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# How does genetic diversity change towards the range periphery? An empirical and theoretical test

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## ABSTRACT

**Question:** How does genetic diversity change as one moves along a species' range, towards the periphery? Previous work shows contradictory evidence for an increase, decrease or no clear trend along the range.

**Hypothesis:** A hump-shaped unimodal pattern of within-population genetic diversity will occur along the range with peak diversity in sub-peripheral populations. This hypothesis incorporates and explains some of the apparent contradictions found in the literature.

**Organism:** Thirteen native chukar partridge (*Alectoris chukar*) populations.

**Location:** A steep environmental gradient towards the periphery of the species' range in Israel.

**Methods:** Genetic diversity was estimated in 26 allozyme loci.

**Conclusions:** A unimodal pattern of within-species genetic diversity, as expressed by measures of heterozygosity, is found along the range. Diversity peaks at the sub-periphery of the chukar range. These populations are located at the ecotone between the Mediterranean and desert climatic regions.

**Appendix:** A mathematical model that explores possible mechanisms generating the unimodal pattern. The model suggests that a unimodal pattern can appear under a range of parameters.

*Keywords*: *Alectoris chukar*, distribution range, genetic diversity, Israel, range periphery, sub-periphery.

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## INTRODUCTION

### Patterns of within-species diversity across the distribution range

How does genetic diversity change over a species' range, and especially as the edge of the range is approached? This question has attracted attention for decades, much of it within the framework of the quest to better understand speciation mechanisms. In recent years, the issue is receiving attention in the face of the rapid threats to biodiversity and the need to provide a venue for evolutionary processes to continue (Smith *et al.*, 2001). In the latter context, studies have focused on patterns and processes shaping range boundaries (e.g. Hoffmann and Blows, 1994; Kirkpatrick and Barton, 1997; Case and Taper, 2000; Holt and Keitt, 2000) and have compared genetic and phenotypic diversity in core versus peripheral populations (e.g. Brussard, 1984; Lammi *et al.*, 1999; Kark *et al.*, 2004).

The literature of recent decades suggests that populations located at the geographical periphery of species' distribution ranges often experience unfavourable ecological conditions (biotic and/or biotic) (Brown, 1984; Wiens, 1989; Gaston, 1990; Brown *et al.*, 1995; Lomolino and Channell, 1995) that lead to reduced fitness and population density (Hoffmann and Blows, 1994; Lesica and Allendorf, 1995; Brown *et al.*, 1996). These populations eventually fade out, and mark the edge of the species' range, a dynamic region that may shift with changing environments (Eldredge, 1995). Further in towards a species' core distribution lies what might be termed the distribution's 'sub-periphery', beyond which populations become ephemeral, increasingly discontinuous (Brown *et al.*, 1996; Lennon *et al.*, 1997), isolated, and more patchily distributed (Boorman and Levitt, 1973; Carter and Prince, 1988; Brown *et al.*, 1996).

At a regional spatial scale encompassing a species' range, three hypotheses concerning trends of within-population genetic diversity across the geographical distribution range, as the periphery is approached, have dominated the literature in the past 70 years (reviewed in Brussard, 1984; Hoffmann and Blows, 1994; Safriel *et al.*, 1994). The first hypothesis postulates that genetic diversity will decrease towards the periphery of the range (Carson, 1959; Mayr, 1963; Lewontin, 1974). This hypothesis assumes that core populations are contiguous, dense, and thus maintain high within-population diversity, whereas peripheral populations are small, isolated, and sparse and thus show lower genetic diversity (Carson, 1959; Mayr, 1963). The hypothesis is supported by 50-year-old observations (e.g. Da Cunha and Dobzhansky, 1954), as well as more recent ones (Hoffmann and Parsons, 1991; Parsons, 1991; reviewed in Lesica and Allendorf, 1995). A second, contradictory, hypothesis predicts that genetic diversity will increase towards the range periphery. Under this hypothesis, peripheral populations are expected to maintain higher genetic diversity than populations from non-peripheral areas of the range. This hypothesis is attributed to the fluctuating conditions at the periphery of the range, which generate diversity within populations over time (Fisher, 1930; Burger, 1988; Hoffmann and Parsons, 1991; Parsons, 1991). This hypothesis, too, is supported by data (e.g. Nevo, 1988; Hoffmann and Parsons, 1991; Parsons, 1991). Finally, the third (null) hypothesis predicts no changes in diversity across the range, hence no clear spatial trends in within-population diversity. This hypothesis has also gained empirical support (Mayr, 1970; Brussard, 1984). These three hypotheses generate three different, contrasting predictions as to the spatial patterns of genetic diversity across a species' range moving towards the periphery. Thus, the literature reveals inconsistencies and apparent contradictions (Parsons, 1989; Safriel *et al.*, 1994). The resolution of these contradictions is becoming increasingly important in the face of population declines and the need to take into account the within-species component in conservation planning.

## Factors contributing to the discrepancies

Some of the contradictions may reflect differences between species and ecological systems or between the genetic and/or morphological diversity markers studied and the methodology used. Within-population genetic diversity can be affected by natural selection, population dynamics, genetic drift, and other stochastic processes. Over the past five decades population genetics studies have used a wide range of approaches, such as chromosomal arrangements, allozyme variants, and nucleotide substitutions, with increasing emphasis on diversity at the DNA level in recent decades. Different markers can show different patterns. Their frequencies in populations can change in response to different pressures and types of selection, or as a result of various population dynamics, isolation, genetic drift, and other stochastic fluctuations (neutral processes) (Nei, 1973).

The frequencies of neutral markers will also vary according to historical and current population factors (e.g. effective population size, demographic fluctuations, bottlenecks, random genetic drift, rates and direction of gene flow). Thus, the patterns of genetic diversity found in populations across a species' range may be controversial with regard to whether the markers are 'neutral' or 'naturally selected'. For example, Carson's (1959) and Mayr's (1963) original theories implicitly refer to a neutral model of gene diversity: large core populations maintain higher diversity because they can harbour more mutations and because they are less vulnerable to drift.

However, the differences between methodologies used in different studies cannot entirely resolve the contradicting empirical results. Even within a single measure of genetic diversity, such as allozyme diversity, contradictory results have been often obtained in different studies comparing diversity patterns within populations across species ranges (see Brussard, 1984; Hoffmann and Parsons, 1991). Therefore, other factors must be involved in generating the discrepancies. One possibility is that in the search for linear patterns, non-linear patterns, which can explain some of the contradictions, may have been overlooked. In addition, studies of core versus periphery often compare two main distribution areas, the one representing the core and the other the periphery (e.g. Siikämaki and Lammi, 1998; Volis *et al.*, 1998; Channell and Lomolino, 2000). Populations are sampled to represent the two main regions, following a dichotomous approach, rather than a more continuous one. However, even when we attempt to sample the range continuously, species' ranges are rarely continuous over space, and the degree of their patchiness depends on the scale at which sampling is done.

In addition, the definitions and logic behind the selection of core versus peripheral areas may differ between studies. As discussed in Schwartz *et al.* (2003), a problem in comparisons of core versus periphery has been the lack of operational definitions, and only few recent studies have addressed this issue. In some cases, samples from the very edge of the range represent peripheral populations. Yet due to scarcity of populations, their small size, and spatial discontinuity near the distribution margins, the populations sampled to represent the periphery may not occur at the very periphery of the range. Some authors divide the distribution range dichotomously into core and periphery, following geographical (geometrical) or ecological criteria. For example, Channell and Lomolino used two approaches: dividing the range into two equal area belts (Lomolino and Channell, 1995), and taking the area falling within a ring around half the distance between a central point and the nearest edge (Channell and Lomolino, 2000). In a study of lynx populations in North America, Schwartz *et al.* (2003) used a biologically based definition, which derives from the size of the home range of the individuals.

We propose that to accurately identify patterns of genetic diversity, and better understand the processes shaping them, we need to focus on sites towards the edge of the range, specifically targeting sections of the range in which non-linearity in ecological conditions occurs, such as in climatic transition areas. Thus the focus will be on populations that are geographically peripheral and ecologically marginal. Sampling along a continuum from these edge populations towards populations that are located (geographically) farther away from the edge will therefore allow peripheral populations to be contrasted with less peripheral populations that often occur in ecologically more favourable areas.

Sampling along a more continuous gradient enables us to identify changes in within-population diversity as we approach the very periphery, and to compare different sections of the outer parts of the range. While this does not require sampling of the whole range, it generates a better understanding of what happens as the geographical periphery is approached than does a simple dichotomous comparison of core and margin. Note also that different kinds of genetic variation (e.g. selected and neutral) can lead to different patterns of diversity. Here, in both our fieldwork analyses and theoretical model (see Appendix), we have chosen to concentrate on one type of genetic variation that has the potential to play some role in adaptation – weakly selected alleles.

## Towards reconciling the contradiction

In this paper, we propose a unifying hypothesis to reconcile the contrasting theories on changes in genetic diversity as one approaches a range margin. To do so we must first clarify terms. The range 'periphery' is here defined as the area beyond which a species' density declines to zero, and where populations are at or near the very edge of the species' range. Further towards the distributional core is an intermediate sector sometimes called the 'turnover zone'. This term is borrowed from a simulation study of range dynamics by Lennon *et al.* (1997), who showed that in the turnover zone, the cell (i.e. population) occupancy fell off steeply, leading to 'rapid spatial thinning of populations' (Lennon *et al.*, 1997, p. 495; see also Carter and Prince, 1988). This area we call the 'sub-periphery' of the range, an area located between the core and the periphery (often rather closer to the periphery) where the species approaches the edge of its more dense and continuous distribution. Thus, sub-peripheral areas are in many cases expected to overlap with areas of sharp environmental transition [i.e. ecotones (see Kark and van Rensburg, 2006)].

We propose here that for many species genetic diversity may be expected to peak in such sub-peripheral regions of a distribution, rather than in the extreme periphery or the distributional core, as is generally thought. This is due to the combination of fluctuating environmental conditions and moderate levels of gene flow typically found in such sub-peripheral regions, with lower genetic diversity expected both in core areas (where conditions are more stable) and in the extreme range periphery (where populations tend to be small and isolated). The idea is presented in greater detail in the Appendix to this paper, where we develop and simulate a model that examines several (though not all possible) scenarios that may lead to the predicted diversity pattern. For example, when different alleles at a certain locus have different effects on the fitness, and population patchiness increases from the core to periphery, heterozygosity in this locus would often peak in the sub-periphery. Our proposed hypothesis encompasses several classical predictions concerning genetic diversity in peripheral versus core populations, which become special

cases. Under this hypothesis, some of the apparently contradictory earlier hypotheses become complementary and can each explain a portion of the overall trend.

In this study, we test the hypothesis in a model species, the chukar partridge (*Alectoris chukar*), along a periphery–sub-periphery–core transect. This case study represents one transect along a distributional gradient, but we predict that similar patterns may be seen for other similar transects. We use a natural setting that enables testing the above hypotheses and predictions – a steep climatic gradient moving away from the very extreme periphery of the species' global range at the Negev Desert of Israel, through the species' sub-periphery, positioned at the ecotone between Mediterranean-type and desert ecosystems, towards the more inner parts of the range in the Mediterranean climatic regions.

## METHODS

### The eco-geographical gradient in the study area

A sharp climatic and ecological gradient occurs in Israel from Mediterranean to desert ecosystems. Numerous species reach the margins of their Mediterranean, Irano-Turanian, and Saharo-Arabian distributions along this gradient (Yom-Tov and Tchernov, 1988; Danin, 1998). Mean annual rainfall in the northern Mediterranean regions of Israel in the Galilee and Golan Heights reaches 850 mm (Table 1). Yet only 300 km away in the southern Negev Desert, mean annual rainfall decreases to less than 50 mm and is highly variable over time (Bitan and Rubin, 1991). An especially steep climatic gradient occurs in the northern Negev, where the ecotone between Mediterranean and desert ecosystems is located (Danin, 1998). In this area, rainfall decreases from over 450 mm to less than 150 mm within approximately 50 km. Many animal and plant species reach the edge of their continuous distributions in this area (Yom-Tov and Tchernov, 1988; Danin, 1998). This setting provides a good opportunity to compare trends in genetic diversity as a species' range periphery is approached in populations that are geographically close, yet experience substantially different environmental conditions.

### Chukar partridge distribution

The chukar (*Alectoris chukar*) is continuously distributed in Israel with high population densities in the Mediterranean climatic regions in the north and centre of Israel (Shirihai, 1996). The sub-periphery (turnover zone) for the species falls in the Mediterranean–desert ecotone, where rapid spatial thinning of chukar populations occurs across short geographic distances (Shirihai, 1996). The distribution becomes patchy and populations become smaller and more isolated south of the ecotone towards the central and southern Negev Desert, where the global periphery of the species' distribution range occurs (Shirihai, 1996). Beyond this area, only a single isolated population, most likely a relict from the Pleistocene, is found in the mountains of the Southern Sinai Desert (Kark *et al.*, 1999). Substantial information is available on the species' biology, distribution (Shirihai, 1996), morphological diversity (Kark *et al.*, 2002), evolutionary history, developmental instability (Kark, 2001; Kark *et al.*, 2001), and physiology (Degen *et al.*, 1984; Carmi-Winkler *et al.*, 1987). The chukar global distribution extends to Turkey in the north and to Central China in the east (although a different sub-species occurs there) (Cramp and Simmons, 1980; Jonsson, 2006). However, the steep gradient in Israel results in environmental conditions in the northern parts of the chukar local range being more similar to those in more northern areas many hundreds of kilometres away than the conditions in the arid desert

**Table 1.** Location and population characteristics and estimates of allelic diversity for chukar populations sampled across the distribution range towards the range periphery in Israel

| Population | Region | Distance to periphery | Mean annual rainfall | Mean temperature | | $n$ | SE $n$ | Mean Ho | SE Ho | Mean He | SE He | Mean A | SE A | %P |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | | | | Jan | Aug | | | | | | | | | |
| Tel Mahfi | Mediterranean | 408 | 847 | 5.2 | 23.2 | 27.0 | 0 | 0.052 | 0.026 | 0.069 | 0.036 | 1.5 | 0.2 | 26.9 |
| Pazra Hill | Mediterranean | 395 | 704 | 6.0 | 24.4 | 24.7 | 0.2 | 0.063 | 0.029 | 0.076 | 0.036 | 1.5 | 0.2 | 26.9 |
| Lawiya-Ramot | Mediterranean | 372 | 499 | 9.3 | 27.0 | 24.1 | 0.7 | 0.079 | 0.031 | 0.080 | 0.032 | 1.4 | 0.2 | 26.9 |
| Bezek Reserve | Mediterranean | 316 | 378 | 9.4 | 25.8 | 26.9 | 0.4 | 0.086 | 0.037 | 0.094 | 0.039 | 1.4 | 0.2 | 17.5 |
| Ben-Gurion Airport | Mediterranean | 264 | 576 | 12.1 | 26.0 | 24.7 | 0.5 | 0.093 | 0.031 | 0.105 | 0.038 | 1.5 | 0.2 | 30.8 |
| Luzit | Mediterranean | 233 | 430 | 11.4 | 25.9 | 28.2 | 0.3 | 0.092 | 0.036 | 0.094 | 0.038 | 1.6 | 0.2 | 30.8 |
| Gvaraam | Ecotone (sub-periphery) | 218 | 432 | 12.1 | 25.3 | 25.9 | 0.1 | 0.120 | 0.043 | 0.115 | 0.041 | 1.6 | 0.2 | 30.8 |
| Yatir | Ecotone (sub-periphery) | 199 | 255 | 9.3 | 25.0 | 19.8 | 0.1 | 0.106 | 0.037 | 0.107 | 0.038 | 1.5 | 0.2 | 34.6 |
| Hirbet Sira | Ecotone (sub-periphery) | 196 | 285 | 10.2 | 25.5 | 28.7 | 0.2 | 0.103 | 0.036 | 0.107 | 0.038 | 1.6 | 0.2 | 34.6 |
| Nevatim | Ecotone (sub-periphery) | 182 | 191 | 10.4 | 26.3 | 28.8 | 0.2 | 0.111 | 0.040 | 0.114 | 0.041 | 1.5 | 0.2 | 30.8 |
| Sede Boqer | Desert (periphery) | 148 | 115 | 9.9 | 25.3 | 27.6 | 0.2 | 0.073 | 0.032 | 0.096 | 0.040 | 1.5 | 0.2 | 26.9 |
| Ramon | Desert (periphery) | 129 | 93 | 9.2 | 24.1 | 31.7 | 0.2 | 0.096 | 0.037 | 0.100 | 0.037 | 1.5 | 0.2 | 34.6 |
| Faran | Desert (periphery) | 86 | 33 | 11.6 | 27.9 | 25.8 | 0.2 | 0.094 | 0.035 | 0.105 | 0.039 | 1.5 | 0.2 | 30.8 |

*Note*: $n$ = mean sample size per locus, SE = standard error, Ho = mean observed heterozygosity, He = mean expected heterozygosity (unbiased estimate based on Hardy-Weinberg equilibrium), A = mean number of alleles per locus, %P = percentage of polymorphic loci (a locus is considered polymorphic when more than one allele is detected). Populations are listed from north to south. Distance from the range periphery (marked in Fig. 1) is in kilometres. Details on the analytical procedures used for generating the climatic maps and their accuracy can be found in Kurtzman and Kadmon (1999).

areas only several dozens of kilometres away. This leads to sharp changes in population densities across the range over short distances and allows us to study changes in genetic variability across a steep environmental gradient over short geographical distances. This also allows us to examine genetic trends as the edge of the range is approached, while minimizing differences associated with human-related histories, climatic changes, and other large-scale processes that occur when very distant populations are compared. Chukars are relatively sedentary and do not exhibit known latitudinal or altitudinal migrations (Shirihai, 1996). Coveys usually remain within a limited area of several square kilometres (Alkon, 1974). Chukars are native to the region and there has been no restocking or introduction of birds from other regions in Israel for hunting purposes, and thus any natural genetic patterns are likely to be relatively undisturbed. Chukar hunting was allowed in Israel in the past, but we chose study sites that had minimal levels and impacts of hunting.

### Sampling and genetic analysis

Between September 1995 and early February 1996, thirteen populations of chukars were sampled in Israel across the distributional gradient from the periphery inwards, from the northern Golan Heights to the southern Negev (Fig. 1). The sampling included four populations from the Mediterranean–desert ecotone region, which represents the species' sub-periphery (Table 1). Birds were sampled by the Israel Nature and Parks Authority rangers and authorized hunters during the non-breeding season when the birds organized into stable coveys (flocks) that maintain relatively fixed home ranges (Alkon, 1974). In most cases one bird (rarely two) was sampled from each covey. To enable comparison, the sampling was done within the same size area (~10 $km^2$) over all regions. This also enabled the sampling of distinct local populations and provides a consistent sampling scale in our results. Between 20 and 32 birds were sampled from each population (Table 1). Heart and liver tissues were dissected from birds in the field, stored in ice coolers, and transferred within several hours to laboratory freezers kept at −20°C or −80°C, except for three populations, in which the birds were dissected in the laboratory. Samples of each tissue were separately homogenized and clear supernatants were collected and stored at −80°C in aliquots. Polyacrylamide gel electrophoresis, staining of allozyme products, and genetic interpretation of electromorph mobility were performed following Randi and Alkon (1994). Twenty-six putative loci were resolved [see Randi and Alkon (1994) for list of loci analysed, except for PEP-2, LDH, SOD-2, mGOT, mIDH, and GDH, which were not resolved here]. Estimates of genetic diversity were computed for each population using BIOSYS-1, v.1.7 (Swofford and Selander, 1989) and GENETIX (Belkhir *et al.*, 2001). These included the mean observed heterozygosity, mean expected heterozygosity based on Hardy-Weinberg equilibrium, and the deviation among the observed and expected values, mean number of alleles per locus, percentage of polymorphic loci, and $F_{st}$-values (Swofford and Selander, 1989). Range periphery was taken as the first square beyond the occupied range in which density decreases to zero based on the density grid system presented in Shirihai (1996), as marked in Fig. 1. Distance from range periphery was measured for each population following Shirihai (1996).

## RESULTS

Nine of the 26 loci studied were polymorphic. Mean observed heterozygosity across all populations ranged between 0.052 and 0.120, mean expected heterozygosity between 0.069

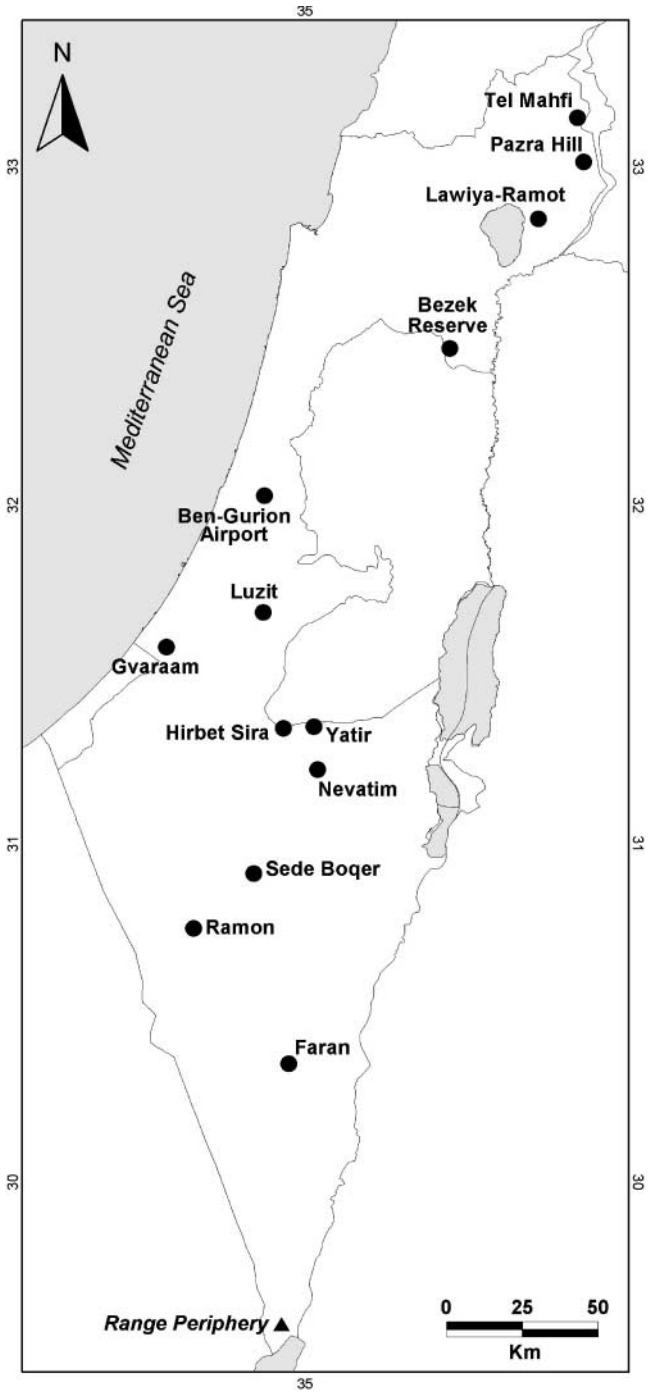


**Fig. 1.** Map of the study area and populations sampled. The chukar partridge range periphery based on Shirihai (1996) is marked with a triangle.

and 0.115, percentage of polymorphic loci between 26.9% and 34.6%, and mean number of alleles per locus between 1.4 and 1.6 (Table 1). No significant correlation ($P > 0.3$) was found between mean sample size per locus and any of the genetic diversity parameters tested. Average pairwise $F_{st}$-values ranged between 0.002 and 0.130 and showed a significant positive correlation with geographic distance among the sampling locations (Pearson $r = 0.44$; $P = 0.01$). Two rare alleles (in two separate loci) were detected only in ecotone populations, while several other alleles were most frequent in the sub-peripheral parts of the range. A cluster analysis using a Wagner tree produced by rooting at the midpoint of the longest path clustered the three peripheral populations separately. The three peripheral populations separated from all four sub-peripheral populations, which were pooled separately from the non-peripheral Mediterranean locations, within which all three populations from the Golan Heights were pooled together. Similar results were seen when using a Wagner tree produced by rooting at the midpoint of the longest path [in all cases the coefficient used was the Modified Rogers distance (Wright, 1978)], and analysis followed the multiple addition criterion procedure of Swofford (1981) and Prager and Wilson (1976). *F*-values were used in selecting partial networks (Swofford and Selander, 1989). These results were also consistent with a cluster analysis using an unweighted pair group method using the Modified Rogers distance coefficient (Wright, 1978).

## Trends in genetic diversity in the chukar partridge in Israel

As predicted, when approaching the range periphery of the chukar partridge in Israel, genetic diversity first rises and then falls towards the very extreme periphery. Peak levels of diversity are obtained for the sub-peripheral populations from the Mediterranean–desert ecotone region (Fig. 2A). A quadratic regression, which better models the unimodal pattern, is highly significant for expected heterozygosity based on Hardy-Weinberg equilibrium ($r^2_{\text{quadratic}} = 0.83$, $P = 0.0001$) and for observed heterozygosity based on a direct count ($r^2_{\text{quadratic}} = 0.70$, $P = 0.0025$). Similar relationships are obtained when the arcsine of mean heterozygosity is taken. The majority of loci are in Hardy-Weinberg equilibrium in most regions. A significant quadratic relationship is also found between mean annual rainfall (see Table 1 for climatic data) in each of the study locations and both expected heterozygosity based on Hardy-Weinberg equilibrium ($r^2_{\text{quadratic}} = 0.58$, $P = 0.002$) and observed heterozygosity ($r^2_{\text{quadratic}} = 0.60$, $P = 0.01$). The linear regression coefficients are lower ($r^2_{\text{linear}} = 0.45$ and $r^2_{\text{linear}} = 0.31$, respectively). Significant quadratic and linear relationships are found between mean temperature in the coldest month, January, and both expected and observed heterozygosity estimates ($r^2_{\text{quadratic}} = 0.60$, $P = 0.002$ and $r^2_{\text{quadratic}} = 0.66$, $P = 0.0007$, respectively) but for the summer month of August the regression coefficients are lower and are non-significant.

To examine the potential effect of sampling, we examined the trends and results obtained when excluding certain sections of the range and comparing the results with those obtained using the full range of our study data. As predicted, when only a portion of the chukar range in Israel is analysed, contradictory patterns appear (Fig. 2). When the analysis excludes the extreme periphery, a statistically significant trend showing increasing diversity from the core towards the periphery of the range appears (Fig. 2C). When the populations from the inner areas of the range are excluded and only populations from the periphery to the sub-periphery are included in the analysis, an opposite trend appears, with a (statistically non-significant) decline in diversity towards the range periphery (Fig. 2B). When the

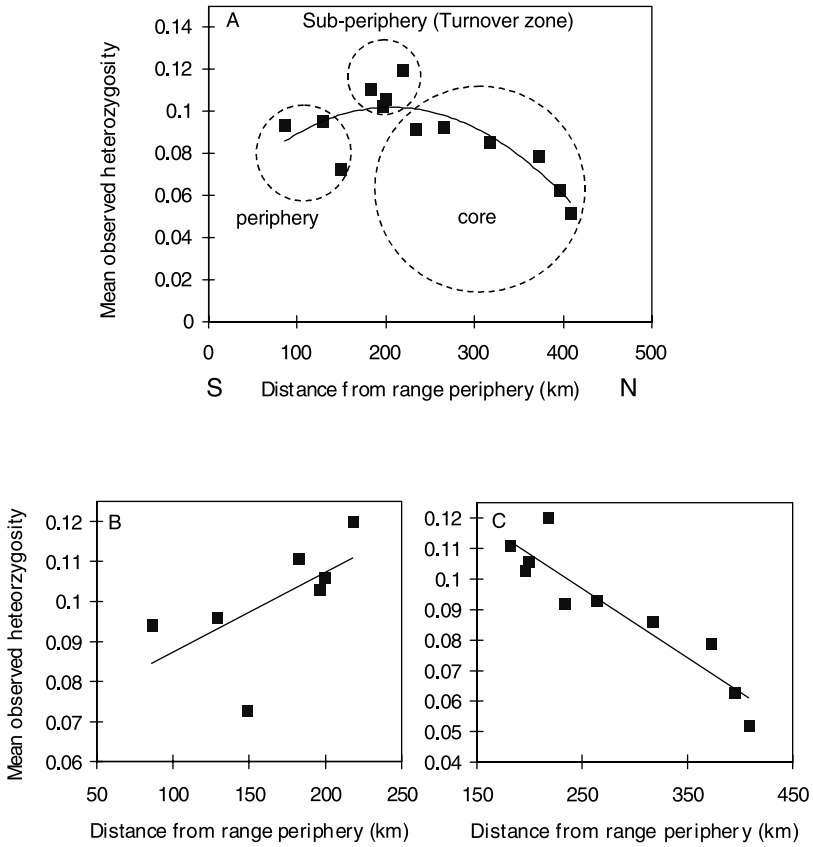


**Fig. 2.** Trends in within-population genetic diversity over the chukar partridge range in Israel, as estimated by mean observed heterozygosity (direct count) versus distance of the study population from the range periphery (marked in Fig. 1). South and north are marked in (A) as S and N, respectively. Panel (A) shows trends across all 13 populations sampled with quadratic regression fit ($r^2 = 0.70$, $P = 0.0025$). Findings for the part of the range from the periphery to the sub-periphery only are shown in (B) with linear regression fit ($r^2 = 0.39$, $r = 0.63$, $P = 0.13$). Panel (C) shows the trends for populations sampled from the sub-periphery towards the core alone, excluding the periphery ($r^2 = 0.86$, $r = -0.93$, $P = 0.0001$).

sub-periphery is excluded from the analysis and only more inner areas versus the periphery are compared, the unimodal pattern completely disappears. Only when a more continuous gradient is sampled from the periphery through the sub-periphery inwards is the unimodal pattern unveiled (Fig. 2A).

## DISCUSSION

Within-population genetic diversity, as estimated by mean allozyme heterozygosity, shows a unimodal pattern in Israel as the chukar partridge range periphery is approached. Peak levels of diversity occur in sub-peripheral populations located in the northern Negev ecotone region. From here, diversity declines towards both the core area and the periphery

of the range. A quadratic regression of population mean heterozygosity versus its distance from the range periphery is highly significant for both observed and expected heterozygosity. These results are congruent with a unimodal pattern of phenotypic diversity found in a study of morphological traits in the same species in Israel and the region (Kark *et al.*, 2002).

## The classical hypotheses are special cases

These results suggest that partial sampling of a species' range may lead to contradictory conclusions regarding the patterns of genetic diversity occurring from core to periphery. They accommodate the two classical hypotheses on core–periphery diversity, as well as the null case in which no clear trends exist across the range. Indeed, our results show that considering only subsets of the genetic gradient could have resulted in data supporting any of the three hypotheses, depending on which regions of the distribution were compared. Only when the sampling includes areas extending over a more complete gradient from the extreme periphery through the sub-periphery to the core does the hump-shaped pattern appear. These results support the unifying hypothesis raised earlier in this paper.

Conflicting results between studies focusing on different species may also arise due to differing spatial patterns in the distribution of different species. For example, the spatial distribution of some species does not include isolated peripheral populations (Caughley *et al.*, 1988) due to an abrupt step-shaped distribution edge caused by environmental or biotic changes that result in a sharp distribution barrier (Caughley *et al.*, 1988; Brown *et al.*, 1996; Kirkpatrick and Barton, 1997; Lennon *et al.*, 1997).

## Possible factors contributing to the unimodal pattern

### *Historical factors*

One could hypothesize that the high diversity found in chukar partridges in the Mediterranean–desert ecotone region is a result of secondary contact of previously isolated populations in a hybrid zone, which may be congruent with the turnover zone. Re-contact of these populations could potentially result in high diversity in the area of contact (Barton and Hewitt, 1989). Indeed, hybridization has been shown to increase diversity in various species (Barton and Hewitt, 1989). Thus secondary re-contact of formerly divergent and isolated populations in a hybrid zone with introgression seems a compelling, simple theory to explain diversity trends in Israeli chukars across the ecotone. If this is the case, re-contact of formerly isolated populations in the region following the Quaternary may have led to hybridization and to increased genetic diversity in the region. Morphological studies and paleontological work suggest that chukar distribution in this region in the past 120,000 years has been contracting rather than expanding (Nissani, 1974; Yom-Tov and Tchernov, 1988). This may have contributed to the patterns seen in the chukar case (Randi *et al.*, 2006). However, if re-contact were the primary factor generating diversity in the ecotone area, we would expect that the elevation in genetic diversity in this region would have been generated by the combination of two separate sets of alleles from the core and the periphery meeting at the intermediate area and thus generating high diversity, or by the combination of the same alleles with different frequencies in the two allopatric population systems. Yet the elevated diversity seen in chukars from the ecotone area is due to greater heterozygosity and higher

polymorphism, caused by the appearance of new rare alleles (the appearance of such alleles could also be a consequence of genetic drift during propagule colonization resulting from recombination), and by an increase in the frequency of rare alleles compared with other populations. As suggested by Randi *et al.* (2006) in an analysis based on mDNA, the observed genetic structure of chukar populations in Israel has likely been determined by a combination of complex historical processes (past fragmentation in allopatry and range expansion) and demographic processes related to long- and short-range dispersal across the environmental gradient.

### *Spatial ecological factors*

The hypothesis predicting a unimodal pattern, as supported in the chukar case study, is based on both population dynamics and natural selection (see theoretical model in Appendix). Although the chukar has a wide range in Israel, where the edge of its global range is approached, we find a steep change in multiple climatic and other environmental factors over relatively short distances that strongly influence the chukar population structure and diversity. Indeed, the levels of developmental instability increase substantially towards the range periphery, suggesting that environmental and genetic stress increase towards the range periphery (Kark, 2001). This may also lead to an increase in mutation rate (Lamb *et al.*, 1998; Hoffmann and Parsons, 1991). It has been shown in many species that when moving towards the periphery of a species' range, population densities often decrease and become temporally and/or spatially fluctuating (Brussard, 1984; Wiens, 1989; Brown *et al.*, 1996). At the periphery, the distribution patterns tend to become less continuous (Brown *et al.*, 1996) and populations become more transient, isolated, and patchily distributed (Boorman and Levitt, 1973), although exceptions exist (Lawton, 1996). Local populations at the extreme periphery exist in isolated and infrequent patches of suitable environment and often experience low rates of gene flow, repeated bottlenecks, and random genetic drift (Hoffmann and Blows, 1994). This would result in reduced genetic diversity within each population at the periphery. Founder effects, caused by the recolonization of peripheral populations by a small number of individuals (Wiens, 1989), further reduce persistence and diversity (Kirkpatrick and Barton, 1997). Thus local sub-populations at the extreme periphery of the range will generally maintain low within-population diversity. However, if many peripheral sub-populations are considered over a larger geographical area, the cumulative genetic diversity over the whole periphery combined may be high again. While within sub-population diversity may decrease towards the extreme periphery of a species' range, between sub-population diversity may rise, if different populations drift towards fixation of different alleles. The spatial scale examined may affect the patterns of genetic diversity seen within and between populations and the definition of a population. Different spatial resolutions might reveal contrasting patterns of core–margin genetic diversity shifts and this may have contributed to some contradictions in the literature. This study was not designed to compare sub-populations within each of the populations studied, so we cannot say whether this is the case here, but it would be interesting to compare genetic diversity within local sub-populations and measure rates of dispersal within and among study populations in future studies.

In the inner core areas of the range, located farther away from the periphery, where environmental conditions are more optimal, it is harder to predict when genetic diversity will decline. This will largely depend on the relationship between spatial and temporal heterogeneity in the core. An interesting possibility is that when populations here are larger and more continuous (Brown, 1984; Hoffmann and Blows, 1994; Lomolino and Channell, 1995) and adaptive

traits (or linked genes) are considered, only those genotypes most adapted to the ecological conditions in the core will prevail (Karlin, 1982). New genotypes, added by dispersal or mutation, will have less chance of competing with the more established ones, which persist in stable, long-lived populations (Lennon *et al.*, 1997). This may lead to relatively low diversity in the inner core areas to a degree which will also depend on the spatial and temporal heterogeneity of these regions.

Finally, in the sub-periphery, within-population diversity is predicted to peak. While populations here are large enough to avoid the effects of genetic drift, levels of gene flow may be sufficient to enable new genotypes to enter the area from neighbouring regions. Genotypes arriving from different peripheries in some years may mix both with each other as well as with those more frequent in the core, leading to a peak in both heterozygosity and the number of alleles. Shifting environmental conditions in both space and time in the transitional area, in which the sub-periphery is often found, allow different alleles to co-exist in temporally fluctuating frequencies that follow the temporally fluctuating environmental conditions. Also, rare alleles can be adaptive under these shifting conditions. Clearly, the precise pattern in each species depends on the interaction between gene flow, population dynamics, mutation, and local selection. The high diversity is likely a result of a combination of high enough gene flow entering the region and the fluctuating and unique environments that give an advantage to unique and rare local alleles.

The hump-shaped pattern in genetic diversity across the distribution range with peak diversity in the sub-periphery is predicted to occur under several implicit assumptions: the distribution limits are caused by abiotic rather than biotic (e.g. predation, interspecific competition) factors; abundance decreases towards the periphery, populations become smaller and more isolated towards the periphery; and similar sized areas are studied across the range (representing populations). We should keep in mind that the degree of continuity depends also on the spatial scale of study, and results may depend on the spatial scale sampled and analysed.

In this study, we focused on the range of a species at a given point in time, assuming that temporal changes occur at a relatively small local spatial scale. Yet we are aware of the fact that species' ranges are dynamic and shift over time such that the location of the core, sub-periphery, and periphery may change. For example, the current sub-periphery of the bird's range in Israel had higher densities in the past when the climate was more mesic and some of the current diversity in the region could be a remnant from the past. However, due to the short distances between sub-periphery and the neighbouring areas, this is likely to have a marginal contribution to current patterns. Different measures of genetic diversity could respond differently to such changes due to their different rates of change. Therefore, the proposed model will be valid mainly in those cases where the short-term temporal shifts of the distribution range occur at a spatial scale that does not lead to restructuring of the main range areas between one generation and the next.

## Analogy to the community level

Theoretical considerations (Tilman, 1982) and empirical results at the community level (Abramsky and Rosenzweig, 1984) indicate a unimodal pattern in species richness along productivity gradients in some cases (reviewed in Waide *et al.*, 1999), partly resolving a prolonged debate between conflicting approaches. Rosenzweig and Abramsky (1993) suggested that the discrepancies in the literature may have partly resulted from the fact that different investigators were looking

at different phases of the gradient, namely, at either the increase or decrease phases rather than at both combined. Only in the latter case is the unimodal trend unveiled. Tilman and Pacala (1993) reason that the prediction of peak species diversity at intermediate productivity is qualitatively similar to that of peak species diversity at intermediate rates of disturbance, also known as the intermediate disturbance hypothesis (Connell, 1978) [see Kondoh (2001) and Kadmon and Benjamini (2006) for a discussion on the relationship between disturbance, productivity, and species richness]. These predictions and evidence are at least partly congruent with the unimodal diversity patterns proposed in this study at the within-species level. Multiple hypotheses have been suggested to explain unimodal species diversity patterns at the community level, as reviewed by Rosenzweig and Abramsky (1993). One of the similarities to the within-species level patterns discussed here is the idea that fewer species can persist at both very high and low primary productivity compared with intermediate levels, possibly due to lower environmental variance or heterogeneity [see discussion on the environmental heterogeneity hypothesis in Rosenzweig and Abramsky (1993) for details]. However, even at the community level, where much more theoretical and empirical work has been done, the processes leading to the patterns (and even the patterns themselves) are not yet entirely clear (Rosenzweig and Abramsky, 1993). As in the case of genetic diversity presented in our study, low species diversity at high productivity levels is the part most difficult to explain. It can result from a variety of processes and is most likely a result of a combination of factors.

## Practical implications

In light of the rapid decline of natural populations (Hughes *et al.*, 1997), there is an increasing perception of the need to set priorities for biodiversity conservation at the within-species level. Our results point at the significance of interconnectedness of different regions along a species' range: the whole might hold considerably more diversity than the sum of the isolated parts. This result is consistent with previous work (Hadany, 2003) that suggested that some migration between areas of different selective pressures may dramatically facilitate complex adaptation. We suggest that sub-peripheral populations deserve further attention as focal points for research and cost-effective conservation efforts aiming to understand the likelihood of maintaining dynamic ecological and evolutionary processes.

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## APPENDIX

### A mathematical model that explores possible mechanisms generating the unimodal pattern suggests that it can appear under a range of demographic and environmental parameters

To better understand some of the factors that may generate a unimodal relationship between heterozygosity and the location of populations along a species' range from its core distribution to the range's boundary, we applied a simple theoretical model. This model does not attempt to cover the whole range of possibilities in the general case or to describe the chukar case study in detail. Instead, the model aims to explore several plausible scenarios under which the unimodal pattern can emerge. We concentrate on weakly selected loci, and assume that the patchiness of the population becomes higher as we approach the periphery. We also assume that the effectiveness of selection against slightly deleterious alleles (which do not have a specific effect on adaptation to the gradient) tends to decrease with the gradient towards the range periphery. Such a change in the effectiveness of selection along the gradient can result from several processes including random drift, reduced intra-species competition, linkage with strongly selected alleles, and possibly a change in the mutation rate. Peripheral populations are relatively small, and thus more prone to genetic drift (Hoffmann and Blows, 1994), resulting in higher expected frequency of weakly deleterious alleles. In addition, peripheral populations may experience an increased mutation rate. An increase in mutation rate towards the periphery can result from an increase in environmental stress caused by factors such as aridity and temperature (Hoffmann and Parsons, 1991; Lamb *et al.*, 1998), though this is not always the case. The net effect of these factors is expected to increase the frequency of the slightly deleterious alleles towards the periphery.

We assumed that the species is distributed along a one-dimensional gradient representing an environmental parameter gradient (e.g. temperature, rainfall). A single locus with two alleles $A$ and $a$ was considered. To try to resemble allozymes (which were used in the genetic analysis of the fieldwork and are either near-neutral or very weakly selected), we assumed that allele $A$ is slightly more advantageous than $a$, such that the relative fitness of genotypes $AA$, $Aa$, and $aa$ are 1, 1-$sh$, and 1-$s$, respectively, where $0 > s$, $h < 1$. However, this advantage is negatively correlated with the ecological gradient. This is in contrast with strongly selected alleles that contribute directly to the fitness of peripheral populations (e.g. genotypes related with stress resistance, such as drought). To simplify the model, we concentrated on the effect of only two factors that change along the distribution range: (a) population subdivision and (b) the intensity of selection. Wright's inbreeding coefficient ($f$) was used as a measure of population subdivision. It increases with the gradient towards the periphery, where populations are patchier. Changes in the frequency of weakly selected alleles along the gradient can result from several processes, including random drift and linkage with strongly selected alleles. Peripheral populations are smaller, and thus are more prone to genetic drift (Hoffmann and Blows, 1994), resulting in higher expected frequency of weakly deleterious alleles. Similarly, weakly deleterious alleles for traits that are not relevant to the gradient may 'hitch-hike' with the strongly selected alleles that are relevant to it. This effect may also increase the frequency of the slightly deleterious alleles towards the periphery, where the selection on the relevant alleles is stronger. The net effect of these two factors is expected to decrease the effective selection on the slightly deleterious alleles. Note that this

is not in contradiction to increased selection towards the periphery on alleles that are directly relevant to the gradient (e.g. stress resistance, such as drought or heat tolerance). For simplicity, we did not explicitly model the underlying causes, but assumed that the selection against weakly deleterious mutations decreases towards the periphery.

Using this simple model, we found that when the selection effectiveness decreases along the distribution gradient towards the periphery, and inbreeding increases along the same gradient (as sub-populations become smaller and more isolated), a unimodal pattern of heterozygosity occurs under a wide range of parameters.

## Model framework

We considered $n$ large populations located along a uni-dimensional gradient, with migration between neighbouring populations. $P_{ij}$ is the frequency of genotype $j$ $\{j \in AA, Aa, aa\}$ in population $i$, whereas $1 \le i \le n$ represents the location of the population along the gradient. The value $i = 1$ represents the periphery of the range, and $i = n$ the population located farthest away from the periphery. For simplicity we assumed that migrants do not move more than one population up or down the gradient over a single generation. Each generation, a frequency $m_{ik}$ of randomly chosen individuals from population $i$ $(1 < i < n)$ disperse to population $k$ for $k = i + 1$, $i - 1$ (in the two boundary cases $i = 1$ and $i = n$ dispersal is to the single neighbouring population, $k = 2$, $k = n - 1$, respectively). In general, both population size and migration rates between populations can vary from one population to another. Symmetric mutation ($A \to a$ and $a \to A$) occurs at rate $\mu$. The dynamics are described in equations (1–8) below.

## Variables used in the model

$P_{ij}$ = the frequency of genotype $j$ in population $i$ before migration
$\tilde{P}_{ij}$ = the frequency of genotype $j$ in population $i$ after migration
$P_{ij}'$ = the frequency of genotype $j$ in population $i$ in the following generation
$P_i$ = the frequency of allele $a$ within the gametes of population $i$
$s_i$ = effective selection against the genotype $aa$ in population $i$
$h$ = dominance coefficient of allele $a$
$\mu$ = mutation rate
$f_i$ = Wright's inbreeding coefficient, a measure of population subdivision in population $i$
$m_{ij}$ = frequency of migration from population $i$ to population $j$

## The recursion equations

Genotype frequencies after migration are as follows:

$$\tilde{p}_{1j} = \frac{p_{1j}(1 - m_{12}) + m_{21} \cdot p_{2j}}{\sum_j [p_{1j}(1 - m_{12}) + m_{21} \cdot p_{2j}]} \tag{1}$$

$$\tilde{p}_{ij} = \frac{p_{ij}(1 - m_{i,i-1} - m_{i,i+1}) + m_{i-1,i} \cdot p_{i-1,j} + m_{i+1,i} \cdot p_{i+1,j}}{\sum_j [p_{ij}(1 - m_{i,i-1} - m_{i,i+1}) + m_{i-1,i} \cdot p_{i-1,j} + m_{i+1,i} \cdot p_{i+1,j}]} \qquad 1 < i < n \tag{2}$$

$$\tilde{p}_{nj} = \frac{p_{nj}(1 - m_{n,n-1}) + m_{n-1,n} \cdot p_{n-1,j}}{\sum_j [p_{nj}(1 - m_{n,n-1}) + m_{n-1,n} \cdot p_{n-1,j}]} \tag{3}$$

Mutation further affects genotype frequencies as follows (where $p_i$ is the frequency of allele $A$ within the gametes in population $i$, and $q_i$ is the frequency of $a$):

$$p_i = (\tilde{p}_{iAA} + 0.5\tilde{p}_{iAa})(1 - \mu) + \mu(\tilde{p}_{iaa} + 0.5\tilde{p}_{iAa}) \qquad 1 \le i \le n \tag{4}$$

Reproduction and selection are modelled as follows (following Agrawal and Chasnov, 2001):

$$p'_{iAA} = (p_i^2 + p_i q_i f_i)/\omega_i \tag{5}$$

$$p'_{iAa} = 2p_i q_i (1 - f_i)(1 - s_i h)/\omega_i \qquad 1 \le i \le n \tag{6}$$

$$p'_{iaa} = (q_i^2 + p_i q_i f_i)(1 - s_i)/\omega_i \tag{7}$$

where $\omega_i$ is the average fitness of newborns in population $i$:

$$\omega_i = (p_i^2 + p_i q_i f_i) + 2p_i q_i (1 - f_i)(1 - s_i h) + (q_i^2 + p_i q_i f_i)(1 - s_i) \tag{8}$$

Iterating equations (1–8), we can find the equilibrium values, where $p_{ij} = p'_{ij}$.

## Model results

We consider a simple version of the model, described in Fig. A1. Two parameters change along the gradient. First, selection levels over the considered traits that are not directly relevant to the gradient decrease linearly with the distance from the core towards the periphery, due to the combination of increased stochastic effects (drift) and increased selection over linked loci that strongly affect fitness in the conditions of the periphery. Second, population subdivision remains constant and low throughout most of the species' range (populations 4–12) and increases linearly towards the edge of the range, representing increasing sub-population patchiness (Fig. A1). We examine the case where the different populations are of the same size, but those closer to the periphery are spread over a larger area, and have a lower migration rate between patches within the population. For simplicity, we present the case where the rate of migration between entire populations is constant at value $m$ (the equations, however, allow us to modify that assumption) and only the rate of migration within populations changes. Interestingly, this simplified scenario is sufficient to generate the hump-shaped pattern. The alleles interact additively ($h = 0.5$). As a result of the change in the effective selection with the gradient, we find that the frequency of allele $a$ increases towards the periphery, and obtains its maximum value in the most peripheral population located farthest away from the core. Since the effective selection against allele $a$ is stronger in the sub-periphery than the periphery, the frequency of $a$ at the periphery in the parameter range studied is a decreasing function of $m$, while the frequency of $a$ in the sub-periphery is an increasing function of $m$. The frequency of heterozygotes shows a more complex behaviour: it increases with the frequency of $a$, but decreases with population subdivision ($f$). As a result, if migration is above a certain (low) threshold and population subdivision at the periphery is above a certain level, the frequency of the heterozygotes will peak at the sub-periphery, as shown in Figs. A2 and A3. The frequency of allele $a$ is highest in the periphery, but it often appears there in a homozygote state. An *aa* individual disper-

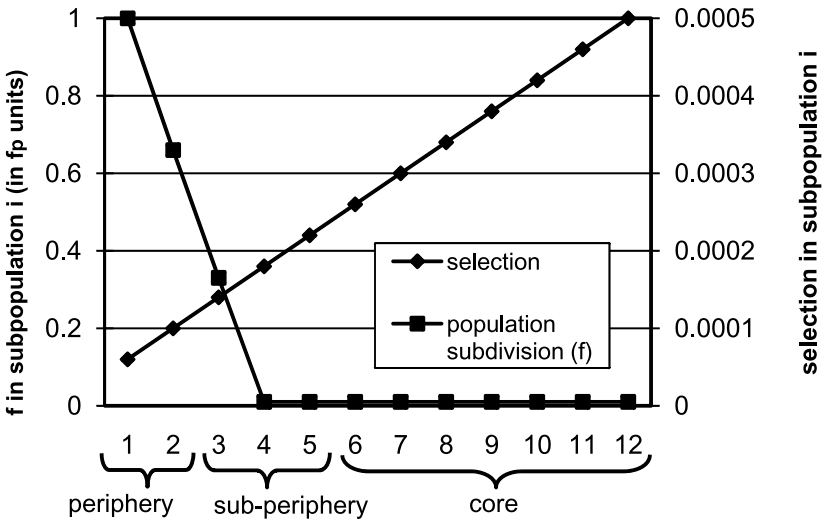


**Fig. A1.** Structure of the theoretical model. A simple version of the model, assuming that the number of populations is 12, where populations 1 and 2 constitute the periphery, where selection against the allele *a* is weak and the population is patchy. Populations 3–5 form the sub-periphery, and populations 6–12 represent the core. The core is assumed to be larger in spatial extent than both the periphery and sub-periphery. Selection decreases linearly with the gradient, whereas population subdivision is low throughout most of the species' range, and increases linearly with the gradient towards the edge. The value of *m* (migration) is equal for all populations. We studied values of $f_p$ ranging from 0.01 to 0.1. Note that *f* values are given in $f_p$ units, where $f_p$ is the maximal value of *f*, obtained at the very periphery (population 1).

sing from a peripheral to a nearby sub-peripheral sub-population is more likely to meet and mate with an *AA* individual and thus to have heterozygote offspring.

The unimodal pattern of heterozygosity is obtained under the assumption of weak selection. As the selection against the allele *a* becomes stronger, the heterozygosity peak moves towards the periphery, and eventually is obtained at the very edge of the range (Fig. A4). At the same time, the relative height of the peak increases with selection, and very weak selection would produce a very low peak. The model does not apply to cases of extremely weak selection, where the allele in question is effectively neutral.

A similar result can be obtained if the decrease in *s* with the gradient is replaced by an increase in $\mu$ with it (Fig. A5). A stronger result can of course be obtained if both processes act in concert. Note that this version of the model, in which *s* is constant along the gradient, can be generalized to a neutral model: if the common allele has no selective advantage over the rare one but the rate of mutation between the two increases with the gradient, we expect a qualitatively similar result.

## Generalizations

We can assume various functions for the dependence of *s* (or $\mu$) and *f* on the gradient (e.g. linear with different starting and/or end points, exponential, etc.). In general, heterozygosity will peak in the intermediate sub-periphery so long as: (i) generation or maintenance of

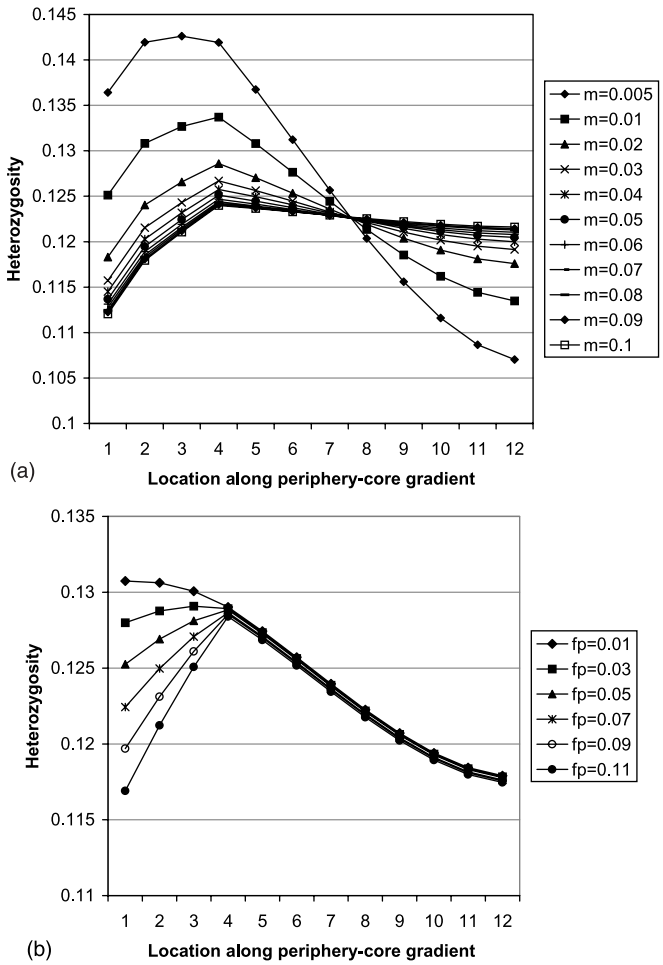


**Fig. A2.** Heterozygosity as a function of the periphery–core gradient. The equilibrium frequency of heterozygotes along the gradient is plotted for different migration rates (a) or population subdivision (b). Number of populations modelled is 12, of which the first two populations (1, 2) constitute the periphery, populations 3–5 form the sub-periphery, and populations 6–12 are at the core. $\mu = 10^{-5}$, $s$ and $f$ change as a function of the gradient as shown in Fig. A1. These assumptions are sufficient to produce a unimodal distribution of heterozygosity along the geographical distribution range for a wide range of parameters. $f_p$ is the maximal value of Wright's inbreeding coefficient, attained at the periphery ($i = 1$). (a) $f_p = 0.1$, (b) $m = 0.02$.

variability increases with the gradient towards the periphery ($s$ decreases or $\mu$ increases); (ii) population subdivision ($f$) increases with the gradient; (iii) $f$ in the periphery is high enough (the threshold determined by the other parameters); (iv) migration is high enough; and (v) the gradient is divided into enough populations, allowing sufficient resolution. For example, if the current model were used with $n = 3$, we would only see a monotonous increase in heterozygosity from core to periphery.

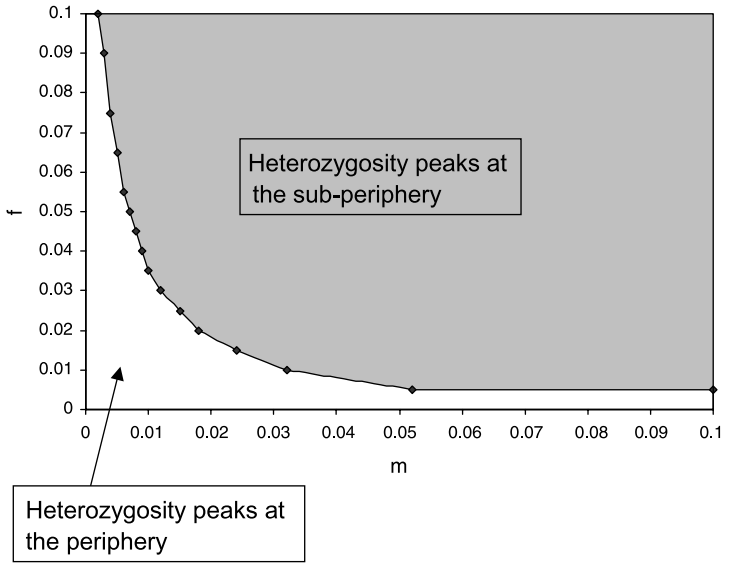


**Fig. A3.** Location along the distribution range (as described in Fig. A1) in which heterozygosity peaks as a function of the migration rate between populations $m$ and population subdivision at the periphery, $f$. In the current model, peak heterozygosity is attained at the sub-periphery in most of the parameter range (shaded area above the line) and at the periphery in the rest of the parameter range (white area below the line), but never at the core. Due to the decrease in selection against allele $a$ with the gradient, its maximal frequency is attained at the periphery, but the difference is very small. The difference in the frequency of $a$ between the periphery and the sub-periphery decreases as $m$ increases (mutants migrate from the periphery to the sub-periphery), whereas the frequency of heterozygotes decreases with $f$. As a result, the critical value of $f$ above which the peak in heterozygosity is attained at the sub-periphery decreases with $m$, and the critical value of $m$ decreases with $f$. It can be seen that for most of the parameter range, heterozygosity peaks at the sub-periphery (area above line). $\mu = 10^{-5}$, $h = 0.5$, $s$ and $f$ change as a function of the gradient, as described in Fig. A1.

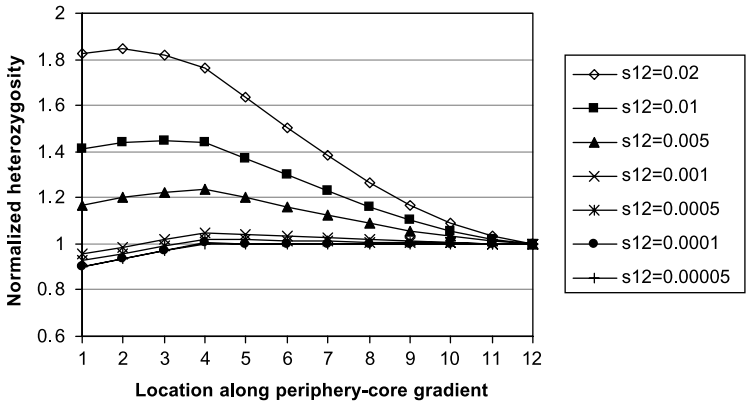


**Fig. A4.** Heterozygosity as a function of the periphery–core gradient, as calculated for different levels of selection. Number of populations modelled is 12, of which the first two populations (1, 2) constitute the periphery, populations 3–5 form the sub-periphery, and populations 6–12 are at the core. The normalized equilibrium frequency of heterozygotes along the gradient (i.e. heterozygosity in population *i*/heterozygosity in population 1) is plotted for different levels of selection. $\mu = 10^{-5}$, $f$ changes as a function of the gradient as shown in Fig. A1. $s_{12}$ is the strength of selection in the core ($i = 12$), but from here selection changes as a function of the gradient as shown in Fig. A1. The difference in selection results in large differences in the frequencies of alleles. To emphasize the effect of selection on the *change* in heterozygosity along the gradient, we normalized the heterozygosity at sub-population $i$ by that value at sub-population 12. Normalizing factors of $s_{12} = 0.00005$ to $s_{12} = 0.02$ were 0.45, 0.37, 0.12, 0.07, 0.01, 0.006, 0.003, correspondingly. $f_p = 0.1$ is the maximal value of Wright's inbreeding coefficient, attained at the periphery ($i = 1$).

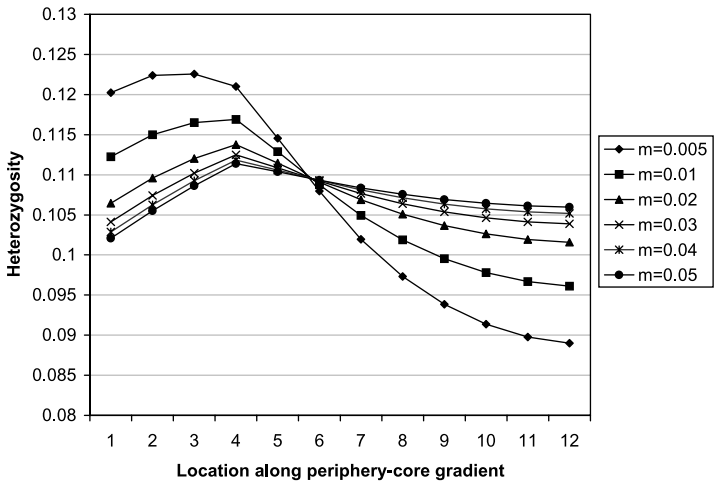


**Fig. A5.** Heterozygosity as a function of the periphery–core gradient when selection is constant but mutation rate increases with the gradient based on the theoretical model. The equilibrium frequency of heterozygotes along the gradient is plotted for different migration rates. Number of populations modelled is 12, of which the first two populations (1, 2) constitute the periphery, populations 3–5 form the sub-periphery, and populations 6–12 are at the core. $m = 0.01$, $\mu$ and $f$ change as a function of the gradient. These assumptions result in a unimodal distribution of heterozygosity along the geographical distribution range for a wide range of parameters. $f_p = 0.1$ is the maximal value of Wright's inbreeding coefficient, attained at the periphery ($i = 1$).