Kin-structured colonization in *Phalacrus substriatus*

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The focus of this work is to examine the genetic structure of newly colonized populations of the mycophagous beetle *Phalacrus substriatus*. The newly colonized populations are characterized by small founding groups, often consisting only of females. Because an all-female colonizing propagule can successfully found a new population, females must be mated prior to dispersal. Furthermore, because of limited dispersal, founders come from only a limited set of populations, thereby increasing their probability of common origin (ϕ). The small founding groups, high probability of common origin and mating patterns of female beetles generate a strong kin-structuring in *P. substriatus* as evidenced by the high average relatedness among first generation offspring ($r = 0.190$, weighted average over populations). The effective number of matings per female (M_e) was estimated to be around 1.5. This yields an estimate of the effective size of the newly colonized populations of 5.2. The probability of common origin was also high (0.80). The results are discussed in the light of how founding events may affect the structuring of genetic variation within and between local populations.

Keywords: colonization, effective population size, *F*-statistics, kin-structure, relatedness.

Introduction

In species experiencing frequent extinctions and recolonizations, most local populations will have undergone a founding event in their recent history, regardless of the current population size (McCauley, 1989). As theoretical models have shown, the size and structure of the newly colonized populations should be the prime focus for understanding how population turnover affects the genetic variation within and genetic differentiation among populations (Wade & McCauley, 1988; Whitlock & McCauley, 1990). As founding groups are often small this generates an additional opportunity for genetic drift to act at the time of colonization. The magnitude of the founder effect will thus be determined by the effective population size of the colonizing propagule, k_e. Apart from the actual number of individuals involved in the colonization event, the effective size is influenced by such factors as variation in sex ratio among colonizers, variation in reproductive success and kin-structuring among the individuals involved (Whitlock & McCauley, 1990). The global estimate of k_e, the effective number of colonizers, will further be influenced by variation

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among different newly founded populations because the appropriate summary statistic is the harmonic mean (Whitlock & McCauley, 1990; McCauley *et al.*, 1995). Because the harmonic mean is always less than or equal to the arithmetic mean, variation in size among different founding groups tends to reduce the global estimate of k_e (Crow & Kimura, 1970; Whitlock & McCauley, 1990). Small founding groups will consequently have a disproportionately large effect on the genetic consequences of colonizations.

The aim of this paper is to quantify the genetic structure of a number of newly founded populations of *Phalacrus substriatus* more thoroughly than in our previous study (Ingvarsson *et al.*, 1997). I am particularly interested in how mating patterns of female beetles influence both the effective size of newly colonized populations and the probability of common origin or individuals in the founding groups. As I have been unable to raise the beetles under laboratory conditions I rely on beetles sampled from field populations. Although this limits the number of newly founded populations that can be studied, these founding events represent naturally occurring colonizations and will therefore be directly applicable to the problem of how founding groups

are composed and how this will affect the population genetic structure in the metapopulation.

A commonly observed phenomenon in many insects is that populations are founded by groups consisting entirely of females. In this case the size of the dispersing unit is larger than is implied by a simple count of individuals, because females carry gametes from a number of males from their source population. On the other hand, females mating with males from the same parental population prior to dispersal, will increase the probability of common origin of alleles (Whitlock & McCauley, 1990). Consequently, the genetic structure of newly colonized populations will depend on the migration patterns, gene identity among members in the source population and on the mating system of the species in question (i.e. number of matings, sperm precedence patterns, etc.).

Wade (1982, 1985a) developed a model for colony formation that takes both multiple founders and multiple inseminations of females into account. In this model the relatedness among individuals in a population is determined by the number of parents and the distribution of maternity and paternity among these individuals (Wade, 1985a). More specifically, the genetic relatedness among diploid individuals in a group is given by (Wade, 1985a):

$$r = \frac{1}{4}\left(1 + \frac{1}{M_e} + \overline{m\sigma_m^2}\right)\left(\frac{1}{N_f} + \overline{N_f\sigma_f^2}\right),\qquad(1)$$

where N_f is the number of breeding females in the founding group and M_e is the harmonic mean number of mates per female. In eqn (1), $\overline{m\sigma_m^2}$ represents the average of the products of the number of males per female and variance in apportionment of paternity among these males. Similarly, $\overline{N_f\sigma_f^2}$ is the average of the product of number of females in a founding population and the variance in apportionment of reproduction among these females (Wade, 1985a). Under the assumption of equal apportionment of reproduction of the female founders and an equal apportionment of paternity among males, both these terms are zero and eqn (1) reduces to:

$$r = \frac{1}{4}\left(1 + \frac{1}{M_e}\right)\left(\frac{1}{N_f}\right).\qquad(2)$$

Equation (2) suggests that it is possible to estimate the effective number of mates, M_e, for the females (N_f) founding a population if the relatedness among the offspring the following generation is known. Rearranging eqn (2) yields:

$$M_e = \frac{1}{4N_f r - 1}.\qquad(3)$$

Local populations of the mycophagous beetle *P. substriatus* turn over rapidly and the expected persistence time of any given population is short, of the order of 4–5 years (Ingvarsson *et al.*, 1997). Because colonization of extinct populations occurs regularly, the persistence of the species is achieved at the metapopulation level as a balance between extinctions and recolonizations (Olivieri *et al.*, 1990; Harrison, 1991).

Previous studies have suggested that a strong kin-structure exists in local *P. substriatus* populations, particularly in newly colonized populations. Previous results also showed a strong female-biased sex ratio in the founding groups with some groups consisting exclusively of females. Because founding groups consisting only of females successfully established new populations, some or all dispersing females must have mated prior to dispersal. As these mated females are carrying the gametes of males from their source population the actual number of colonizers will be higher than a simple count of individuals would indicate. Although we had no detailed data on mating patterns in *P. substriatus*, we suggested that the sizes of the founding populations were at least twice the number estimated from a simple count of individuals (Ingvarsson *et al.*, 1997). Furthermore, we also showed that members of the founding groups came from a limited set of populations which suggests that individuals involved in the founding events could be related. Because both kin-structuring and inbreeding among colonizers are known to reduce the effective size of the founding populations (Whitlock & McCauley, 1990), we predicted that turnover would lead to an increase in genetic differentiation among populations. This observation was also verified by data from an analysis of genetic differentiation of 40 local populations of *P. substriatus* (Ingvarsson *et al.*, 1997).

Material and methods

Studied species

Phalacrus substriatus (Coleoptera: Phalacrideae) is a univoltine beetle found mainly on tussocks of the sedge *Carex nigra* infected by the anthracoid smut *Anthracoidea heterospora*. The adult beetles are active from early June to early July. During this period the adult beetles feed both on *C. nigra* pollen and on smut spores of *A. heterospora*. Eggs are laid either on the surface of, or in a hole bitten in, the

perigynium of host plant. Larvae hatch after approximately 1 week and feed in developing smut sori (Kontkanen, 1936). The larval period lasts 3–4 weeks after which pupation occurs in the sorus. Adult beetles emerge after 3 weeks and appear to overwinter as adults at the base of the tussock (P. K. Ingvarsson, pers. obs.).

Mark–recapture studies have shown beetles to be fairly sedentary and a tussock of the host plant corresponds quite well to a local population of *P. substriatus* (Ingvarsson *et al.*, 1997). Individual *P. substriatus* beetles do not show any flight tendencies either in the field or in the laboratory, even though they have fully developed wings (P. K. Ingvarsson, pers. obs.). Thus, dispersal is probably achieved by beetles crawling between tussocks, resulting in low migration rates between different local populations.

There is substantial temporal variation in local population size and populations have been shown to have extinction rates of about 25% per year (Ingvarsson *et al.*, 1997). The main reason for local extinctions is prolonged periods of high water levels when tussocks become submerged under water, mainly occurring during fall storms.

Colonization experiment

The experiment was performed on three islands in the Skeppsvik archipelogo, 20 km east of Umeå, Sweden. In early June 1995, a total of 45 new populations were artificially created, divided equally among the three study islands, by transplanting tussocks of the host plant *C. nigra* from an island where *P. substriatus* was known not to occur. The transplanted tussocks could not be visually distinguished from other tussocks of *C. nigra* on the islands and, after transplantation, they continued to flower throughout the season and again the following year. All populations were repeatedly censused over a period of approximately 3 weeks to record any naturally occurring colonizations. At the same time, mark–recapture experiments were performed at the studied islands. All beetles captured were individually marked with a three-colour code on the elytra and released in the same population where they were found. Because the origins of all marked beetles were known (I assumed that beetles originated in the population where they were first caught and marked) it was possible to determine the numbers of source populations that were represented in the founding groups. In early July, after egg laying had progressed for approximately 3 weeks, all populations were sweep-netted repeat-edly over 3 days until no more beetles could be found in the tussocks. I was able to recapture over 85% of all beetles that had been marked in the populations. All captured beetles were brought back to the laboratory where they were sexed and subsequently frozen at $-70°C$ until they could be further processed for enzyme electrophoresis. All beetles were assayed for five polymorphic enzyme systems, aconitate hydratase (Acn; EC 4.2.1.3), isocitrate dehydrogenase (Idh; EC 1.1.1.42), malate dehydrogenase (Mdh; EC 1.1.1.37), phosphoglucoisomerse (Pgi; EC 5.3.1.9) and triose-phosphate isomerase (Tpi; EC 5.3.1.1). A smaller set of the populations involved in this colonization experiment is described in Ingvarsson *et al.* (1997), where a more detailed description of the electrophoretic procedures can also be found. At the start of the activity period of *P. substriatus* in early June 1996, all artificial populations that had received at least one female colonizer in 1995, were revisited for three consecutive days. If beetles are sampled early in the season, before any migration has occurred between different populations, all individuals can safely be assumed to be locally derived. In this case, the artificially created populations do provide an opportunity to test the genetic composition of founder populations after one winter. All beetles collected in 1996 were treated as described above.

Individuals were scored for their genotypes at the five enzyme systems and Wright's *F*-statistics were calculated for the three islands separately using the method of Weir & Cockerham (1984). This method partitions the total inbreeding coefficient (F_{IT}) into components of nonrandom mating in subpopulations (F_{IS}) and genetic differentiation among different subpopulations (F_{ST}). Standard errors were estimated by jack-knifing over loci (Weir & Cockerham, 1984). All *F*-statistics were calculated using the program FSTAT (Goudet, 1995).

Genetic relatedness

The average genetic relatedness *r*, of individuals in the newly founded populations was calculated from the estimated *F*-statistics using the formula (Hamilton, 1972; Pamilo, 1989):

$$r = \frac{2F_{ST}}{1+F_{IT}}. \qquad (4)$$

This method estimates the average relatedness of the sampled populations rather than the degree of relatedness of any particular group. There are small, but statistically significant, differences in allele

frequencies between the three different islands (Ingvarsson & Olsson, 1997). To avoid artificially inflating the estimates of relatedness, r was therefore calculated for the three islands separately (Pamilo, 1984, 1989). Standard errors of r were obtained by jack-knifing over loci and standard errors were then used to estimate 95 per cent confidence intervals using standard techniques (Sokal & Rohlf, 1981).

As mentioned above, r is calculated as an average over all newly colonized populations on any given island. To use eqn (3) to estimate the effective number of mates, M_e, it is therefore necessary to calculate an average of the number of female founders in the populations. The appropriate summary statistic in this case is the harmonic mean number of females found in the newly colonized populations.

In populations consisting of a mixture of sib-groups the estimate of F_{IS} is expected to be negative, because in this case alleles within individuals tend to be less, or equally, correlated, than if they were randomly combined in the population (Wright, 1965; Cockerham, 1973; Michod, 1980). Furthermore, in a population subdivided largely into kin-groups a positive F_{ST} and a F_{IT} close to zero are expected (Michod, 1980).

Effective population size

What ultimately determines the impact of founding events on the genetic structure of the metapopulation is the relationship between the effective population size of the founding groups and the migration rates among extant populations (Wade & McCauley, 1988; Whitlock & McCauley, 1990). The effective size of a population with variable numbers of males and females is given by (Wright, 1938; Caballero, 1994):

$$N_e = \frac{4N_f N_m}{N_f + N_m}, \tag{5}$$

where N_f and N_m are the number of females and males in the population, respectively. Because M_e is the effective number of mates per female, the effective number of males in a population is given by $N_f M_e$ (i.e. the number of females times the effective number of mates per female). Note that if the same males mate with multiple females, the average relatedness among the offspring in the population is increased. This will consequently reduce M_e. An M_e estimate of less than one would thus indicate some degree of mate sharing between females. Substituting $N_f M_e$ for N_m in eqn (5), where M_e is given by eqn (3), yields after rearranging:

$$N_e = \frac{1}{r}. \tag{6}$$

It is thus possible to estimate the effective size of a colonizing propagule in this case by the reciprocal of the genetic relatedness among the offspring in the following generation. This result can be derived more generally from the fact that in a randomly mating population the relatedness between two individuals is equal to twice the probability that a randomly chosen gamete from the two individuals is identical by descent. If population size varies over time (as it does for newly colonized populations of *P. substriatus*), gene identity in a population (and hence relatedness) depends on the population size in the previous generation. The probability of identity by descent is, by definition, equal to the inbreeding coefficient in the population, F (and hence is $r = 2F$, where both r and F are defined relative to the previous generation; Hartl & Clark, 1989). Because in an ideal population $F = 1/2N_e$, eqn (6) follows directly.

Results

Successful colonizations occurred in 16 of the artificially created populations. For a colonization event to be regarded as successful: (i) at least one female beetle had to be among the founding individuals in 1995, and (ii) the population had to be extant the following year. The average number of female colonizers in 1995 was 2.8 (harmonic mean 2.2, Table 1).

Of the 16 populations, 11 were colonized by groups consisting entirely of females. The other five populations received both male and female colonizers, with an average of 1.4 males (Table 1). Consequently there was a strong female bias in the newly founded populations and 84% of the colonizers were females. The average size of the populations in the year following the colonization event was 10.2 (Table 2), which does not differ ($t_{45} = 0.34$, $P > 0.5$) from the average populations size seen in *P. substriatus* (Ingvarsson *et al.*, 1997).

The inbreeding coefficient, F_{IS}, was zero or negative in 14 out of the 16 populations (Table 2) and the combined estimated of F_{IS} was significantly negative for all three islands (Table 3). The different newly colonized populations were strongly differentiated, as evidenced by the high F_{ST} values. F_{IT} was slightly negative in all cases, but in only one case was the estimate significantly different from zero. There is thus clear evidence for kin-structuring in newly colonized populations of *P. substriatus*.

Table 1 The number of adult male and female *Phalacrus substriatus* founders at each of the artificially created populations in 1995

Population	Island 1		Island 2		Island 3	
	Males	Females	Males	Females	Males	Females
1	0	2	0	1	1	4
2	0	1	0	2	0	1
3	0	2	1	3	2	2
4	2	2	0	4	0	3
5	1	3	0	2	0	1
6	—	—	—	—	0	3
Total	3	10	1	12	3	14

The kin-structure is also confirmed by the estimates of genetic relatedness for the different islands (Table 3). The degree of relatedness was always high and the weighted average equalled 0.190 over the three islands. None of the estimates was significantly different from either $r = 0.250$ or $r = 0.188$. A value of r of 0.250 is expected when offspring groups consist of an equal mixture of sib-groups from two unrelated females each mated once and $r = 0.188$ is expected when offspring groups consist of an equal mixture of sib-groups from two unrelated females, each mated twice.

Replacing N_f in eqn (3) with the harmonic mean of females founding populations on the separate islands yields an average value of M_e of 1.39. The estimates of M_e per island and the 95 per cent confidence intervals are given in Table 4. The confidence intervals for M_e are estimated by taking a fixed N_f and using the symmetric confidence intervals obtained for r.

The low M_e estimates are in agreement with between one or two mates per female. Note however that M_e could also be reduced if the different females (or males) responsible for the matings within each subpopulation were themselves related or if the different females mate with the same males. The effective number of mates is represented by the harmonic mean number of males mated to a female and as such it will be sensitive both to the distribution of the number of mates per female in the population and to variations in the distribution of paternity of different males. As it is conceivable that there is variation both among males in the number of eggs fertilized and in the number of matings per female, the potential number of sires of a single

Table 2 Number of offspring of founders sampled in each population of *Phalacrus substriatus* in 1996 and the per population estimate of F_{IS}. Also given is the average over populations of F_{IS}, weighted by sample size

Population	Island 1		Island 2		Island 3	
	n	F_{IS}	n	F_{IS}	n	F_{IS}
1	8	0.005	7	−0.358	14	−0.163
2	9	−0.429	10	−0.227	8	0.00
3	10	0.094	5	−0.116	11	−0.25
4	11	−0.377	18	−0.017	15	−0.048
5	15	−0.144	7	−0.212	6	−0.167
6	—	—	—	—	9	−0.215
Average	10.6	−0.219	9.4	−0.124	10.5	−0.152

Table 3 F-statistics and estimates of genetic relatedness for the three groups of newly founded populations of *Phalacrus substriatus*. Jack-knifed standard errors are given in parentheses. Values significantly different from zero are given in bold

Island	F_{IT} (SE)	F_{ST} (SE)	F_{IS} (SE)	r (SE)
1	−0.118 (0.060)	**0.080** (0.013)	**−0.219** (0.053)	**0.181** (0.040)
2	−0.012 (0.030)	**0.099** (0.008)	**−0.124** (0.026)	**0.200** (0.013)
3	**−0.047** (0.005)	**0.093** (0.026)	**−0.152** (0.025)	**0.195** (0.032)

Table 4 The calculated effective number of mates, M_e, for *Phalacrus substriatus*

Island	M_e	95% C.I.
1	1.34	0.89–2.72
2	1.51	1.15–2.21
3	1.53	0.84–8.36

female's brood may be greater than the figure of one or two males estimated here.

Because the genotypes of the maternal founders are known it is also possible to detect multiple paternities in a group of individuals by demonstrating incompatible genotype classes in the offspring. Multiple paternities can be confirmed whenever more than three paternally derived alleles can be identified in the brood of a single female (McCauley & O'Donnell, 1984; Costa & Ross, 1993). However, as only one enzyme system in this study (Acn) had more than two common alleles, it is difficult to infer multiple paternities based on this method. Of the four populations that were founded by single females it is possible to identify unambiguously more than three paternal alleles in only two of the populations (population 1 on island 2 and population 2 on island 3). When populations are founded by multiple females, it is even more difficult to find evidence for multiple paternities because the number of alleles required to demonstrate multiple paternities unambiguously is dependent upon the number of females in the population. Given the lack of enzyme systems with more than four alleles, this method is effectively ruled out for detecting multiple paternities in these populations. Although these data are inconclusive, they provide some indication that the offspring in some broods of *P. substriatus* can be sired by more than one male.

The effective population size averaged over all three islands was 5.2 (Table 5). This value is slightly larger than the estimate of 4.0 provided in Ingvarsson *et al*. (1997), where we assumed that females were mated to a single male.

Discussion

'Kin-founding', the founding of new populations by groups of relatives, is known to enhance the effects of population turnover, because kin-structuring reduces the effective population size of the founding groups (Lawrence, 1986; Whitlock & McCauley, 1990). Newly colonized populations of *P. substriatus* show a characteristic kin-structuring which can largely be attributed to the dispersal biology and mating patterns of the female beetles. Dispersal in *P. substriatus* is strongly female-biased and male beetles are rare in recently established populations (Ingvarsson *et al*., 1997). Consequently, most females will be inseminated in their native population, prior to dispersal. Moreover, dispersal distances are short, of the order of a few metres (Ingvarsson *et al*., 1997), resulting in only a few source populations being represented among the colonizing individuals. This increases the potential kin-structure even further because the different founding females may either be related or may share some of the mates in their native population.

Both the estimates of M_e and the data on incompatible genotype classes in the offspring show that female beetles may be multiply mated, although the effective number of mates per female appears to be low, 1.5 or less. Multiple matings reduce the average relatedness among offspring in the brood of a single female. The extent to which relatedness is reduced depends both on the number of males a female mates with and also on variation in reproductive apportionment among different males (Wade, 1985a). However, the effective number of mates is given by the harmonic rather than the arithmetic mean and, therefore, females with low effective numbers of mates will have a disproportionately large influence on the average relatedness in a population (Wade, 1982, 1985a). Thus, even though some female beetles mate with multiple males, the net effect on the average relatedness in a newly colonized population will be only slightly affected. Moreover, the number of female founders in general exerts a much larger influence on the average relatedness in newly colonized populations than does the average number of matings per female (Wade, 1978, 1985a).

The effective population size of the founding groups estimated here ($k_e = 5.2$) is somewhat higher than previously estimated. Ingvarsson *et al*. (1997) used demographic data from naturally occurring

Table 5 The effective population sizes, k_e, for the different newly colonized populations of *Phalacrus substriatus*

Island	k_e	95% C.I.
1	5.51	4.53–7.02
2	4.99	4.43–5.7
3	5.12	3.87–7.57

colonizations and estimated k_e to be 4.0. This conclusion was reached without prior knowledge of the specific mating patterns of *P. substriatus*, by assuming that every female was, on average, mated to a single male. The data presented here show that the assumption of $M_e = 1$ is an underestimate of the true M_e and, consequently, leads to a k_e estimate which is too low. The effective population size is about double the population size estimate by a simple count of individuals. This somewhat paradoxial observation arises from the fact that, because colonization is almost exclusively achieved by females, observing the number of colonizers ignores the contribution of males that are only 'present' in the form of stored sperm in the colonizing females. This observation highlights the importance of specifically taking demographic processes, such as mating and dispersal patterns, into account when trying to work out the effect of population turnover.

In the earlier study we also suggested that the probability of common origin among colonizers, ϕ, was at least 0.5 but did not provide a more exact estimate because we only had data on the number of source populations from five newly colonized populations. The more detailed data set presented here provides an opportunity to estimate ϕ more precisely. The probability of common origin when alleles move only in diploids (in dispersing females) can be calculated according to Whitlock & McCauley (1990, eqn 7). Using their equation the probability of common origin of diploid individuals, averaged over all newly founded populations, is 0.78. This translates into an estimate of ϕ equal to 0.80, almost 60% greater than previously estimated. Although the size of the extant populations of *P. substriatus* is small ($n = 11.1$), newly founded populations are about 60 per cent smaller ($k_e = 5.2$). Because the strength of genetic drift is proportional to the reciprocal of the population size, the bottleneck at the time of colonization generates an additional opportunity for genetic drift to act. As a result, the founding event will convert genetic variation within populations to variance among populations, therby increasing the genetic differentiation among populations.

The conversion of genetic variation from within to among populations opens up the possibilities for group and kin selection, processes that require substantial genetic variation among groups to operate successfully (Uyenoyama & Feldman, 1980, Wade, 1985b). Consequently, demographic processes that increase the among-group component of genetic variation, such as population turnover and/or kin-structuring, will generate conditions that are more favourable for the evolution of group-specific traits; for example, in a series of studies of the imported willow leaf beetle, *Plagiodera versicolora*, Wade and his colleagues have shown that the evolution of social behaviours in this beetle are determined by a balance between selection at two levels of population structure (McCauley *et al.*, 1988; Breden & Wade, 1989; Wade, 1994 and references therein). The study of McCauley *et al.* (1988) showed that there was variation in group relatedness in individual larval colonies, both between different localities but also between years at any given locality. They argued that this could lead to situations where ecological conditions favoured the evolution of social behaviours in some generations and locations but not in others. They also pointed out the importance of both within-population demographic processes and turnover of local populations as factors for determining the outcome of the evolution of social behaviours. Whether selection at different hierarchical levels of population structure (within and between groups) will be of importance in *P. substriatus* remains to be seen. However, the typical nonequilibrium population structure documented in this and previous studies does provide a background that is generally favourable for such evolution to occur.

Acknowledgements

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