.259 51.2    3.65
## 15   11.96 5.29 22.8 3.151 20.0 6.751 13.0    1.22

summary(out.all, threshold=3, format="allpheno")

##           chr   pos     bp     hr     bw heart_wt
## c2.loc54    2 59.8 0.860 4.192 0.637    0.631
## c7.loc45    7 47.7 6.107 0.208 0.531    0.473
## c12.loc49  12 51.2 0.124 1.590 1.871    3.649
## c15.loc8   15 12.0 5.290 1.616 5.423    1.216
## c15.loc16  15 20.0 4.374 2.967 6.751    1.095
## D15MIT184 15 22.8 3.778 3.151 6.610    1.017

summary(out.all, threshold=3, format="tabByCol")

## bp:
##           chr   pos ci.low ci.high lod
## c7.loc45    7 47.7 36.71    56.7 6.11
## c15.loc8   15 12.0  3.96    22.8 5.29
##
```

```

## hr:
##           chr pos ci.low ci.high lod
## c2.loc54    2 59.8   14.8    87.8 4.19
## D15MIT184  15 22.8   12.0    36.0 3.15
##
## bw:
##           chr pos ci.low ci.high lod
## c15.loc16  15  20     11      30 6.75
##
## heart_wt:
##           chr pos ci.low ci.high lod
## c12.loc49  12 51.2   28.2    62.2 3.65

summary(out.all, threshold=3, format="tabByChr")

```

```

## Chr 2:
##           chr pos ci.low ci.high lod
## hr : c2.loc54  2 59.8   14.8    87.8 4.19
##
## Chr 7:
##           chr pos ci.low ci.high lod
## bp : c7.loc45  7 47.7   36.7    56.7 6.11
##
## Chr 12:
##           chr pos ci.low ci.high lod
## heart_wt : c12.loc49 12 51.2   28.2    62.2 3.65
##
## Chr 15:
##           chr pos ci.low ci.high lod
## bp : c15.loc8  15 12.0   3.96    22.8 5.29
## hr : D15MIT184 15 22.8   11.96   36.0 3.15
## bw : c15.loc16 15 20.0   10.96   30.0 6.75

```

## 0.7 Two-dimensional, two-QTL scans

Two-dimensional, two-QTL scans offer the opportunity to detect interacting loci or to separate pairs of linked QTL. Analysis is performed with ‘scantwo’, which is much like scanone.

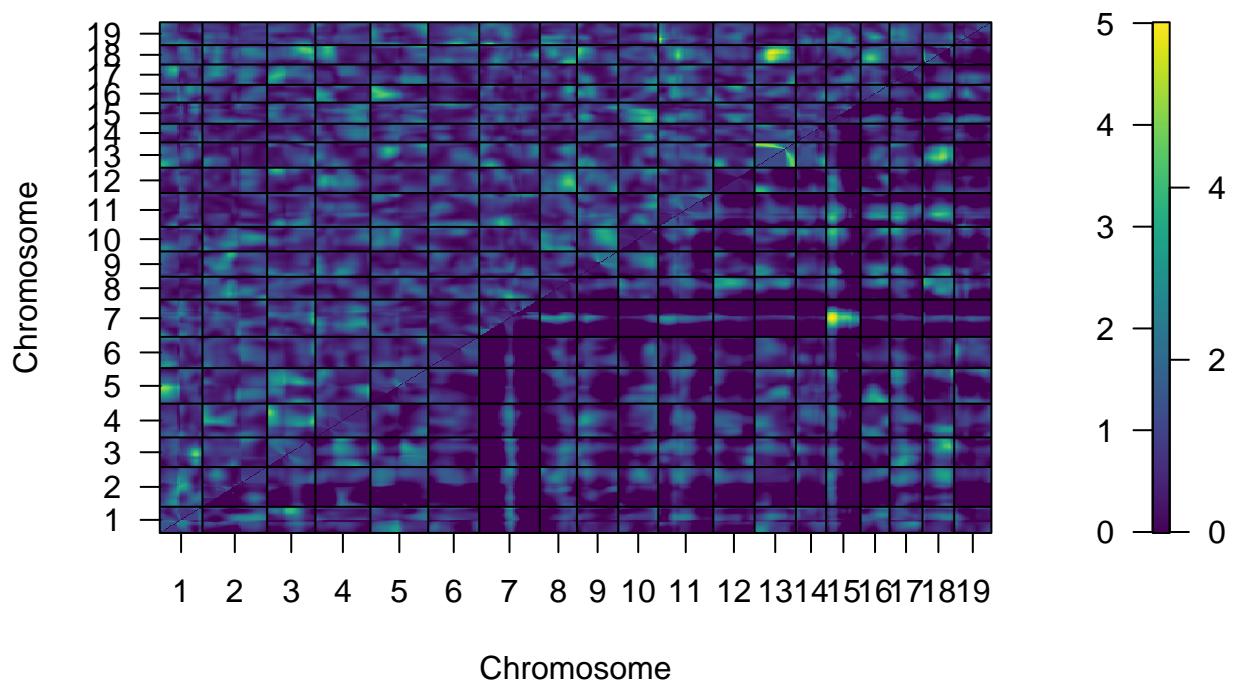
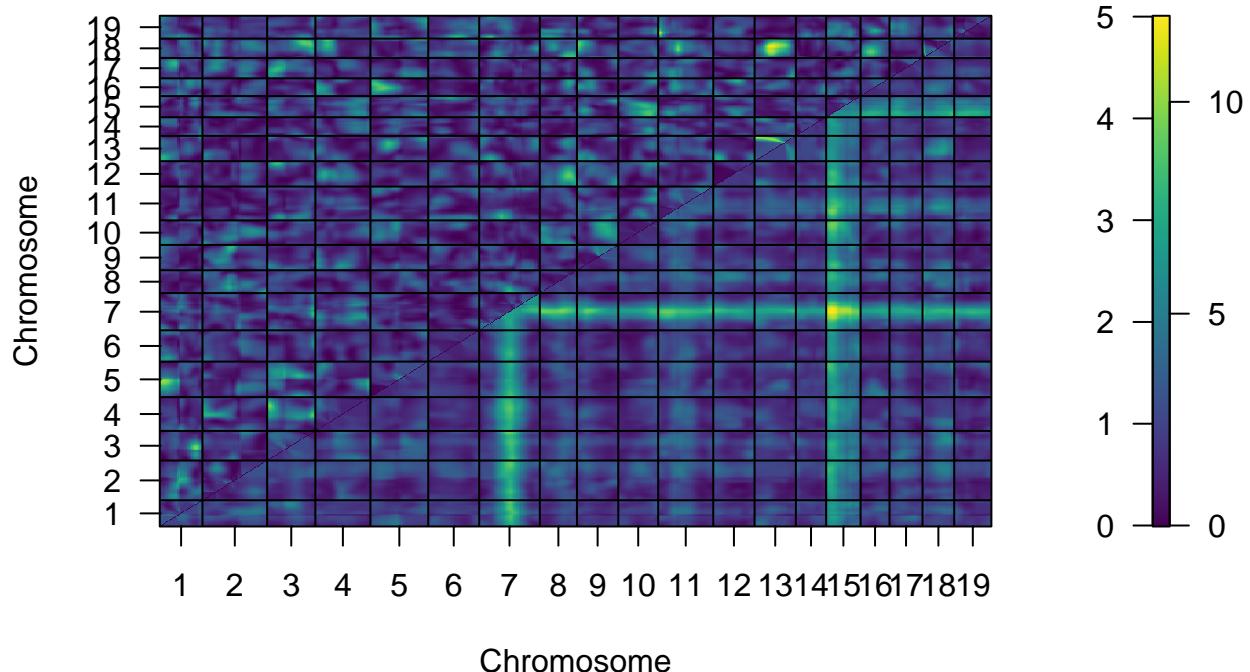
```

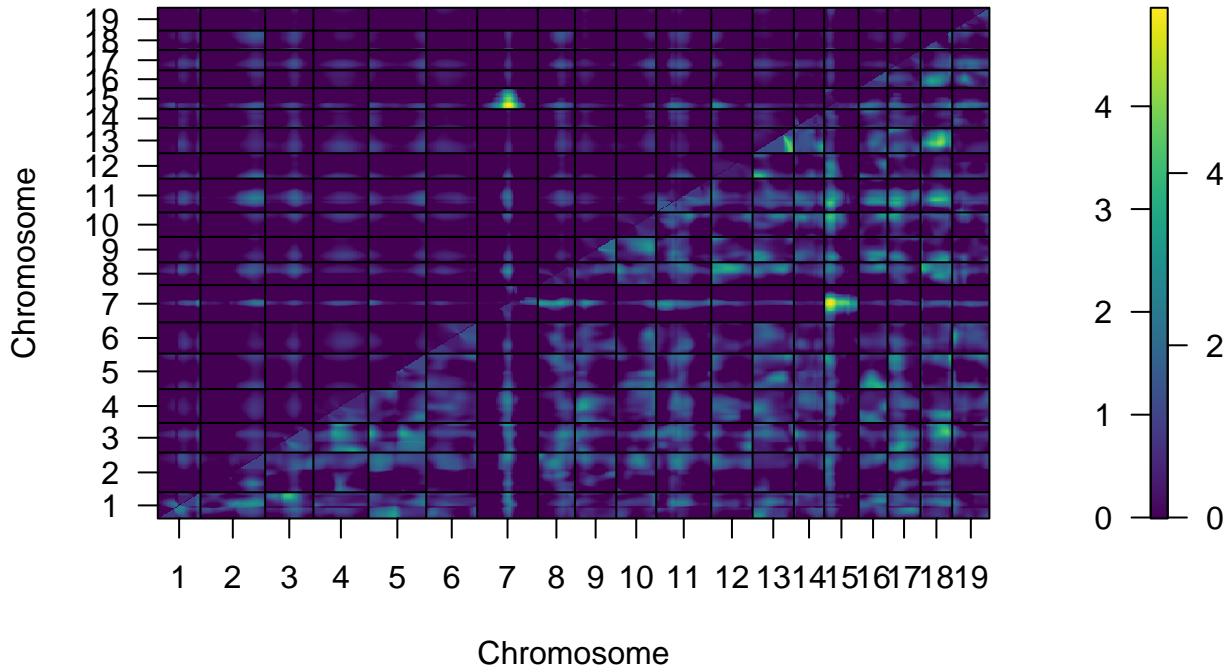
sug <- calc.genoprob(sug, step=2)

out2 <- scantwo(sug, method="hk", verbose = FALSE)

plot(out2)

```





```
operm2 <- scantwo(sug, method="hk", n.perm=5)

## Doing permutation in batch mode ...

summary(out2, perms=operm2, alpha=0.2, pvalues=TRUE)
```

	pos1f	pos2f	lod.full	pval	lod.fv1	pval	lod.int	pval	pos1a	pos2a
## c1 :c7	75.40	48.7	10.06	0.0	3.96	1.0	1.493	1	75.40	48.7
## c2 :c7	93.80	48.7	8.99	0.2	2.89	1.0	0.852	1	89.80	48.7
## c2 :c11	77.80	34.7	4.92	1.0	2.70	1.0	0.602	1	85.80	36.7
## c5 :c7	3.37	48.7	8.60	0.2	2.50	1.0	0.551	1	3.37	48.7
## c7 :c8	48.71	52.9	9.55	0.0	3.45	1.0	0.971	1	48.71	52.9
## c7 :c15	46.71	12.0	12.01	0.0	5.91	0.2	0.961	1	46.71	14.0
## c11:c15	26.70	12.0	9.62	0.0	4.32	1.0	2.349	1	30.70	12.0
## c12:c15	2.23	12.0	8.41	0.2	3.12	1.0	0.554	1	4.23	12.0
##			lod.add	pval	lod.av1	pval				
## c1 :c7			8.57	0.0	2.47	0.0				
## c2 :c7			8.13	0.0	2.04	0.2				
## c2 :c11			4.31	0.2	2.10	0.2				
## c5 :c7			8.04	0.0	1.95	0.2				
## c7 :c8			8.57	0.0	2.47	0.0				
## c7 :c15			11.05	0.0	4.95	0.0				
## c11:c15			7.27	0.0	1.98	0.2				
## c12:c15			7.85	0.0	2.56	0.0				

## 0.8 Multiple-QTL analyses

After performing the single- and two-QTL genome scans, it's best to bring the identified loci together into a joint model, which we then refine from which we may explore the possibility of further QTL. In this effort, we work with "QTL objects" created by 'makeqtl'. We fit multiple-QTL models with 'fitqtl'. A number of additional functions will be introduced below.

```

sug <- calc.genoprob(sug, step=1)
qtl <- makeqtl(sug, chr=c(7,15), pos=c(47.7, 12), what="prob")
out.fq <- fitqtl(sug, qtl=qtl, method="hk")
summary(out.fq)

##
##      fitqtl summary
##
## Method: Haley-Knott regression
## Model: normal phenotype
## Number of observations : 155
##
## Full model result
## -----
## Model formula: y ~ Q1 + Q2
##
##      df      SS      MS      LOD      %var Pvalue(Chi2)  Pvalue(F)
## Model    4  3206.168 801.54191 11.02961 27.94195 2.465709e-10 4.653179e-10
## Error 150   8268.219   55.12146
## Total 154  11474.387
##
## 
## Drop one QTL at a time ANOVA table:
## -----
##      df Type III SS      LOD      %var F value Pvalue(Chi2)  Pvalue(F)
## 7@47.7    2        1537 5.739 13.40     13.94          0 2.79e-06 *** 
## 15@12.0    2        1302 4.923 11.35     11.81          0 1.72e-05 *** 
## --- 
## Signif. codes:  0 '***' 0.001 '**' 0.01 '*' 0.05 '.' 0.1 ' ' 1

```

We may obtain the estimated effects of the QTL via get.est=TRUE. We use dropone=FALSE to suppress the drop-one-term analysis.

```

summary(fitqtl(sug, qtl=qtl, method="hk", get.est=TRUE, dropone=FALSE))

## Warning in fitqtlengine(pheno = pheno, qtl = qtl, covar = covar, formula = formula, : Dropping 8 ind

##
##      fitqtl summary
##
## Method: Haley-Knott regression
## Model: normal phenotype
## Number of observations : 155
##
## Full model result
## -----
## Model formula: y ~ Q1 + Q2
##
##      df      SS      MS      LOD      %var Pvalue(Chi2)  Pvalue(F)
## Model    4  3206.168 801.54191 11.02961 27.94195 2.465709e-10 4.653179e-10
## Error 150   8268.219   55.12146
## Total 154  11474.387

```

```

## 
## 
## Estimated effects:
## -----
##           est      SE      t
## Intercept 103.7934  0.6157 168.584
## 7@47.7a    3.0403  0.8811   3.451
## 7@47.7d   -4.0269  1.3228  -3.044
## 15@12.0a   -4.7880  0.9854  -4.859
## 15@12.0d   -0.3855  1.5633  -0.247

```

To assess the possibility of an interaction between the two QTL, we may fit the model with the interaction, indicated via a model “formula”. The QTL are referred to as Q1 and Q2 in the formula, and we may indicate the interaction in a couple of different ways.

```
out.fqi <- fitqtl(sug, qtl=qtl, method="hk", formula=y~Q1*Q2)
```

```
## Warning in fitqtlengine(pheno = pheno, qtl = qtl, covar = covar, formula = formula, : Dropping 8 ind...
```

```
out.fqi <- fitqtl(sug, qtl=qtl, method="hk", formula=y~Q1+Q2+Q1:Q2)
```

```
## Warning in fitqtlengine(pheno = pheno, qtl = qtl, covar = covar, formula = formula, : Dropping 8 ind...
```

```
summary(out.fqi)
```

```

## 
##     fitqtl summary
## 
## Method: Haley-Knott regression
## Model: normal phenotype
## Number of observations : 155
## 
## Full model result
## -----
## Model formula: y ~ Q1 + Q2 + Q1:Q2
## 
##           df      SS      MS      LOD      %var Pvalue(Chi2)      Pvalue(F)
## Model     8  3426.482 428.31024 11.93861 29.862 4.455906e-09 1.171762e-08
## Error  146  8047.905  55.12264
## Total   154 11474.387
## 
## 
## Drop one QTL at a time ANOVA table:
## -----
##           df Type III SS      LOD      %var F value Pvalue(Chi2) Pvalue(F)
## 7@47.7       6      1757.6 6.648 15.32  5.3142      0.000 5.51e-05 ***
## 15@12.0      6      1522.5 5.832 13.27  4.6032      0.000 0.00026 ***
## 7@47.7:15@12.0  4      220.3 0.909  1.92  0.9992      0.381 0.41009
## --- 
## Signif. codes:  0 '***' 0.001 '**' 0.01 '*' 0.05 '.' 0.1 ' ' 1

```

Another way to assess interactions is with the function ‘addint’, which adds one interaction at a time, in the context of a multiple-QTL model. This is most useful when there are more than two QTL being considered.

```
addint(sug, qtl=qtl, method="hk")

## Warning in addint(sug, qtl = qtl, method = "hk"): Dropping 8 individuals with missing phenotypes.

## Method: Haley-Knott regression
## Model: normal phenotype
## Model formula: y ~ Q1 + Q2
##
## Add one pairwise interaction at a time table:
## -----
##          df Type III SS    LOD %var F value Pvalue(Chi2) Pvalue(F)
## 7@47.7:15@12.0  4        220.3 0.909 1.92  0.9992      0.381      0.41
```

The locations of the two QTL are as estimated via the single-QTL scan. We may refine our estimates of QTL location in the context of the multiple-QTL model via refineqtl. This function uses a greedy algorithm to iteratively refines the locations of the QTL, one at a time, at each step seeking to improve the overall fit.

```
rqt1 <- refineqtl(sug, qtl=qtl, method="hk")
```

```
## pos: 47.71 11.96
## Iteration 1
##   Q1 pos: 47.71 -> 46.71
##     LOD increase:  0.008
##   Q2 pos: 11.96 -> 12.96
##     LOD increase:  0.021
## all pos: 47.71 11.96 -> 46.71 12.96
## LOD increase at this iteration:  0.029
## Iteration 2
##   Q2 pos: 12.96 -> 12.96
##     LOD increase:  0
##   Q1 pos: 46.71 -> 46.71
##     LOD increase:  0
## all pos: 46.71 12.96 -> 46.71 12.96
## LOD increase at this iteration:  0
## overall pos: 47.71 11.96 -> 46.71 12.96
## LOD increase overall:  0.029
```

```
rqt1
```

```
##   QTL object containing genotype probabilities.
##
##       name chr  pos n.gen
## Q1  7@46.7    7 46.71     3
## Q2  15@13.0   15 12.96     3
```

```
summary(out.fqr <- fitqtl(sug, qtl=rqt1, method="hk"))
```

```
## Warning in fitqtlengine(pheno = pheno, qtl = qtl, covar = covar, formula = formula, : Dropping 8 ind
```

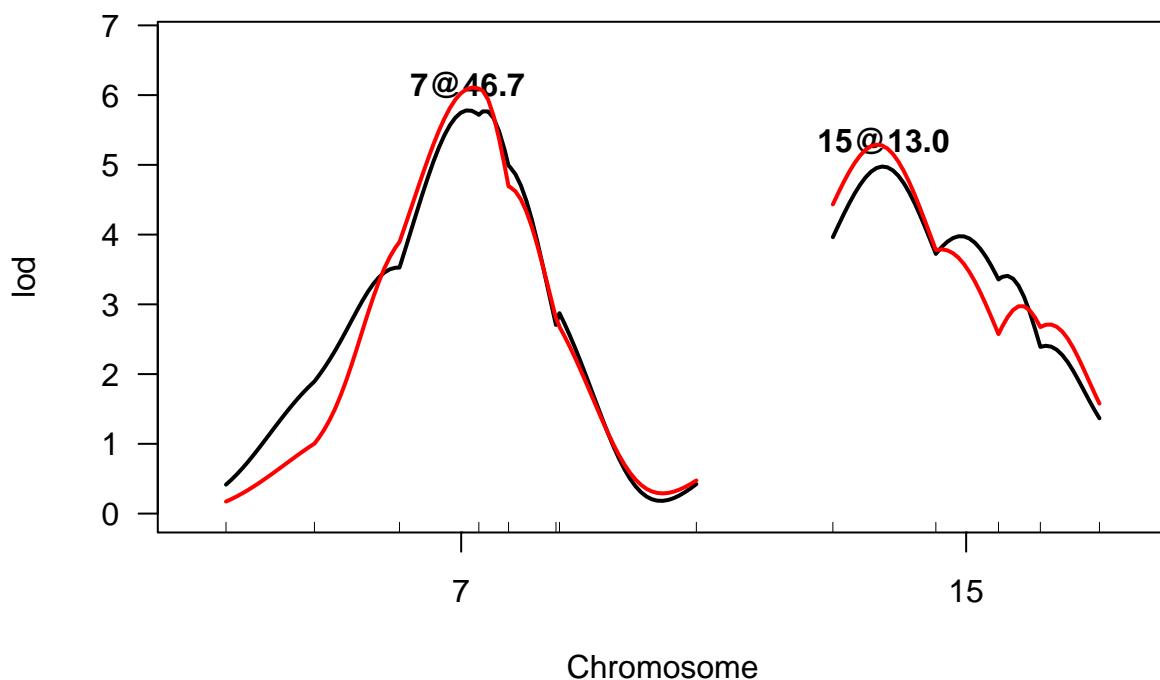
```

##      fitqtl summary
##
## Method: Haley-Knott regression
## Model: normal phenotype
## Number of observations : 155
##
## Full model result
## -----
## Model formula: y ~ Q1 + Q2
##
##      df      SS      MS      LOD      %var Pvalue(Chi2)   Pvalue(F)
## Model    4  3213.341 803.33536 11.05882 28.00447 2.311169e-10 4.369214e-10
## Error 150  8261.046  55.07364
## Total 154 11474.387
##
## Drop one QTL at a time ANOVA table:
## -----
##      df Type III SS      LOD      %var F value Pvalue(Chi2)   Pvalue(F)
## 7@46.7    2          1548 5.780 13.49    14.05      0 2.55e-06 ***
## 15@13.0    2          1316 4.976 11.47    11.95      0 1.53e-05 ***
## ---
## Signif. codes:  0 '***' 0.001 '**' 0.01 '*' 0.05 '.' 0.1 ' ' 1

plotLodProfile(rqtl)

plot(out.hk, chr=c(7,15), col="red", add=TRUE)

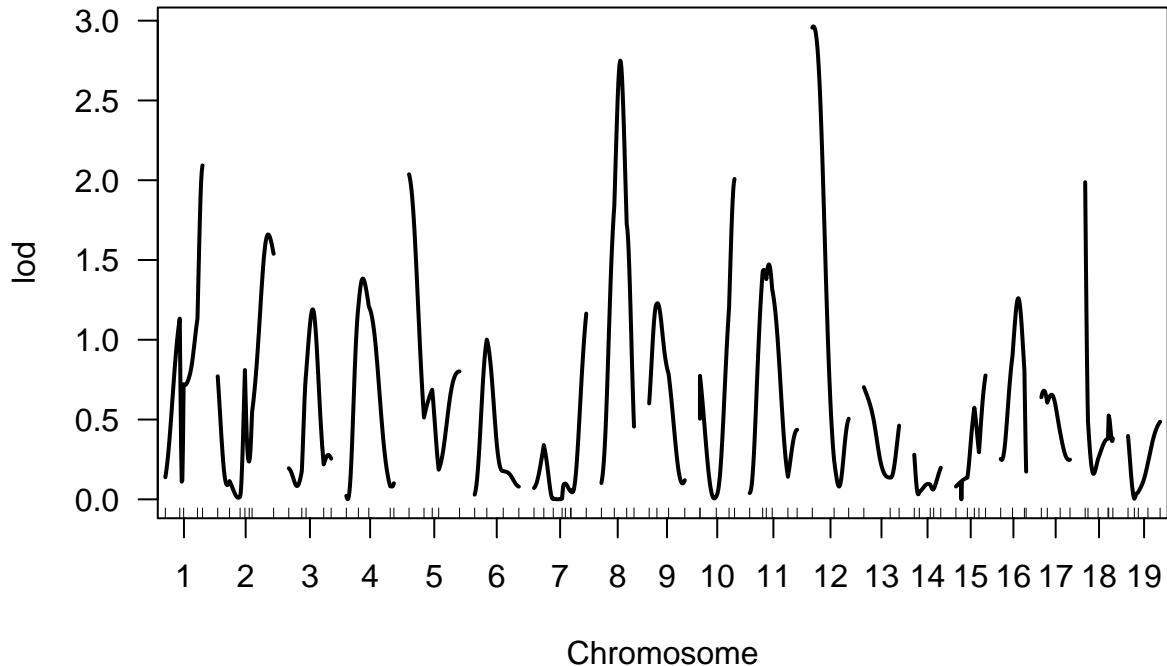
```



```
out.aq <- addqtl(sug, qtl=rqtl, method="hk")
```

```
## Warning in addqtl(sug, qtl = rqtl, method = "hk"): Dropping 8 individuals with missing phenotypes.
```

```
plot(out.aq)
```



Finally, we consider the function `stepwiseqtl`, which is our fully automated stepwise algorithm to optimize the penalized LOD scores of Manichaikul et al. (2009). We first need to calculate the appropriate penalties from the twodimensional permutation results.

```
print(pen <- calc.penalties(operm2))
```

```
##      main     heavy     light
## 2.770221 7.947069 5.505152
```

We then run `stepwiseqtl`, using `max.qtl=5`. It will perform forward selection to a model with 5 QTL, followed by backward elimination, and will report the model giving the largest penalized LOD score. The output is a QTL object.

```
out.sq <- stepwiseqtl(sug, max.qtl=5, penalties=pen, method="hk", verbose=2)
```

```
## -Initial scan
## initial lod:  6.107099
## ** new best ** (pLOD increased by 3.3369)
##    no.qtl =  1  pLOD = 3.336878  formula: y ~ Q1
##    qtl: 7@47.7
## -Step 1
## ---Scanning for additive qtl
##     plod = 5.513487
## ---Scanning for QTL interacting with Q1
##     plod = 0.8930199
## ---Refining positions
## --- Moved a bit
##    no.qtl =  2  pLOD = 5.518379  formula: y ~ Q1 + Q2
```

```

##          qtl: 7@46.7 15@13
## ** new best ** (pLOD increased by 2.1815)
## -Step 2
## ---Scanning for additive qtl
##      plod = 5.712007
## ---Scanning for QTL interacting with Q1
##      plod = 1.229681
## ---Scanning for QTL interacting with Q2
##      plod = 1.902743
## ---Look for additional interactions
##      plod = 0.949707
## ---Refining positions
## --- Moved a bit
##      no.qtl = 3   pLOD = 5.7151   formula: y ~ Q1 + Q2 + Q3
##      qtl: 7@47.7 15@13 12@4.2
## ** new best ** (pLOD increased by 0.1967)
## -Step 3
## ---Scanning for additive qtl
##      plod = 5.424769
## ---Scanning for QTL interacting with Q1
##      plod = 1.301826
## ---Scanning for QTL interacting with Q2
##      plod = 1.710722
## ---Scanning for QTL interacting with Q3
##      plod = 2.521311
## ---Look for additional interactions
##      plod = 1.198123
## ---Refining positions
## --- Moved a bit
##      no.qtl = 4   pLOD = 5.462236   formula: y ~ Q1 + Q2 + Q3 + Q4
##      qtl: 7@46.7 15@13 12@2.2 8@50.9
## -Step 4
## ---Scanning for additive qtl
##      plod = 4.79462
## ---Scanning for QTL interacting with Q1
##      plod = 0.9458758
## ---Scanning for QTL interacting with Q2
##      plod = 1.458711
## ---Scanning for QTL interacting with Q3
##      plod = 1.909949
## ---Scanning for QTL interacting with Q4
##      plod = 0.9068932
## ---Look for additional interactions
##      plod = 2.503296
## ---Refining positions
## --- Moved a bit
##      no.qtl = 5   pLOD = 4.916621   formula: y ~ Q1 + Q2 + Q3 + Q4 + Q5
##      qtl: 7@49.7 15@13 12@8.2 8@49.9 18@13.4
## -Starting backward deletion
## ---Dropping Q4
##      no.qtl = 4   pLOD = 5.540272   formula: y ~ Q1 + Q2 + Q3 + Q4
##      qtl: 7:49.7 15:13 12:8.2 18:13.4
## ---Refining positions
## --- Moved a bit

```

```

## ---Dropping Q4
##   no.qtl = 3   pLOD = 5.412899   formula: y ~ Q1 + Q2 + Q3
##   qtl: 7:51.7 15:12 12:10.2
## ---Refining positions
##   --- Moved a bit
## ---Dropping Q3
##   no.qtl = 2   pLOD = 5.513487   formula: y ~ Q1 + Q2
##   qtl: 7:47.7 15:13
## ---Refining positions
##   --- Moved a bit
## ---Dropping Q2
##   no.qtl = 1   pLOD = 3.312696   formula: y ~ Q1
##   qtl: 7:46.7
## ---Refining positions
##   --- Moved a bit
## ---One last pass through refineqtl

```

out.sq

```

## QTL object containing genotype probabilities.
##
##      name chr pos n.gen
## Q1 7@47.7 7 47.71 3
## Q2 12@4.2 12 4.23 3
## Q3 15@13.0 15 12.96 3
##
## Formula: y ~ Q1 + Q2 + Q3
##
## pLOD: 5.715

```