

SPATIAL CHARACTERISTICS OF HABITAT PATCHES AND POPULATION SURVIVAL

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ABSTRACT

Lefkovitch, L.P. and Fahrig, L., 1985. Spatial characteristics of habitat patches and population survival. *Ecol. Modelling*, 30: 297–308.

The effect of the spatial arrangement of habitat patches on the survival of resident populations were considered in a stochastic model using population parameters appropriate to *Peromyscus leucopus*. The 34 possible arrangements of connections among five otherwise identical patches were simulated in order to determine the survival probabilities and population sizes.

The main findings are that populations in completely isolated patches have lower survival probabilities than those in patches that are connected to other patches, and that the survival probabilities of populations in connected patches increases with the size of the largest geometric figure of which the patch is a part. The results are discussed in the context of resource management.

INTRODUCTION

Although most species live in heterogeneous environments composed of 'patches' of suitable and unsuitable habitats (Emmel, 1976; Cowie and Krebs, 1979; McNamara, 1982), most ecological models assume that the environment is homogeneous (e.g., see Lotka, 1925; Leslie, 1945; Wiegert, 1974; Beddington et al., 1975; Anderson, 1979; Hansen and Tuckwell, 1981). It has been shown, both theoretically and empirically, that this assumption produces inaccurate predictions about population survival (Levin, 1976;

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Goldstein, 1977; Southwood, 1977; Fahrig and Merriam, in press). However, apart from a preliminary study by Fahrig et al. (1983), it appears that there is no description of the way in which habitat heterogeneity changes model predictions. The problem is complex since every heterogeneous environment in nature is a unique spatial arrangement of habitat patches.

Based on simulations of all eleven arrangements of four woodlots, Fahrig et al. (1983) suggested the importance of isolation, but explanations for differences in population survival among the connected patches were not offered. The present study of the 34 arrangements of five patches, which clearly include those of four as a subset, was undertaken to remedy this. It does not seem likely that a further study of the arrangements of six, of which there are 156, will yield any further insights.

The purpose of this study was to understand which aspects of the spatial characteristics of groups of habitat patches are important predictors of the survival of resident populations.

METHODS

To study the problem, a number of arrangements of habitat patches were chosen, and the population sizes in the patches were simulated over time. The simulation results were then analysed to determine which features of the spatial arrangement of patches appear to be important for population survival.

Choice of arrangements

The spatial arrangements of habitat patches (see Fig. 1) were chosen to satisfy the following conditions: (a) there are five habitat patches; (b) each patch may or may not be 'connected' to one or more of the other four, where the existence of a connection allows individuals to move through the inter-patch region, e.g. the patches may be sufficiently close together to allow this movement, or a physical 'corridor' of suitable habitat may link them; (c) all connections are of equal 'strength', i.e. the probability that individuals move between two connected patches is the same for all connections; (d) all patches are otherwise equivalent.

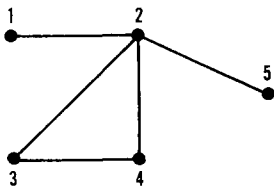


Fig. 1. A suggested arrangement of five habitat patches; circles are patches, lines are connections.

Under these restrictions, all 34 distinct spatial arrangements (Riordan, 1958, p. 146) of the five patches were examined.

Simulation experiments

To make the simulations biologically meaningful, published information was used on the white-footed mouse *Peromyscus leucopus* for populations in southeastern Ontario, which is the northern edge of its range. *P. leucopus* appears to prefer habitats with vegetational cover in the form of shrubs and trees and to avoid open areas such as fields (Bendell, 1961; Whitaker, 1967; M'Closkey and Lajoie, 1975; Hansen and Warnock, 1978). The hypothetical habitat patches can be thought of as woodlots separated from each other by fields, but sometimes linked by 'fencerows', which are fencelines along which trees and shrubs are growing; the latter have been suggested as corridors for movement of *P. leucopus* (Wegner and Merriam, 1979; Fahrig and Merriam, in press).

The model (presented in detail in Fahrig et al., 1983) is stochastic and is structured to follow the population sizes in four age classes in a series of interconnected patches through time. Within a patch, additions to the youngest age class occur through births, and to the other classes through aging, while losses occur through deaths. Between-patch dynamics consist of additions due to immigration from connected patches, and losses due to emigration. Since the age classes are of unequal duration, the underlying deterministic model is intermediate between the equal age class model of Leslie (1945) and the stage class model of Lefkovich (1965).

The basic operator of the model is a transition matrix, for each time period. Each matrix has a block form. An element of the off-diagonal block, $p(i, j, k, t)$, is the proportion of organisms in class k moving from patch j to patch i during the time t to $t + 1$.

The probabilities of remaining are elements in the diagonal blocks (i.e. $i = j$), which also include birth and death rates, so that a typical diagonal element is

$$p(i, j, k, t) = 1 - \sum_{\substack{j=1 \\ j \neq i}}^m p(j, i, k, t) + b(i, k, t) - d(i, k, t)$$

where $b(i, k, t)$ is the birth rate in patch i for class k during t to $t + 1$, $d(i, k, t)$ is the death rate, and m is the total number of patches. Parameters estimated from the literature were used as means. In the simulations for each year a new random estimate was chosen, assuming a normal distribution, with standard deviation equal to 10% of the mean. The vector of population sizes of the various age classes in the different patches at time $t + 1$ was then

obtained as the product of the (random) transition matrix for time t with the vector of population sizes at time t .

Detailed discussion of the parameter values is found in Fahrig et al. (1983), but the following points should be noted. First, there is no evidence that any of the probabilities of giving birth, dying, and dispersing from a woodlot are density-dependent for *P. leucopus*. Second, as no evidence to the contrary was found, it was assumed that *P. leucopus* disperse irrespective of whether or not a dispersal corridor exists. Individuals dispersing in the absence of a corridor are assumed to be lost due to predation. Third, the adult population in each woodlot in the spring is assumed to be 15% of the population in the previous fall (Taylor, 1978; Middleton, 1979). Fourth, all connections between woodlots are assumed to be biologically equi-distant (same length, width, plant species composition, etc.) and all woodlots are biologically equivalent. Fifth, the mice leaving a woodlot are divided equally among the connections.

The population sizes were calculated for each week from the 3rd week of March to the 2nd week of October for each woodlot in each spatial arrangement, and are summarized by the population sizes at the end of the year.

The average yearly final population sizes (in the 2nd week of October), and their variances were calculated for each woodlot. The simulations were terminated at 100 years; if a population did not survive for 100 years, the year in which it died out was noted.

Analysis of results

Those aspects of the spatial arrangement important for population survival were determined by analysis of variance of three dependent variables, which, in appropriately transformed scales, are:

(1) YEAR = $\log[\text{population survival in years}/(100 - \text{survival in years})]$, i.e. the logit transformation of the probability of surviving 100 years.

(2) PRES = $\log(\text{average yearly final population size})$, i.e. the mean number of mice at the end of the year in a logarithmic scale.

(3) PREV = $\log(\text{variance of PRES})$.

The following features of spatial arrangement were considered to be possible explanatory factors. For each patch:

(1) DEGRE: the degree of a patch is defined as the number of other patches to which it is connected.

(2) NEIGH: the neighbouring degree of a patch is the average degree of all patches to which it is connected.

(3) ISO: a patch is either isolated (DEGRE = 0) or is connected (DEGRE > 0).

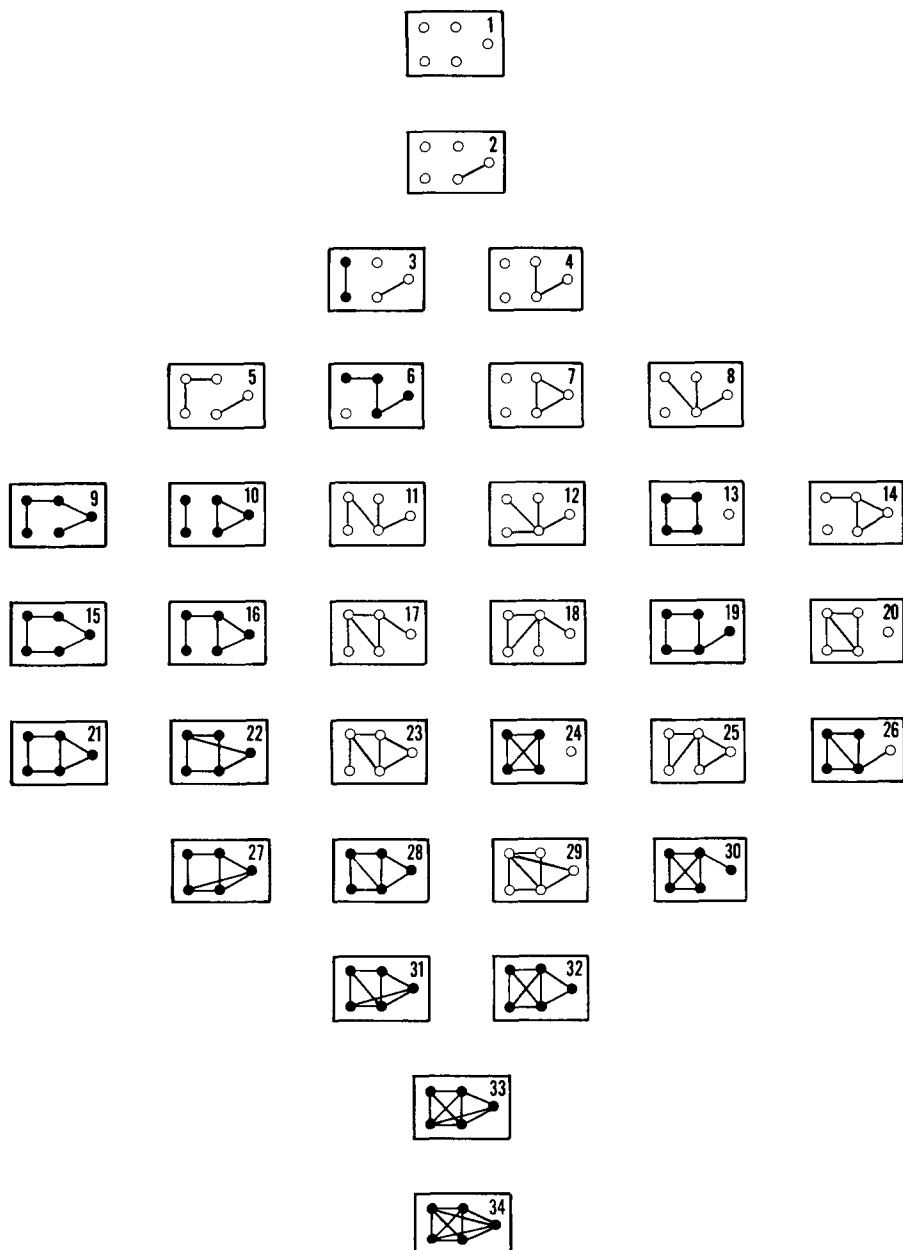


Fig. 2. All unique spatial arrangements of five unlabelled habitat patches; circles are patches, lines are connections. Populations in patches shown as open circles died out within the 100-year simulation.

(4) CRIT: a critical patch is one which, if removed from the spatial arrangement, separates the arrangement into two or more components. For example, in Fig. 1, only patch 2 is critical.

(5) GG: connected patches may be distinguished according to the largest geometrical figure of which they are a part. The only possibilities for five patches are a line, triangle, square, and pentagon. For example, in Fig. 1, patches 1 and 5 belong to a line, and patches 2, 3 and 4 belong to a triangle.

These explanatory factors are not completely independent, and, for example, CRIT and GG may be regarded as one factor with five levels. Two other predictors, namely, the orbits of the graphs and their structural information content (Mowshowitz, 1968) were also considered but found not to play a detectable role, and are not considered further in this paper.

Analyses of variance were performed to determine which of the factors, if any, were important sources of variation for the dependent variables described above. Because of the lack of balance, the analyses used instrumental variables.

RESULTS

All possible arrangements of five patches, under the constraints listed in Section Choice of arrangements, are illustrated in Fig. 2. A summary of the

TABLE 1

Summary analysis of variance giving mean squares for the (transformed) dependent variables

Transformation used	DF	YEAR (Survival) logit	PRES (Abundance) logarithm	PREV (Variability) logarithm
<i>Source of variation</i>				
ISO	1	237.664 *	90.923 *	69.881 *
GG within ISO	3	94.158 *	4.197 *	0.726
CRIT within GG within ISO	3	5.405	1.171	0.594
Covariates (NEIGH, DEGRE)	2	5.600	0.907	3.852
Residual	160	4.331	0.666	1.077
Means (back-transformed)		Probability of surviving 100 years	Mean numbers at end of year	Estimated variance at end of year
ISO 1 (isolated)		0.0085	0.1554	1.1219
ISO 2 (connected)				
GG2 (line)		0.6660	10.0744	61.992
GG3 (triangle)		0.6770	10.0442	47.323
GG4 (square)		0.9773	19.9654	67.357
GG5		0.9942	25.0031	68.855

* $p < 0.05$.

simulation results after transformations, together with the possible explanatory factors used in the analysis are given in Appendix 1.

The results of the analyses of variance are given in Table 1. Most of the variation in YEAR, PRES and PREV is explained by the contrast between isolated and nonisolated patches (i.e., factor ISO). Populations in isolated patches died out much earlier, had lower average population sizes and variances, but higher coefficients of variability than those in connected patches.

For YEAR and PRES, a significant portion of the variance not explained by ISO was attributed to GG (the largest geometrical figure). The means (Table 1) show that woodlots forming part of a square ($GG = 4$) or a pentagon ($GG = 5$) had higher population sizes and probabilities of survival for 100 years than those which formed part of a line ($GG = 2$) or a triangle ($GG = 3$). None of the other factors nor the covariates could be shown to play an additional significant role for any of the dependent variables.

DISCUSSION

The factors identified in the analyses as being the most important for population survival are whether the patch is isolated or not and, if not, then the size of the largest geometrical figure to which it belongs. The set of predictor variables used in the analyses of variance, however, are not independent. For example, degree zero corresponds to isolation, and so an isolated patch can never be critical, and the mean degree of its neighbours is necessarily zero (or undefined). Furthermore, since isolated patches represent the smallest possible geometrical figure, ISO and GG although treated separately here, are better regarded as a single factor of five levels. Finally, if an arrangement is not closed, there is a positive association between DEGRE and CRIT. Thus the explanatory factors imply both more and less than their original definitions.

Data for a decisive test of the results are difficult to obtain. This would require studies of *Peromyscus leucopus* population in a very large number of woodlots, which are interconnected in a variety of ways. However, Fahrig and Merriam (in press) studied *P. leucopus* populations in six woodlots, of which two were apparently completely isolated, while the other four were inter-connected by fencerows to form a square. The populations were studied over a summer using smoked paper tracking (Justice, 1961). Since the number of tracks (per 100 tracking stations per week) was shown to be correlated with the number of animals trapped in live traps (Fahrig and Merriam, in press), it is a measure of relative population size. The number of tracks per week for 12 weeks in the six woodlots, given in Table 2, are consistent with the results of the present study, since all four inter-connected

TABLE 2

(a) Number of tracks per 100 tracking stations in each of 12 weeks, June–September, 1982, in six woodlots

	Week												Mean	
	1	2	3	4	5	6	7	8	9	10	11	12		
Isolated														
1	0	3	6	2	0	4	10	12	2	2	9	8	4.8	} 5.5
2	0	1	0	2	5	8	14	12	13	13	6	5	6.3	
Interconnected														
1	0	1	1	1	1	4	5	19	16	5	15	11	6.6	} 8.4
2	0	1	2	0	9	19	19	18	14	3	3	20	9.0	
3	0	2	2	1	5	5	9	10	27	6	8	7	6.8	
4	1	18	1	2	26	26	8	19	13	2	9	14	11.2	

(b) Analysis of deviance for the above data using a log-linear model and Poisson errors

Model	Model		Change in	
	DF	Deviance	DF	Deviance (χ^2)
Mean	71	477.517		
+ Weeks (W)	60	206.794	11	270.723 *
+ Connections (C)	59	188.374	1	18.420 *
+ Interaction (W.C)	48	163.508	11	24.866 *

* $p < 0.01$.

woodlots had higher mean population sizes than either of the two isolated ones. A log-linear analysis, rating the number of tracks as a Poisson variate (see Table 2), not surprisingly shows a significant time effect, but also an isolation and an interaction effect at the 0.1% level.

The sensitivity of any simulation model to the input values is important for its refining and interpretation. While insensitive parameters are perhaps superfluous, those which are sensitive may require further study. Although an extended analysis has not been performed, the only sensitive parameter appears to be the overwintering survival rate; small increases result in a population explosion, while small decreases result in rapid extinction. Since mortality in the model is not density dependent, the sensitivity to overwintering survival is not surprising.

In interpreting the results of this study, the assumptions in the model and the special characteristics of the population dynamics of *P. leucopus* must be remembered:

(1) There is an assumption that a proportion of each population dispersed, irrespective of the number of connections. In the absence of connec-

tions, mice are supposed to have dispersed into the open fields where they had no chance of survival. This explains the importance of ISO (isolation) in the results of the simulation. For a species whose populations do not disperse when isolated, ISO may not be as important.

(2) The birth, mortality and dispersal rates of *P. leucopus* are all assumed to be density-independent. If, for another species, at low population densities, birth rate is high, mortality and dispersal rates low, with the reverse for high population densities, then populations will tend to persist for longer. Populations of such species, in arrangements such as no. 25 in Fig. 2, may not then die out. As the relative importance of stabilizing density-dependent factors increases, it must be expected that the probability of survival of populations in isolated habitats will increase.

(3) The assumptions that all patches are equivalent and all connections equally strong, allow other aspects of spatial arrangement to be considered. In nature, neither of these assumptions need be true, so that further work will be necessary to determine their importance.

Although interpretation of the results must recognize these limitations, three inferences have important implications for applied ecology:

(1) If the species is a pest (e.g. apple tree leaf mites), so far as is possible, its habitat patches (e.g. apple trees) should be arranged in patterns that minimize not only the possible connections between trees but also the sizes of figures formed by connections between neighbouring patches (e.g., two trees sufficiently close to allow mite dispersal constitute a connection). Isolation is best, but if it is not possible to arrange this, separated rows or small figures are to be preferred.

(2) If the species is harvestable or produces a harvestable product (e.g. honey bees), the opposite is true. The patches (e.g. bee hives) should be arranged in well-connected, large closed figures. This also follows from the studies of linear arrangements in which drift to an adjacent position occurs with non-zero probability in a finite number of positions (Jay, 1965).

(3) For rare species needing conservation, the provision of a number of suitable habitats each of sufficient size to maintain a population is obvious, but this study also suggests that establishing links able to be traversed by individuals can be a major factor in their long-term survival.

If the model described in this paper is a reasonable picture of reality for a species, it follows that the recognition of the connection possibilities among patchily distributed populations is essential to an understanding of its dynamics, survival, and gene flow.

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APPENDIX 1

Summary of simulation results after transformations YEAR, PRES, PREV, CFFV, (DEGRE, NEIGH, ORBIT, STRUC, CRIT, ISO, GEDG)

	YEAR	PRES	PREV	CFFV	DEGRE	NEIGH	ORBIT	STRUC	CRIT	ISO	GEDG	
-3.	4864	-1	4692	0. 9781	7. 1584	0	0. 000	1	0. 0000	0	1	1
-3.	4864	-1	3036	-1. 0475	9. 9229	0	0. 000	1	0. 0000	0	1	1
-3.	4864	-1	9937	-1. 4357	9. 9055	0	0. 000	1	0. 0000	0	1	1
-3.	4864	-1	9937	-1. 4357	9. 9055	0	0. 000	1	0. 0000	0	1	1
-3.	4864	-1	9937	-1. 4357	9. 9055	0	0. 000	1	0. 0000	0	1	1
-3.	4864	-1	6089	0. 6757	7. 0077	0	0. 000	1	0. 0000	0	1	1
-3.	4864	-1	5245	-1. 2376	6. 7172	0	0. 000	1	0. 0000	0	1	1
-3.	4864	-1	3036	-1. 0475	9. 9229	0	0. 000	1	0. 0000	0	1	1
-3.	4864	-1	3289	-0. 2384	1. 2328	1	1. 000	1	0. 0000	0	1	1
-3.	4864	-1	1744	-0. 5678	8. 8934	1	1. 000	1	0. 0000	0	1	1
-3.	6052	4	4344	-0. 0285	3. 9906	1	1. 000	1	0. 0000	0	1	1
-3.	4864	-1	6593	-0. 9770	6. 6779	0	0. 000	1	0. 0000	0	1	1
-3.	6052	4	4720	-0. 9917	9. 3693	1	1. 000	1	0. 0000	0	1	1
-1.	7463	1	1537	4. 4504	9. 9176	1	1. 000	1	0. 0000	0	1	1
-1.	7463	1	2147	4. 5255	1. 8514	1	1. 000	1	0. 0000	0	1	1
-1.	4864	-1	8134	-1. 9541	6. 2675	0	0. 000	1	0. 0000	0	1	1
-1.	4864	-1	3711	0. 6089	1. 9650	0	0. 000	1	0. 0000	0	1	1
-1.	4864	-1	7348	-1. 0129	3. 2979	0	0. 000	1	0. 0000	0	1	1
-1.	4864	-1	1103	0. 0000	8. 8609	0	0. 000	1	0. 0000	0	1	1
-1.	4864	-1	7103	-0. 7103	8. 8876	1	1. 000	1	0. 0000	0	1	1
-1.	2083	9	924	9. 8477	5. 5124	1	1. 000	1	0. 0000	0	1	1
-1.	3246	4	7443	4. 4220	0. 4803	1	1. 000	1	0. 0000	0	1	1
-1.	1019	9	9098	4. 3346	0. 4759	2	2. 000	1	0. 0000	0	1	1
-1.	8615	2	2507	6. 148	1. 7449	1	1. 000	1	0. 0000	0	1	1
-1.	8615	2	2507	6. 148	1. 7449	1	1. 000	1	0. 0000	0	1	1
-1.	6052	4	6345	-0. 3450	0. 3445	1	1. 500	1	0. 0000	0	1	1
-1.	6052	4	6345	-0. 3450	0. 3445	1	1. 500	1	0. 0000	0	1	1
-1.	4864	-1	5257	-0. 6760	8. 8265	0	0. 000	1	0. 0000	0	1	1
-1.	6052	4	6859	0. 3063	3. 3560	1	1. 500	1	0. 0000	0	1	1
-1.	6052	4	1497	-4. 2887	3. 3659	2	2. 000	1	0. 0000	0	1	1
-1.	4864	-1	0410	-0. 3660	4. 4110	0	0. 000	1	0. 0000	0	1	1
-1.	4864	-1	0620	-0. 2132	3. 2824	2	2. 000	1	0. 0000	0	1	1
-1.	4864	-1	0217	-0. 2384	4. 4656	0	0. 000	1	0. 0000	0	1	1
-1.	4864	-1	1223	0. 6380	3. 3092	0	0. 000	1	0. 0000	0	1	1
-1.	4864	-1	1279	0. 4616	8. 8913	0	0. 000	1	0. 0000	0	1	1
-1.	1019	9	7883	4. 4176	1. 3228	1	1. 000	1	0. 0000	0	1	1
-1.	0037	9	8837	-1. 8699	1. 0518	1	1. 000	1	0. 0000	0	1	1
-1.	4864	-1	0403	-0. 3917	3. 3260	0	0. 000	1	0. 0000	0	1	1
-1.	0037	9	8918	-0. 3974	8. 8498	0	0. 000	1	0. 0000	0	1	1
-1.	0037	9	8918	-0. 3974	8. 8498	0	0. 000	1	0. 0000	0	1	1
-1.	6052	4	4654	5. 5101	0. 4915	1	1. 500	1	0. 0000	0	1	1
-1.	6052	4	4423	4. 6464	0. 3266	1	1. 000	1	0. 0000	0	1	1
-1.	6052	4	7688	4. 6755	6. 6563	1	1. 000	1	0. 0000	0	1	1
-1.	6052	4	7174	4. 4443	4. 4980	1	1. 500	1	0. 0000	0	1	1
-1.	6052	4	2639	0. 7653	3. 3374	1	1. 500	1	0. 0000	0	1	1
-1.	6052	4	1864	4. 6150	0. 3076	1	1. 000	1	0. 0000	0	1	1
-1.	6052	4	4187	4. 7164	3. 3463	1	1. 000	1	0. 0000	0	1	1
-1.	6052	4	4992	4. 7012	0. 3171	1	1. 000	1	0. 0000	0	1	1
-1.	6052	4	4727	0. 0236	3. 3823	1	1. 000	1	0. 0000	0	1	1
-1.	6052	4	4256	4. 6263	3. 3289	1	1. 000	1	0. 0000	0	1	1
-1.	1787	4	4833	0. 6055	6. 6050	0	0. 000	1	0. 0000	0	1	1
-1.	3399	1	1968	0. 3909	8. 8671	1	1. 000	1	0. 0000	0	1	1
-1.	2187	1	0388	0. 3503	6. 6751	1	1. 000	1	0. 0000	0	1	1
-1.	2187	1	5767	4. 5718	7. 7329	1	1. 333	1	0. 0000	0	1	1
-1.	3399	1	4971	3. 4561	1. 2599	1	1. 000	1	0. 0000	0	1	1
-1.	0082	1	6837	4. 6156	0. 6867	1	1. 000	1	0. 0000	0	1	1
-1.	1119	9	5659	4. 587	8. 8497	1	1. 000	1	0. 0000	0	1	1
-1.	1119	9	5659	4. 587	8. 8497	1	1. 000	1	0. 0000	0	1	1
-1.	9583	6	8334	6. 6364	4. 6364	1	1. 000	1	0. 0000	0	1	1
-1.	0082	1	6257	4. 7092	0. 7626	1	1. 000	1	0. 0000	0	1	1
-1.	6052	4	0175	0. 4486	0. 7459	1	1. 000	1	0. 0000	0	1	1
-1.	6052	4	0127	6. 6499	0. 8289	1	1. 000	1	0. 0000	0	1	1
-1.	6052	4	0072	9. 9316	0. 5878	1	1. 000	1	0. 0000	0	1	1

