The Ecology Of Homostyle And Heterostyle Primroses
Primula vulgaris Huds.

Thesis

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The ecology of homostyle and heterostyle primroses

*Primula vulgaris* Huds.

by

Mark Allen Boyd BSc(Hons) Loughborough

Submitted for the degree of PhD

on 17th December 1986
CHAPTER 5
SURVIVAL IN EXPERIMENTAL PRIMROSE POPULATIONS.

It is apparent from the data for seed output (Chapter 4.5) and population composition (Chapter 3.2) that most seeds and seedlings do not survive to maturity. It is also clear that though homostyles produce more seeds per plant than the other morphs on average they do not spread through the population as rapidly as might be expected. It would appear, then, that the ratio of the adult phenotypes in a population is not a direct reflection of the ratios that would be expected from a seed crop.

The seeds of the three morphs tend to be of different sizes (Chapter 4.4). It is possible that this has some consequence for the timing or success of germination of seeds of the three morphs. In addition it is possible that selfing by homostyles reduces the viability of their seeds relative to the heterostyle morphs.

There is reason to believe from the history of the population at Batcombe that the survival of plants to maturity differs between the morphs. Crosby (1949) found a small proportion of homostyle plants in this population but they have now entirely disappeared. Either random mortality has resulted in homostyles dying out or they differ in their juvenile mortality relative to the other morphs.

A knowledge of juvenile mortality of the three morphs would be of interest and is important for any models of
population growth.

This chapter describes experiments which attempt to discover whether there are differences between primrose morphs in juvenile mortality and whether any such differences are correlated with differences in seed size.

A life table analysis was carried out to examine any differences in the mortality of the three morphs. The technique used was similar to that used by Ennos (1981) on morphs of white clover *Trifolium repens* in which selection is assessed by comparing the performance of plants under field and ideal conditions. The growth to flowering of primrose seed which could be reasonably expected to contain all three morphs was compared between greenhouse conditions and artificial populations set up at a site with a wild heterostyle population (Woburn) and one with a wild homostyle population (Witheridge).

If mortality in the greenhouse can be kept at a very low level, the difference in the numbers and proportions of the three morphs between the greenhouse and the experimental populations can be taken as a measure of the selection for or against a particular morph.

Juvenile mortality has not been assessed before in this species and it is considered in the following sections in this chapter.

1) Methods

2) Survival in the greenhouse

3) The use of seeded quadrats
4) Morph numbers and proportions in the experimental populations

5) Selection in primrose morphs before flowering

6) The germination of seeds of different size
METHODS 5.1

A total of 26,000 seeds were collected from 200 plants at Wyke in June 1981 and stored under cool, dark conditions until the autumn. Because of the population composition at Wyke, it is reasonable to assume that this seed would yield plants of all three morphs. This seed was mixed and random quantities of 600 seed were separated from it. 2,400 Seed (4 groups of 600) were germinated in the greenhouse in four seed trays and tended in individual pots until flowering. The ratio of the morphs in these greenhouse 'quadrats' is taken to be the original ratio of morphs present in the 26,000 seeds originally used.

Other batches of 600 seeds were used in seeded quadrats which were placed at random on a grid system in the two populations of Woburn and Witheridge. Twelve seeded quadrats were put into each of the populations in January 1982 and the plants which emerged in them were brought back to the greenhouse at intervals over the following two years. Four quadrats were removed from the populations every six months and the plants in each of them were transferred to individual pots and grown to flowering in the greenhouse. Conditions in the greenhouse ensured maximum survival of plants. This meant that any selection which may have been operating in the field was halted when plants were brought back to the greenhouse. The ratios of the morphs which flowered in the retrieved quadrats were compared with the ratios of morphs in those
plants which had been grown from seed in the greenhouse. The difference between these two figures was taken as a measure of the selection operating in the field up to the time of the retrieval of the field quadrats. The timing of the retrieval of the field quadrats is shown in Figure 5.1.

Six fallow quadrats were created in each population (Figure 5.1). Any plants which were found in these were brought back to the greenhouse and grown to flowering to check for the possibility of natural regeneration of primroses from the seed pool interfering with the observed ratio of morphs.

The design of this experiment assumes that a greenhouse with adequate supplies of water, light and nutrients and a control over the level of insect pests and competition represents an ideal 'selection-free' environment for the growth of all three primrose morphs. To gain the maximum reliability of the results from this experiment, as many of the seeds which are germinated should be raised to flowering in the greenhouse as possible. Any mortality in the greenhouse could mask results from the field quadrats particularly as it would be difficult to determine whether there had been any differential mortality in the greenhouse itself. The greenhouse conditions are described below.

A total of 2,400 seeds (4 groups of 600) from the same batch used in the field quadrats were used in the greenhouse. Each group of 600 seeds was germinated in Levingtons potting compost in seed trays. This was found to be the most suitable
<table>
<thead>
<tr>
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<th>WOBURN</th>
<th>GREENHOUSE</th>
</tr>
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<tbody>
<tr>
<td>JAN 1983</td>
<td>6 fallow</td>
<td>6 fallow</td>
<td>4 seeded</td>
</tr>
<tr>
<td></td>
<td>12 seeded</td>
<td>12 seeded</td>
<td></td>
</tr>
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Figure 5.1 The timing of quadrat retrieval from the experimental populations
readily-available growing medium. The progress of germination in each tray was measured by counting the numbers of seedlings emerging at approximately four day intervals. Each seedling was transferred to an individual pot once its first true leaves had expanded. These pots were labelled with the date of the transfer and the number of the seed tray from which the seedling came. These seedlings were than raised to flowering. The plants were maintained with adequate amounts of water and Phostrogen compound fertiliser. They were fumigated when necessary and were repotted twice before flowering thus ensuring adequate growth free from the usual limiting factors such as nutrients and competition.

This growing regime ensured a high level of survival (see below) and comparisons between the morph proportions between replicate trays could be made to provide a check on the conditions for germination.
In this section I will present the germination and survival rates of primroses grown in the four greenhouse replicates which will result in 'control' figures for the proportions of morphs that can be compared to the morph proportions found in the field quadrats.

The number and percentage of seeds which germinated in the four greenhouse trays are given in Table 5.2a.

The seedlings emerging in the four trays were transferred to individual pots and raised to flowering. Many of the seedlings were killed before flowering by insect pests and some did not survive the hot summer of 1984. The numbers of the three morphs which survived to flowering are given in Table 5.2b.

It is interesting that there is a significant difference in the number of seeds which germinated in each of the trays. 82% was the highest figure for germination and so it might appear that between 18% and 53% of the potential number of plants are lost from the greenhouse proportions at this stage. However, the proportions of the three morphs which flowered in the four trays do not differ significantly even though the numbers of plants involved do. I would suggest that there are no differences in the survival of the three morphs in ideal conditions and that any difference in the proportions of the three morphs grown from the field quadrats compared with the greenhouse will be indicative of selection.
<table>
<thead>
<tr>
<th>TRAY NUMBER</th>
<th>NUMBER OF SEEDLINGS</th>
<th>% GERMINATION</th>
</tr>
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<td>492</td>
<td>82</td>
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<tr>
<td>2</td>
<td>378</td>
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<tr>
<td>4</td>
<td>282</td>
<td>47</td>
</tr>
</tbody>
</table>

Table 5.2a. The number and percentage of seeds germinating in the four greenhouse seeds trays. $X^2 = 62.2$, $p < 0.05$. 
Table 5.2b. The numbers of primroses of the three morphs flowering in the four greenhouse trays. Morph ratios do not differ significantly between the trays ($x^2 = 2.65, p < 0.05$).
induced by the environment.

The proportions of the three morphs which will be used as the original proportions in the seed stock are given below in Table 5.2c.

It is apparent that thrums are represented by the lowest percentage of plants in the original stock but they are sufficiently abundant for comparisons of their numbers in the greenhouse and field situations to be made. Under the simplest of assumptions regarding the genetics in Chapter 2, a population with morph proportions as present in Wyke in 1982 would be expected to yield seeds in the proportions 35:35:30, pin:thrum:homostyle. This assumes that all the homostyles are heterozygous and that pollen flow is completely random. If homozygous homostyles occurred or if pollen flow was restricted thrums would be expected to comprise a smaller proportion of the seed crop.
<table>
<thead>
<tr>
<th>PIN</th>
<th>THRUM</th>
<th>HOMOSTYLE</th>
</tr>
</thead>
<tbody>
<tr>
<td>45</td>
<td>21</td>
<td>34</td>
</tr>
</tbody>
</table>

Table 5.2c. The proportions of morphs raised from the greenhouse.
THE USE OF SEEDED QUADRATS 5.3

The seeds which were to be used in the field populations had to be organised so that their positioning was as natural as possible and also so that they were relatively easy to transfer back to the greenhouse as seedlings.

25 x 25 cm\(^2\) Quadrats were chosen at random on a grid system within the populations. The quadrats were marked with corner posts and cleared of vegetation if necessary. The soil surface was broken up to prevent the seeds from blowing away. In this way, the quadrats represented reasonably good sites for germination that might be considered similar to those resulting from scratching by animals such as rabbits.

600 Seeds were scattered on the surface of each quadrat. A number of fallow quadrats were prepared in a similar manner to the seeded quadrats. The fallow quadrats were a control to check for the possibility of recruitment into the experimental populations from a seed pool.

To bring the seedlings back to the greenhouse, the entire turf of the seeded quadrat was removed with a spade. The seedlings were separated from the turf in the greenhouse and each was potted individually. Survival in the greenhouse was better than in the field quadrats and so the retrieval of quadrats from the field can be regarded as halting selection in them. These seedlings were raised to flowering in the greenhouse in the same way as plants which had been in the greenhouse throughout. Retrieval of field quadrats at...
different times of the year helps to show how selection for a particular morph changes with time and season.
MORPH NUMBERS AND PROPORTIONS IN THE FIELD EXPERIMENTS

5.4

The numbers and proportions of primrose morphs raised from the seeded quadrats in the experimental populations of Woburn and Witheridge are given in Table 5.4. The initial ratios of the morphs are indicated by the proportions in the greenhouse stock.

In general, replicate quadrats retrieved at the same time from the field had similar morph proportions and contained similar numbers of plants. This would be expected if the original proportions of morphs in the seed batches were similar. What is more interesting is that there was a shift in the proportion of the morphs over the course of the experiment away from the initial proportions in the greenhouse.

In both experimental populations the proportion of pin plants flowering remained fairly constant. The proportion of thrum plants was initially higher than in the greenhouse but fell thereafter in both populations. The proportion of homostyles in the quadrats increased over the course of the experiment at both sites. The similarity between the two sites is expected given that the plants were all grown from the same seed mix. Homostyles have not been previously grown in a heterostyle population and this experiment suggests that they are capable of growing outside their usual range.

The differences in the numbers and proportions of morphs
<table>
<thead>
<tr>
<th>Location</th>
<th>PIN %</th>
<th>THRUM %</th>
<th>HOMSTYLE %</th>
<th>N</th>
</tr>
</thead>
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<tr>
<td>GREENHOUSE</td>
<td>45</td>
<td>21</td>
<td>34</td>
<td>1369</td>
</tr>
<tr>
<td>WOBBURN</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>May 1983</td>
<td>46</td>
<td>23</td>
<td>31</td>
<td>303</td>
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<td>Sept. 1983</td>
<td>46</td>
<td>18</td>
<td>36</td>
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<td>May 1984</td>
<td>43</td>
<td>16</td>
<td>41</td>
<td>143</td>
</tr>
<tr>
<td>WITHERIDGE</td>
<td></td>
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<td></td>
</tr>
<tr>
<td>May 1983*</td>
<td>37</td>
<td>35</td>
<td>28</td>
<td>63</td>
</tr>
<tr>
<td>Sept. 1983</td>
<td>36</td>
<td>32</td>
<td>32</td>
<td>56</td>
</tr>
<tr>
<td>May 1984*</td>
<td>37</td>
<td>24</td>
<td>39</td>
<td>71</td>
</tr>
</tbody>
</table>

Table 5.4. The proportion of morphs and the total numbers of plants raised from seeded quadrats retrieved from Woburn and Witheridge. All percentages are the means of four replicates. Replicate quadrats marked * differed significantly from one another ($X^2$, $p < 0.05$).
grown from seeded quadrats from the two experimental populations can be explained by an examination of the ground cover present in the two sites. Witheridge is a beech wood and so has a dense ground cover of leaf litter (Chapter 2). It was apparent, particularly on retrieval of the first quadrats, that many seedlings had failed to emerge through this leaf litter. Etiolated seedlings were present at the first census which died before they could be transferred to individual pots in the greenhouse. By contrast, Woburn had a considerably sparser ground cover when most of the seedlings were emerging and so a greater number of them were able to become established.

The suggestion is that thrum seedlings are stronger on emergence than those of the other two morphs and so were able to push their way through the leaf litter at Witheridge better. This may be a consequence of the differences in mean seed size noted in Chapter 4.4.

One result of the difference in the numbers of plants between Woburn and Witheridge is that seedling densities differ greatly between the two sites. The similarity in the proportion of morphs under these different densities suggests that either seedling density does not have a differential effect on mortality of the three morphs or that any such differences are masked by differences in the conditions between the two sites. The maximum density of seedlings in any one quadrat was equivalent to 328/m² which is comparable to that which may occur if a plant sheds seed from one or
more capsules in a small gap suitable for germination.
SELECTION IN PRIMROSE MORPHS BEFORE FLOWERING 5.5

Selection was measured by the relative change in the proportions of the three morphs between the greenhouse stock and plants grown from the seeded quadrats. The plants grown from each census were compared with the original proportions in the greenhouse as well as with the previous census. In this way, it is possible to see both the total extent of selection against a morph over its juvenile stage as well as the changes in selection which occur during that stage. These results are expressed graphically below.

It is apparent (Figures 5.5a, b, c) that there is a change in the proportion of morphs relative to the greenhouse right from the first field census. It would appear that thrum seeds have a better chance of germinating and surviving to the first census than those of either of the other two morphs, particularly at Witheridge. One might expect seeds from thrum plants to germinate more successfully than those of the other morphs if pollination is incomplete. Seeds are larger if there are relatively few per capsule and it might be expected that this would be advantageous. If this were not so, one might expect the resources used to make these larger seeds to be diverted for other uses. However, there is no reason to suppose that seeds from thrum plants will have a higher proportion of thrums than those from other plants. Thrum seeds must be of heterostyle genotype (Chapter 2) and if larger ones do have a higher germination rate this can only
Figure 5.5a The percentage of morphs in the quadrats raised from the experimental populations.
(census 1 = greenhouse proportions)
Figure 5.5b Changes in the proportions of morphs from the previous census showing the pattern of selection over the year at Woburn. (census 1 = greenhouse proportions)
Figure 5.5c Changes in the proportion of morphs from the previous census showing the pattern of selection over the year at Witheridge. (census 1 = greenhouse proportions)
favour heterostyly.

Of greater interest is the change in the proportion of morphs after germination. Despite the initial predominance of thrum seedlings in the first census at both sites, homostyles increase in proportion over the course of the experiment. This increase is at the expense of thrums and mirrors the direction of selection predicted by Crosby (1949). Crosby (1949), however, predicted that such a change would occur over generations rather than within the seedlings of a single generation.
The seeds of homostyles tend to be smaller than those of the heterostyle morphs if pollinators are limiting (Chapter 4.4). Thrum seeds are smaller than pin seeds for a given number of seeds in a capsule but thrums will have a higher mean seed weight if pollination is limiting.

In this section an experiment is described to investigate the effects of seed size and morph on the germination rate. Seeds from the three morphs were separated into three size categories by eye. Seeds from ten different plants were mixed in each category. Seeds were planted in seed trays in the greenhouse in five replicates of 60 seeds each making a total of 2,700 seeds.

The seeds were kept moist and allowed to germinate. Seedlings were removed at ten day intervals. The results are expressed as the number of seeds which germinated after a total of three months.

The smallest seeds of all three morphs had the lowest germination rate but there was little difference between germination in the two larger size categories. There was no significant difference between the germination of seeds from the three morphs (Table 5.6). The peak of germination of all categories was around similar dates. This suggests that the predominance of large seeds in the seed pool noted in Chapter 4.6 is the result of their potential longevity in relation to smaller seeds rather than of the possibility that they are
<table>
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<th>HOMOSTYLE</th>
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<td>29</td>
<td>27</td>
</tr>
<tr>
<td>MEDIUM (Mean 0.73mg)</td>
<td>39</td>
<td>37</td>
<td>39</td>
</tr>
<tr>
<td>LARGE (Mean 0.84mg)</td>
<td>42</td>
<td>40</td>
<td>37</td>
</tr>
</tbody>
</table>

Table 5.6. The mean numbers of seeds germinating of different size categories. Figures are the means of five replicates of 60 seeds of each type. There is no significant difference in germination between morphs (F = 0.11, p > 0.2) but there is a significant difference in the germination of seeds of different sizes (F = 18.8, p < 0.05).
the only ones left after the smaller seeds have germinated.

It is interesting that homostyles had similar germination rates to the heterostyle morphs. Selfing does not seem to have resulted in inviable homostyle seeds and it seems more likely that homostyles are at a disadvantage because of their smaller mean seed size rather than through inbreeding depression.

It is possible that the difference in the germination of seeds of different sizes would be accentuated under field conditions particularly if larger seeds gave rise to seedlings better able to emerge through leaf litter. Larger seeds are found in capsules which have not been fully pollinated. It is possible that differences in the pollination of the morphs between years would have an effect on the proportion of morphs in the following years seedling crop as well as on the number of seeds produced by each morph. The data on seed germination combined with the seed pool data of Chapter 4.6 provides a possible explanation for the stability of homostyle populations.
Life tables provide a formalised summary of the mortality of a group of individuals throughout the lifespan and are particularly useful in providing the transition probabilities for matrix models of population change. This chapter presents life tables for the three morphs and uses them in models of population growth.
Age-specific life tables are constructed by following the fates of a cohort of individuals of known age (from a single generation) through from their birth (or germination for plants) to the death of the last individual (Southwood, 1978). This technique is the best where applicable because the mortality of individuals is observed directly.

Time-specific life tables (Southwood, 1978) are used on long-lived species where an age-specific life table would not be practical. This technique depends on being able to assess the age structure of the population at a specified time. It is a useful technique for trees and other long-lived species where the age structure can be easily assessed. However, mortality is not observed directly by this technique and more rigorous assumptions about population stability have to be made.

Both the above techniques result in a life table from which the transition probabilities between age classes can be obtained. However, the probability of an individual dying may be more closely related to its stage of growth than its age. Stage-specific life tables can be constructed from the transition probabilities between growth stages as readily as the other techniques described above.

Stage-specific life tables are often particularly appropriate for plants because of the plasticity of plant growth in relation to different environmental conditions. The stage of a plant may often prove to be a better predictor of
its fate than its chronological age (eg Werner and Caswell, 1977).

In this study age-specific life tables were constructed independently for seedlings of the three morphs. These were used in preference to stage-specific life tables because the removal of individual seedlings from the field quadrats once they had reached a certain size would have been more time-consuming and, more importantly, more risky to the plants concerned than retrieving the entire turf at once. The removal of individuals from quadrats once they had reached a certain size would also have changed the conditions of those plants which remained in the field in terms of density and shade.

Normally, age-specific life tables are created by following the fate of all members of a cohort of individuals through from their birth (germination) to the death of the last individual of that cohort. This avoids any problems which may be encountered with overlapping generations. However, this is not possible with primroses in so short a study and so the data for the life tables are drawn from more than one source. The data on juvenile mortality are obtained from the experiment at Woburn (Chapter 5) and the data for adult mortality are obtained from Wyke as described in Chapter 3.

The data for Woburn are used for each of the three morphs because there was not sufficient germination and survival at Witheridge to justify a life table analysis. In addition, the only difference between the two sites appeared to be the result of differences in ground cover (Chapter 5.5).
The adult mortality figures are obtained from Wyke only. Although the data from Batcombe would be as good for the heterostyle morphs, it is better to use data for all three morphs from a single source within age categories so that any difference between the morphs is not obscured by differences between sites.

Two fecundity schedules for each morph are presented with the data for seed production being taken for the best and worst years at Wyke. The pattern of seed production between the morphs varies between years depending not only on whether the year in question is a good one for primrose flowering but also whether it is a good year for the pollinator species. For this reason, a mean seed production figure for each of the three morphs would not be as meaningful as considering years when pollination is more or less complete and years when pollination limits seed production.

The life tables and fecundity schedules for the three morphs are presented below (Tables 6.1a, b, c, d).

It can be seen from the life tables (Tables 6.1a, b, c) that the general pattern of mortality was similar in all three morphs. Most of the mortality took place between sowing and the first census. Mortality in the juvenile stages is much greater than after plants have survived to their first flowering episode. In addition, only 5-13% of seeds present at the start of the year survive to flowering.

Thrums have a higher survival to the first census than the other two morphs but their survival is lower than either of the other morphs thereafter. Homostyle survival is lowest to
<table>
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<tr>
<th>Sources of data</th>
<th>Census number</th>
<th>Length of age interval, days</th>
<th>Age in days at census</th>
<th>Nos alive</th>
<th>Survivorship</th>
<th>Nos dying</th>
<th>Mortality rate per X-(X+1) day</th>
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</thead>
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<tr>
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<td>0</td>
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<td>1.000</td>
<td>131</td>
<td>0.00408</td>
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<td>119</td>
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<td>1214</td>
<td>32</td>
<td>0.120</td>
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Table 6.1a Life table for pin primroses. Data are taken from the field experiments of Chapter 5 and from the mapping of Wyke reported in Chapter 3.
Table 6.1b Life table for thrum primroses. Data are taken from the field experiments of Chapter 5 and from the mapping at Wyke described in Chapter 3.
<table>
<thead>
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<th>Age in days at census</th>
<th>Nos alive</th>
<th>Survivorship</th>
<th>Nos dying during X-(X+1) day</th>
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</tr>
<tr>
<td>quadrats</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Field</td>
<td>4</td>
<td>243</td>
<td>484</td>
<td>59</td>
<td>0.287</td>
<td>33</td>
<td>0.00153</td>
</tr>
<tr>
<td>quadrats</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Surv. at Wyke</td>
<td>5</td>
<td>365</td>
<td>849</td>
<td>26</td>
<td>0.129</td>
<td>1</td>
<td>0.0001054</td>
</tr>
<tr>
<td>Surv. at Wyke</td>
<td>6</td>
<td>365</td>
<td>1214</td>
<td>25</td>
<td>0.124</td>
<td>-</td>
<td>-</td>
</tr>
</tbody>
</table>

Table 6.2c Life table for homostyle primroses. Data are taken from the field experiments of Chapter 5 and from the mapping of Wyke described in Chapter 3.
Table 6.1d Fecundity schedules for the three primrose morphs in 'good' and 'bad' years for seed production. The dates in inverted commas are extrapolated from the life tables but help to make sense of the schedules.

<table>
<thead>
<tr>
<th>Morph</th>
<th>X</th>
<th>l_x</th>
<th>b_x</th>
<th>l_xb_x</th>
</tr>
</thead>
<tbody>
<tr>
<td>Pins (bx 1983)</td>
<td>Jun 83 - May 84</td>
<td>1.000</td>
<td>0</td>
<td>0</td>
</tr>
<tr>
<td></td>
<td>'May 84 - May 85'</td>
<td>0.126</td>
<td>77.5</td>
<td>9.765</td>
</tr>
<tr>
<td></td>
<td>'May 85 - May 86'</td>
<td>0.120</td>
<td>77.5</td>
<td>9.3</td>
</tr>
<tr>
<td>Pins (bx 1984)</td>
<td>Jun 83 - May 84</td>
<td>1.000</td>
<td>0</td>
<td>0</td>
</tr>
<tr>
<td></td>
<td>'May 84 - May 85'</td>
<td>0.126</td>
<td>214</td>
<td>26.964</td>
</tr>
<tr>
<td></td>
<td>'May 85 - May 86'</td>
<td>0.120</td>
<td>214</td>
<td>25.68</td>
</tr>
<tr>
<td>Thrums (bx 1983)</td>
<td>Jun 83 - May 84</td>
<td>1.000</td>
<td>0</td>
<td>0</td>
</tr>
<tr>
<td></td>
<td>'May 84 - May 85'</td>
<td>0.052</td>
<td>74.6</td>
<td>3.8792</td>
</tr>
<tr>
<td></td>
<td>'May 85 - May 86'</td>
<td>0.048</td>
<td>74.6</td>
<td>3.5806</td>
</tr>
<tr>
<td>Thrums (bx 1984)</td>
<td>Jun 83 - May 84</td>
<td>1.000</td>
<td>0</td>
<td>0</td>
</tr>
<tr>
<td></td>
<td>'May 84 - May 85'</td>
<td>0.052</td>
<td>324</td>
<td>16.848</td>
</tr>
<tr>
<td></td>
<td>'May 85 - May 86'</td>
<td>0.048</td>
<td>324</td>
<td>15.552</td>
</tr>
<tr>
<td>Homostyles (bx 1983)</td>
<td>Jun 83 - May 84</td>
<td>1.000</td>
<td>0</td>
<td>0</td>
</tr>
<tr>
<td></td>
<td>'May 84 - May 85'</td>
<td>0.129</td>
<td>143</td>
<td>18.447</td>
</tr>
<tr>
<td></td>
<td>'May 85 - May 86'</td>
<td>0.124</td>
<td>143</td>
<td>17.732</td>
</tr>
<tr>
<td>Homostyles (bx 1984)</td>
<td>Jun 83 - May 84</td>
<td>1.000</td>
<td>0</td>
<td>0</td>
</tr>
<tr>
<td></td>
<td>'May 84 - May 85'</td>
<td>0.129</td>
<td>269</td>
<td>34.701</td>
</tr>
<tr>
<td></td>
<td>'May 85 - May 86'</td>
<td>0.124</td>
<td>269</td>
<td>33.356</td>
</tr>
</tbody>
</table>
the first census but is highest thereafter. The result of this is that for a given number of seeds in the start of the life tables, thrums end up with the lowest number of flowering plants followed by pins and then homostyles with the highest.

In a population at equilibrium, the sum of the $l_x b_x$ columns in the fecundity schedules over the lifetime of the individuals concerned is a measure of the fitness of the morphs involved. If fecundity and survival remain constant over the reproductive phase of the lifetime of the subjects, the $l_x b_x$ figure in any one year can be regarded as partial fitnesses.

A direct comparison of the partial fitnesses of the three morphs would not be valid because pins produce seeds of both pin and thrum genotype. However, a comparison between the partial fitnesses of homostyles and heterostyles can be made if certain assumptions are followed. If all homostyles are homozygous and only self and pins and thrums produce seeds in the ratios 50:50, pin:thrum, the partial fitnesses of the heterostyle and homostyle morphs are calculated as follows:

\[
\text{Partial heterostyle fitness} = \frac{l_x b_x^{\text{pin}} + l_x b_x^{\text{thrum}}}{2}
\]
\[
\text{Partial homostyle fitness} = l_x b_x^{\text{homostyle}}
\]

These partial fitnesses are based upon ecological parameters with the minimum of assumptions regarding the mating system. For poor years where pollination is incomplete the ecological partial fitness for heterostyles is 0.35:1.
compared to homostyles and in good years where pollination is relatively complete the same ratio has a value of 0.6:1. The implications of this are that clearly the rapidity with which homostyles spread through a heterostyle population depends on the pollinators.
Life tables provide the raw materials for models of population change and one of the most useful techniques is matrix modelling. Transition probabilities between age classes are taken from life tables and entered into a transition matrix. These transition probabilities are multiplied by a vector representing the population age structure and iterated until a stable age structure is reached. The construction of the transition matrix is relatively easy for each morph but some assumptions about the genetics of the breeding system are required to make sense of the iterative process. The transition matrix for homostyle primroses can be constructed without difficulty and is presented below.

The elements of the matrix \((i,j)\) are arrived at as follows. Element \((1,1)\) is the probability that a seed present in one year will also be present in the following year. A seed can remain in the seed pool with a probability of element \((1,1)\) or it can germinate and be present in the following year as a seedling with a probability of element \((2,1)\) or it can die. Element \((1,1)\) is assumed to be zero here because although there is a seed pool (Chapter 4.8) there is no information available about recruitment to it.

Element \((1,4)\) can have two values. Each of these values is derived from the probability that an adult plant will flower in a given year multiplied by the seed production of plants which do actually flower. The two values for this element
### Table 6.2a Transition matrix for homostyle primroses

The four age classes roughly correspond to the classes: Seed (S), Seedling (C), non-flowering rosette (J), and Adult (A). Rows = i, Columns = j.

<table>
<thead>
<tr>
<th></th>
<th>S</th>
<th>C</th>
<th>J</th>
<th>A</th>
</tr>
</thead>
<tbody>
<tr>
<td><strong>S</strong></td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>137 or 258</td>
</tr>
<tr>
<td><strong>YEAR (X+1)</strong></td>
<td><strong>C</strong></td>
<td>0.46</td>
<td>0</td>
<td>0</td>
</tr>
<tr>
<td><strong>J</strong></td>
<td>0</td>
<td>0.628</td>
<td>0.05</td>
<td>0</td>
</tr>
<tr>
<td><strong>A</strong></td>
<td>0</td>
<td>0</td>
<td>0.441</td>
<td>0.962</td>
</tr>
</tbody>
</table>

---
represent the seed production in good or bad years. The consideration of the two extremes is more biologically meaningful because of the qualitative differences in seed production between morphs in the two different types of year. The assumption inherent in calculating this element is that all seeds of homostyles are homozygous and do not outcross. This assumption is not correct (otherwise no pin plant would produce seeds of homostyle genotype under natural conditions) but it is simple and is used as there is no information regarding the genotypes of morphs from this study.

Elements (3,3) and (4,3) represent the probabilities of a second stage seedling (J) remaining in that stage until the following year or making the transition to flowering plant respectively. Element (3,2) represents the transition from seedling (C) to non-flowering rosette (J) and element (4,4) represents adult survival. All other elements are zero because they are either nonsensical or no such transitions were found in the present study.

The transition matrices for the two heterostyle morphs are similar to that for homostyles but they are not entirely independent of one another during the iterative process. The transition matrices for the two heterostyle morphs are presented below (Tables 6.2b, c).

The elements for the heterostyle transition matrices are derived in a similar manner to those for the homostyle matrix. However, the elements (1,4) in both heterostyle matrices are one half the seed production of plants multiplied by the probability of an adult flowering in any one year.
Table 6.2b Transition matrix for pin primroses. The four age classes roughly correspond with the stages; Seed (S), Seedling (C), non-flowering rosette (J), and Adult (A). Rows = i, Columns = j.

<table>
<thead>
<tr>
<th></th>
<th>S</th>
<th>C</th>
<th>J</th>
<th>A</th>
</tr>
</thead>
<tbody>
<tr>
<td>S</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>37.2 or 102.7</td>
</tr>
<tr>
<td>YEAR (X+1)</td>
<td>C</td>
<td>0.515</td>
<td>0</td>
<td>0</td>
</tr>
<tr>
<td>J</td>
<td>0</td>
<td>0.438</td>
<td>0.05</td>
<td>0</td>
</tr>
<tr>
<td>A</td>
<td>0</td>
<td>0</td>
<td>0.557</td>
<td>0.94</td>
</tr>
</tbody>
</table>
Table 6.2c Transition matrix for thrum primroses. The four age classes roughly correspond to the stages; Seed (S), Seedling (C), non-flowering rosette (J) and Adult (A). Rows = i, Columns = j.

<table>
<thead>
<tr>
<th></th>
<th>S</th>
<th>C</th>
<th>J</th>
<th>A</th>
</tr>
</thead>
<tbody>
<tr>
<td>S</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>33.2 or 144.2</td>
</tr>
<tr>
<td>YEAR (X+1)</td>
<td>C 0.556</td>
<td>0</td>
<td>0</td>
<td>0</td>
</tr>
<tr>
<td>J</td>
<td>0</td>
<td>0.329</td>
<td>0.004</td>
<td>0</td>
</tr>
<tr>
<td>A</td>
<td>0</td>
<td>0</td>
<td>0.304</td>
<td>0.857</td>
</tr>
</tbody>
</table>
The iterations of the age structure vectors for the heterostyles are not independent. If the vector for the age distribution is:

\[
\begin{bmatrix}
S \\
C \\
J \\
A
\end{bmatrix}
\]

The calculation of the elements C, J and A is straightforward but the calculation of S is only possible if the two matrices for the pin and thrum morph are iterated at the same time. They are calculated as follows:

\[
S_{\text{pin}, t+1} = (M_{\text{pin}, 1, 4} \times S_{\text{pin}, t}) + (M_{\text{thrum}, 1, 4} \times S_{\text{pin}, t})
\]

\[
S_{\text{thrum}, t+1} = (M_{\text{thrum}, 1, 4} \times S_{\text{thrum}, t}) + (M_{\text{pin}, 1, 4} \times S_{\text{thrum}, t})
\]

\[S = \text{vector element (S)}, \ M_{1, 4} = \text{transition element (1, 4)}.\]

The result of this is that whatever the differences in the age structure between the two morphs which may appear over the course of the iterations, the production of seeds of the two heterostyle morphs will be equal. This assumes that the heterostyle morphs only outcross.

The values of the elements in the age structure vector were all set at 100 to overcome the problems of rounding errors and the iterations were continued until a stable age structure was reached. This proved to be 30 iterations where each iteration represents one year. The results of the matrix iterations are illustrated graphically in Figure 6.2.
Figure 6.2a Matrix model for homostyle seeds (solid line) and heterostyle seeds using the original matrix for 'good' years.
Figure 6.2b Matrix model for primrose seedlings using the original matrix for 'good' years
Figure 6.2c Matrix model for primrose "juveniles" using the original matrix for 'good' years.
Figure 6.2d Matrix model for primrose adults using the original matrix for 'good' years.
The three morphs increase differentially over time (Figure 6.2). With the original values for the transition elements, homostyles increase more rapidly than either of the two heterostyle morphs. The heterostyle morphs increase together but for a given number of heterostyle genets thrums would have a lower number of flowering plants at any one time. This model suggests that survival differences between the heterostyle morphs are sufficient to explain a bias in the distribution of morphs within a heterostyle population in favour of pins. The extent of this bias will be discussed later.

It is apparent from this model that small changes in the relative survival of the morphs will have a great effect on the morph proportions measured by a census of flowering plants. To determine how changes in the values of the transition elements would affect the outcome of the iterations a sensitivity analysis was carried out.
SENSITIVITY ANALYSIS 6.3

A sensitivity analysis (Caswell, 1978; Pinero et al 1984) is used to determine where the model is most affected by small changes in the values of the transition probabilities. This would help show which changes in the life history parameters would have the most effect on population growth and morph fitness.

In essence, the reproductive value (Caswell, 1978) for each age class is multiplied by the values in the stable age structure vector for that age class and entered into a new matrix known as the sensitivity matrix. The stable age structure values in this case were percentage values rather than absolute values after 30 iterations to keep the numbers down to a manageable level. The magnitude of the values of the elements in the sensitivity matrix indicate the transitions whose values are the most important in determining the population growth rates. The sensitivity matrices for each of the three morphs in the two types of year are given below in Tables 6.3a-f.

The sensitivity analysis shows the model to be most sensitive to changes in the transition elements (2,1) in all three morphs. The values of the element (2,1) are the least realistic in the model because they represent survival to May of plants planted in the previous January. Element (2,1) should also take into account the loss of seeds between shedding in June and the following January. For example, the values of 0.515 for element (2,1) of the pin transition matrix is correct for this experimental study but in nature
<table>
<thead>
<tr>
<th>YEAR X</th>
<th>S</th>
<th>C</th>
<th>J</th>
<th>A</th>
</tr>
</thead>
<tbody>
<tr>
<td>S</td>
<td>-</td>
<td>-</td>
<td>-</td>
<td>6.7</td>
</tr>
<tr>
<td>YEAR (X+1)</td>
<td>C</td>
<td>962</td>
<td>-</td>
<td>-</td>
</tr>
<tr>
<td>J</td>
<td>-</td>
<td>434</td>
<td>87</td>
<td>-</td>
</tr>
<tr>
<td>A</td>
<td>-</td>
<td>-</td>
<td>149</td>
<td>51</td>
</tr>
</tbody>
</table>

Table 6.3a Sensitivity matrix for pin primroses using the transition matrix for good years for seed production.
<table>
<thead>
<tr>
<th></th>
<th>S</th>
<th>C</th>
<th>J</th>
<th>A</th>
</tr>
</thead>
<tbody>
<tr>
<td>S</td>
<td>-</td>
<td>-</td>
<td>-</td>
<td>6.4</td>
</tr>
<tr>
<td>YEAR (X+1)</td>
<td>C</td>
<td>334</td>
<td>-</td>
<td>-</td>
</tr>
<tr>
<td>J</td>
<td>-</td>
<td>197</td>
<td>47</td>
<td>-</td>
</tr>
<tr>
<td>A</td>
<td>-</td>
<td>-</td>
<td>90</td>
<td>52</td>
</tr>
</tbody>
</table>

Table 6.3b Sensitivity matrix for pin primroses using the transition matrix for poor years for seed production.
<table>
<thead>
<tr>
<th>YEAR X</th>
<th>S</th>
<th>C</th>
<th>J</th>
<th>A</th>
</tr>
</thead>
<tbody>
<tr>
<td>S</td>
<td>-</td>
<td>-</td>
<td>-</td>
<td>0.76</td>
</tr>
<tr>
<td>YEAR (X+1)</td>
<td>C</td>
<td>244</td>
<td>-</td>
<td>-</td>
</tr>
<tr>
<td>J</td>
<td>-</td>
<td>178</td>
<td>26</td>
<td>-</td>
</tr>
<tr>
<td>A</td>
<td>-</td>
<td>-</td>
<td>96</td>
<td>17.5</td>
</tr>
</tbody>
</table>

Table 6.3c Sensitivity matrix for thrum primroses using the transition matrix for good years for seed production.
<table>
<thead>
<tr>
<th></th>
<th>S</th>
<th>C</th>
<th>J</th>
<th>A</th>
</tr>
</thead>
<tbody>
<tr>
<td>YEAR X</td>
<td></td>
<td></td>
<td></td>
<td>0.15</td>
</tr>
<tr>
<td>C</td>
<td></td>
<td>56</td>
<td></td>
<td></td>
</tr>
<tr>
<td>J</td>
<td></td>
<td></td>
<td>44</td>
<td>7.8</td>
</tr>
<tr>
<td>A</td>
<td></td>
<td></td>
<td>42</td>
<td>12</td>
</tr>
</tbody>
</table>

Table 6.3d Sensitivity matrix for thrum primroses using the transition matrix for poor years for seed production.
Table 6.3e Sensitivity matrix for homostyle primroses using the transition matrix for good years for seed production.
<table>
<thead>
<tr>
<th></th>
<th>S</th>
<th>C</th>
<th>J</th>
<th>A</th>
</tr>
</thead>
<tbody>
<tr>
<td>YEAR X</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>S</td>
<td>-</td>
<td>-</td>
<td>-</td>
<td>8</td>
</tr>
<tr>
<td>YEAR (X+1)</td>
<td>C</td>
<td>1095</td>
<td>-</td>
<td>-</td>
</tr>
<tr>
<td>J</td>
<td>-</td>
<td>356</td>
<td>101</td>
<td>-</td>
</tr>
<tr>
<td>A</td>
<td>-</td>
<td>-</td>
<td>215</td>
<td>64</td>
</tr>
</tbody>
</table>

Table 6.3f Sensitivity matrix for homostyle primroses using the transition matrix for poor years for seeds production.
seed loss before germination must be greater and so this figure should be reduced.

From the matrix model described above, pin adults would outnumber thrum adults by a ratio of 1:0.41 for a run of 'good' years and by 1:0.397 for a run of 'bad' years after 30 iterations. This is despite the fact that the two matrices are linked during iteration such that the annual rate of increase of both morphs is the same. Such a degree of bias is obviously unrealistic but it is important that survival differences can be shown to influence the morph ratios so markedly.

To attempt to bring the increase of the heterostyle morphs into more alignment with the observed ratios in field populations, changes in the values of the element (2,1) in the transition matrices were made. Element (2,1) was reduced by a factor of ten in all three transition matrices to bring seed survival down to a more realistic level. Element (2,1) in the pin matrix became 0.0515 while that in the thrum and homostyle matrices became 0.0556 and 0.046 respectively. All other transition values remained the same as before. After 30 iterations of these new ratios, the ratio of pin adults to thrum adults was 1:0.375 and 1:0.34 in 'good' and 'bad' years respectively. A blanket reduction in the transition element (2,1) by an order of magnitude favoured pins.

Summing the values for pin and thrum, it is of interest that the ratio of homostyles to heterostyles starts as 1:2 but after 30 iterations of the original transition matrices homostyles outnumber heterostyles in the ratio of 1:0.087 and 1:0.0036 for runs of 'good' and 'bad' years respectively. An
allround reduction in the value of transition element (2,1) by a factor of ten increases the proportion of heterostyle adults and the same ratios become 1:0.11 and 1:0.012 respectively.

There is reason to believe that although the transition element (2,1) should be reduced for all matrices, this reduction should not be the same for all morphs. The differences noted in the germination of seeds of different sizes (Chapter 5.7) and the numbers of the three morphs raised from seed collected from the seed pool in the Somerset populations suggest that element (2,1) should be reduced less for thrums than for the other two morphs. If the proportion of morphs raised from the seed pool is taken as an indication that there is differential survival of seeds in the soil before germination then a reduction in the transition element (2,1) in accord with the seed pool data is justified.

From the seed pool data at Batcombe (Table 4.6b), 8 pins and 17 thrums were raised to flowering. The transition elements (2,1) in the heterostyle matrices were multiplied by 0.08 and 0.17 for pin and thrum respectively. All other elements of the transition matrices remained as those of the original model. After 30 iterations using these new matrices, the ratio of pin adults to thrum adults was 1:0.803 and 1:0.83 for 'good' and 'bad' years respectively. This new ratio of pin to thrum adults compares favourably with those found at Batcombe (Table 3.2b).

4 Pins, 13 thrums and 1 homostyle were raised from the seed pool at Wyke (Table 4.6b). Although these numbers are
extremely low it was decided to use them in the model rather than purely arbitrary figures. Elements (2,1) from the original matrices were multiplied by 0.04, 0.13, and 0.01 for pin, thrum and homostyle respectively to account for seed loss at Wyke. Element (2,1) of the original matrices then became 0.0206 for pins, 0.07228 for thrums and 0.0046 for homostyles. All other elements in the original transition matrices remained unchanged.

After 30 iterations using the new matrices incorporating Wyke seed pool data, thrums outnumbered pins so that the ratio of pin to thrum adults had become 1:1.19 for 'good' years and 1:1.017 for 'bad' years. Homostyles fared worse in this version of the model than they had previously and the ratio of homostyles to heterostyles had become 1:460 for 'good' years and 1:10.4 for 'bad' years respectively. Homostyles are massively outnumbered by heterostyles if seeds survival in the soil can be taken as a measure of seed loss between shedding and germination. It is clear, however, that a better understanding of the ratio of morphs in the seed pool and seed survival is needed.
DISCUSSION 6.4

The matrix models and sensitivity analysis presented in this chapter are the first ecological models of this species which incorporate juvenile survival and are the first which have not worked entirely within a genetic framework.

This model has, however, required the assumption that homostyles do not outcross and are effectively homozygous in all circumstances. In addition it is assumed that the genotypes of heterostyle seed are 50% pin and 50% thrum. There is no information from the present study about the frequency or behaviour of plants with different genotypes and so only the simplest genetic assumptions have been made.

In this discussion I intend to explore some of the assumptions made in these models and show how they relate to the spread of homostyles through heterostyle populations.

Under conditions of complete homozygosity and in the absence of competition between the three morphs, homostyles had a greater growth rate than either of the heterostyle morphs even if they do not outcross. From the original matrices, the annual growth rate of homostyles is 2.79 in 'good' years and 2.39 in 'bad' years. The corresponding figures for the two heterostyle morphs are 2.5 and 1.9 and are the same for pin and thrum because of the link between the two morphs during iteration. Crosby (1949) suggests that homozygous homostyles may suffer reduced viability as the result of inbreeding depression. This may well be important over the first few generations of inbreeding but after that many of the deleterious recessive genes will have been
selected out and so, without contrary evidence, there is no reason to believe that homozygous homostyles have reduced fitness in comparison with heterozygotes.

One unrealistic assumption in this model is that homostyles only self. If this were so, then no pin plant would give rise to homostyle offspring and there would be no reason to suppose that thrums would be excluded any faster than pins from a population invaded by homostyles. Any outcrossing by homostyles would increase the rate of increase of homostyles at the expense, initially, of thrums. With this in mind, it can be said that the model presented in this chapter represents the minimum spread of homostyles based on ecological parameters and that the speed of homostyle spread will be determined by their level of outcrossing.

It would seem, then, that homostyles should spread through populations very rapidly given their ecological and genetic advantage over the heterostyle morphs. However, homostyles have been reported as stable in many populations (Curtis and Curtis 1984a) and they appear to have died out from Batcombe. The increase in the level of homostyly in Wyke noted in the present study (Chapter 3.2) suggests the possibility that homostyles have increased more rapidly in some areas than has been previously observed. This is probably the result of differences in census techniques between workers in some cases but there is, I believe, considerable variation in the speed with which homostyles can spread through a population.

In this chapter it was demonstrated that the growth rate of the three morphs was dependent on seed survival from shedding to the first census in the experiments described in
Chapter 5. If heterostyle seeds are produced in equal proportions in a heterostyle population, the change in seed survival in the original model to take into account the possible differences in survival of seeds in the soil is, to some extent, justifiable. That is to say, variations in the survival of pin and thrum seeds in the soil may counter survival differences noted in heterostyle plants with the result that most populations appear to consist of the two morphs in approximately equal numbers.

It is hard to justify differences in seed survival so great as those incorporated into the model when considering homostyles. However, even under those conditions where the homostyle transition probability between seeds and the seedlings present at the first census is an order of magnitude lower than for the heterostyle morphs, the annual growth rate of homostyles is positive at 1.17 for 'good' years and 1.09 for 'bad' years.

It has been shown in Chapter 4.6 that homostyles may suffer reduced germination in relation to the other two morphs as a result of their lower mean seed size.

If there is some outcrossing of homostyles though, seeds of homostyle genotype from pin mothers would be larger than those from homozygous homostyles particularly if pollination were incomplete.

It is clear that a knowledge of the sizes of seeds of homostyle genotype and a better understanding of the survival of seeds in the soil may be important in understanding the nature of the spread of homostyle primroses.

Vegetative spread was not considered in this model. The
three morphs showed similar rates of clonal growth under experimental conditions (cf Chapter 3.8) and there is no evidence to suggest that clonal growth differs between morphs in the field. Caswell (1986) has suggested that clonal growth should be incorporated in matrix models of population growth but without data on the transitions involved this is not possible in the current study.

The models presented in this chapter clearly show that a firm grasp of the ecology of the whole primrose life cycle is vital for an understanding of homostyle spread.
This thesis has been concerned with whether ecological differences between primrose morphs exist and whether any such differences are important for the spread of homostyly.

The model presented in Chapter 6 demonstrates that differences in the ecology of the three morphs may affect their spread and in this chapter I intend to discuss the nature of those differences as a whole as well as the implications of this work for ecologists and population geneticists.

It is apparent that the differences in seed size between morphs, which resulted from incomplete pollination of heterostyles could be important for the spread of homostyles. During the course of this work the following hypothesis was developed; The very advantage over heterostyles which homostyles appear to enjoy in terms of their higher seed output may be their downfall because of fitness trades-off between seed number and seed size.

Further work on the differences found between the three morphs is required and will be discussed below.
ECOLOGICAL DIFFERENCES BETWEEN PRIMROSE MORPHS 7.2

Figure 1.2 of the introduction shows a diagrammatic life history of the primrose giving the stages of growth where ecological differences between morphs may be expected to occur if they were present. It is apparent from the preceding chapters that ecological differences can be found at almost every stage of the life cycle. For most stages of the life cycle, homostyles were the most successful morph and thrums were the least successful. These differences are incorporated into the model of Chapter 6.

The model of Chapter 6 is useful for determining the growth rates of the three morphs under different conditions but it also obscures some of the differences found between morphs. For example, the model takes into account differences in adult survival but it does not indicate the causes of those differences. In this section I would like to summarise all the differences found between the morphs.

Two differences between thrums and the other morphs appear to be important in that they have consequences for other stages of the life cycle. The number of flowers and the flower architecture of thrums both results in thrums performing worse than either pins or homostyles in other aspects.

Thrums have more flowers than the other morphs (Chapter 4.1) and this has important implications for both adult survival (Chapter 3.6) and potential seed output (Chapter 4.5). Plants which show a greater than normal number of
flowers have a reduced probability of surviving to the next flowering season and, as thrums do not appear to have compensated for their high flower production by other means, this means that adult survival of thrums is lower than for the other two morphs. Thrum plants which have similar flower numbers to the other morphs do not suffer greater mortality (Chapter 3.6).

Because thrums have the greatest number of flowers, they also have the largest potential seed output of any of the three morphs. It can be seen, however, that thrums normally produce the lowest number of seeds of any morph (Chapter 4.5).

The flower architecture of thrums is such that insect visitors are more likely to remove pollen from thrums but they are also the least likely to receive legitimate pollinations (Chapter 4.2). If pollinators are scarce, thrums fare disproportionately badly in terms of seed production in relation to pins and homostyles. For a given number of seeds per capsule, thrum seeds are lighter than for either of the other two morphs (Chapter 4.4) but because pollination of thrums is rarely complete (Chapter 4.2) and because of the relationship between seed number per capsule and seed weight (Chapter 4.4), thrums tend to produce heavier seeds than those of either of the other two morphs. This results in seeds from thrum parentage having a higher rate of emergence than either of the other morphs (Chapter 5.7). After emergence, however, thrum seedlings have a lower survival than those of the other morphs (Chapter 5.5) but the reason
for this is unknown.

The differences above have been used in the model of Chapter 6 but, for example, the difference in flower number between the morphs and differences in the pollination rate have been combined in the figure for seed production.

It is clear from the sensitivity analysis of Chapter 6 that it would be of value to obtain estimates of the level of persistence of seed in the soil from one year to the next as well as a measure of the rate at which the longer term seed pool is supplemented. The work in this thesis points to the importance of the relative recruitment from seed of the three morphs in determining the rate at which homostyles may be expected to spread through a heterostyle population.

Seeds from the soil in the Somerset populations were collected from soil cores taken just prior to the shedding of the next seed crop. It was not possible to determine the age of the seed and it is likely that the flotation technique and oven-drying used to separate the seeds from the soil cores resulted in an under-estimate of the viability but not the numbers of seeds in the pool.

The accumulation of seeds in the soil could be investigated experimentally by sowing seeds in a suitable area and retrieving them over a period of years and running germination tests on them. In this way, a measure of the survival of seeds between their shedding and germination could be obtained. The results of such an experiment could be incorporated into the matrix model of Chapter 6 by changes in the transition element (2,1).
Models to explain the distribution of homostyly have previously concerned only the genetics of the breeding system under different assumptions on the level of homostyle outcrossing and homzygote viability (Crosby, 1949, 1959; Bodmer, 1960). Recently these assumptions have been tested (Piper et al., 1984) and there is also a model which considers frequency dependent selection of homostyles (Curtis and Curtis, 1984a). These models do not consider survival differences between the morphs or the other ecological differences considered in this thesis.

The results from the present study suggest that homostyles would be expected to increase in relation to heterostyles on purely ecological grounds. If outcrossing of homostyles was incorporated into the models of Chapter 6 it would seem that homostyles would be destined to increase with even greater rapidity. That is to say, the ecological results from this thesis appear only to strengthen the dilemma of why homostyles have not spread rapidly through heterostyle populations in which they have become established. Measures of seed persistence, as indicated in the previous section, may hold the answer.

Many of the findings in this work could be incorporated into population genetic models without too much difficulty but the resulting predictions would be radically different from those of current models. One of the most important lessons to be gained from this thesis is that neither
ecologists or geneticists in isolation will solve all the mysteries of the primrose homostyle/heterostyle system.
This thesis demonstrates that although ecologists may be interested in the differences between morphs as exemplifying differences between mating strategies within a species, it is important to consider the whole of the life cycle rather than just the reproductive episodes. The only apparent differences between morphs may be in their floral structure but survival differences between morphs in their juvenile stages may also be present. Meagher (1982) recognised that life history differences between the sexes in the dioecious species Chamaelirium luteum had to be incorporated into matrix models predicting population growth for that species but otherwise such parameters have been largely ignored. This thesis is further proof that techniques are available to study differences in the survival of morphs even before they can be visually identified.

This thesis is also important as far as models of breeding systems are concerned. It would appear that both survival and reproductive consequences of the switch from one breeding system to another are important in considerations of different life histories. For example, heterostyly has evolved towards dioecy on several occasions (Lloyd, 1979) and if flower production is a significant cost to primroses (cf Chapter 3.6) then a switch from heterostyly to dioecy should be considered in both survival and reproductive terms.

Ecologists specifically concerned with primroses will find that this thesis suggests further work. I will now discuss
some of the work which still needs to be done and how it could be accomplished.

Within the limitations of this study in terms of time and material available, the data for juvenile survival reported in Chapter 5 are correct. The differences in survival cannot, however, be safely assumed correct at other seedling densities despite the similarities between the results from Woburn and Witheridge. The density of seeds used (600/25cm²) is similar to those which may be expected in nature but it is possible that the actual density of seedlings may be far higher than in the experiments. If, for example, several capsules shed seed into an area of bare ground such as produced by rodent scratchings, the seedling densities may be far greater than in the quadrats. Seedlings in the quadrats were never so densely packed that they markedly interfered with each other at the first census. The result of this is that by later censuses the initial advantage of the stronger seedlings has been lost although the mechanism behind this is uncertain. At higher seedling densities the initial advantage of thrum plants may be maintained if they smother seedlings of the other morphs before they are able to catch up their growth. A repeat of the experiment of Chapter 5 using a range of seedling densities and with more early censuses would show whether relative survival of the juvenile primrose morphs changed with density. If they did, the transition elements of the model in Chapter 6 could not be regarded as constant over the iterations.

In addition to density-dependent seedling survival, the
persistence of seeds in the soil is in need of further investigation. This could be done either in seed trays or in the field as has been described in the previous section.

It would also be of interest to discover whether the differences in the ecology of the three morphs reported in this thesis vary with differing environmental conditions. The sharp divisions between areas containing homostyles and those areas which contain only heterostyle plants in some of the Somerset primrose populations is striking in both its nature and its stability over the last 40 years. It is possible that homostyles may be even more limited by the environment under some conditions than has been suggested in this thesis.

Concurrently with the experiments in Chapter 5 an experiment was devised to see whether there were differences in the performance of the three morphs under different environmental regimes. Seeds from the original greenhouse stock were grown under conditions of shade, high nutrient levels and with slug pellets. These were compared with seed grown in pots without any additional treatment as a control. The results of this experiment were inconclusive because too few plants grew to maturity for analysis of the results to be worthwhile. A repeat of this experiment with greater numbers of seed and replicates may prove illuminating.

Another point worth emphasising is that had the differences in pollination of the three morphs reported in this work and by Piper et al (1984) not been discovered, one may be tempted to see the smaller numbers of seeds produced by thrums in some years as a shift away from female function.
rather than as a consequence of pollinator activity. Bierzychudek (1981) has warned against mistaking pollinator limitation for resource partitioning and it seems that this needs to be considered when discussing the evolution of dioecy from heterostyly.

Finally, it is clear that both homostyles and heterostyles have complex ecologies which cannot be explained by simple differences in their seed output or their genetics alone.
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