GENE FLOW AND SELECTION IN A NATURAL POPULATION OF *DROSOPHILA MELANOGASTER*

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Manuscript received September 23, 1974

ABSTRACT

A marked genetic differentiation to the presence of alcohol in the environment has been shown to occur between inside cellar and adjacent outside sections of a vineyard population of *D. melanogaster* (McKENZIE and PARSONS 1974). Estimates of migration during the vintage period suggest considerable movement occurs from outside into the cellar and that the most tolerant genotypes are the most successful migrants. A quantitative model of this system suggests that the selection intensity may not be a limiting factor in maintaining the differentiation. It also suggests that gene flow must be restricted between sections of the population at all but vintage periods if this differentiation is to persist.

THERE has been considerable discussion concerning the relative importance and interaction of gene flow and selection in determining genetic differentiation. Gene flow has been considered by some authorities as a critical factor in maintaining continuity between populations (MAYR 1963); others have thought it far less relevant (EHRlich and RAVEN 1969; ENDLER 1973).

The degree to which genetic differentiation occurs across an environmental gradient may be related to the relative magnitude of selection and gene flow in different areas of the gradient (JAIN and BRADSHAW 1966). At the microenvironmental level the maintenance of a genetic polymorphism in a heterogeneous environment can also be considered in terms of gene flow and selection (LEVENE 1953; DEAKIN 1966).

The effect of gene flow is potentially greatest where there are relatively few populations in a cline (ENDLER 1973). The maximum effect of gene flow thus occurs in the extreme case of a two-population system since the effect cannot be diminished by the introduction of genes from other areas (PARSONS 1963). For such a two-population system the maintenance of clines and of polymorphism in a heterogeneous environment is synonymous. Thus, both are determined by the relative fitness of genotypes in each population and the extent of gene exchange between populations. Consequently, such a simple system may be useful in providing a more general model, for, while clines have been reported for a number of characters (see ENDLER 1973 for references), information on the effect of gene flow and selection in these cases is limited. Indeed, the amount of gene exchange

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that may occur between sections of a natural population is a matter of some conjecture (GLEAVES 1973).

One obvious limitation to the usefulness of such a two-population system is the difficulty of defining an observable component of environmental heterogeneity that is of direct relevance to the populations considered. Without a clearly defined environmental gradient, or discontinuity, it is virtually impossible to explain the relevance of changes in gene frequency. This limitation has been overcome in plant populations where the microenvironment can be adequately specified (BRADSHAW 1972). This paper deals with a similar situation in a population of *Drosophila melanogaster*.

A combination of laboratory and field experiments suggest that *D. melanogaster* is more able to utilize an alcohol-associated resource than the sibling species *D. simulans* (MCKENZIE and PARSONS 1972). Laboratory studies with adults have shown *D. melanogaster* to be more tolerant to the presence of alcohol in the environment than *D. simulans*. The percentage of larvae that emerge as adults after development on alcohol-supplemented media is also greater for *D. melanogaster*, while gravid females of this species show similar preference for oviposition sites in both standard and alcohol-impregnated media. *D. simulans*, however, demonstrates a marked preference for the former sites (MCKENZIE and PARSONS 1972). Within a population at the "Chateau Tahbilk" vineyard in Victoria adults of both species occur outside the cellar, but only *D. melanogaster* is found within it and larvae and pupae of this species may be collected in the seepage from the wine casks. The outside adult distribution of the species is also affected during vintage by the presence of alcohol fumes from the fermentation area above the cellar. *D. melanogaster* is more common nearer the fermentation area at this time (see MCKENZIE 1974 for discussion and a ground plan of the vineyard). The excess of females repeatedly found in the cellar and near the fermentation area during vintage is explained by an increased mortality of males in these areas (MCKENZIE 1974).

A marked microdifferentiation for tolerance to the presence of alcohol has occurred between the cellar and outside sections of the *D. melanogaster* population. Thus, larvae from strains derived from the cellar were more tolerant to the presence of alcohol in the environment than those of strains from outside the cellar (MCKENZIE and PARSONS 1974). Furthermore, there was evidence of gene flow between the sub-sections of the population. Therefore, this situation is useful in analyzing the factors affecting the extent of differentiation in the presence of gene flow and dynamics of such a system.

METHODS

Population Structure at "Chateau Tahbilk"

The population of *D. melanogaster* outside, but adjacent to, the cellar undergoes marked numerical fluctuations. During the winter months few flies can be collected outside the cellar by hand or by banana bait trapping (see MCKENZIE and PARSONS 1972; MCKENZIE 1974 for trapping procedure); indeed it is difficult to obtain more than 50 flies in monthly samples of 5 hours duration during non-vintage periods, although numbers do increase in the months just

prior to vintage. During vintage there is a rapid numerical increase in the population, and for a similar sampling period more than 500 flies can be readily collected in each sample. Similar changes are observed in the cellar. During the non-vintage period the cellar population is greater than that outside the cellar, while the reverse is true during vintage, although the values are more similar at this time (Table 1). Samples which produced no adults from either area are not included. The outside numbers are based on a trapping grid up to 60 meters from the fermentation area (McKENZIE 1974). Movement of *D. melanogaster* appears to be directed toward the cellar during vintage, but is apparently random at other times (McKENZIE 1974). Any mass movement into the cellar from outside is, therefore, most likely to occur during vintage. Preliminary studies have shown this to be so and hence any attempt to measure the extent of gene flow should be restricted to this period.

Pre-vintage Releases and Collections

A demonstration of movement of flies into the cellar from the outside section of the population does not necessarily provide evidence of gene flow. It must be shown that migrants contribute to the cellar gene pool. Estimates of the amount of migration and of the genetic effect of migrants on the cellar population are most conveniently made if the stages of the life cycle (adults, larvae and pupae) scored in the cellar have a different phenotype from that of the migrants. For a numerical estimate of migration to be made it is also necessary that individuals with a marker phenotype survive during the experimental period. For these reasons control releases into the cellar population were made in the pre-vintage period. This allowed the cellar population to be marked with a line carrying the single recessive mutant, orange (*or*). The release line was derived by crossing a homozygous laboratory marker stock to a recently derived heterogeneous cellar stock from "Chateau Tahbilk". F_2 individuals of this cross carrying the marker phenotype were then crossed to the heterogeneous "Tahbilk" stock. This procedure was repeated for at least 2 cycles before the release of the marker was made.

Three such releases were made, involving 2500 (release 1, December 1973), 4000 (release 2, February 1974) and 4000 (release 3, March 1974) flies. Approximately equal numbers of each sex were released. Because of the low numbers of flies in the cellar at the times of release, the introduction ensured that at least 95% of the cellar population was homozygous for the marker immediately after release.

Subsequent sampling in the cellar was by hand trapping and by banana bait. These methods provide similar sample ratios (McKENZIE 1974) and, as there was no significant difference in the proportion of the orange phenotype collected by either method, the data presented are based on pooled values.

Vintage Release and Collection

A fourth release of 1500 marker flies of each sex was made into the cellar population one week after the commencement of the vintage period (release 4, April 1974). At this time the outside population was beginning to increase rapidly. The release is again assumed to have marked

TABLE 1

Paired comparison t-tests (after angular transformation) and mean proportions of Drosophila melanogaster collected inside and outside the cellar during vintage and non-vintage periods (based on monthly collections from January 1972 to April 1974, with a single vintage sample being taken each year)

	Inside	Vintage Outside	t_1	Inside	Non-vintage Outside	t_2
♂	0.22	0.78	8.13*	0.79	0.21	7.11***
♀	0.33	0.67	3.70	0.87	0.13	8.30***
Number of collections	3			23		
	* $P < 0.05$			*** $P < 0.001$

FIGURE 1.—The proportion of orange homozygotes in collections made after releases in December 1973 (R_1), February 1974 (R_2), March 1974 (R_3) and April 1974 (R_4). The time scale is from the first release.

95% of the cellar population, as population numbers were still relatively small at this time and the proportion of orange homozygotes was relatively high both prior to and at the first collection subsequent to the release (Figures 1 and 2).

After the release at 1000 hours, collections were made by hand trapping individual flies in food vials at the specified sample times for periods each lasting 30 minutes. The first collections were made at 1200 and 1600 hours of the release day. Subsequent collections were made daily at 0900 and 1600 hours for the remainder of the collection period. In all, 9 collections were made. The samples were made without replacement.

Outside the cellar, collections were made 1 meter from the fermentation area (McKENZIE 1974) by hand trapping for 30 minutes. Times of collection were at 1630 hours on the day of the 4th release and thereafter daily at 0930 and 1630 hours. After the final collection 1500 marker flies of each sex were released at the same site outside the cellar and the population was again sampled for 30 minutes. Absolute population size for this period was then estimated from the number of marked animals in the total collected. It should be noted that because of the directed movement of flies toward the cellar at this time (McKENZIE 1974) the population numbers at the site outside the cellar may be continuously changing and, therefore, the absolute population size estimate will only be approximate for even a restricted sample period. However, relative changes in the total number of animals collected during each fixed 30-minute sample period are thought to reflect changes in the absolute population (SOUTHWOOD 1966). For this reason, total population size estimates for each sample period were made by comparing the numbers of

FIGURE 2.—The proportion of orange homozygotes in collections made after the release in the vintage period of 1974 (R_4). Time is in hours (actual ■ or daylight ▲) after the release. The estimates of population size in the transition zone outside the cellar are plotted (solid line) against the daylight hour scale.

animals collected in each period and relating these to the absolute population size estimate obtained above.

RESULTS

The proportion of orange homozygotes in the population steadily decreases with time after the various releases, but during the non-vintage releases ($R_1 - R_3$) this occurs more gradually (Figure 1). The decrease in these control experiments is considered to be largely due to the lower fitness of the orange homozygote and the heterozygote relative to the wild-type homozygote. The genotypes of wild-phenotype males were ascertained by crossing with homozygous orange females, while the genotype of the wild-phenotype female and that of the male she had mated with was estimated from their progeny or by crossing the progeny to orange homozygotes. Because of the problem of multiple insemination, some female data were inconclusive; but these procedures showed a deficiency of het-

erozygotes ($P < 0.05$) relative to Hardy-Weinberg expectations and an increased mating performance by wild-type homozygotes ($P < 0.001$). The proportion of orange homozygotes obtained for adults, larvae and pupae of a given sample was similar, showing that the released genotype can breed and persist in the cellar environment for a considerable time.

The decrease of the mutant homozygote is very rapid after the vintage release (R_4 , Figure 1). That this decrease is not due to a decreased survival of the marker phenotype, relative to the control releases, may be seen from Table 2. Until the fourth collection the number of wild-phenotype flies increases ($\chi^2_3 = 117.64$, $P < 0.001$) but the number of orange homozygotes for each sample period remains relatively constant ($\chi^2_3 = 6.73$, $P > 0.05$). For subsequent collections the numbers of the wild phenotype collected in each sample are not significantly different ($\chi^2_4 = 4.25$, $P > 0.1$) but the numbers of the orange phenotype collected are different ($\chi^2_4 = 56.96$, $P < 0.001$), primarily because of the fifth sample. The maximum number of flies collected in a given sample period is 171. Once this number is reached the total numbers collected in each subsequent sample are similar, presumably because it represents the maximum number of flies that can be individually hand-trapped in a 30-minute sample period regardless of the actual population size. Results of other collection periods are in agreement with this. Therefore, the decrease in the numbers of the orange marker phenotype collected after the fourth sample most likely reflects a sampling probability rather than an increased mortality. The relative consistency of the number of orange-phenotype flies collected from the sixth collection onward is thought to reflect the lack of movement of wild-phenotype flies from outside into the cellar during this period.

The data of this period are represented in an expanded form in Figure 2. Male and female data have been combined for presentation, as they show the same trends and as the population estimates of the sexes are significantly correlated ($P < 0.001$). Estimates of the population size at the site 1 meter from the fer-

TABLE 2

The number of orange phenotype and the total number of flies collected during 30-minute sample periods in the cellar during vintage

Collection number	Number of orange flies collected	Total number of flies collected
1	75	83
2	61	74
3	93	131
4	78	170
5	48	171
6*	13	161
7	11	147
8	12	161
9	10	163

* The similarity of the number of orange-phenotype individuals collected from the sixth collection presumably reflects the lack of additional movement of wild-phenotype individuals into the cellar. See text.

mentation area are also provided in Figure 2, with male and female data being combined for the reasons presented above. This site represents a transition zone between the inside and the outside of the cellar so that the population estimates for the site are considerably below those of the entire outside population. There appears to be a direct relationship between the increase of the population in this transition zone and the decrease in the proportion of the marker phenotype in the cellar up to 30 daylight hours after the cellar release (Figure 2). Prior to the next collection (0900) the outside site was sprayed with insecticide by the vineyard staff. This resulted in a depression of population numbers. Further spraying occurred prior to the 1630 collection of the same day and was continued after the sample was taken. No further decrease in the proportion of the orange phenotype within the cellar was observed during this period.

These results imply that the rate of movement of wild-phenotype individuals into the cellar is related to the population size in the area directly outside the cellar. Given the directed movement of *D. melanogaster* at this time (McKENZIE 1974), this result is not surprising.

Some comment is necessary on the final increase in the population outside the cellar, since this does not produce a corresponding increase within the cellar (Figure 2). The increase occurs between an evening and a morning collection. The concordance of the decrease of orange homozygotes for either time scale (i.e., daylight or actual hours in Figure 2) suggests that there is no significant movement of *D. melanogaster* outside daylight hours. As insecticide was applied after the evening collection, the increase of the population in the transition zone is most likely to have occurred in the few hours of daylight before the morning sample by movement of flies from surrounding unsprayed areas. Therefore, it is improbable that there was sufficient time for this increase to influence cellar numbers before the final sample.

An evaluation of the amount of migration that occurs can be gained from estimates of the number of wild-phenotype adults in the cellar population. At the time of release the population was estimated at approximately 200 from the proportions of orange and wild-phenotype adults collected, while at the conclusion of sampling the comparable estimate was 62,000.

Larval samples also provide an indication of the effect of migration. Because of the rapid mating of the species after eclosion, any female moving into the cellar is likely to be fertilized and capable of immediate oviposition. The contribution of migrant individuals during the sample period can be estimated from the change in frequency of the marker phenotype in adults emerging from larvae collected in the cellar at the time of release and 120 hours later, by which time eggs oviposited by migrants, or by females mated by migrants, will have begun to hatch.

The frequencies of orange homozygotes emerging from larval samples are given in Table 3. Data for pupal samples are also provided. The proportion of the marker phenotype decreases in the larvae, while there is an increase in the pupae. The decrease of the proportion of the marker phenotype in the larvae demonstrates the rapid effect migrants have on the cellar population, as any contribution derived solely from the orange homozygotes of the fourth cellar release has

TABLE 3

The number of adults emerging from larvae and pupae collected in the cellar at the time of release (R_4) and in the final sample 120 hours later

The percentage of the orange phenotype in the emerging individuals is also given.

	Larvae				Pupae			
	Number Release	Number Final	Percent orange Release	Percent orange Final	Number Release	Number Final	Percent orange Release	Percent orange Final
♂	47	91	36.1	21.9	26	15	15.3	33.3
♀	48	102	39.6	20.6	26	31	11.5	19.4
Combined sexes	95	193	37.9	21.2	52	46	13.5	23.9

been overshadowed. The temperature in the cellar during the sampling period was consistently near 21°C. Hence, any eggs oviposited by females of the fourth cellar release or by migrant females would not have reached the pupal stage of development in the time available between the two samples. Therefore, their contribution would not influence the proportion of the orange phenotype in the pupal stage. The increase observed is due to the subsequent development of the larval phenotype of the first sample period.

Larvae and pupae were each sampled for 30 minutes at both collection times. The number of larvae collected is much larger in the final sample, while the number of pupae remains essentially the same (Table 3). This again suggests that migrant individuals make a rapid contribution to the gene pool of the cellar population. However, as the phenotypes of the pupae collected in the final sample may be explained by the development of larvae available at the time of the original sample, it appears that any interaction caused by increased larval numbers is small. This suggests that the cellar's alcohol-associated resources were not being totally utilized by the original population, particularly as the availability of pupation sites is not limiting. The influx of migrants allows for a potentially more efficient exploitation of these resources. This is especially significant over the vintage period, when the amount of potential resource available is increased by spillage and seepage during transfer of the recently fermented wine to the storage casks in the cellar.

As the experimental period is approximately 1/5th of the entire vintage period, it is reasonable to conclude that the pre-vintage cellar population will be completely "swamped" by migrants from outside during vintage if the rate of influx remains constant. Indeed, the proportion of orange homozygotes was less than 1% in samples of larvae, pupae and adults made 3 weeks after the final collection of the experimental period. It is therefore necessary to consider how the differentiation between inside and outside sections of the population (McKENZIE and PARSONS 1974) is maintained in the presence of such gene flow.

A MODEL SYSTEM

McKENZIE and PARSONS (1974) found that tolerance to alcohol in the environment involved both additive and dominant genetic components. The mechanism could not be explained by a simple 1 locus-2 allele system and, in addition, the

FIGURE 3.—Distribution of the percentage of adults emerging from 2 replicates of 25 larvae each on 0% and 9% alcohol-supplemented media for strains of *D. melanogaster* derived from inside and outside the cellar at "Chateau Tahbilk." Each unit on the ordinate represents the mean for one strain. Values are pooled for 10 strains from each of the months of May 1972 and February to April 1973. Standard deviations are given after angular transformation (derived from the data of McKENZIE and PARSONS 1974).

distribution of adults emerging from larvae on 9% alcohol media (Figure 3) indicates a polygenic component.

If it is assumed that the alcohol tolerance system is controlled by a polygenic mechanism, a model can be framed to incorporate a shift in the distribution with the mean of the outside section of the population to a distribution with the mean tolerance of the cellar section. The model further assumes that the cellar section of the population is "swamped" by migration from outside during vintage and that gene exchange is then excluded between the sections of the population.

Given that $R = h^2_n S$, where R is the response to selection, h^2_n is the narrow-sense heritability and S is the selection differential (FALCONER 1960), it is possible to estimate S on the assumption that both heritability and response remain constant over generations (see LEE and PARSONS 1968). Since the patterns of

TABLE 4

Mean cellar temperature, with standard deviations, for 1972 and 1973

The number of months with temperatures greater than 14° and the mean temperatures and standard deviations for these months are also given.

Year	Mean temperature °C		n	Temperature > 14°C Mean	°C
1972	15.1	±3.6	8	17.2	±2.0
1973	14.4	±3.9	7	17.1	±2.4

tolerance are normally distributed ($P > 0.1$), the proportion of population above the mean tolerance of individuals selected in each generation can be calculated. This proportion provides an indication of the selection intensity required to produce the required change in mean tolerance. The estimate will, of course, be greater than the actual selection intensity required. For the "Chateau Tahbilk" system, R is equivalent to the shift in the mean of the outside section of the population to the mean of the cellar population, as discussed in the preceding paragraph. To achieve this, selection must act on the original population; it is from this population that the estimate of selection intensity will derive.

The temperatures in the cellar (Table 4) are likely to limit the number of generations between 2 successive vintage periods to a maximum of 10. Since it is unlikely that oviposition occurs in the cellar at temperatures less than approximately 14° (McKENZIE, unpublished) it is possible that the number of generations will be less than this. Five generations has therefore been assumed as a minimum value.

Any estimate of heritability can apply only to the specific population in time which supplied the data used in the calculation (SPRAGUE 1955). Heritability values of 0.1 to 0.5 have been arbitrarily chosen, as this is the range commonly observed for quantitative characters (FALCONER 1960). As the additive genetic effects of tolerance contribute significantly to the overall variance (McKENZIE and PARSONS 1974), the actual heritability may approach the upper limits of this range.

The results of the model are given in Table 5. The two population comparisons are for the pooled outside and cellar populations and for the outside vintage pop-

TABLE 5

The proportion of the "outside" population with a tolerance greater than the mean of the selected individuals of that population for the specified heritabilities (h^2_n) over selection periods of 5 or 10 generations (data used for calculations after McKenzie and Parsons 1974)

Population comparison	Response (R)	Generations of selection	Heritability (h^2_n)				
			0.1	0.2	0.3	0.4	0.5
Total (Cellar)	8.2	5	0.04	0.17	0.28	0.33	0.36
Total (Outside)		10	0.17	0.33	0.38	0.41	0.43
February (Pre-vintage, Cellar)	17.7	5	0.01	0.10	0.19	0.26	0.30
March (Vintage, Outside)		10	0.10	0.26	0.33	0.38	0.40

ulation (March) to the pre-vintage (February) cellar population. The latter comparison is one in which selection has the maximum time to act. To produce the shift in mean required (R) does not demand particularly stringent selection intensities at any heritability greater than 0.2. Therefore, the observed differentiation will be maintained if the cellar population is "swamped" during vintage and left in isolation until the subsequent vintage. Gene flow *into* the cellar must be restricted at other times. In addition, gene flow *from* the cellar must also be limited, since the difference between genotypes in a non-alcohol-associated environment appears to be small (Figure 3) and there is no significant difference between the cellar and non-cellar sections of the population for the 0% alcohol comparison (McKENZIE and PARSONS 1974).

DISCUSSION

During the vintage period alcohol-associated resources become more readily available both within and in the vicinity of the cellar. If the environment is to be most effectively exploited, migrants to these areas must be able to utilize these resources. The present model of the cycle of gene flow, isolation and selection allows for effective utilization but does not explain how differentiation is maintained between the sections of the population during the vintage period itself (McKENZIE and PARSONS 1974). For this to occur it is clear that selection must act on individuals that move into the cellar. Experimental verification of this is currently being investigated, but in other situations different genotypes have been shown to possess different dispersal and migration potential (SAKAI *et al.* 1958; KREBS *et al.* 1973), and it would appear that preferential migration may also occur in the case under consideration. Under these circumstances the probability of differentiation is enhanced because more tolerant individuals will have a greater probability of reaching the cellar. However, in this case the intensity of selection will be significant. In terms of the model, the shift in the mean (R) must effectively occur over 1 generation. Even allowing for a heritability of 0.5, the proportion of the outside population with a tolerance greater than that of the mean of the selected individuals will be 0.04 for the Total (Cellar) : Total (Outside) comparison of Table 5. For the February (Cellar) : March (Outside) comparison this proportion is 0.004. Clearly, for lower heritabilities the intensity of selection will be even more acute.

The potential for selection certainly exists both outside and inside the cellar during vintage, since a high male mortality is observed near the fermentation area at this time (McKENZIE 1974). After the vintage period the selection pressures in the cellar are sufficient to maintain the differentiation, though it seems likely that the migrants reaching the cellar during the vintage period are genotypically most capable of utilizing the alcohol-associated resource.

There is some evidence that gene flow may occur from the cellar during the spring (McKENZIE 1974). As the outside population adjacent to the cellar is low at this time, any resistant genotypes undergoing migration could contribute to the subsequent population increase, which would lead to a de-differentiating effect.

SLATKIN (1973) has suggested that drastic changes in gene frequency will only occur at a barrier to dispersal when almost all individuals attempting to cross the barrier are prevented from doing so. The present results are in agreement with this; continual gene flow would lead to continuity between both sections of the population, more particularly because the differences between the viabilities of the genotypes in the outside environment are not large. MCKENZIE and PARSONS (1974) have suggested that the more resistant genotypes must be at a disadvantage in the outside environment for differentiation to be maintained. The smaller this disadvantage the greater the restriction on gene flow from the cellar must be. This effect is likely to be localized. While individuals of *Drosophila* are certainly capable of considerable dispersive movement (YERINGTON and WARNER 1961), the majority of any population show restricted movement (DOBZHANSKY and WRIGHT 1943; RICHARDSON 1969; WALLACE 1970). This appears also to apply to the "Chateau Tahbilk" population, particularly during non-vintage periods (MCKENZIE 1974). During vintage it is likely that the outside population is increased by recruits transported with grapes from the fields which are not in the immediate vicinity of the cellar. Significantly, the level of tolerance of the outside population is lowest at this time (MCKENZIE and PARSONS 1974). Such a recruitment of individuals also enhances the chances of differentiation being maintained.

Before any model system is applied to a natural system it is essential that a detailed knowledge of the environment and of the functions of natural selection and gene flow in that system is available (ENDLER 1973). Considerable gene flow does occur at "Chateau Tahbilk" between the cellar and outside selections of the population, but differentiation is still maintained. However, mass movement appears only likely to occur during a restricted period when an increased alcohol-associated resource is available. The balance between selection pressure and gene flow must be critical in the determination of differentiation between sections of a population. The importance of either component will vary in different systems, and ultimately the relative fitness of different genotypes in different environments will be an important factor in determining the relevance of gene flow.

I should like to thank PROF. P. A. PARSONS for his encouragement during all stages of the work and PROF. B. JOHN and DR. G. HEWITT for their helpful advice and, with DRS. J. DEARN and D. SHAW, for critically reading the manuscript. The comments of DR. R. H. RICHARDSON and an anonymous referee have also been most useful. Financial assistance was provided by an Australian Research Grants Committee grant to PROF. PARSONS.

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