

Within-P opulation D iversity
in the D istribution R ange:
P artridges as a R esearch M odel

A dissertation for the degree of Doctor of Philosophy

by

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A c k n o w l e d g m e n t s

"...All the sciences and arts are taught as if they were separate. They are separate only in the classroom."

Aldo Leopold

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A b s t r a c t

This thesis focuses on spatial patterns in within-population diversity in natural populations. Populations across a species distribution range differ in the ecological and evolutionary processes they undergo, and thus in their patterns of within-population diversity. A long-lasting debate between two major contradictory hypotheses concerning trends in within-population diversity across a species range, from core to periphery, appears in the scientific literature. One hypothesis postulates that diversity within populations will decrease along this cline, while the other suggests increasing diversity towards the range periphery. The first hypothesis predicts that core populations, which undergo balancing selection, will maintain high genetic diversity, while peripheral populations, being small, fragmented and isolated will show low genetic variability. The second hypothesis derives from speciation considerations and argues that core populations undergo stabilizing selection and maintain lower genetic diversity compared to peripheral populations, which undergo fluctuating selection and therefore sustain higher levels of genetic diversity. This hypothesis postulates maintenance of diversity by non-stabilizing environmental heterogeneity near the periphery. This heterogeneity may occur at both the spatial and temporal dimension.

Due to the central relevance of this topic to the understanding of speciation and extinction processes, these hypotheses were tested in various species. A review of the empirical literature revealed apparent contradictions - some evidence supporting one, and other evidence - the second hypothesis. An examination of this literature suggested that some of these apparent contradictions may result from differences in the planning, undertaking and in the analysis of the findings in different studies. These classical hypotheses, and especially their spatial implications, recently gain significance in a novel context, that of biodiversity conservation in the face of the predicted Global Environmental Changes.

In this thesis, I propose that the above hypotheses may be complementary rather than contradictory, and may be reconciled within the framework of a unifying hypothesis for spatial trends in within-population diversity across the range. The proposed hypothesis predicts a hump-shaped uni-modal diversity pattern along a species range, from core to periphery, with peak diversity in “turnover zone” populations located at the intermediate transition area between the core and the periphery. In this area, the species reaches the edge of its continuous distribution and beyond it, towards the range periphery, populations become small and isolated. In many species, this zone will fall in areas of ecological transition (i.e. ecotones).

This work includes several levels:

1. A test of spatial patterns in genetic diversity across the distribution range, from core to periphery.
2. A test of spatial patterns in morphological diversity across the range.
3. A test of spatial patterns in morphological asymmetry within populations, a measure for developmental instability.
4. A test of the relationship between genetic diversity, as estimated by heterozygosity, and fluctuating asymmetry.
5. A summary of the findings and their integration, with a focus on scientifically based conservation decision-making.

In order to test the above hypotheses, and especially the proposed hump-shaped hypothesis, there was a need to locate an area where steep climatic and environmental gradients occur across short geographical distances. In addition, there was a need to focus on a model species which changes its distribution across this cline, to enable a comparison of populations from continuous areas of the distribution, where population density is usually high (termed core), through ecotonal areas at the margins of the species continuous distribution, to areas with small isolated populations at the extreme margins of the species range.

Located at the congruence of several climatic, bio- and zoogeographical regions, steep climatic and ecological gradients occur in Israel along relatively short geographical distances. Mean annual rainfall declines from up to 1000 mm in the

north to less than 25 mm only several dozens of km away to the south and east, with an especially steep cline occurring at the Northern Negev ecotone. These sharp natural gradients provide us with a unique opportunity to examine trends in diversity within populations of a species which are geographically proximal (and are potentially connected by gene flow), but experience very contrasting environments.

I chose the chukar partridge (*Alectoris chukar*) in Israel as a research model for various reasons: The chukar has a continuous distribution in Israel and its population density is high from the Mediterranean areas in the north to the Mediterranean-desert ecotone. The margin of the species continuous range is located in the semi-arid transition zone of the northern Negev, where annual rainfall changes from approximately 450 to 150 mm. Chukars in this area undergo rapid environmental spatial and temporal variations. Chukar distribution becomes patchy and the populations smaller and more isolated in areas with less than 100 mm rainfall in the Negev and Sinai deserts, where the global margin of the species' distribution range is found. As far as known, the chukar is a sedentary bird species, and birds do not exhibit latitudinal or altitudinal migrations, a fact that enables the comparison of local populations.

Using existing and originally collected data sets, I studied trends in within-population diversity in chukar populations along the gradient in Israel and Sinai at two major levels, which included genetic and morphological diversity. At the first stage of the study, five chukar populations were sampled across the distribution gradient in Israel from the core to the species turnover zone, located at the ecotone region. I took the samples to Dr. E. Randi's laboratory in Italy for allozyme electrophoretic analysis. This gives estimates of genetic diversity at the coding level and enables the calculation of various diversity estimates. Significant results were found at this stage of the study: diversity, as estimated by all measures (observed and expected heterozygosity, percent of polymorphic loci and mean number of alleles per locus) monotonously increased towards the ecotone.

Following these findings, during August 1995 to February 1996, a wider sampling of chukar populations was undertaken, which included a detailed sampling

of the ecotone region and of the extreme periphery. Seventeen populations were studied from core to periphery. Thirteen study regions in which modern human-related disturbance are minimal were carefully selected. For comparison with these natural areas, a neighboring population was sampled in four of the regions in areas with intense game hunting and irrigated agriculture. Samples were analyzed using methods similar as those used in the previous year. A total of 26 allozyme loci were resolved for approximately 25-35 birds from each population.

The results supported the proposed hypothesis: genetic diversity showed a hump-shaped pattern across the species range, with peak diversity in turnover zone populations, which were located at the Northern Negev ecotone, where the edge of the species' continuous range occurs. A quadratic regression between distance from range periphery as the independent variable and each of the genetic diversity estimates, especially mean observed and mean Hardy-Weinberg expected heterozygosity, explained some 73 and 80 percent of the total variance, respectively, and was highly significant ($p < 0.0025$ and $p < 0.001$, respectively). The polynomial model explained a significantly higher proportion of the variance than a linear regression (increasing or decreasing) model. Partial sampling of the range would have led to contradicting conclusions and to support of different hypotheses regarding trends in diversity across the range for each of the different sections: If the sampling would have included only the 10 populations from the core to the ecotone (without the extreme periphery), a significant trend ($r^2 = 0.86$, $r = -0.93$, $p = 0.0001$) of decreasing diversity with increasing distance from the range periphery would have been found. On the contrary, if the core would not have been sampled, a trend of decreasing diversity towards the range periphery would have appeared across the seven populations included, although it was not significant ($r^2 = 0.39$, $r = 0.63$, $p = 0.13$). If the turnover zone were not sampled and only core vs. extreme periphery were compared (9 populations), the hump-shaped pattern would not have been apparent at all. Only when the range is sampled across a more complete continuum, does the hump-shaped trend appear, thus resolving the contradiction between the two hypotheses. Each of the two hypothesis predicts the trends for a different part of the

range. This is similar to the study of trends in species diversity across productivity gradients, in which contradictory findings showing a decrease vs. increase in diversity were partly resolved by a wider sampling of the gradient, showing a hump-shaped pattern.

At the phenotypic level, I tested trends in within-population diversity from a data set collected by R. Nissani (1974), which was computerized and used for the purposes of this work. Populations were sampled across the chukar range from the Upper Galilee to the extreme arid periphery, including the isolated relict populations from the Sinai Mountain region. Each bird was measured for 35 traits and 23 ratios were calculated. This gave a relatively large number of traits which enabled comparison across the range. In equivalence to the estimates used at the genetic level, a statistic termed *Estimator in a Dependent Sample* (EDS) was developed. It enables to calculate one diversity value for each population based on the coefficient of variation, taking into account all individuals, traits and the correlation between all traits. The results showed similar trends to those observed at the genetic level: within-population diversity had a hump-shaped pattern across the chukar range, from core to periphery. Peak levels were found at the ecotone region and decreased towards the core and the periphery in both males and females, traits and ratios.

All animal and plant species have a confined distribution range with areas that mark the edge of their range. The fact that the distribution ends beyond these region suggests that individuals in these regions may confront high levels of stress than in other areas. However, populations located near the edge of the range often have a patchy distribution pattern and are located in resource rich patches. In these rich patches, individuals may actually experience relatively favorable environments, similar to the environment in the core. In order to test whether individuals across the range perceive different environments, I compared levels of bilateral asymmetry, an estimator of developmental instability.

Three major types of deviations from bilateral symmetry in morphological traits within a population are known. These include fluctuating asymmetry (FA; small random deviations from symmetry), directional asymmetry (DA; where one side is

consistently larger than the other) and antisymmetry (handedness, where most individuals deviate from symmetry showing either right or left asymmetry). As far as known, the development of both sides of a bilaterally symmetrical trait is coded by the same genes. Therefore, deviation from perfect symmetry may reflect the ability of individuals to develop in a stable path. FA is widely considered as an indicator of developmental instability, yet DA and antisymmetry have only recently been argued as possible estimates for developmental instability, predicting a continuum between the three asymmetry types. I examined asymmetry in the third toe length across the range, from core to periphery, in 11 chukar partridge populations in Israel. A strong and significant correlation between distance from the range periphery and FA was found, with a leap in FA at the ecotone. This suggests that geographically peripheral populations are ecologically marginal and are prone to higher levels of stress. While most individuals in the Mediterranean-core were symmetrical and the populations showed a distribution close to that expected for FA, the directional component of asymmetry and antisymmetry significantly increased towards the periphery. Asymmetry patterns shifted along the range from more fluctuating to more directional and antisymmetrical. Only when the range was widely sampled across a continuum, was the shift in asymmetry types resolved. This provides primary empirical evidence for shifts in levels and type of asymmetry across a species' natural range, showing a continuum between asymmetry types and supporting the notion that all three asymmetry types can reflect developmental instability. Chukars are not well adapted to desert conditions. In arid environments they are distributed mainly in food and water-rich patches. Even within these apparently "favorable" resource rich patches, individuals confront higher stress relative to those from other areas across the range. This work indicates that the ecotone, as perceived by the birds, is an area of transition between lower to higher levels of stress confronted.

The relation between genetic diversity and asymmetry was examined. Genetic diversity, as estimated using both observed and expected heterozygosity, was not associated with FA at either the population or individual level when tested across the entire range from core to periphery. Partial sampling of the selected range would

have revealed opposing trends. A detailed and well-planned sampling of the distribution range, which includes core, turnover and peripheral zones, is essential for understanding trends in genetic diversity, in developmental stability, and in their association.

A long-term goal of the work is to guide conservation policies with considerations that hitherto were not elicited. In this context, directing further research and conservation efforts towards the ecotone region may prove to be a practical direction because: (1) This region was shown to be especially rich on diversity, comprising a within-species diversity hotspot; (2) it was rich in unique (“endemic”) alleles, not found in other populations; (3) it represented other distribution areas included in this study in genetic composition. Populations from this intermediate area of the range not only had nearly all alleles found in populations from all other areas of the distribution, but they also had additional alleles, not found in other populations.

Ecotones harbor numerous species, many of which have turnover zones in these areas of environmental change. Hence by conserving the ecotone region, which is relatively small in size yet rich in diversity, we may manage to conserve high diversity at both the within and between species scales; this may prove to be a cost-effective strategy. I recommend that turnover zone populations within the ecotone area should receive high research attention as potential speciation centers and genetic reservoirs for the species, which may potentially guarantee the maintenance of high diversity and future speciation processes. Further studies should test the generality of these ideas focusing on other ecotone regions and on careful sampling of distribution gradients. This is essential in the face of the Global Climatic and Environmental Changes and the need to plan large-scale spatially-based conservation and environmental programs for sustaining biodiversity.

Note to the reader

This thesis comprises seven chapters and an appendix (see details in “Outline of the thesis” chapter below). The first and final chapters (1 and 7) present a general introduction and discussion in which I provide an overview of the study questions, their theoretical underpinnings and the research findings. Chapters 2-6 and the appendix comprise scientific papers which were published, submitted or are in final stages of preparation before submission to peer-reviewed journals. I tried, in this framework, to build the chapters of this thesis together as a single comprehensive work, from which they originally derived and to avoid repetitions. Repetition, however, was unavoidable in some cases due to the fact that every scientific paper must stand alone and necessitates a description of the species, the research area etc, which are rather similar in most of the papers deriving from this work. I compiled all the references in a single list at the end of the work, except for Chapter 2, to which the references are attached.

General Introduction - Chapter 1

The study of biological diversity (biodiversity) is receiving wide scientific attention in recent decades. Biodiversity has been defined in various ways (Gaston and Spicer, 1998). Discussion regarding its definition is dynamic, with shifts between the more traditional emphasis on the community level to emphasis on the ecosystem and population levels. One of the definitions, proposed by the United Nations Convention on Biological Diversity (1992) is "the diversity within species, between species and of ecosystems". The within-species component of diversity is further defined as "the frequency and diversity of different genes and/or genomes..." (IUCN, 1993), as estimated by the genetic and morphological diversity within species.

While research and conservation discussion in the past century focused mainly on the community level, in the past decade it has been extended to include the lower within-species and the higher ecosystem levels. "With the interest in conservation biology shifting...to populations from communities" (Hanski, 1989), ecologists are increasingly dealing with the population level, as a prerequisite to community-level studies. The component comprising *within-species genetic and morphological diversity* is increasingly emphasized as an important element of biodiversity (UN Convention, 1992). Recent studies suggest that patterns of genetic diversity significantly influence the viability and persistence of local populations (Frankham, 1996; Lacy, 1997; Riddle, 1996). Genetic diversity among interbreeding individuals within geographical areas can be detected by morphological (Lynch, 1996; Roy and Foote, 1997) and molecular (Avise, 1994; Loeschecke et al., 1994) tools.

This thesis focuses on the spatial component of within-population diversity, testing hypotheses regarding spatial trends in diversity across the distribution range. Revealing patterns in within-species diversity across species ranges is highly relevant for scientific and utilitarian purposes. It is central to our scientific understanding of ecological and evolutionary (e.g. speciation and extinction) processes (Smith et al.,

1997) and for the determination of conservation priorities, which are often set on a map-based spatial basis. Thus awareness of this component may be vital in criteria definition and prioritizing for conservation and wise use of genetic resources (Brooks et al., 1992). This may enable to reach explicit decisional procedures that allow systematic rather than opportunistic selection of populations and areas for *in situ* protection (Pressey et al., 1993). It is especially important in the face of the recent Global Climatic and Environmental Changes (Safriel et al., 1994).

Much scientific and conservation focus at the community (multi-species) level is aimed at detecting areas especially rich in biological diversity, i.e. “diversity hotspots”, a term coined by Myers (1989; 1990; reviewed in Reid, 1998) and Mittermeier et al., 1998). This approach focuses attention towards revealing areas rich in species diversity, endemism, rare and endangered species (Mittermeier et al., 1998). Similarly, at the within-species level, revealing areas and populations sustaining rare and unique genetic structures and especially high diversity, may be highly important for basic and applied research and for setting conservation and management priorities. The identification of such areas may facilitate our understanding of the potential role of different parts of the distribution range in evolutionary and ecological processes (Smith et al., 1997). Hence a long-term goal of the work is to guide conservation policies with considerations that hitherto were traditionally not elicited.

Core and periphery

Patterns in within-species diversity may be revealed by comparing populations across a species distribution range along a cline from the very edge of the range to those at more inner areas (Brussard, 1984; Carson, 1959; Da Cunha and Dobzhansky, 1954; Lennon et al., 1997; Lesica and Allendorf, 1995; Mayr, 1963). Within a single species’ distribution range, the terms “periphery” and “core” are often used in a geographical context, referring to the physical location of a population within the geometry of the range (Brown et al., 1996). While the term peripheral populations often refers to those located at the very edge of the distribution, core populations are

those found further away from the range boundaries (Brown et al., 1996). This geographical distinction may also be related to a more ecological one, as separated by Brussard (1984): "Marginal" areas are the ecologically most unfavorable, unpredictable and least suitable parts of the range (Hengeveld and Haeck, 1981), where extinction probabilities are high (Lennon et al., 1997). In contrast, "central" areas of the distribution range are over time the most favorable and predictable for the species, and where extinction probabilities are lowest (Brown, 1984; Gaston, 1990; Lesica and Allendorf, 1995; Lomolino and Channell, 1995; Wiens, 1989; see discussion in Brussard 1984 regarding terminology). There are specific cases where the geographical and ecological areas are not congruent (Brussard, 1984; Gaston, 1990; Lesica and Allendorf, 1995), but in many cases they coincide (Brussard, 1984; Gaston, 1990; Hoffmann and Blows, 1994; Lesica and Allendorf, 1995; Wiens, 1989).

Trends in populations along the distribution range

Crossing the geographical distribution range of a species along a transect from the core towards the periphery, a change in the biotic and abiotic factors that affect individuals of the species is expected (Andrewartha and Birch, 1954; Brown et al., 1995; Lawton, 1995; Lesica and Allendorf, 1995). Across the range, factors limiting population size may vary (Brown et al., 1995) and the change may be gradual or abrupt (Caughley et al., 1988; Kirkpatrick and Barton, 1997; Lennon et al., 1997). Movement along the range to one direction may result in harsher abiotic conditions, while movement to a different direction may lead to stronger biotic stress (Brown et al., 1996). In many cases, the optimal combination of ecological, environmental and biotic factors for a species is found within the core of its range (Lesica and Allendorf, 1995; Wiens, 1989). Moving from the core towards the periphery of the geographic range, ecological favorability often decreases (Brown, 1984; Brussard, 1984; Gaston, 1990; Hengeveld and Haeck, 1981; Lesica and Allendorf, 1995; Wiens, 1989) and extinction probability of local populations increases (Lennon et al., 1997). Population densities generally decrease and become more fluctuating along such a cline (Brown,

1984; Brown et al., 1995; Brussard, 1984; Caughley et al., 1988; Collins and Glenn, 1991; Gaston, 1990; Hengeveld and Haeck, 1981; Hoffmann and Blows, 1994; Lomolino and Channell, 1995; Vrijenhoek et al., 1985; Wiens, 1989), the range tends to become less continuous (Brown et al., 1996), and populations become more isolated, transient (Lomolino and Channell, 1995) and patchily distributed (Boorman and Levitt, 1973; Carter and Prince, 1988), although exceptions to these trends exist (Lawton, 1995; Svensson, 1992). Brussard (1984) suggests for *Drosophila* that while *“moving away from the optimum physical conditions in the central part of the gradient, there will be intermediate areas where the average population size is lower and fluctuates more. Although permanent populations are generally maintained in this region, fluctuations in numbers related to variation in the physical environment will be common and pronounced...Populations inhabiting the ecologically marginal areas of the gradient will be even smaller and fluctuate more than those in the intermediate areas”*. Fluctuations in population size and growth rate at the periphery may result in temporary peaks (Carter and Prince, 1981; Prince et al., 1985), as well as declines to very low levels (Brussard, 1984), and in the lack of sufficient dispersal from neighboring populations, may lead to the extinction of local populations (Harrison, 1994; Lennon et al., 1997; Thomas and Hanski, 1997).

Classical hypotheses

Two main contradictory hypotheses concerning trends in genetic diversity across a species range, from periphery to core, are found in the literature (reviewed in Safriel et al., 1994):

Increasing diversity from periphery to core - the Carson hypothesis

The first hypothesis, developed by Carson (1959), argues that genetic diversity will increase from the range periphery towards the core (Fig. 1). Carson (1959) suggested that core populations, continuous and dense, will maintain higher genetic diversity, undergoing balancing selection, while peripheral populations, being small, fragmented and isolated, will have lower levels of within-population diversity

(Carson, 1959; Mayr, 1963). This theory implicitly refers to a neutral model of gene diversity: large core population maintain higher genetic diversity because they harbor more mutations and because genetic drift is less effective in them as compared to small isolated peripheral populations. Yet theoretically, this prediction may also be expected based on selection considerations: diversity near the periphery of the range in adaptive traits will be low because only the few genotypes which can cope and survive in these extreme conditions will persist, whereas others will perish (Hoffmann and Parsons, 1991). This hypothesis is supported in many classical papers (e.g., Da Cunha and Dobzhansky, 1954), as well as more recent work (see Hoffmann and Parsons, 1991; Parsons, 1991a; Vrijenhoek et al., 1985; reviewed in Lesica and Allendorf 1995).

Mayr suggested that in some cases gene flow from the core may compensate for the effects of local selection and genetic drift at the periphery. In such cases genetic diversity may actually be homogenous throughout the species' range (Mayr, 1963; Mayr, 1970). This may be derived from the Carson hypothesis and termed the "Mayr

Decreasing diversity from periphery to core - the Fisher hypothesis

A competing hypothesis predicts that genetic diversity will decrease as one moves away from the range periphery towards the core (Fig. 1). Peripheral populations will sustain higher levels of genetic diversity, undergoing balancing selection in spatially heterogeneous and unpredictable environments while core populations will experience stabilizing selection, which will reduce genetic diversity (Burger, 1988; Fisher, 1930; Hoffmann and Parsons, 1991; Parsons, 1989). This theory implicitly refers to adaptive considerations and mainly to the type and strength of natural selection pressures. Empirical evidence for increased genetic diversity at the periphery of species distribution ranges exists in the literature from various regions and species (Hoffmann and Parsons, 1991; Nevo and Beiles, 1988; Parsons, 1991a).

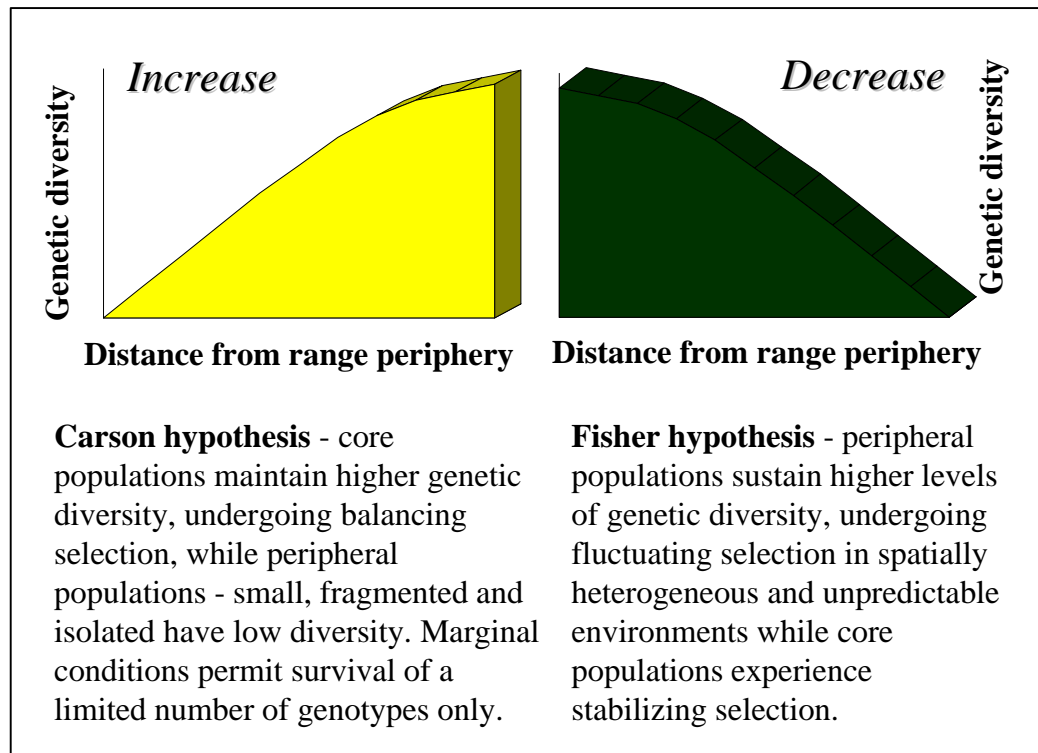


Figure 1. Trends in genetic diversity within populations vs. distance from the species' range periphery based on the two major found hypotheses in the literature.

Motivation driving hypothesis testing

The classical hypotheses presented above have been the focus of theoretical and empirical tests, central to the fields of ecology and evolution, for decades. Early evolutionary ecology studies aimed to reveal areas of active speciation (Eldredge, 1995). Being small and isolated, peripheral populations were suggested as potential speciation centers (Fisher, 1930) and as suitable areas for the study of speciation processes. Over the last two decades the focus has shifted to add the conservation dimension. Due to increasing recognition of the role of genetic diversity in the viability and performance of natural populations (see above and Lacy, 1997), the description and understanding of spatial patterns in genetic and morphological diversity at the within-species level has become an important component of

biodiversity studies (Lande, 1988). Conservation decisions and priority setting increasingly integrate scientific knowledge regarding genetic diversity (Kark et al., 1999). As mentioned, this approach includes an effort to reveal areas rich in genetic diversity and areas where populations are especially rich in rare and unique genetic structure. Recently, increased interest has focused on the role of ecotones (i.e. areas of transition) as speciation centers (Smith et al., 1997; Smith et al., 1999), in biodiversity conservation and as potential diversity hotspots (Smith et al., 1999; Kark et al., 1999) and areas rich in unique and rare genetic structures (Kark et al., 1999).

Review of previous studies

Early work done in the 50's to test the above hypotheses yielded contradictory results. One of the earliest studies was performed by da Cunha and Dobzhansky (1954), who compared chromosomal polymorphism in core vs. peripheral populations of *Drosophila*. According to their working hypothesis, the amount of adaptive polymorphism carried in a population is a function of the variety of the ecological niches it exploits. They found that core *Drosophila willistoni* populations were highly polymorphic relative to those at the periphery, where the species was less common and less ubiquitous than its competitors. They interpreted this result in a 'Carsonian' fashion (da Cunha and Dobzhansky 1954). White (1951), however, found no diminution of chromosomal variability towards the distribution periphery (White, 1951). Other early studies found an increase in genetic diversity at the periphery of the range (summarized by Hoffmann and Parsons 1991).

The topic continues to draw investigation, but no clear pattern has yet emerged (e.g. Brussard 1984; Nevo 1988; Parsons 1991a; Vrijenhoek *et al.* 1985). Work focusing on a wide range of animal and plant species has tested these hypotheses using various phenotypic and molecular genetic estimates. A review of the literature revealed a confused situation, with substantial empirical evidence supporting each of the above hypotheses (Table 1). In addition, there are cases where no obvious spatial trends in the levels of within-population diversity emerge (Brussard, 1984). Reviewing the case of protein electrophoretic diversity, Parsons (1989, p.43) notes

that: “...variability levels in central vs. marginal populations have revealed a rather confused situation. For an endangered fish, *Poeciliopsis occidentalis*, in Arizona, geographically peripheral populations show less electrophoretic variation than do central populations. In contrast, some *Drosophila* populations show higher electrophoretic variability at the margins...Hence, comparisons of electrophoretic variability under differing ecological circumstances must be approached with extreme caution.” These inconsistencies invited closer investigation, especially in the context of the new practical spatial implications for biodiversity conservation (Lesica and Allendorf, 1995; Lomolino and Channell, 1995; Smith et al., 1997).

Genetic diversity within a population may be affected by stochastic factors, including gene flow, population dynamics, random processes such as genetic drift (Wright, 1932; Slatkin, 1994; Wade and Goodnight, 1998) and by natural selection. The interaction between the neutral factors and the type and levels of selection pressures will largely determine the levels of genetic diversity in populations. While Carson’s theory implicitly refers to a neutral model of gene diversity, the Fisher hypothesis of hyper-variable marginal populations due to fluctuating environments refers to selected markers and to more complicated genetic models which involve natural selection. Therefore, different trends in genetic diversity may be obtained by studying traits controlled by “neutral” vs. “naturally selected” genes (Futuyma, 1997; see also [Chapter 4](#)) or when comparing different loci. This may lead to contradictory results in different studies, because genes may be submitted to varying pressures of natural selection, which are very difficult to detect and quantify in natural populations. In addition, along the years workers have used different genetic and molecular methods to reveal genetic diversity (e.g. chromosome inversions vs. microsatellites) which may be affected to a different extent by random vs. selective processes ([Chapter 4](#)), leading to contradictions between the investigations. However, an extensive review of the literature suggests that these factors do not fully resolve the debates and discrepancies between the hypotheses and their empirical evidence seen in the literature along the years. Even within a single estimate of genetic diversity, such as allozymes, contradictory results are often revealed between studies

testing trends across species ranges (e.g. Brussard, 1984; Hoffmann and Parsons, 1991a).

Discrepancies between the hypotheses

Some of these contradictions may reflect a real dichotomy, resulting from the fact that studies work on different species and in various ecological systems, which show inconsistent spatial patterns in genetic diversity. Yet there appear to be several other major factors which have contributed to the controversy. An examination of methodology of various empirical and theoretical studies suggests that there may be additional underlying factors which have, up to now, been overlooked and have contributed to the confused situation.

Often, studies of core vs. periphery compare two main distribution areas, the one representing periphery and the other core. Populations are sampled from two extremes rather than along a continuum. The definition and logic behind the selection of these two areas very often differs between studies (Antonovics et al., 1994). In some cases, peripheral populations are sampled from the edge of the species *continuous* range, where population density declines rapidly (Lennon et al., 1997). Yet this intermediate area of the range may not represent the very edge of the range. Alternatively, peripheral populations may be sampled at the very extreme periphery of the range, representing small and isolated fragmented populations (Antonovics et al., 1994). In these cases populations from intermediate areas of the range, located in-between the extreme periphery and the core, are not included in the study. These differences in sampling alone may lead to contradictory conclusions, because different sections of the distribution range are compared. In addition, in some cases the two distribution areas representing core vs. periphery are compared in populations which are geographically very distant (Brussard, 1984), in some cases from different continents (see for example comparison of marginal vs. central populations of birds in

Table 1. A summary of results of studies testing trends in within-population diversity in core vs. peripheral populations. Among the papers published between 1978-1998 dealing with diversity in peripheral vs. core populations, some show evidence for higher diversity in core populations, supporting the Carson hypothesis, while others show evidence for the opposite trend, supporting the Fisher hypothesis. Several papers show no consistent trends or significant differences between core and peripheral populations. Only papers where authors refer to both core (or central) and peripheral (or marginal) populations rather than only one of these were included. Incomplete data were not filled in.

Study area	Species studied	Number of populations studied	Type of diversity measured	Hypothesis supported	Comments	Source reference
Europe	<i>Quercus petrea</i>	81	genetic (allozyme)	Inconsistent	Higher heterozygosity in core than in peripheral populations, but higher number of alleles per locus in the periphery than in the core	(Zanet to and Kremer, 1994)
Central and western Mediterranean basin; French Atlantic coast region	<i>Quercus ilex</i> (holm oak)		genetic (allozyme)	Carson	Six main disjunct regions of the range	(Michaud et al., 1995)
Central and northern Japan - Hokkaido and Honshu Islands	<i>Pinus pumila</i> (stone pine)	18	genetic (allozyme)	Carson Fisher for some loci	15 enzyme systems, generally lower in peripheral populations (in some alleles higher in peripheral populations)	(Tani et al., 1996)
Western North America	<i>Bromus tectorum</i> (cheatgrass)	6	genetic (quantitative)	Inconsistent mixed	Introduced species	(Rice and Mack, 1991)
California	<i>Avena barbata</i>	97	genetic (allozyme)	Hump-shaped	Genetic diversity in polymorphic populations was positively related to microhabitat heterogeneity (spatio-temporal). which had a bell shape. 35 loci	(Allard et al., 1978)
Israel	<i>Avena barbata</i>	31	genetic (allozyme)	Inconsistent	35 loci	(Allard et al., 1978)
Canada - USA	<i>Carex lasiocarpa</i>	39	genetic (allozyme)	Fisher	12 loci	(McClintock and Waterway, 1993)
Canada - USA	<i>Carex pellita</i>	20	genetic (allozyme)	Inconsistent	12 loci	(McClintock and Waterway, 1993)
Utha	<i>Hordeum jubatum</i>		genetic (allozyme)	Carson	18 loci	(Shumaker and Babbie, 1980)

Turkmenistan and Israel	<i>Hordeum spontaneum</i> (wild barley)		morphological	Fisher	Seeds germinated in greenhouse. Higher in peripheral populations in most traits (14 of 18)	(Volis et al., 1998)
Israel	<i>Hordeum spontaneum</i> (wild barley)		genetic (allozyme)	Fisher		(Nevo and Beiles, 1988)
Utah	<i>Pseudotsua menziesii</i>		genetic (allozyme)	Carson	20 loci	(Schnabel et al., 1993)
New Zealand	<i>Leptosepermum scoparium</i> (Myrtaceae)	17	morphological	inconsistent mixed	Inconsistent for different traits studied	(Wilson et al., 1991)
Australian coast	<i>Drosophila serrata</i>		genetic (quantitative)	Carson		(Blows and Hoffmann, 1993)
Kenya, Morocco, Italy, Reunion, Australia	<i>Ceratitis capitata</i> (Medfly)		genetic (allozyme and DNA)	Carson		(Baruffi et al., 1995)
Southeastern France	<i>Parnassius mnemosyne</i> (Papilionidae)	24	morphological and genetic (allozyme)	Carson for genetic and inconsistent for phenotypic	23 loci; Lower in periphery in allozyme analysis, non-regular yet “slightly impaired” in periphery in morphological traits	(Descimon and Napolitano, 1993)
Israel	<i>Theba pisana</i> (Helicidae)		genetic (allozyme)	Fisher		(Nevo and Beiles, 1988)
Israel	<i>Hyla arborea</i> (Hylidae)		genetic (allozyme)	Fisher		(Nevo and Beiles, 1988)
Israel	<i>Bufo viridis</i> (Bufonidae)		genetic (allozyme)	Fisher		(Nevo and Beiles, 1988)
Israel	<i>Gryllotalpa gryllotalpa</i> (Gryllotalpidae, mole cricket)		genetic (allozyme)	Hump-shaped	Diversity first increases but declines towards the range extreme periphery	(Nevo and Beiles, 1989)
Israel	<i>Acomys cahirinus</i> (Muridae)		genetic (allozyme)	Fisher		(Nevo and Beiles, 1988)
Israel	<i>Agama stellio</i> (Agamidae)		genetic (allozyme)	Fisher		(Nevo and Beiles, 1988)
Arizona vs. Sonora, Mexico	<i>Poeciliopsis occidentalis</i>	21 (16 Sonoran)	genetic (allozyme)	Carson	Heterozygosity	(Vrijenhoek et al., 1985)

Møller, 1995). Populations from very distant areas may experience completely different recent disturbances affecting their patterns of genetic diversity.

Another difference may arise due to sampling of areas with differing levels of human-related disturbance. Because sampling of the extreme edge of the range may be very difficult, populations sampled from these areas are often sampled in non-natural resource rich (e.g. agricultural) and human-impacted areas, especially when the periphery occurs in the desert. These areas may actually have different patterns of genetic diversity relative to the more natural surrounding environment, where density is lower and sampling becomes more difficult (see discussion in Kark et al., 1999).

Sampling of the distribution range

I suggest that in order to reveal patterns in diversity and partly resolve some of the contradictions between the above hypotheses, the distribution range should be approached along a continuum rather than a core-periphery dichotomy or should be divided more finely, into at least three areas rather than only two. These include the core, the periphery and an intermediate area located in-between the periphery and the core which I term the “turnover zone” (based on Lennon et al., 1997), where “rapid spatial thinning of populations” occurs (Lennon et al. 1997:495; see also Carter and Prince 1981), and where the edge of the species continuous distribution is found.

Turnover zones and ecotones

Areas of ecological transition, i.e. ecotones, have recently received increasing interest due to their potential importance as biodiversity hotspots and in biodiversity conservation (Kark et al., 1999; Smith et al., 1997). In these areas of steep ecological transition between ecosystems many species reach the limits of their continuous distributions (Danin, 1998; Endler, 1982) and their turnover zone. From here towards the most extreme periphery of the range populations become small, isolated and eventually fade out, marking the edge of the species’ range (Chapter 3, Kark et al., ms

in preparation). Thus “turnover zones” of various species are predicted to often occur at areas of ecological transition, leading to congruence of the ecotone between ecosystems and the species’ turnover zone (Kark et al., 1999). In this thesis, I will use the term “ecotone” for ecosystem-related transition zones (i.e. areas of transition between ecosystems) and the term “turnover zone” for density and distribution-related changes within a single species’ range (i.e. transition between core and periphery).

Integrating hypothesis

As mentioned earlier, paying particular attention to areas of steep ecological gradients may help draw a more continuous picture of the changes in within-population diversity across a species range. Contradicting patterns at the community level were partly resolved by wider sampling of productivity gradients. These revealed a hump-shaped pattern of species diversity across this gradient, resolving long-lasting debates (Rosenzweig and Abramsky, 1993). The contradictions emanating from empirical studies (as discussed above) and theoretical considerations (see [Chapters 3 and 7](#)) led me to the prediction that wider sampling of the range, which includes areas of transition, will reveal a unimodal pattern of genetic diversity across the species range, and resolve some of the previous apparent contradictions appearing in the literature.

In this work, I suggest, discuss and test a novel hypothesis regarding trends in within-population diversity across the distribution range. I argue that it may partly resolve some of discrepancies appearing in the literature and described above. This hypothesis predicts that genetic diversity within populations will show a hump-shaped pattern across the range, with peak levels of diversity at intermediate turnover zones of the range (Fig. 1). This hypothesis predicts that when only part of the range will be sampled, from the core to the turnover zone or from turnover zone to periphery, contradicting trends will appear. In addition, it predicts that if the turnover zone, where diversity is expected to peak will not be included in the sampling, the hump-shaped pattern will not be revealed at all. Thus partial sampling

of different sections may lead to contradictory results. In order to test the hypothesized trends, one would need to sample the distribution range more continuously and focus on the turnover zone located in the ecotone area in more detail due to the steepness of the ecological gradient there. The proposed hypothesis and its logic are discussed in detail in the General Discussion ([Chapter 7](#)).

Hypothesis testing

In order to test the proposed hypotheses one would need to: (a) identify an area where steep environmental changes occur across short geographical distances and (b) select a species which is distributed along this gradient with continuous core populations, turnover zone populations at the edge of their more continuous range as well as small and isolated populations at the extreme periphery of the species' range.

The eco-geographical gradient in the study area

In Israel, which comprises a narrow land bridge between Europe, Asia and Africa, steep climatic and ecological clines occur within relatively short distances (Safriel et al., 1994). The sharp climatic and ecological gradient in Israel from Mediterranean to desert ecosystems is congruent with northern, western and southern margins of Mediterranean, Irano-Turanian and Saharo-Arabian species' distributions, respectively (Danin, 1998; Yom-Tov and Tchernov, 1988). While mean annual rainfall in the Mediterranean Galilee and Golan Heights in the north can reach over 900 mm, only several dozen to hundreds of km away in the southern Negev desert mean annual rainfall decreases to less than 30 mm and is highly variable among the years (data from the Israel Meteorological Service and Bitan and Rubin, 1991; Fig. 2). An especially steep climatic gradient occurs in the northern Negev, where the ecotone between Mediterranean and desert ecosystems is found (Danin, 1998; Kark et al., 1999). In this area, rainfall decreases from over 450 mm to less than 150 mm within a narrow belt of less than 60 km. Many species reach the edge of their continuous distributions in this area (Bitan and Rubin, 1991; Kadmon and Danin, 1997; Safriel et al., 1994; Yom-Tov and Tchernov, 1988). Thus, the steep cline in this

region offers a unique opportunity to compare geographically proximate populations within species ranges which are potentially connected by dispersal and gene flow, yet may experience very different environments and ecological conditions.

Figure 2. Mean annual rainfall in Israel. The map was made based on data in the GIS laboratory of the Hebrew University of Jerusalem. Note the sharp changes in rainfall across short geographical distances, and especially the Mediterranean-desert ecotone region where rainfall rapidly declines to the south and to the east.

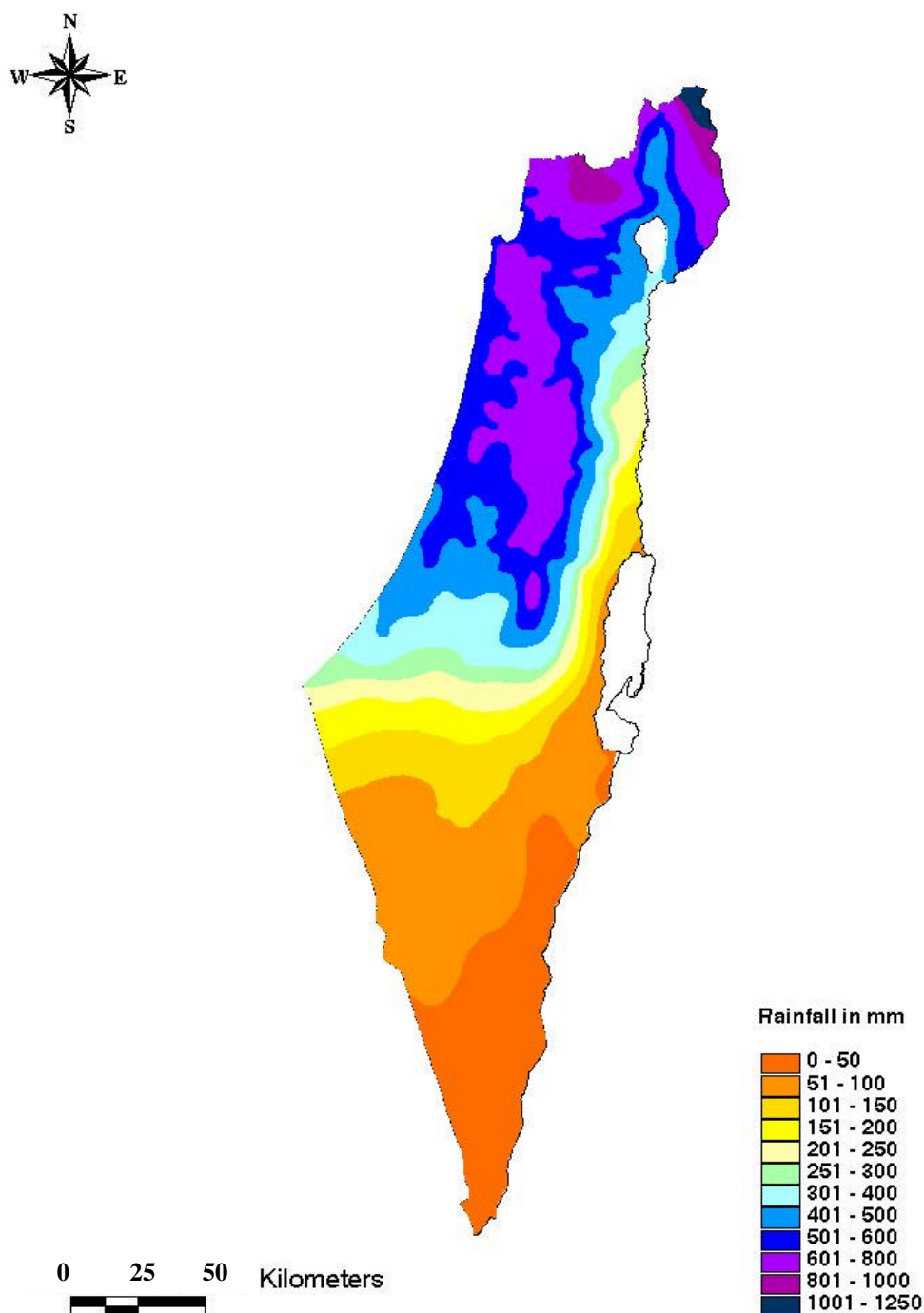


Figure 3. Chukar partridges (*Alectoris chukar*)



Photos from Dan Cowell and Donald Mathis

This setting provides a good opportunity to test the hypotheses presented, comparing trends in genetic diversity in species distributed along this gradient. This is important because, as mentioned, comparison of very remote populations along too wide an area may involve many confounding variables (Carter and Prince, 1988).

The chukar partridge

I chose the chukar partridge (*Alectoris chukar*) (Fig. 3) as a research model for testing the above hypotheses for various reasons:

1. Chukar distribution: The chukar generally inhabits the mesic and semi-arid areas, and has continuous populations in Mediterranean and steppe parts of the range (Shirihai, 1996). The species occurs in deserts only at the margins of its range in isolated and sparse populations (Shirihai, 1996; Liu Naifa, pers. comm.). The extreme desert regions of the southern Negev and Sinai comprise the south-western border of the chukar global distribution range. In the chukar-continuous Mediterranean areas in the north, which comprise part of the species' "core", environmental conditions are relatively favorable, mean annual rainfall is over 400 mm, variability in rainfall among the years is relatively low and population density is high (Cramp and Simmons, 1980; Shirihai, 1996). The semiarid ecotone region of the northern Negev, which separates the arid region (desert) from the dry subhumid (non desert) region (United Nations Environment Programme, 1992), where mean annual rainfall decreases to approximately 150-450 mm, and variability in rainfall among the years is higher (data from the Israel Meteorological Service) is the edge of the species' continuous distribution. This area, which is the ecotone between Mediterranean-type and desert ecosystems and where a sharp climatic gradient occurs (Kadmon and Danin, 1997), comprises the "turnover zone" of the species' range in Israel, where rapid thinning of chukar populations occurs across short geographic distances (Shirihai, 1996). Marginal to the Negev Highlands in the south of Israel and towards the Sinai Desert, where mean annual rainfall is <100 mm and is highly variable among the years, chukar density decreases, distribution becomes discontinuous and local populations become patchy and isolated (Degen et al., 1984; Pinshow et al.,

1982; Shirihi, 1996). This area comprises the extreme periphery of the chukar range. An additional isolated population, most probably a relict from the late Pleistocene, is found in the mountains of the Southern Sinai desert (see Kark et al., 1999).

The chukar generally inhabits mesic and semi-arid areas, and occurs in deserts only at the margins of its range. It is not typical of extremely arid regions, where the species usually occurs in patchily distributed more food-rich locales (Carmi-Winkler et al., 1987; Pinshow et al., 1983). Chukars do not possess physiological adaptations to heat stress (Carmi-Winkler et al., 1987; Frumkin, 1983; Kam, 1986), especially as compared with the partly sympatric sand partridge (*Ammoperdix heyi*) which is well adapted to the desert (Carmi-Winkler et al., 1987; Degen et al., 1984; Pinshow et al., 1982). A main limiting factor in the desert is the chukars' ability to forage long enough to obtain their energy requirements without risking their heat balance. In arid hot environments extremely high temperatures limit their foraging activity levels to approximately one hour a day, which cannot suffice for their energy and water demands (Carmi-Winkler et al., 1987). Therefore, in these marginal habitats the species occurs discontinuously in isolated populations limited to temporary food and water patches (Carmi-Winkler et al., 1987; Shirihi, 1996; Kark, unpublished data). These habitat patches must be rich enough to meet the birds' energetic needs in the short available foraging time, limited to the early morning hours (Carmi-Winkler et al., 1987; Degen et al., 1983; Pinshow et al., 1983). It must also provide sufficient water during the dry months when chukars probably need to drink water on a regular daily basis (Carmi-Winkler et al., 1987; Degen et al., 1983; Pinshow et al., 1983).

2. Substantial information has been accumulated regarding chukar morphology (Nissani, 1974; Chapter 5; Kark, unpublished data), physiology (e.g., Degen et al., 1982; Degen et al., 1983; Pinshow et al., 1983), behavior, social organization (Alkon, 1979) and genetic characteristics (Randi and Alkon, 1994).

3. Life history: Chukars are easy to locate, map and follow in the field. Much information is available on their life histories. They are diurnal, and can be followed during their daily activity. The chukars are organized in social groups (coveys)

consisting of 10-20 individuals during the non-breeding season, and in the breeding season (February-May in northern Israel; Alkon, 1974) they form breeding pairs. The clutch size is relatively large (the mean at Ramat Issachar in the eastern Galilee was 12.2 ± 3 , range 8-17 eggs (Alkon, 1974), and usually the female alone takes care of the brood for a few months, until coveys are reformed during autumn (Alkon, 1974).

4. Sedentary species: As far as known, chukars do not exhibit long-distance spatial or altitudinal migrations (Paz, 1987), and available information from marked chukars in Israel suggests that movements of individual birds are restricted to a few kilometers in both northern and southern populations (Alkon, 1974; P. Alkon unpublished data). Coveys usually remain within a limited area of several square km (Alkon, 1974). This enables to compare local populations.

5. Chukars occur in both relatively “natural traditional” and “modern-human related” environments (see below), enabling a comparison between neighboring populations, which are exposed to different modern human-related selective pressures and population dynamics.

All these factors combined made the chukar in Israel a good candidate for testing trends in diversity across the range. In this work, I test trends in genetic and phenotypic diversity in populations across a steep environmental gradient in the distribution range. Focusing on the chukar partridge (*Alectoris chukar*) as a research model, I compare diversity within populations from continuous areas of the distribution, termed core, through populations in the turnover zone, located at the edge of the species continuous distribution to the extreme periphery of the species range.

Human related effects

Human-related activity, including traditional agriculture, controlled burning and grazing by domestic animals have been dominant in Israel and the region for thousands of years (Holzapfel et al., 1992), and have affected the Mediterranean region, as well as the ecotone and the desert regions (Danin, 1998). Yet these

activities have changed their character in the 19th-20th centuries, with increased human immigration to the area (Kark, 1989). While some areas of Israel were largely affected by these changes, others, mainly consisting of grazing areas, remained relatively similar to their previous condition. This provides a setting to compare between two types of habitats across the gradient in order to try to detect whether differences in diversity trends exist based on the type of environment sampled across the range (see [Chapter 4](#)). The two included highly “modern-disturbed” regions along the gradient, where modern agriculture, irrigation and intense game hunting are dominant vs. “natural” areas, where some grazing and cultivation may occur yet where modern agriculture and game hunting are absent. The latter areas better represent the typical environment of the area in the past hundreds, perhaps thousands of years.

Trends in environmental stress across the range

A central question that arises when comparing trends in diversity across species ranges is whether individuals from populations sampled across different parts of a species range actually experience different environments and confront different levels of environmental stress. It is especially interesting to test whether populations located near the periphery of the species range confront higher levels of environmental stress than those further towards the interior of the range. Physiological evidence suggests that chukars are stressed in arid environments, especially as compared to the partly sympatric sand partridge (see above). Yet this does not actually support the argument that individual chukars near the species’ range periphery experience and perceive more stressful environments than those further away. Chukars in the desert have patchy populations and occur in water, food and resource-rich patches (Kark et al., 1999). Therefore, one might argue that the immediate environment that a bird actually perceives in the patch at the periphery where it is located is similar to that of non-peripheral populations.

Finding and developing tools that enable to study the way in which individuals perceive their environment and to compare this variable in natural populations is

essential. A promising direction towards this goal, which is recently receiving substantial interest, is the study of asymmetry as an estimator of developmental instability and the impact of environmental stress (Lens et al., 1999; Sarre et al., 1994). This tool presents a promising direction to conservation biology, ecology, developmental biology and evolutionary research (Møller and Swaddle, 1997), as discussed in Chapters 6 and 7 in more detail.

As far as known, the development of a trait on both sides of a bilaterally symmetrical individual is under the influence of an identical set of genes (Clarke, 1993). Therefore, it has been suggested by various authors that deviation from perfect symmetry towards the right or the left side of the body does not have a significant genetic basis and represents variation of environmental origin (e.g. Palmer and Strobeck, 1986), although the tendency to develop in a stable path and to exhibit asymmetry (to either side) may have a heritable component (Møller and Swaddle, 1997; Palmer and Strobeck, 1986). In order to test whether individuals comprising populations across the range actually perceive different environments, I compared levels of an estimator of developmental stability termed fluctuating asymmetry, across the populations studied for diversity.

Three main types of asymmetry (i.e. deviation from perfect symmetry between the right and left sides of a bilaterally symmetrical individual) appear in the literature. These include fluctuating asymmetry (FA), directional asymmetry (DA) and antisymmetry (Van Valen, 1962; Palmer & Strobeck, 1986; Leary & Allendorf, 1989; Palmer, 1994; Møller & Swaddle, 1997 for definitions; see Fig. 4 for details). The three types of asymmetry differ in the distribution of the signed difference between the right and the left sides of the trait (R-L) in a population (Fig. 4). Increasing evidence suggests that the three forms of asymmetry can be used as estimates of developmental instability (Graham et al., 1998; Graham et al., 1993). Asymmetry types and their ecological implications are discussed in detail in Chapter 6 and Fig. 4.

Fluctuating asymmetry, and based on novel theory and empirical evidence, also directional asymmetry and antisymmetry, reflect the ability of individuals to buffer themselves during development in the face of stress (Leary and Allendorf, 1989;

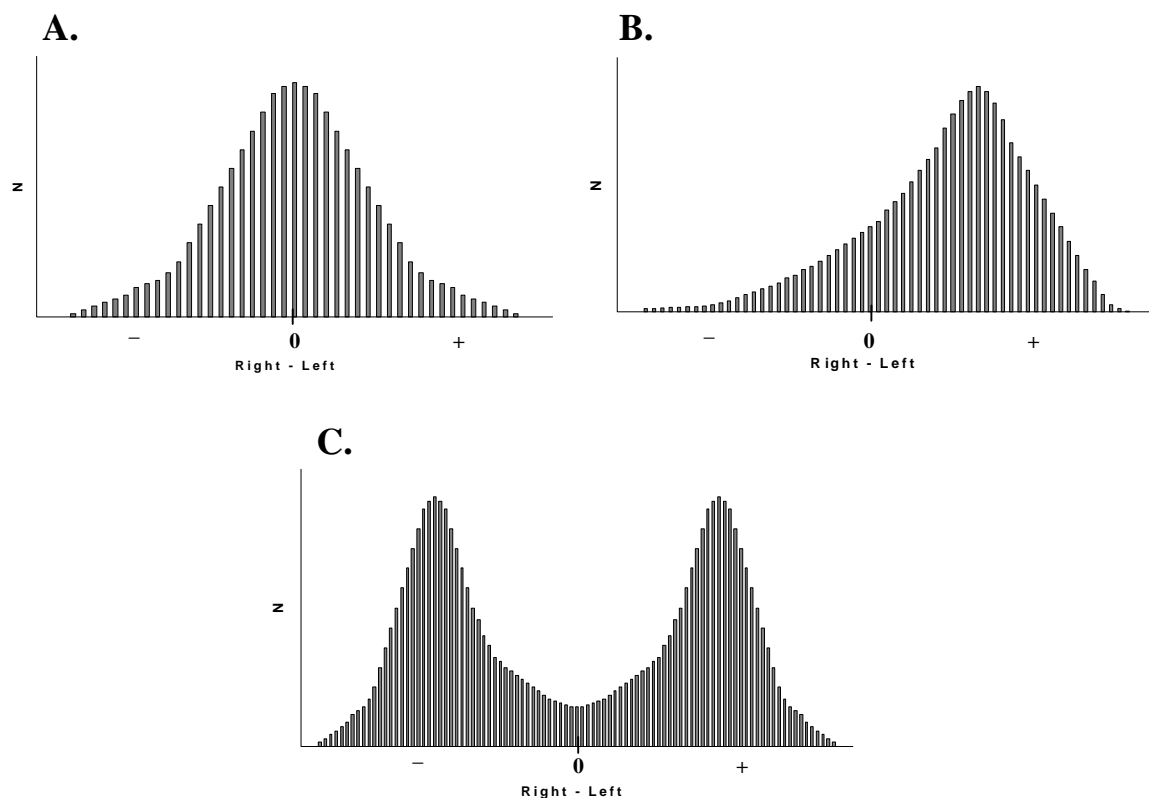


Figure 4. Three major types of bilateral asymmetry: A. Fluctuating asymmetry: small random deviations from perfect symmetry where symmetry is the normal state. The difference between the two sides of a trait shows for the population a normal distribution of signed right minus left (R-L) values with a mean of zero. B. Directional asymmetry: distribution of signed R-L values shows a unimodal pattern yet is not normal. One side is consistently larger than the other in a population and the distribution does not have a mean of zero. C. Antisymmetry (handedness): The population has a bimodal or a broad-peaked (platykurtic) distribution of signed R-L about a mean of zero, where most individuals are asymmetrical, the direction is unpredictable. All three types are population parameters.

(Leary and Allendorf, 1989; Swaddle and Cuthill, 1994; Watson and Thornhill, 1994). Both experimental and observational work suggests that symmetry is significantly associated with increased performance (Leary and Allendorf, 1989; Møller and Swaddle, 1997). For example, in an experimental manipulation, Møller (1991) showed higher maneuverability performance in passing aerial obstacle courses in more symmetrical male barn swallows. Similar results were obtained for European Starlings (Swaddle et al., 1996). Møller and Swaddle (1997) summarize that both proximal (e.g. mechanistic aerodynamic factors) and indirect factors may be contributing to this relationship.

Wide evidence exists showing relationship between asymmetry and various fitness components (reviewed in Clarke, 1995; Møller, 1997; but see also Clarke, 1998a). Developmental stability has been shown to be positively correlated with survival, growth rate, competitive ability, fecundity and reproductive success (reviewed in Møller and Swaddle, 1997). A meta-analysis of studies dealing with the relationship between asymmetry and reproductive success of birds revealed a reduction in litter or in clutch size, in the number of clutches or the quality of offspring with high asymmetry in 14 of the 15 studies reviewed (Møller and Swaddle, 1997). In humans, developmental instability, as estimated by fluctuating asymmetry, was shown to be correlated with child maltreatment by parents, abortion rate, child aggression, various disorders, physiological and mental health (Thornhill and Møller, 1997). FA has been shown to play a role in sexual selection in various species, including humans. For example, ratings of facial attractiveness of photographs presented to study participants of the opposite sex were positively correlated with symmetry in both sexes (Thornhill and Møller, 1997). Yet interestingly, computer generated faces which were perfectly symmetrical were rated lower than faces with some asymmetry (Swaddle and Cuthill, 1995). More symmetrical men started sexual intercourse earlier in life, had a larger number of sex partners and had more extra pair copulations. Female partners of more symmetrical men reported a higher proportion of copulation accompanied by orgasm (Thornhill et al., 1995). A literature review by Møller and Swaddle (1997) shows that inbreeding is also strongly related to increased levels of FA. Approximately 78% of 77 studies of 29 species reported that inbreeding is related to unstable developmental pathways while only 9% showed an opposite relationship (Møller and Swaddle, 1997).

The use of asymmetry as a tool for estimating developmental instability, fitness and stress still deserves much research, especially in natural populations. However, substantial evidence suggests that asymmetry may provide a useful tool for estimating the ability of individuals to buffer development in the face of environmental stress, as perceived by individuals. It provides “*an unbiased estimate of the way in which individuals have experienced their environment*” (Thornhill and Møller, 1997:502).

and therefore, can potentially be used to compare levels of stress posed to individuals from different environments and across both spatial and temporal clines within species' distributions.

R e s e a r c h G o a l s

The goals of this work are:

1. To critically test classical hypotheses regarding trends in genetic diversity within populations across a species range.
2. To present and test a novel hypothesis regarding spatial trends in within-population diversity, which predicts a hump-shaped pattern of diversity across the range with peak levels in turnover zone populations located at the edge of the species continuous range. For the chukar partridge and many other species this area is found at the ecotone region. Populations in this study area are therefore predicted to harbor especially high levels of genetic and phenotypic diversity, comprising within-species "diversity hotspots". This will be tested at the genetic and morphological levels.
3. To test trends in asymmetry and shifts between asymmetry types across this gradient and to test the hypothesis that fluctuating asymmetry, an estimate of developmental instability, increases across a species range, from core to periphery.
4. Based on the prior, to discuss recommendations for future research and for biodiversity conservation, and to set spatially-based conservation priorities based on scientific knowledge.

The hypotheses in paragraphs 1 through 3 are tested focusing on the chukar partridge (*Alectoris chukar*) in Israel as a research model.

Outline of the Thesis

Following the general introduction and background presented in the first Chapter, Chapter 2 provides the first evidence for the test of the hypotheses on genetic diversity across the range in a conservation biology context, with a focus on areas of transition between ecosystems (i.e. ecotones). The paper presents a test of trends in allozyme diversity across five chukar populations sampled in two separate years of study (1990, 1993) in Israel from the Mediterranean-core towards the ecotone. It shows a significant increase in within-population diversity from the core towards the ecotone, where peak levels of diversity were revealed. This Chapter discusses the factors contributing to the observed pattern, focusing on the interaction between population dynamics and selection pressures. Although the trends are very clear and significant, this earlier part of this study alone did not enable to test the proposed hump-shaped hypothesis, because it did not include the extreme periphery of the range. Therefore, as presented in the Preface to Chapters 3 and 4 and in the chapters, a wider and more conclusive sampling was planned and done in 1995 to test the proposed hump-shaped hypothesis (see above). I tested trends in diversity across a more complete distribution gradient, focusing on sampling methodology, carefully defining and studying populations based on area size and human-impact levels, selecting areas where modern human-related disturbance is minimal. These were compared with areas where disturbance is especially high. This chapter shortly presents and discusses the predictions, the general pattern observed, and the empirical evidence for the hump-shaped pattern of genetic diversity observed across the chukar range. Chapter 4 presents and discusses these results and ideas in more detail and adds a comparison between modern human-related and natural environments. Chapter 5 presents a test of the hypotheses at the morphological level, using an extensive data set collected over 25 years ago and kindly made available for this work by Rachel Nissani. I computerized and re-analyzed this data set, which was collected for a

different purpose, yet allowed a test of my research hypotheses. This Chapter also presents a weighted average statistic, which enables to calculate morphological diversity within populations, taking into account the correlation between multiple traits used. The findings at the morphological level draw a very similar pattern to that revealed at the genetic level. The findings presented in Chapters 3 to 5 emphasize the importance of the study and sampling design in resolving patterns across the range. When only part of the range is sampled contradictory results and confused patterns appear. Chapter 6 focuses on the study of trends in asymmetry and its expression across the range and shows a significant increase in asymmetry along the chukar range, from core to periphery across a steep Mediterranean-desert ecotone with an abrupt step in the ecotone region. In addition, it presents evidence that the expression of directional asymmetry elements increases along this gradient. Asymmetry shifts along the range vary from more fluctuating to more directional and antisymmetrical. Only when the range is widely sampled across a continuum, is the shift in asymmetry types clearly resolved. This provides primary empirical evidence for shifts in levels and type of asymmetry across a species' natural range, showing a continuum between the major asymmetry types known, and supporting the notion that all three asymmetry types can reflect developmental instability. Chapter 7 summarizes the major findings and significance of this thesis and discusses the theoretical and empirical basis and the implications of this work, including the implications for conservation. The appendix in Chapter 8, presents a test and discussion of the correlation between diversity and asymmetry.

P r e f a c e t o C h a p t e r 2

This Chapter presents a test of trends in within-population allozyme diversity in the chukar partridge in Israel for the part of the range from the Mediterranean core to the species' turnover zone (see [Chapter 1](#) for definitions), located at the Mediterranean-desert ecotone. The extreme periphery of the chukar range in the southern Negev was not included in this first part of the work. The study includes a comparison of two years, 1990 and 1993. Five populations were sampled in each of the two years. The sampling in 1990 was done by Ettore Randi and Philip Alkon as part of a systematic and population genetic study (Randi and Alkon, 1994). To test my research hypotheses, I planned the sampling in 1993 in co-ordination with Randi and Alkon. It was designed to include three of the five populations sampled in 1990 in order to enable a comparison among years and to test robustness and variability of the trends along short-term time scales. Two additional populations which were not sampled in 1990 were included in the 1993 sampling in order to emphasize the ecotone region, which is an important component in the hypotheses being tested and to enable a comparison between the Golan Heights and the Galilee. I did the genetic analyses in E. Randi's molecular genetics laboratory in the Istituto Nazionale per la Fauna Selvatica, Bolgna, Italy. This enabled a best comparison of the two years' data, which were resolved in the same laboratory, using the same techniques and similar protocols. It also enabled to resolve samples from both years together, on a single gel, when significant differences were detected. This allowed to test whether differences detected between the two years are due to methodological factors or reflect real short-term variability in genetic diversity. Overall, trends revealed in both years were very similar and showed a significant and clear trend across the gradient from the core to the ecotone. These results are presented in the following Chapter, which discusses the possible underlying factors and processes contributing to the patterns revealed, and their implications for conservation biology and planning.

Chapter 2

Conservation Priorities for Chukar Partridge in Israel Based on Genetic Diversity Across an Ecological Gradient

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Preface to Chapters 3 and 4

The findings presented in Chapter 2 for the portion of the chukar distribution from the core to the turnover zone at the ecotone show clear trends. However, as suggested in Chapter 1, some important components were missing in this earlier sampling, which were central for testing the research hypotheses presented in Chapter 1:

1. The part of the range from the turnover zone at the Mediterranean-desert ecotone to the extreme periphery at the central and southern Negev was not included in the early part of the study (Chapter 2). I was interested to test whether the trend revealed from the core towards the ecotone will continue increasing for the part from the ecotone towards the extreme periphery, will reach a plateau, or, as predicted by the integrating hypothesis presented earlier in this work (Chapter 1) and discussed in Chapters 3 and 7, will decrease, showing a hump-shaped diversity pattern across the range, from core to periphery.
2. Results were clear and statistically significant for most allozyme diversity estimates, yet they were based on only five populations in each of the two years.
3. The most southern populations sampled in the two years (Ezuz and Sede Boqer (SB) in 1990 and SB in 1993) were not sampled in a “natural” environment (see Chapter 1). They were sampled in areas with modern-human related disturbance (orchards with some hunting in ‘Sede Boqer Orchards’ and crop fields in ‘Ezuz’). Therefore, these populations may actually show increased genetic diversity due to the fact that birds are attracted to these resource-rich patches from the neighboring more extreme environment. Chukars in these non-natural areas most probably experience different selection pressures and population dynamics compared to more natural surrounding environments, leading to differences in levels of genetic diversity within and among populations (Carmi-Winkler, 1985), as discussed in more detail in Chapters 2 and 4.

The following two Chapters follow on the previous, and present an extended test of the research hypotheses regarding trends in diversity across the core-periphery

distribution gradient in Israel. In order to test the hypotheses, a wider and more conclusive sampling was undertaken in 1995. I extensively planned this sampling effort along a more complete gradient in Israel, from the northern Golan Heights through the northern Negev ecotone to the southern Negev Desert. This was designed carefully, with a larger number of populations, and with emphasis on the sampling design and selection of sampling sites with regard to levels of human-impact and disturbance. Populations were sampled in two types of environments, including what I term “natural” vs. “modern human-related” environments (see [Chapter 1](#) for details). Each populations from the “natural” environments included in the study was selected and sampled paying special attention to these pre-determined criteria:

1. Open or semi-open habitats (in contrast with dense maquis);
2. Areas which are at least five km from modern irrigated agricultural fields or orchards;
3. Areas where there is very low or no game hunting;
4. Areas without major roads, settlements or other major modern human-related disturbances;
5. Areas for which information regarding hunting and agricultural history is available;
6. When possible, populations were sampled in areas which were studied in the two previous years of the study ([Chapter 2](#)) to enable a comparison of short-term temporal trends in diversity.

Overall, seventeen populations were sampled along the gradient (see details in [Chapter 4](#)) of which 13 were sampled in “natural” environments. In order to enable a comparison with neighboring populations from disturbed non-natural environments, four additional populations were sampled in orchards or agricultural fields, where more extensive game hunting occurs. These were located approximately 10 km from a paired natural population. Sample size included 25-30 birds from each location, following the experimental design presented in Randi and Alkon (1994). Based on earlier work ([Chapter 2](#)), this sample size was known to be sufficient for identifying

significant trends in genetic diversity among populations, when many loci (over twenty) are resolved (Randi and Alkon, 1994). The sampling was done during as short a period as possible, to avoid confounding by temporal (within-year) fluctuations. It was done during the non-breeding season, when the birds in all areas are in a social structure of coveys, before separation of coveys to breeding pairs begins (Alkon, 1974; Alkon, 1979), and when juveniles are already similar in appearance to adult birds (Alkon, 1979). Each of the study areas was determined following several preliminary trips to the region together with the regional Nature Reserves Authority ranger and scientific division, and based on information available from prior research on the species in the area (Alkon, 1974; Carmi-Winkler, 1985; Degen et al., 1984; Kark et al., 1994; Kark et al., 1999; Nissani, 1974; Pinshow et al., 1982; Randi and Alkon, 1994; P. Alkon, B. Pinshow, E. Tchernov, personal communication), from the Israeli Nature Reserves Authority (Shay, 1995), and from other data sets (P. Alkon, unpublished data). Using the Geographical Information Systems ArcInfo program of the Hebrew University GIS Center, I described each site for various ecological characteristics, including mean annual rainfall, annual mean temperatures, July and January mean temperatures, altitude, latitude. Information regarding hunting intensity and history, modern human-related disturbance intensity and history was collected for all areas. Plant community chorotype distributions for each of the study areas were kindly provided by A. Danin (unpublished data) (see Additional Figure attached at the end of [Chapter 4](#)).

Spatial scale of study and population definition

This work focuses on a comparison of populations across a core-periphery gradient within a species distribution range. It has been argued that in the case of the chukar partridge in Israel that the more arid environment near the periphery of the range is more spatially and temporally heterogeneous than compared to areas further away from the margins of the range, as measured by climatic conditions (see Pg. 14). Yet it is important to mention that spatial heterogeneity occurs in all environments at different scales, from local to regional and global (Allard *et al.*, 1978). Therefore, an

important factor in studies focusing on spatial comparisons is to define in advance the scale that the study is addressing and design the work taking this into account. This has been done in this study when the population comparison across the chukar range was designed.

Comparisons of spatial diversity across different scales, from the local, through the sub-regional, regional and to the global, are all important for the understanding the processes determining diversity patterns and for conservation decisions. The scale which scientists focus their studies towards should be determined by the goals of their study. In my work, I focused on the sub- and regional scale based on my research goals (Chapter 1) and aimed to provide spatial recommendations for conservation at this scale, which is often the scale that decision makers focus on when designing nature reserves. The scale of study also depends on the size and traits of the organism studied, and in the case of the chukar, the selected regional scale for comparison seemed the most appropriate for the purposes of this work. This work later incorporated local comparisons, when testing for differences between “natural”

-disturbed” regions or comparing populations within a region, such as the Mediterranean-arid ecotone, as discussed in detail in Chapters 4-7. In organisms with zero or short-range mobility and short-range gene flow, such as some plants, invertebrates and small mammals, it may be desirable to study smaller spatial scales. However, larger organisms, such as the chukars, perceive a larger spatial scale. Individuals integrate local conditions over several to several dozens of square km. This was considered when defining population size and defining it at a scale of 10 km².

The term *population* has been defined in various ways, yet most definitions have a spatial basis. For example, Begon *et al.* (1996) define *population* as: “a group of individuals of one species in an area, though the size and nature of the area is defined, often arbitrarily, by the purposes of the studies being undertaken”. I defined *population* area size of 10 square km. Within this area, there are heterogeneous patches and mosaics. However, relative to the body size and available knowledge on the movement of the chukar (Alkon, 1974 and Alkon, personal communication), this

area size seemed best for the comparing within-population diversity, thus enabling a regional scale comparison along the distribution range. The goals of this work focus it primarily towards a comparison of populations within the distribution range, with reference to the ecological factors and their changes across the range, rather than the climatic factors alone (e.g. Mediterranean-arid gradient). As discussed in [Chapter 7](#) in detail, I followed the response of a species to its environment, as reflected by its distribution range (where the edge of the range represents an area beyond which the species cannot persist through time), rather than an approach that focuses on the climatic factors alone (e.g. arid vs. mesic) and tends to treat all species across this cline similarly. The latter approach is important, yet does not acknowledge the fact that various species respond differently to different environments ([Chapter 6 and 7](#)). For example, in the case of the chukar partridge, the extreme desert delimits the edge of the distribution range, and individuals of this species do not persist under very arid conditions (see [Chapter 1](#), pgs. 17-19). Yet, a closely related species, the sand partridge (*Ammoperdix heyi*) occurs only in the desert, and non-arid areas mark the edge of its range. Therefore, an approach following climatic variables alone, without taking into account spatial patterns of abundances and densities along species' distribution ranges may lead to the fact that scientists overlook the real environmental factors and processes that determine the levels of genetic and morphological diversity for a species. These examples suggest that an approach taken from the study species' perspective, as followed in this study, may be more representative of the environmental conditions. For detailed discussion of these questions see [Chapter 7](#).

The following two Chapters present the findings from this wider sampling across the range and discuss the theoretical background, the findings and their implications. [Chapter 3](#) presents, for the first time, the hump-shaped hypothesis and gives an outline of its empirical test in the chukar partridge. [Chapter 4](#) discusses the findings in more detail and presents the comparison of genetic diversity in the “natural” vs. non-natural environments across the chukar range in Israel.

Chapter 3

Trends In Within-Population Diversity Across A Species Range Reconsidered

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Two contradictory hypotheses concerning trends in within-population genetic (allozyme) diversity across a species range are found in the literature. One postulates that diversity within populations decreases from core to periphery (Carson, 1959; Lewontin, 1974; Mayr, 1963), while the other suggests increasing diversity towards the periphery of the range (Fisher, 1930). There is empirical evidence supporting both hypotheses (Da Cunha and Dobzhansky, 1954; Lesica and Allendorf, 1995). A literature review reveals a rather confused situation and apparent contradictions (Parsons, 1989; Safriel et al., 1994). We propose that the hypotheses may be complementary rather than contradictory and in some cases may be reconciled within the framework of a hypothesis that predicts a hump-shaped pattern of genetic diversity along the species range. Peak diversity is expected in turnover zone (Lennon et al., 1997) ecotonal populations located in the intermediate transition area between the core and the periphery, as an amalgam of the older conflicting hypotheses. The hypothesis is tested in the chukar partridge (*Alectoris chukar*) across a core-periphery gradient in Israel. Within-population genetic diversity trends across the chukar range, as estimated using measures of heterozygosity in 26 allozyme loci, reveal a hump-shaped pattern with peak levels of heterozygosity in turnover zone populations located at the ecotone. Only when the intermediate area is sampled is the trend revealed. These findings support the proposed hypothesis.

We tested the hypothesis that genetic diversity within populations will show a hump-shaped pattern across the species' range, with maximal levels of diversity at the intermediate turnover zone of the range focusing on the chukar partridge (*Alectoris chukar*) in Israel. Chukars are sedentary birds and do not exhibit known altitudinal or latitudinal migrations (Shirihai, 1996). In the chukar-continuous Mediterranean areas in the centre and north of Israel, environmental conditions are relatively favourable, mean annual rainfall is over 450 mm (Bitan and Rubin, 1991), variability in rainfall among the years is relatively low (Bitan and Rubin, 1991) and population density is high (Shirihai, 1996). The desert border ecotone of the northern Negev, where mean annual rainfall decreases from over 450 to less than 150 mm within 50 km and

temporal variability in rainfall is higher (Bitan and Rubin, 1991), is the edge of the chukar continuous distribution in Israel (Kark et al., 1999). This area, which is the ecotone between Mediterranean and desert ecosystems and where a sharp climatic gradient occurs (Kark et al., 1999), represents the “turnover zone” of the species’ range in Israel, where rapid spatial thinning of populations occurs (Lennon et al., 1997). Environmental conditions, as perceived by the birds, change rapidly in this area, as reflected by an abrupt increase in mean levels of fluctuating asymmetry, which estimates developmental instability in the populations. Towards the Negev and Sinai Deserts, where rainfall is <100 mm and is highly variable among the years chukar density decreases, distribution becomes discontinuous and local populations become patchy and isolated (Shirihai, 1996; Kark et al., 1999). This area comprises the extreme periphery of the species range.

Between September 1995 and early February 1996, thirteen chukar populations were sampled in Israel across the steep rainfall gradient from the northern Golan Heights to the southern Negev (Fig 1). 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, of which nine were polymorphic (see Randi and Alkon (1994) for loci analysed, except PEP-2, LDH, SOD-2, mGOT, mIDH, GDH which were not resolved). Estimates of genetic diversity were computed using BIOSYS-1 (Swofford and Selander, 1989). Distance from range periphery was calculated for each population based on Shirihai (1996). Birds were sampled by Nature Reserves Authority rangers and authorised hunters following Randi and Alkon (1994) during the non-breeding hunting season when organised in stable coveys that maintain relatively fixed home ranges. Two or less (in most cases one) individuals from each covey were sampled. A population was defined based on area size (ca 10 km²), and was selected from regions with minimum modern human-related disturbance (e.g. hunting, agriculture and irrigation).

Within-population genetic diversity, as estimated by mean population heterozygosity levels, shows a hump-shaped pattern across the chukar range in Israel

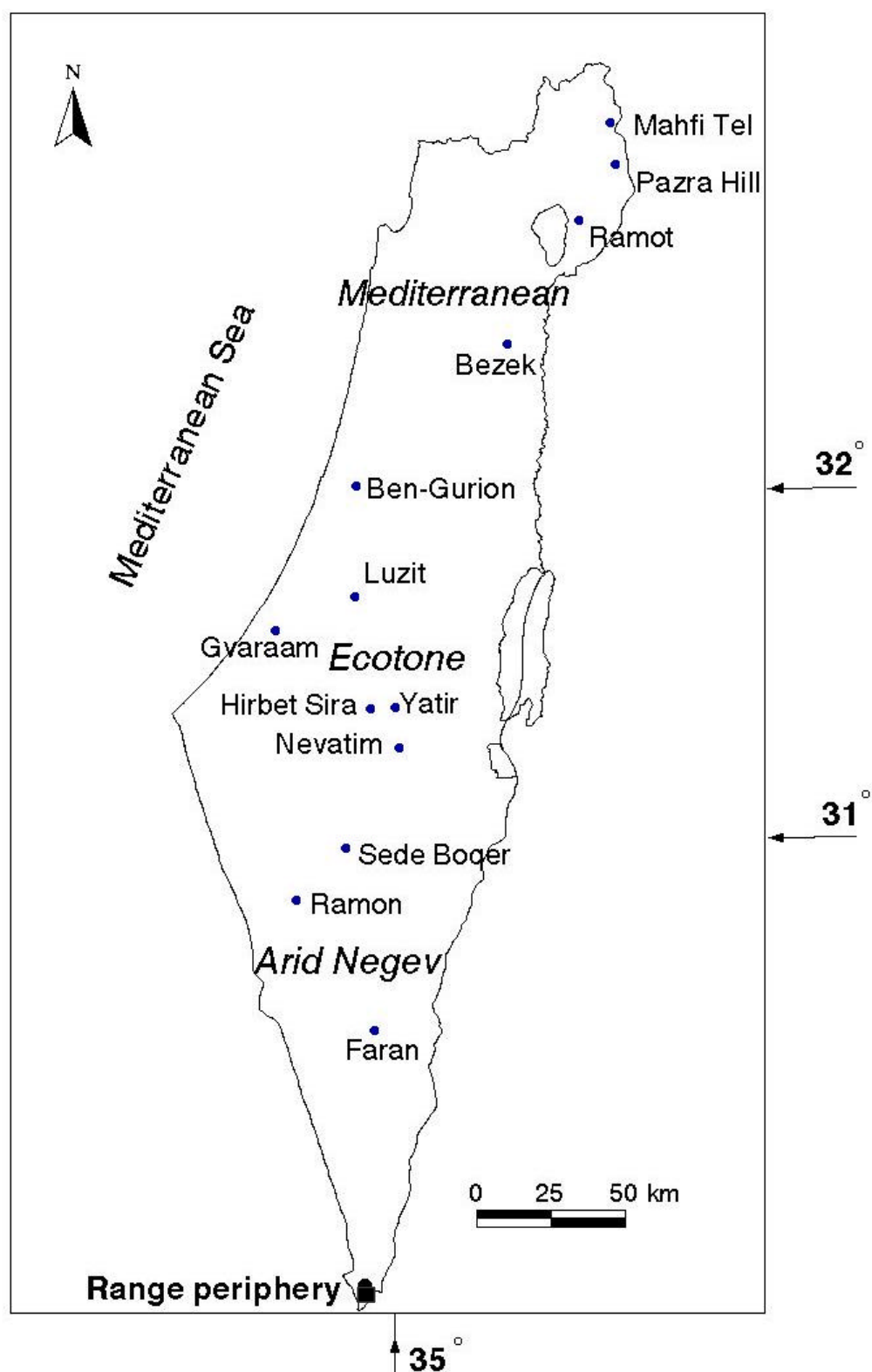


Figure 1. Map of study area, populations sampled and range periphery.

Table 1

Population characteristics and estimates of heterozygosity for chukar populations sampled from core to periphery (n = mean sample size per locus, H_o = mean observed heterozygosity, SE = standard error, H_e = mean expected heterozygosity¹). Populations are listed from north to south (see Fig. 1 for locations).

Population	Distance from range periphery	n	SE n	mean H_o	SE H_o	mean H_e	SE H_e
Tel Mahfi	408	27	0	0.052	0.026	0.069	0.036
Pazra Hill	395	24.7	0.2	0.063	0.029	0.076	0.036
Ramot	372	24.1	0.7	0.079	0.031	0.080	0.032
Bezek	316	26.9	0.4	0.086	0.037	0.094	0.039
BG Airport	264	24.7	0.5	0.093	0.031	0.105	0.038
Luzit	233	28.2	0.3	0.092	0.036	0.094	0.038
Gvaraam	218	25.9	0.1	0.120	0.043	0.115	0.041
Yatir	199	19.8	0.1	0.106	0.037	0.107	0.038
Hirbet Sira	196	28.7	0.2	0.103	0.036	0.107	0.038
Nevatim	182	28.8	0.2	0.111	0.04	0.114	0.041
Sede Boqer	148	27.6	0.2	0.073	0.032	0.096	0.004
Ramon	129	31.7	0.2	0.096	0.037	0.100	0.037
Faran	86	25.8	0.2	0.094	0.035	0.105	0.039

1. Unbiased estimate based on Hardy-Weinberg Equilibrium

from core to periphery. Peak levels of diversity occur in all four populations from the northern Negev ecotone, as compared to both core and peripheral populations (Table 1, Fig. 2a). Diversity decreases from the ecotone towards the Mediterranean core in a monotonous fashion, and towards the extreme periphery, although not monotonously. A quadratic regression of mean heterozygosity within the population vs. distance from the range periphery was highly significant with $r^2 = 0.70$, $p = 0.0025$ for observed heterozygosity and $r^2 = 0.83$, $p = 0.0001$ for Hardy-Weinberg expected heterozygosity. Similar results are obtained after an arcsine transformation of mean heterozygosity levels. When only part of the range is sampled contradicting trends appear (Fig. 2).

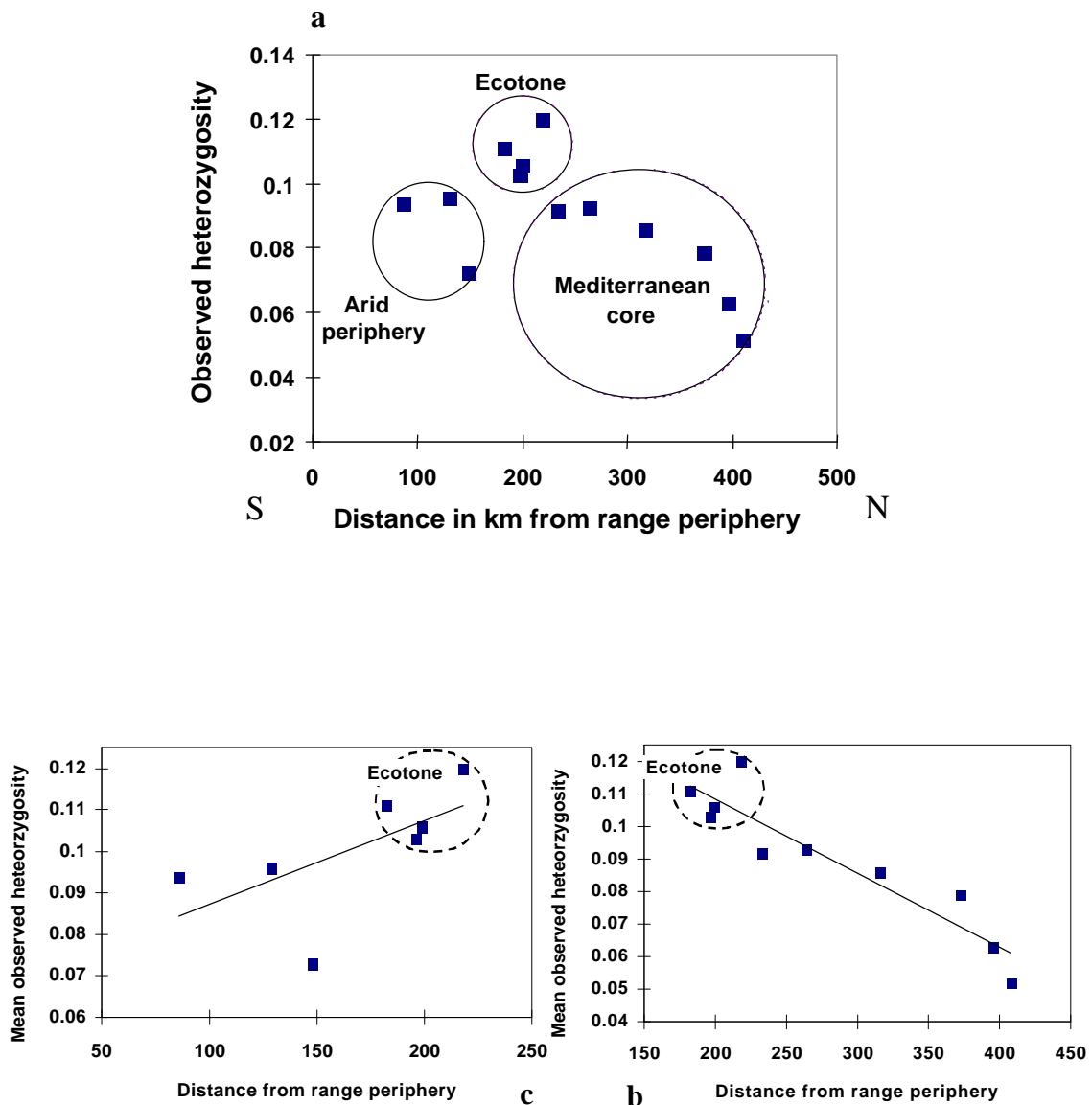
The hypothesis predicting a hump-shaped pattern, as supported in the chukar case study, is based on both population dynamics and selective considerations. Moving towards the periphery of a species range, population densities often decrease and become more fluctuating (Wiens, 1989; Brown, 1984; Brussard, 1984; Hoffmann and Blows, 1994), the range tends to become less continuous (Brown et al., 1996), and populations become more isolated, transient and patchily distributed (Boorman and Levitt, 1973), although exceptions exist (Lawton, 1995). Local populations at the extreme periphery exist in isolated and infrequent patches of suitable environment. Occupancy of patches over time is dynamic (Lennon et al., 1997), populations often experience low rates of gene flow, repeated bottlenecks, random genetic drift (Hoffmann and Blows, 1994) and reduced genetic diversity (Lomolino and Channell, 1995). As population persistence time is low (Lacy and Lindenmayer, 1995), new genotypes may not have enough time to base themselves before the local population in which they are found experiences genetic drift or goes extinct (Lesica and Allendorf, 1995). Founder effects, caused by the recolonization of these populations by a small number of individuals from an adjacent population (Wiens, 1989), may reduce genetic diversity (Lesica and Allendorf, 1995) and persistence (Kirkpatrick and Barton, 1997). When dealing with adaptive genes under selection, only those few genotypes which can cope with these extreme conditions can persist, whereas others will perish (Hoffmann and Parsons, 1991). Thus local populations at the extreme

periphery of the range will maintain low levels of within-population diversity. Nevertheless, when combining many local peripheral sub-populations across a wider geographical area, genetic diversity in total may be higher. Yet local extinctions and low levels of gene flow may prevent the persistence of unique local genotypes here along time.

In the central areas of the range, where environmental conditions are over time near optimal for the species, low diversity is again expected. Populations tend to be larger and continuous (Brown, 1984; Hengeveld and Haack, 1982; Hoffmann and Blows, 1994; Lomolino and Channell, 1995; Wiens, 1989). Although large population size may contribute to the maintenance of some within-population diversity, relatively high rates of gene flow here may result in uniformity of allele frequencies (Mills and Allendorf, 1996) and prevent the persistence of unique local genotypes. When adaptive selected traits (or linked genes) are considered, only the genotypes most fit to the ecological conditions in the core will prevail (Karlin, 1982). New genotypes, added by dispersal or mutation will have low chances of competing with the more established genotypes which persist in stable, long-lived populations (Lennon et al., 1997). This will lead to relatively low diversity in the core.

In the turnover zone, where environmentally induced fluctuations in population performance and density are intermediate, within-population diversity will be maximal, compared with both core and periphery. Gene flow among local populations here, intermediate relative to the continuous core and the isolated periphery, will enable new genotypes to enter local populations and establish themselves. Environmental shifts will enable various alleles to coexist in fluctuating frequencies. From adaptive considerations, different genotypes will be the fittest at different times, but may have a chance to maintain themselves also in periods less optimal for them because conditions do not go to extremes. When the turnover zone falls in the ecotonal areas and is congruent with areas of steep climatic and environmental gradients, selection is expected to be disruptive rather than directional, being affected by diverse shifting environments, leading to high diversity.

Figure 2. Trends in genetic diversity, as estimated by mean observed heterozygosity vs. distance from chukar range periphery in Israel in km. North and South are marked in Fig. 2a as N and S, respectively. When the sampling includes only the 10 populations from the core to the ecotone (the extreme periphery is not included), a significant linear trend ($r^2 = 0.86$, $r = -0.93$, $p = 0.0001$) of decreasing diversity with increasing distance from the range periphery appears (Fig. 2b). On the contrary, when the core is not sampled, a linear trend of decreasing diversity towards the range periphery appears across the 6 populations included, although it is not significant ($r^2 = 0.39$, $r = 0.63$, $p = 0.13$; Fig. 2c). Linear regression fit is marked in Figs. 2b and 2c. When the turnover zone is not sampled and only core vs. extreme periphery are compared (9 populations), the hump-shaped pattern is not apparent. Only when the full range, from core through ecotone to extreme periphery is sampled, does the hump-shaped pattern appear (Fig. 2a).



Additionally, secondary contact (Arnold, 1997) may contribute to higher levels of diversity in the ecotone.

This hypothesis predicts a hump-shaped diversity pattern along a species range, peaking in the turnover zone. Diversity may eventually reach a plateau as distance from the turnover zone increases. The precise pattern in each species will depend on the interaction between gene flow, metapopulation dynamics and local selection. The proposed hypothesis encompasses the two classical hypotheses concerning genetic diversity in peripheral vs. core populations, which become special cases, and allows also for more complex situations. Under the hypothesis, the apparently contradictory and controversial earlier hypotheses are accommodated and become complementary. They can each explain a portion of the general picture: The case of higher diversity in what appears in the literature as “peripheral” populations may be observed when populations from the turnover zone (rather than the extreme isolated periphery) are compared with those from the core. The case of lower within-population diversity at the periphery may be observed when populations from the most extreme periphery of the range, often small isolates, are compared with populations from the turnover zone. As in the case of productivity and species diversity patterns (Rosenzweig and Abramsky, 1993), when sampling of the range is incomplete and includes only the increase or decrease phase, or when the ecotone is not sampled or is not separately analysed, confused patterns and apparent discrepancies may appear.

Conflicts may also result from differing patterns of spatial distribution of different species. For example, the distribution of some species does not include isolated peripheral populations due to an abrupt step-shaped distribution edge caused by a sharp environmental barrier (Lennon et al., 1997; Kirkpatrick and Barton, 1997; Brown et al., 1996) or by human-induced factors. In these cases the most peripheral populations observed may actually be those typical of what we termed the turnover zone. In other cases, because sampling of the extreme periphery is practically difficult, this area may not be sampled. We suggest that a more continuous sampling and a finer differentiation of the range into core, turnover zone and periphery may be helpful in revealing complete patterns in within-population diversity across species

ranges. Similarly, a long-lasting debate regarding trends in species diversity across productivity gradients was partly resolved by wider sampling of gradients, revealing a hump-shaped pattern (Rosenzweig and Abramsky, 1993) . In addition, it may be advised to search for non-linear and non-monotonous trends in order to test for a hump-shaped pattern, which will not be revealed by a linear regression or correlation analysis. While the chukar case study supports the hypothesis predicting a unimodal pattern of diversity across the range, the precise pattern in each species will depend on the interaction between gene flow, metapopulation dynamics and local selection. For example, when the edge of the continuous range is geographically close to the extreme periphery, diversity is predicted to show a unimodal, yet left-skewed distribution.

Detecting spatial patterns in within-species diversity across species ranges is highly important for understanding speciation processes and for conservation. In the chukar case study, the ecotone, which harbours the highest genetic diversity as well as proportion of unique (“endemic”) alleles, may well deserve high conservation focus to enable dynamic evolutionary (Smith et al., 1997) and ecological processes.

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Chapter 4

Trends in allozyme diversity in chukar populations reveal a hump-shaped pattern across the ecotone in Israel

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Abstract

The study of spatial trends in within-population diversity across species ranges is receiving wide attention in recent decades due to its implication to biodiversity conservation and to the understanding of speciation patterns and processes. Recent studies focusing on the chukar partridge, across a steep distributional gradient in Israel as a research model, showed a pattern of increasing diversity from the Mediterranean-type core regions towards the Mediterranean-desert ecotone, where the edge of the chukars' continuous range occurs, also termed the species' "turnover zone". In this work, we tested the hypothesis that sampling across a wider part of the species' range, to include the extreme periphery (the "decay zone"), where populations become small and isolated, will reveal a unimodal pattern of within-population genetic diversity with peak diversity maintained at the ecotone region. This paper presents a detailed test of this hypothesis, focusing on allozyme diversity in chukar partridge populations from Israel. In this work, populations were carefully selected to distinguish between "natural" and "modern-disturbed" environments and a wide gradient was studied. We sampled 17 populations across the chukar range in Israel, including four pairs of adjacent populations from natural vs. non-natural environments. Results of this study support the above hypotheses. Diversity shows a hump-shaped pattern across a gradient which includes the core, the turnover zone and the periphery, with peak levels in the turnover zone. Differences in genetic diversity between natural and disturbed environments exist, yet change across the range. This work suggests that only a wide sampling of the range along a relatively continuous gradient can reveal the actual patterns of diversity and may partly resolve previous discrepancies among studies. This is especially important in the context of recent practical spatial implications for biodiversity conservation.

Introduction

“Biological diversity” has been defined by the United Nations Convention on Biological Diversity signed in 1992 as “the diversity within species, between species and of ecosystems”. The within-species component of diversity has been defined as “the frequency and diversity of different genes and/or genomes...” (IUCN 1993, pg. 17). In equivalence to approaches at the community level, revealing spatial patterns of diversity within species ranges and detecting areas especially rich in biological diversity (i.e. “diversity hotspots”), may be important for determining conservation priorities and in understanding the potential role of different areas of the distribution range in speciation and extinction processes (Smith, 1997).

Of central importance in studies of trends across species ranges are populations located at the edge of the range, termed “peripheral populations” (Brown et al., 1996; Fisher, 1930; Hoffmann and Blows, 1994; Lawton, 1993). Comparison of diversity in peripheral and non-peripheral (core) populations has been the focus of various studies at both the genetic and phenotypic levels (reviewed in Blows and Hoffmann, 1993; Brussard, 1984; Parsons, 1991a). Two major contradictory hypotheses concerning trends in genetic diversity in peripheral vs. core populations are current in the literature, each having different spatial implications (Safriel et al., 1994). These hypotheses were developed over 40 years ago, and were discussed mainly in the context of speciation processes. The first hypothesis argues that core populations are continuous, dense and maintain high within-population diversity whereas peripheral populations are small, isolated, sparse and maintain lower genetic diversity (Carson, 1959; Mayr, 1963). According to this rationale, genetic diversity within populations is expected to increase from the periphery to the core across a species range. This idea is supported in classical papers (e.g., Da Cunha and Dobzhansky, 1954), and in more recent work (e.g. Hoffmann and Parsons, 1991; Parsons, 1991a; Vrijenhoek et al., 1985; reviewed in Lesica and Allendorf, 1995).

The competing hypothesis predicts that populations from peripheral areas of a species range will maintain higher genetic diversity levels (Burger, 1988; Fisher, 1930; Hoffmann and Parsons, 1991; Parsons, 1989). Based on this hypothesis, diversity is expected to decrease from the periphery, where the environment is more fluctuating and less predictable, towards the core. Empirical evidence for increased genetic diversity at the margins of species distributions exists in the literature from various regions and species (e.g. Hoffmann and Parsons, 1991; Parsons, 1991a; Nevo and Beiles, 1988). Thus there seems to be empirical evidence supporting each of the two hypotheses. In addition, there are cases where there appear no obvious spatial trends in the levels of within-population diversity (Brussard, 1984).

Genetic diversity within a population may be affected by both natural selection and stochastic factors, including population dynamics and genetic drift. The major types of genetic diversity revealed in population genetics studies include chromosomal arrangements, allozyme variants and nucleotide substitutions. These may be either selected or not, and their frequencies in the populations may change in response to different pressures and types of natural selection, or as a result of neutral (stochastic) fluctuations. Other variants are apparently unselected, and their frequencies vary according to historical and current populations factors (e.g. random genetic drift, effective population size, demographic fluctuations, bottlenecks, gene flow). Thus, it is possible to obtain different estimates of genetic diversity when studying traits controlled by “neutral” vs. “naturally selected” genes. Contradictory results can be the unavoidable consequences of using selected and neutral genetic markers of population diversity. For example, Carson’s (1959) and Mayr’s (1963) original theories implicitly refer to a neutral model of gene diversity: large core population can maintain higher gene diversity because they can harbour more mutations and drift is less effective in them. But classical geneticists have often used selected markers (e.g. chromosome inversions) and have obtained contradictory results. On the other hand, theories of hypervariable marginal populations due to fluctuating environments (Fisher, 1930) refer to selected markers and to more complicated genetic models which involve natural selection. In this case too, we may

expect contradictory results, because genes can be submitted to varying pressures of natural selections, which are very difficult to detect and compare across natural populations. However, this does not fully resolve the debates, as even within a single estimate of genetic diversity, such as allozymes, contradictory results are often revealed between studies testing trends across species ranges (e.g. see Brussard, 1984; Hoffmann and Parsons, 1991). Some of these contradictions may reflect a real dichotomy, resulting from the fact that studies work on different species and in various ecological systems, which show inconsistent spatial patterns in genetic diversity. Yet there appear to be a few other major factors which have contributed to the controversy. Often, studies of core vs. periphery compare two main distribution areas, the one representing core and the other periphery. Populations are sampled from two extremes rather than along a continuum. The definitions and logic behind the selection of these two areas may differ between studies (Antonovics et al., 1994). Peripheral populations may be represented by those from the edge of the species continuous range, where population density declines rapidly (Lennon et al., 1997). Yet this area may not represent the very extreme edge of the range, where populations are more fluctuating and may not be present some of the time due to local extinction, followed by recolonization (Lennon et al., 1997). Alternatively, peripheral populations studied may be sampled at the very extreme periphery of the range, representing small and isolated fragmented populations (Antonovics et al., 1994). In these cases populations from intermediate areas of the range, located in-between the extreme periphery and the core, are not included in the study. These differences in the sampling may lead to contradictory conclusions, as different sections of the distribution range are compared. In addition, in some cases the two distribution areas representing core vs. periphery are compared in populations which are geographically very distant (Brussard, 1984), sometimes from different continents (see for example comparison of asymmetry in marginal vs. central populations of birds in Møller (1995). Populations from very distant areas may experience completely different evolutionary histories. This may cause distinct patterns of genetic diversity within populations. Another difference may arise due to sampling of areas with differing

levels of human-related disturbance. Because sampling of populations at the extreme edge of the range may be very difficult, populations sampled from these areas may often represent areas where the species is abundant relative to the surrounding environment, often related to agriculture and human-related effects. These areas may actually have different patterns of genetic diversity relative to the more natural surrounding environment, where density is lower and sampling becomes more difficult (see discussion in [Chapter 2](#)). Thus trends revealed across the range may strongly depend on whether populations are sampled in relatively “natural” areas across the gradient, as compared to areas with high human-related disturbances, especially near the periphery of the range. Testing the above hypotheses is especially relevant in the context of new practical spatial implications for biodiversity conservation (Lesica and Allendorf, 1995; Lomolino and Channell, 1995; Smith et al., 1997) and thus the importance of better understanding and revealing patterns across the species range.

In this work, we aim to test the above hypotheses across a periphery-core gradient focusing on the chukar partridge across a steep distributional gradient in Israel as a research model. We argue that the competing hypotheses are not necessarily contradictory and in some cases may rather be complementary. This may be revealed when sampling of the range is planned carefully in a detailed and continuous design. This includes small and isolated populations located at the very extreme periphery of the range, through transition areas within the range, termed ‘turnover zones’ (Lennon et al., 1997), where rapid spatial thinning of populations occurs (see below), to the continuous and dense core. We here discuss the importance of intermediate areas of transition, located in-between the core and the periphery, at the edge of the species continuous distribution, for understanding speciation processes and spatial patterns of biodiversity.

In order to make the comparison across the range more robust, we divide the distribution range into three areas. This division of the range is in agreement with three regions within a species distribution identified by Lennon et al. (1997) in a simulation study of metapopulation range dynamics, which included: ‘outland’,

‘turnover zone’ and ‘homeland’. This was based on the percentage of the time in which a local population within the metapopulation is present at a given location in space. The ‘periphery’ is somewhat equivalent to the ‘outland’ identified by Lennon et al. (1997) at the outermost part of the range, where populations were least frequent and were ephemeral relative to other areas. The ‘core’ is equivalent to the main geographical range, termed ‘homeland’, where populations were long-lived, were present during a relatively high percent of the time and showed low turnover. In the intermediate “turnover zone” of the simulation study, cell (i.e., population) occupancy fell off steeply, leading to “rapid spatial thinning of populations” (Lennon et al., 1997:495; see also Carter and Prince, 1981). We adopt the terminology for the turnover zone in this paper, yet maintain the classical terms periphery and core.

Areas of ecological transition, ecotones, have recently received attention due to their potential importance as biodiversity hotspots and as their role in biodiversity conservation (Kark et al., 1999; Smith et al., 1997). We test the role of ecotones as diversity hotspots. In these areas of steep ecological transition between ecosystems various species reach the limits of their continuous distributions (Danin, 1998; Endler, 1982) and beyond here, towards the most extreme periphery of the range populations become small, isolated and eventually fade out, marking the edge of the species range (Kark et al., 1999). We use the term “ecotone” for ecosystem related transition zones (i.e. areas of transition between ecosystems) and the term “turnover
ution-related changes within a single species' range (i.e. transition between core and peripheral distribution). The latter turnover zone may often occur at areas of ecological transition, leading to their congruence.

The goals of this work are to examine trends in genetic diversity in populations across a steep environmental gradient from core to periphery within a species distribution range for testing current hypotheses on core-periphery within-population diversity. We compare diversity within populations of a model bird species from continuous areas of the distribution, termed core, through populations in the turnover zone, located at the margins of the species continuous distribution to the extreme margins of the species range.

Material and Methods

The gradient in Israel

A sharp climatic and ecological gradient in Israel from Mediterranean to desert ecosystems is congruent with northern, western and southern margins of Mediterranean, Irano-Turanian and Saharo-Arabian species' distributions, respectively (Danin, 1998; Yom-Tov and Tchernov, 1988). While mean annual rainfall in the Mediterranean Galilee and Golan Heights in the north is over 900 mm, only 250 km away in the southern Negev desert mean annual rainfall decreases to ca 30 mm and is highly variable among the years (data from the Israel Meteorological Service and Bitan and Rubin (1991). This steep gradient across short geographical distances offers a unique opportunity to test hypotheses regarding trends in diversity across the range in populations which are geographically proximate yet experience very contrasting environments. A 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 <150 mm along approximately 50-60 km. Many species reach the edge of their continuous distributions in this area (Yom-Tov and Tchernov, 1988). This setting provides a good opportunity to compare trends in genetic diversity from core to periphery across a species range in populations which are geographically proximate yet experience steep climatic and ecological gradients.

The species - chukar partridge

We chose the chukar partridge (*Alectoris chukar*) as a research model for testing the above hypotheses for several reasons: The chukar is continuously distributed in Israel and population density is high from the Mediterranean areas in the north to the desert border ecotone (Shirihai, 1996). The margin of the species continuous range is found in the northern Negev ecotone which is the turnover zone for the species. Distribution

becomes patchy and populations smaller and more isolated south of here towards the central and southern Negev desert, where the global periphery of the species' distribution range occurs (Shirihai, 1996). An additional isolated population, most probably a relict from the late Pleistocene, is found in the mountains of the Southern Sinai desert (Kark et al., 1999). Chukars are sedentary, and do not migrate seasonally. Coveys usually remain within a limited area of several square km (Alkon, 1974). Chukars are found in both more natural and human-related habitats, enabling a comparison between these areas. These factors make the chukar in Israel a good candidate for testing trends across the range.

Human effects

While human-related activity, including traditional agriculture, controlled burning and grazing by domestic animals have been dominant in Israel and the region for thousands of years, and have affected the Mediterranean, as well as desert ecosystems (Danin, 1998), they have changed their character in the 19-20th centuries, with large human immigration to the area (Kark, 1989). In this work, we sampled two types of habitats across the gradient in order to try to detect whether differences in diversity trends exist based on the type of environment sampled across the range. These two included highly “modern-disturbed” regions along the gradient, where modern agriculture, irrigation and intense game hunting are dominant vs. “natural” areas, where some grazing and cultivation may occur yet where modern agriculture and game hunting are very subtle. The latter areas better represent the typical environment of the area in the past hundreds, perhaps thousands of years.

Field work

During fall 1995 to winter 1996 (September through early February), 17 populations of chukars were sampled in Israel across the steep gradient from the northern Golan Heights to the southern Negev (Fig. 1). Five of these populations were sampled within the ecotone region. Thirteen natural populations were sampled across the gradient in Israel. Four of these populations were compared with adjacent

paired populations from highly disturbed (termed “modern-disturbed”) areas, where modern agriculture, irrigation and more intense game hunting are dominant (see Fig. 1 for locations). Sampling was done during the non-breeding season when birds are organized in stable coveys that maintain relatively fixed home ranges (Alkon, 1974). Analysis of genetic diversity was done for the 13 populations from the natural environments separately. The four coupled “modern-disturbed” populations were compared with their paired “natural” populations using a paired t-test.

Sampling and genetic analysis

‘Population’ was defined based on area size. Each population was sampled in an area of ca 10 square km. Sampling was done following Randi and Alkon (1994). Hunters were joined and briefed in the field in all cases, except for populations Bezek, Ben-Gurion and Nevatim, in which hunters worked in a clearly confined area. 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 the three populations mentioned above, in which the birds were dissected in the laboratory. Tissue homogenization, 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 Alkon and Randi, 1994 for list of loci analyzed, except PEP-2, LDH, SOD-2, mGOT, mIDH, GDH which were not resolved here). A locus was considered polymorphic if more than one allele was present. Estimates of genetic diversity were computed for each population using BIOSYS-1, v.1.7 (Swofford and Selander, 1989). The following estimates of genetic diversity were computed for each population: percent of polymorphic loci (P), mean number of alleles per locus (A), mean observed heterozygosity (H_o), mean Hardy-Weinberg (HW) expected heterozygosity (H_e).

Regression analyses

Linear and polynomial regressions were calculated between distance from the chukar range periphery and these genetic diversity estimates: observed heterozygosity (direct count) (H_o) and Hardy-Weinberg expected heterozygosity (H_e). Correlation between sample size and all diversity estimates was computed to assure that results were not confounded by this factor. Statistics were calculated using JMP 3.1.5 for Windows (SAS Institute Inc. 1990).

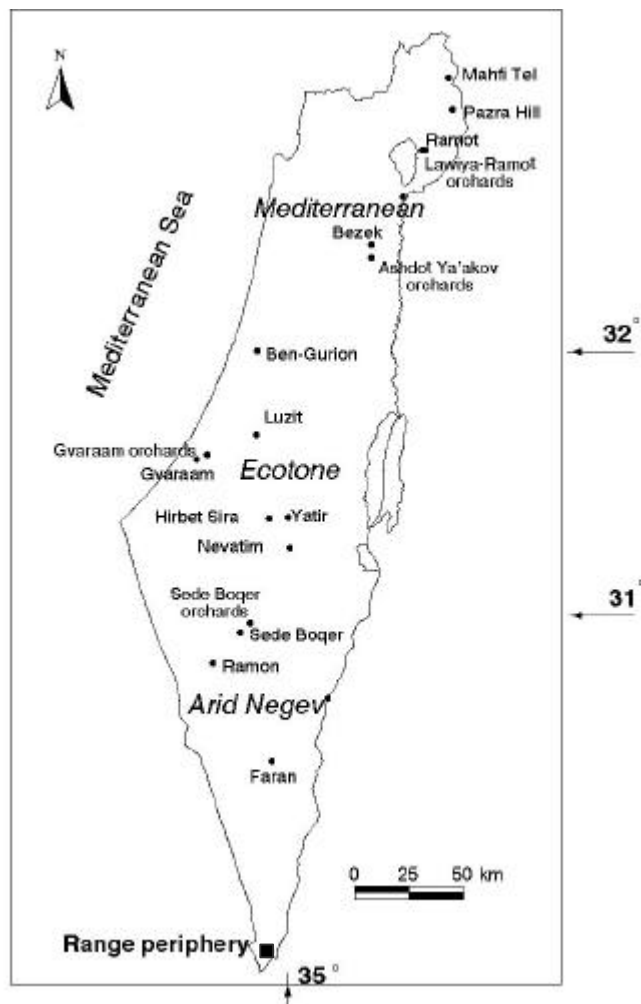


Figure 1. Map of study area and chukar populations sampled. Range periphery is marked with a square and was determined as the center of the grid in which chukar distribution decreases to zero based on Shirihai (1996).

Results

Allozyme diversity in the studied populations

Nine of the 26 studied loci were polymorphic. See Table 1 for allele frequencies across populations. Mean observed heterozygosity across all 17 studied populations ranged between 0.052-0.12, mean expected heterozygosity between 0.069-0.115, percentage of polymorphic loci between 26.9-34.6% and mean number of alleles per locus was between 1.4-1.7 (see Table 1). No significant correlation ($P>0.3$) was found between mean sample size per locus and any of the genetic diversity parameters tested. F_{st} values were between 0.032-0.11 for all populations at single loci and 0.064 at all loci combined (Table 2).

Trends in genetic diversity along the gradient

Overall, trends revealed across the species range in the 13 “natura a hump-shaped trend of within-population diversity from core to periphery of the range. Diversity peaked at the ecotone (Table 3). Maximal levels of diversity were obtained for populations from the northern Negev ecotone, at the steepest parts of the climatic gradient, and the edge of the species continuous range. Diversity decreased from the ecotone towards both the Mediterranean core regions in a monotonous fashion, and towards the extreme periphery, although not monotonously. These trends were especially strong and significant for observed and expected levels of heterozygosity. A polynomial quadratic regression for each of these two diversity estimates vs. distance from the periphery (as the independent variable) was highly significant with an r^2 of 0.70 ($P<0.0025$) and 0.83 ($P<0.001$) for observed and expected heterozygosity, respectively. The trend of decreasing diversity from the ecotone towards the core was found also in the percentage of polymorphic loci and in mean number of alleles per locus, yet decrease towards the extreme periphery was not as clear.

Table 1. List of allele frequencies of polymorphic loci in populations of chukars sampled in Israel, with area codes below population location. Populations are listed from north to south. Mean sample size for each locus is marked as (N).

	Location	Mahfi Tel	Pazra Hill	Ramot Gamla orchards	Lawiya Ramot	Ashdot Ya'akov orchards	Bezek Reserve	Luzit	Ben- Gurion Airport	Gvaram orchards	Gvaram	Hirbet Yatir	Hirbet Sira	Nevatim	Sede Boqer orchards	Sede Boqer natural	Ramon	Faran
Locus	Allele	MT	PH	RG	LR	AY	BR	LU	BG	SV	GV	HY	HS	NV	SB	SN	RM	FR
PGM	(N)	27	25	14	24	17	17	28	25	31	26	20	29	2	28	28	32	26
	A	0	0	0	0	0	0	0	0.04	0	0	0	0	0	0	0	0.016	0
	B	0.981	1	0.964	1	1	0.941	0.982	0.72	0.952	0.962	0.9	0.879	0.948	0.982	1	0.984	0.981
SGOT	(N)	27	25	11	25	17	18	29	25	31	25	20	29	29	28	28	32	26
	A	0	0.04	0	0	0	0	0	0	0	0	0	0	0	0	0		0
	B	0.963	0.84	0.909	0.88	0.882	0.75	0.724	0.86	0.86	0.6	0.75	0.776	0.69	0.911	0.768	0.68	0.712
	C	0.019	0.12	0.091	0.12	0.118	0.25	0.276	0.14	0.177	0.26	0.25	0.224	0.31	0.071	0.143	0.33	0.288
ADH	D	0.019	0	0	0	0	0	0	0	0.06	0.14	0	0	0	0.08	0.089	0	0
	(N)	27	21	14	22	17	18	26	25	32	26	20	28	29	28	28	31	26
	A	0	0.071	0	0	0	0	0	0	0	0	0.05	0.05	0	0.08	0	0.05	0
AC	B	1	0.929	1	1	1	1	1	1	1	1	0.975	0.946	1	0.982	1	0.35	1
	(N)	27	25	14	25	17	18	29	25	32	26	20	28	29	27	28	3	26
	A	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0		0
	B	0	0	0	0.08	0	0	0	0	0.078	0.135	0.125	0.125	0.155	0.111	0.018	0.129	0.058
PEP-1	C	1	0.98	1	0.92	1	1	0.948	0.96	0.922	0.865	0.85	0.857	0.845	0.833	0.982	0.871	0.942
	D	0	0.02	0	0	0	0	0.052	0.04	0	0	0.025	0.018	0	0.056	0	0	0
	(N)	26	25	9	25	16	18	28	25	24	25	18	28	29	27	28	32	26
	A	0.115	0.02	0	0.12	0.125	0.028	0.071	0.08	0.104	0.04	0.056	0.161	0.103	0.093	0.446	0.406	0.346
	B	0.558	0.62	0.444	0.62	0.688	0.417	0.571	0.24	0.375	0.54	0.306	0.339	0.414	0.611	0.321	0.563	0.596
	C	0.327	0.36	0.556	0.26	0.188	0.556	0.357	0.68	0.521	0.42	0.639	0.5	0.483	0.296	0.232	0.031	0.058

Locus	Allele	MT	PH	RG	LR	AY	BR	LU	BG	SV	GV	HY	HS	NV	SB	SN	RM	FR
PEP-2	(N)	27	25	12	25	17	16	28	25	29	26	20	29	29	27	24	31	26
	A	0.944	0.98	0.875	0.9	0.882	0.875	0.857	0.78	0.914	0.904	0.825	0.879	0.776	0.87	0.833	0.887	0.75
	B	0.019	0.02	0.083	0.1	0.118	0.125	0.036	0.1	0.086	0.096	0.175	0.086	0.103	0.056	0.146	0.048	0.135
	C	0.037	0	0.042	0	0	0	0.107	0.12	0	0	0	0.034	0.121	0.074	0.021	0.065	0.115
CK	(N)	27	21	13	6	1	9	17	16	24	26	19	25	29	21	23	26	23
	A	0.037	0	0.077	0.083	0	0.056	0.029	0.09	0.104	0.192	0.105	0.06	0.034	0.071	0.109	0.058	0.13
	B	0.963	1	0.923	0.917	1	0.944	0.971	0.96	0.896	0.769	0.895	0.94	0.966	0.929	0.891	0.942	0.87
	C	0	0	0	0	0	0	0	0	0	0.038	0	0	0	0	0	0	0
6PGD	(N)	27	25	14	25	17	18	29	25	31	26	20	29	29	28	28	32	26
	A	0.093	0.06	0.107	0.12	0.088	0.167	0.017	0.08	0	0.019	0	0.086	0.224	0.107	0.089	0.109	0.038
	B	0	0.06	0	0	0.118	0	0.155	0	0.081	0.154	0.075	0	0.017	0.15	0	0	0.135
	C	0.907	0.88	0.893	0.88	0.794	0.833	0.81	0.88	0.919	0.827	0.925	0.897	0.759	0.68	0.911	0.891	0.827
	D	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
	E	0	0	0	0	0	0	0.017	0.04	0	0	0	0	0	0	0	0	0
	F	0	0	0	0	0	0	0	0	0	0	0	0.017	0	0	0	0	0
	G	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
EST-2	(N)	27	24	14	24	17	18	27	25	31	25	19	27	25	25	27	32	23
	A	0	0	0	0	0.059	0	0	0	0	0	0	0	0.02	0	0	0	0
	B	0.278	0.333	0.5	0.583	0.206	0.25	0.37	0.36	0.242	0.32	0.263	0.222	0.32	0.2	0.185	0.359	0.174
	C	0.167	0.104	0.107	0.125	0.118	0.222	0.185	0.34	0.161	0.2	0.132	0.204	0.06	0.24	0.389	0.234	0.5
	D	0.352	0.271	0.107	0.229	0.294	0.278	0.352	0.18	0.371	0.4	0.368	0.444	0.32	0.34	0.185	0.297	0.196
	E	0	0.042	0.107	0.021	0.265	0.167	0.019	0	0.097	0.06	0	0.019	0	0.14	0.037	0	0.022
	F	0.204	0.25	0.179	0.042	0.059	0.083	0.074	0.12	0.129	0.02	0.237	0.111	0.28	0.08	0.204	0.109	0.109

Monomorphic loci were: Hb-1, Hb-2, post-ALB-1, post-ALB-2, ALB H-PT-1, H-PT-2, H-PT-3, LDH1, LDH2, SOD-1, PGI, MPI, sMDH, FUM, EST-1, EST-3

Table 2. Summary of F statistics for polymorphic loci studied (see chapter 2 for statistics)

Locus	F_{is}	F_{st}	F_{it}
PGM	-.0926	.0885	.0041
SGOT	-.1507	.0542	-.0883
ADH	-.0597	.0426	-.0146
ACP	-.0254	.0502	.0261
PEP-1	.1182	.1132	.2180
PEP-2	.0563	.0315	.0860
CK	-.0418	.0371	-.0031
6PGD	.1063	.0393	.1414
EST-2	.1169	.0521	.1629
Mean	.0485	.0637	.1092

“Natural” vs. “modern-disturbed” areas

A comparison of the four paired populations from the “natural” vs. modern-disturbed areas shows differences in the effect of disturbance on diversity across the range appear (Table 4). In the Mediterranean core and ecotone regions “modern-disturbed” populations from areas with intense modern agriculture (orchards) and hunting had similar or lower genetic diversity levels than in paired populations from “natural” areas with very little agriculture and no hunting (see Table 3). Yet a comparison of the populations from the two types of environs in the arid periphery (Sede Boqer Natural vs. Sede Boqer orchards) reveals an opposite trend: the population from the irrigated orchards had higher levels of diversity in all estimates of genetic diversity tested as compared with its coupled population from the more natural environment, although a t-test comparing mean observed heterozygosity over all loci in the two populations was not statistically significant at the 0.05 level.

Table 3. Population characteristics and estimates of allelic diversity for chukar populations sampled in “natural” environments across the chukar range from core to periphery (n = mean sample size per locus, H_o = mean observed heterozygosity, H_e = mean expected heterozygosity¹, A = mean number of alleles per locus, P = percentage of polymorphic loci²). Populations are listed from north to south. Distance from the range periphery is in km (see Fig. 1). Distance from the range periphery (Distance) was determined for each population. Range periphery was taken as the center of the grid square where density becomes zero at the Southern Negev (Eilat Mountains) region of Israel based on Shirihai (1996; see Fig. 1 and text).

Population	Area Code	Region ³	Distance	n	SE n	Mean H _o	SE H _o	mean H _e	SE H _e	A	SE A	P
Tel Mahfi	MT	Core	408	27	0	0.052	0.026	0.069	0.036	1.5	0.2	26.9
Pazra Hill	PH	Core	395	24.7	0.2	0.063	0.029	0.076	0.036	1.5	0.2	26.9
Lawiya-Ramot	LR	Core	372	24.1	0.7	0.079	0.031	0.08	0.032	1.4	0.2	26.9
Bezek Reserve	BR	Core	316	26.9	0.4	0.086	0.037	0.094	0.039	1.4	0.2	17.5
Ben-Gurion Airport	BG	Core	264	24.7	0.5	0.093	0.031	0.105	0.038	1.5	0.2	30.8
Luzit	LU	Core	233	28.2	0.3	0.092	0.036	0.094	0.038	1.6	0.2	30.8
Gvaraam	GV	Ecotone	218	25.9	0.1	0.120	0.043	0.115	0.041	1.6	0.2	30.8
Yatir	HY	Ecotone	199	19.8	0.1	0.106	0.037	0.107	0.038	1.5	0.2	34.6
Hirbet Sira	HS	Ecotone	196	28.7	0.2	0.103	0.036	0.107	0.038	1.6	0.2	34.6
Nevatim	NV	Ecotone	182	28.8	0.2	0.111	0.04	0.114	0.041	1.5	0.2	30.8
Sede Boqer	SN	Periphery	148	27.6	0.2	0.073	0.032	0.096	0.04	1.5	0.2	26.9
Ramon	RM	Periphery	129	31.7	0.2	0.096	0.037	0.1	0.037	1.5	0.2	34.6
Faran	FR	Periphery	86	25.8	0.2	0.094	0.035	0.105	0.039	1.5	0.2	30.8

1. Unbiased estimate based on Hardy-Weinberg Equilibrium (see text);

2. A locus is considered polymorphic when more than one allele is detected;

3. Region type is based on a phytogeographical analysis for sampling sites. The proportion of plant species belonging to the major floral chorotypes found in Israel was determined for each

population area. Data was provided by A. Danin (unpublished data) based on a grid of 5x5 km for the whole of Israel. In each square, all plant species, of all life forms, were divided based on their chorotype. In two of the regions (Gvara'am and Ramon) where data for the square from which the chukar population originated was insufficient, an adjacent square was used. Based on this phytogeographical classification, populations were pooled into three main regions: Mediterranean (6 populations), ecotone (4 populations) and periphery (3 populations), see Fig. 1 for population areas and Additional Figure (Fig. 3) at the end of this chapter for distribution of plant chorotypes across sampling locations for the 13 populations from natural environments.

Table 4. Estimates of allelic diversity in pairs of populations of chukars sampled in “natural” vs. modern-disturbed environments across distribution gradient from core to periphery (n = mean sample size per locus, H_o = mean observed heterozygosity, H_e = mean expected heterozygosity¹, A = mean number of alleles per locus, P = percentage of polymorphic loci²). Populations are listed from north to south.

Location	Area	Type	n	H_o	H_e	A	P
Lawiya Ramot	Core	“natural”	24.1	0.079	0.080	1.4	26.9
Ramot Gamla orchards	Core	modern-disturbed	13.6	0.081	0.079	1.4	26.9
Bezek Reserve	Core	“natural”	17.5	0.086	0.094	1.4	26.9
Ashdot Ya'akov orchards	Core	modern-disturbed	16.3	0.073	0.08	1.4	19.2
Gvaraam	Ecotone		25.9	0.12	0.115	1.6	30.8
Gvaraam orchards	Ecotone	modern-disturbed	31.1	0.086	0.093	1.5	30.8
SedeBoqer natural	Periphery	“natural”	27.6	0.073	0.096	1.5	26.9
Sede Boqer orchards	Periphery	Modern-disturbed	27.5	0.096	0.101	1.7	34.6

1. Unbiased estimate based on Hardy-Weinberg Equilibrium (see text)
2. A locus is considered polymorphic when more than one allele is detected

Trends in PEP-1

An interesting trend appeared in the locus PEP-1, where three alleles were resolved. While allele A had relatively low frequencies in Mediterranean and ecotone populations, its rates were much higher in all three peripheral populations, including Sede Boqer natural, Ramon and Faran, ranging from 0.35-0.45 (see Fig. 2). Yet the population from the Sede Boqer orchards showed completely different frequencies compared to the three arid peripheral populations, which were much more similar to those in the more northern non-peripheral locations. This may possibly reflect an advantage of this allele or a linked allele in arid environments. The environment where Sede Boqer orchards population persists may thus be more similar to that in the more mesic locations dozens km away than to that of the surrounding desert environment, and even to that of the neighboring “natural” population of Sede Boqer (SN), located only several km away. Thus this allele may be reflecting natural selection rather than exclusively neutral processes.

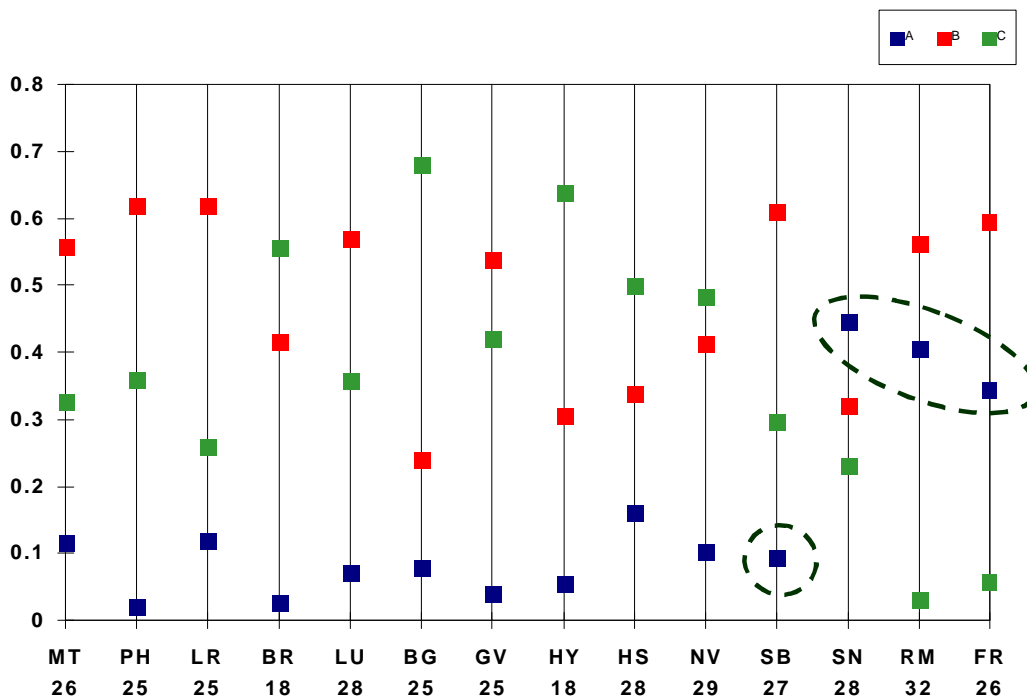


Figure 2. Shift in frequency of alleles in PEP- 1 across study populations, from north to south. Arid peripheral populations (SN, RM, FR) and Sede Boqer orchard population (SB) are marked in dashed circles. See Table 1 for population codes.

Discussion

Pattern of genetic diversity across the range

Trends in within-population genetic diversity for the chukar partridge in Israel show peak levels of diversity at intermediate areas of the range, decreasing both towards the core and the extreme periphery of the species distribution. Populations from the turnover zone, which in the chukar is congruent with the ecotone, sustain especially high levels of within-population genetic diversity, as measured by various estimates, and especially as reflected in levels of observed and expected heterozygosity. These results are apparent in the chukar in Israel across the sharp gradient from the Mediterranean core, where conditions are relatively favorable and population density is high through the ecotone, where the edge of the species continuous distribution occurs, to the extreme periphery, where environmental conditions are less favorable and population density is lower (Shirihai, 1996). The latter area we suggest can also be termed the “decay zone” of the species range.

A potential explanation for the findings, which is worthwhile exploring, is secondary contact of previously isolated populations in a hybrid zone. Recontact of these populations may bring to increased genetic diversity in the contact area (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 alternative theory to explain diversity trends in Israeli chukars across the ecotone. Two morphological sub-species of chukar (*A. c. cypriotes* and *A. c. sinaica*) were traditionally recognized in the region (Cramp and Simmons, 1980), with a putative contact zone occurring around the Mediterranean-desert ecotone region. If this is the case, recontact of formerly isolated populations in the region following the Quaternary glacials may have lead to hybridization and increased genetic diversity. More detailed morphological studies (Nissani, 1974) and some available paleontological findings (Yom-Tov and Tchernov, 1988) suggest that clearly distinct

A. c. sinaica occur only in the southern Sinai desert and that the extant isolated population in the Sinai Mountains is a post-glacial relict (Tchernov, 1988) from the Upper Pleistocene glacial period. Actually, as discussed by Kark et al. (1999) chukar distribution in this region in the past 120,000 years seems to have contracted rather than expanded. Distribution of chukars during those periods was rather continuous throughout the southern parts of Israel and Sinai, including currently more arid areas where chukars are not present or are very rare (Tchernov, pers. comm., Shirihai, 1996). This is because during the glacials the area which is now the southern desert and edge of the chukar range was more mesic and cooler and has since changed into more extreme desert. Thus, as suggested by Kark et al. (1999), the argument for historical recontact and hybridization in the Mediterranean-desert ecotone causing increased diversity does not seem highly probable at this time. Yet current molecular analyses of the mtDNA control region of the same individuals for which allozyme and morphological data are available may contribute to resolving this issue.

Relation to previous years' results

Two previous years of study across the chukar range in Israel (1990 and 1993) showed a pattern of increasing diversity from the core to the turnover zone, consistent with the findings presented here for the same part of the range (Kark et al., 1999). The previous work showed that chukar populations exhibit some isolation by distance effects in the face of substantial gene flow. Kark et al. (1999) suggest that the interplay between the homogenizing effects of gene flow and the divergent pressure of natural selection among populations in different habitat conditions may generate different functional adaptations, increase genetic diversity, enabling divergence with gene flow. Results of this work support these findings, pointing again to populations structuring across short distances and in the face of gene flow. Based on results from that previous sampling (Kark et al., 1999), which did not include the extreme periphery, yet covered a gradient from the core towards the turnover zone, one may have extrapolated for the extreme periphery and concluded that the trend is one of increasing diversity from the core towards the range periphery. Following that work,

we hypothesized that when the extreme periphery will be sampled, genetic diversity will again decline, revealing a hump-shaped pattern (Kark et al., 1999). Testing this prediction was the motivation for the third, comprehensive year of the study, presented here. Populations were sampled across a wider range in Israel to include the extreme periphery. A larger number of populations was studied. We hypothesized that when chukar populations in natural and neighboring irrigated agricultural environments in the desert will be compared there will be local differences in patterns of genetic diversity, which may confound trends if the effect is not controlled across the range. Therefore, in this work, populations were carefully selected to distinguish between “natural” and “modern-disturbed” environments. Area of sampling was confined to 10 square km for each population.

The results of this work support the above hypothesis. Sampling across a gradient which includes core, turnover zone and periphery reveals a hump-shaped pattern of within-population diversity, as estimated by heterozygosity levels. Differences in genetic diversity between natural and disturbed environments exist. In many studies, it is practically difficult to sample populations at the extreme periphery (the “decay zone”) and thus it may be appealing to sample more dense and rich patches, some which are man-made. Yet one should be aware of the fact that these may not represent the genetic structure in more natural, even adjacent environments. While comparing populations from the two types of areas in this study, it is important to recall that this comparison is based on only four pairs, each from a different part of the core-periphery gradient, where the populations from the more disturbed areas were not controlled for the effects of hunting vs. those of agriculture and irrigation. The interplay between these two factors alone may have a crucial role in determining the levels of genetic diversity in the populations from the modern-disturbed areas. These populations were rather chosen to compare with the selected “natural” gradient as areas with very high total disturbance levels. The important point to note here is that if we were to sample and compare only populations from non-natural, disturbed environments, we would have possibly revealed a different trend than that detected when populations from “natural” environments are sampled, especially due to the

decrease of genetic diversity in natural populations near the arid periphery of the range (Table 4). Thus sampling of the range and publication of more detailed description of field work and especially sampling methods and criteria for site selection would help in interpretation of findings, and may help in solving some of the contradictions seen in the literature.

Conservation implications

This work suggests that ecotone areas across the species range may be worth substantial investment for ensuring further dynamic existence of the species, with potential for speciation processes. Rapid shifts in this environment from more mesic to arid and back over short temporal scales (Danin, 1998) may provide an arena for sustaining biological diversity and for speciation processes. Many species, with Saharo-Arabian, Mediterranean, Palaearctic and Irano-Turanian distribution patterns, reach the edge of their continuous distributions in the Mediterranean-desert ecotone region of Israel (Danin, 1998). Being relatively small in size, if ecotones are further shown to be rich in diversity, directing further conservation efforts towards them may prove to be a cost-effective strategy.

In the bird species studied, and possibly numerous other animal species, irrigation-based agriculture and settlement in the desert is creating rich habitat patches in areas that formerly supported only sparse populations, and seems to be changing patterns of distribution (Kark et al., 1999; Shirihi, 1996). The two chukar populations from Sede Boqer exhibited very different levels and patterns of genetic diversity. While the population from the more natural desert environment showed relatively low levels of diversity, as estimated by various measures, the modern-disturbed area population, located in relatively small recently established local “islands” of orchards and agricultural fields within the surrounding arid (mean annual rainfall ca. 100 mm; Israel Meteorological Service) environment in which chukar density is lower. These recent changes seem to have been affecting patterns of genetic diversity. The opposite trend was observed at the ecotone area, where the disturbed areas exhibited lower levels of diversity. Thus conservation decisions

across the steep environmental cline in Israel should not be general but rather area-specific, taking into account the local effects of human-related activity on genetic diversity patterns.

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Additional figure (for Ph.D. thesis only)

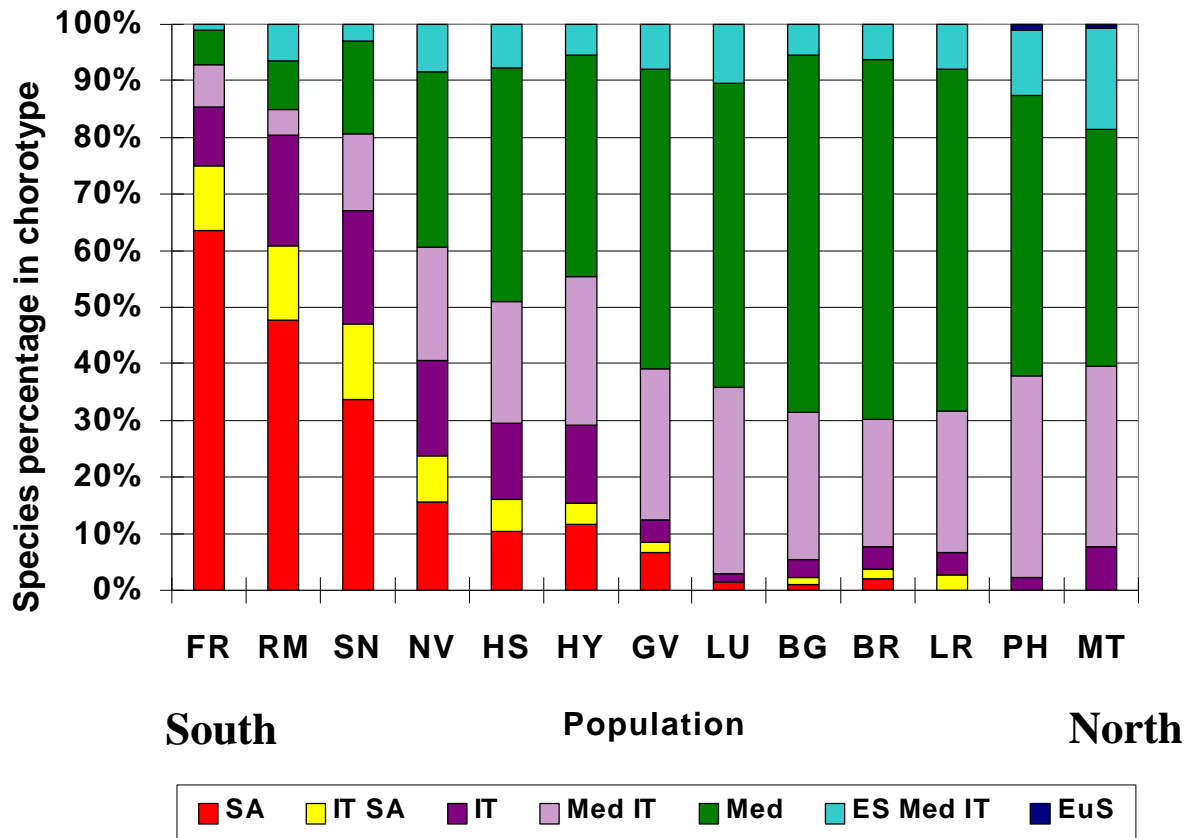


Figure 3. Distribution of plant chorotypes in each of the study areas of the "natural" environments only (as described in text). Populations appear from south to north. Population location codes appear in Table 1 of [Chapter 4](#). The shift between Mediterranean and Saharo-Arabia (desert) chorotypes is apparent in the ecotone region. Mediterranean-desert ecotone region. Chorotype codes: SA - Saharo-Arabian, IT - Irano-Turanian, ES (EuS)- Euro-Siberian, combinations of the main types (see Danin, 1998 for more details).

Data courtesy of Avinoam Danin (unpublished data).

Preface to Chapter 5

Trends in genetic diversity, as estimated by various measures of allozyme diversity, show a hump-shaped pattern of diversity from core to periphery across the chukar range in Israel with peak levels at the turnover zone located in the ecotone (presented in Chapters 2-4). Comparison of trends at the genetic level with those at the morphological level could add another dimension to this work, testing for the generality of patterns across scales and revealing factors which are affecting these patterns. The study of variation within and between species has been the basis of evolutionary theory since Darwin (1859). While comparison of population means is rather simple to plan, the study of trends in variances across the range is usually more complex. This is mainly due to the fact that variances, unlike means, are not normally distributed but are rather F-distributed. Due to this, much larger sample sizes or many more measurements for each individual are required in order to reveal statistically significant differences among populations. This demands a very large amount of work, is time consuming and is therefore expensive. The same is often true for quantitative genetics studies (Lynch, 1996; Roy and Foote, 1997). Yet these fields are receiving increasing attention due the understanding of their major importance in applied and conceptual studies as well as biodiversity research (Roy and Foote, 1997).

In this work, I used a data set collected by Rachel Nissani, as part of her M.Sc. thesis at the Hebrew University of Jerusalem in the early seventies. The goal of that work (Nissani, 1974) was to test Begmann's Law (Begon et al., 1996) by comparing means of traits (and ratios between traits) in populations of the chukar partridge. Populations were sampled across a gradient from the Upper Galilee to the arid periphery, including the isolated relict populations from the Sinai Mountain region. This data set was very useful due to the fact birds were measured for 35 traits and 23

ratios were calculated. This gave a relatively large number of traits which enabled comparison across the range. With permission from Nissani and Tchernov, I computerized this data set and used it for further work. I was interested to find a way to compare within-population diversity (variation), equivalent to the estimates at the genetic level (e.g. mean heterozygosity), which gives one diversity estimate for each sex within each population based on all traits measured in each individual. Sample size was too small to enable a comparison of diversity of single traits across populations. Therefore, the inclusion of all traits was crucial in order to obtain a large enough “effective” sample size for comparisons. A statistic was developed for this work together with A. Darvasi, which enables to calculate one diversity value for each population, taking into account all individuals, traits and the correlation matrix between all traits. The latter was important as many of the traits were inter-correlated. Although only five populations were available with large enough sample sizes, when results are interpreted together with those of the allozyme (genetic) data set, similar trends appear and add an important dimension. The following paper presents the results of this work.

Chapter 5

Increased Phenotypic Diversity at the Ecotone: A Study across the Chukar Partridge Range Using Data from Multiple Correlated Traits

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Abstract

We studied trends in within-species morphological diversity across the chukar partridge (*Alectoris chukar*) range in Israel and the Sinai Peninsula. Five populations distributed along the distribution gradient, from core to periphery, were measured for 35 traits and 23 ratios between traits. We used a simple weighted average statistic which we term ‘Estimator in a Dependent Sample’ (EDS) to compare levels of within-population diversity. It provides an estimate of morphological diversity for each population using data for the coefficient of variation from multiple-correlated traits. Our results indicate that when an intermediate distribution area termed the ‘turnover zone’ (Lennon et al. 1997) is included in the study, a hump-shaped non-monotonic trend in morphological diversity appears across the range. Levels of diversity were maximal in the chukar turnover zone, at the edge of the species’ main distribution. This falls within the Mediterranean-desert ecotone. We suggest that the study of patterns in morphological diversity across species ranges using multiple traits may be important for understanding speciation processes and in determining priorities for biodiversity conservation. If the patterns revealed in this study prove more general, ecotones should be given higher priority in conservation planning serving as diversity hotspots.

Keywords: biodiversity, chukar partridge; core-periphery; distribution range; ecotone; Estimator in a Dependent Sample (EDS); morphological diversity; multiple-correlated traits; turnover zone.

Introduction

The importance of focusing on the study of populations located in ecotone regions and along steep environmental gradients has recently been emphasized (Kark et al., 1999; Smith et al., 1999; Smith et al., 1997). Ecological transition zones (i.e. ecotones) may play a crucial role in generating and maintaining biodiversity and speciation processes (Kark et al., 1999; Smith et al., 1997). Morphological differentiation may be produced by divergent selection in the presence of high gene flow across ecotones between contiguous populations (the divergence-with-gene-flow model of speciation; Rice and Hostert, 1993; Smith et al., 1999; Smith et al., 1997). Morphological divergence is generated at small geographic scales even in species that have great potential for dispersal and gene flow across environmental gradients (Mitchell-Olds, 1992; Peterson, 1995). Accordingly, ecotones may serve as "hot-spots" of within-population diversity across species' ranges, and thereby may warrant high conservation priority processes (Kark et al., 1999; Smith et al., 1997). In these areas of change the distributions of many species become non-continuous and various species approach their main distribution limits (Danin, 1998; Safriel et al., 1994). As a result, major contact zones between subspecies and species are found in ecotones (Endler, 1977; Endler, 1982; Smith et al., 1999). In this paper we adopt the terminology suggested by Lennon et al. (1997) for a single species. Thus in distributional terms we call areas of the range where environmental conditions change from near optimal to sub-optimal and where the main distribution becomes non-continuous 'turnover zones'. Beyond these regions, the species may still maintain small, ephemeral and fluctuating populations towards the very extreme periphery of their range (Lennon et al., 1997) where environments are least suitable (Eldredge, 1995) and where distribution eventually fades out (Lennon et al., 1997).

We here test the hypothesis predicting that within-population morphological variability will increase from the core to the turnover zone and will then drop again toward the periphery. Thus variability is expected to be a hump-shaped function of distance from periphery to core with a maximum at the turnover zone. We test this

hypothesis in the chukar partridge (*Alectoris chukar*) distributed along the Mediterranean-desert ecotone in Israel and Sinai, Egypt.

In Israel, which comprises a narrow land bridge between Europe, Asia and Africa, steep climatic and ecological gradients occur within relatively short distances (Bitan and Rubin, 1991; Danin et al., 1998; Yom-Tov and Tchernov, 1988). The northern mesic regions are characterised by Mediterranean climate, with over 400 mm mean annual rainfall (up to 1000 mm), precipitated largely during October through May. The geographically close southern Negev Desert and Arava Valley are arid, with mean annual rainfall ≤ 50 mm (data from the Israel Meteorological Service; Bitan and Rubin, 1991). A very sharp climatic gradient occurs at the Mediterranean-desert ecotone of the southern Shefela-northern Negev (Kadmon and Danin, 1997; Safriel et al., 1994, fig. 1). Thus, the region offers a unique opportunity to compare geographically proximate populations within a species range, which are potentially connected by dispersal and gene flow, yet experience extremely different environments and ecological conditions.

The chukar generally inhabits the mesic and semi-arid areas, and has large and continuous populations in Mediterranean and steppe parts of the range (Shirihai, 1996). The species occurs in deserts only at the margins of its range in isolated and sparse populations (Shirihai, 1996; Liu Naifa, pers. comm.). The extreme desert regions of the southern Negev and Sinai comprise the south-western border of the chukar global distribution (Shirihai, 1996). The northern Negev ecotone is the edge of the chukar continuous distribution (Kark et al., 1999, fig. 1). This area of transition between Mediterranean and desert ecosystems, where between-years rainfall variability is higher than in the core (data from the Israel Meteorological Service), is the turnover zone of the chukar range in Israel (Kark et al., 1999; Shirihai, 1996).

In the central and southern Negev desert in Israel and the Sinai desert in Egypt, where annual rainfall is <100 mm and is highly variable among the years, chukar density decreases, distribution becomes discontinuous and local populations become small and patchy (Degen et al., 1984; Pinshow et al., 1983; Shirihai, 1996). This area is the extreme periphery of the chukar range. Chukars do not possess physiological

adaptations to heat stress (Carmi-Winkler et al., 1987; Frumkin, 1983; Kam, 1986; Kark et al., 1999), especially as compared with the partly sympatric sand partridge (*Ammoperdix heyi*) which is well adapted to the desert environment (Carmi-Winkler et al., 1987; Degen et al., 1983; Pinshow et al., 1983). A main limiting factor for chukars in the desert is their ability to forage long enough without risking their heat balance. Extremely high temperatures limit the birds' foraging activity to levels which cannot suffice for their energy and water demands (Carmi-Winkler et al., 1987). Therefore, in these marginal habitats the species occurs discontinuously and is usually limited to temporary food and water patches (Shirihai, 1996; S. Kark, unpublished data). These habitat patches must be rich enough to suffice for the birds' energetic needs in the short available daily foraging time, which is limited to the early morning. They must provide sufficient water during the hot and dry summer months when chukars probably need to drink water on a regular daily basis (Carmi-Winkler et al., 1987; Degen et al., 1983; Pinshow et al., 1983). The southern Sinai population is isolated in the Sinai mountains and is most probably a relict from the last glacial periods of the Upper Pleistocene when chukar distribution extended more continuously into areas which are today arid deserts in the Sinai Peninsula (Kark et al., 1999).

Methods

The data set

In this work we use extensive morphological data collected by Nissani (1974) from populations of chukars sampled in Israel and Sinai between 1971-1973. The birds were studied along a steep climatic gradient ranging from the continuous Mediterranean core areas of the species range in the Upper Galilee through the chukar turnover zone at the Mediterranean-desert ecotone (Northern Negev area), to the isolated population of Mount Sinai region at the very extreme periphery of the species range. The populations included from core to periphery (name of site of collection in parenthesis): Upper Galilee (Yiftach), Jerusalem Mountains (Ness Harim), Northern

Negev (Mishmar Hanegev), Negev Highlands (Sede Boqer), and Southern Sinai Mountains (Saint Catherine) (see Table 1). Sample size in each region ranged between 25 to 33 individuals (sexes pooled) for a total of 150 chukars (Table 2).

Trait measurements

Nissani (1974) sampled chukars and compared means between populations, testing for Bergmann and Allen's ecogeographic rules (Begon et al., 1996). The data is used here to examine trends in within-population morphological diversity along the core-periphery gradient to test the proposed hypothesis. Thirty-five morphological traits were measured in all adult individuals and 23 ratios between traits were calculated by Nissani (1974). For detailed description of traits, ratios and measuring methodology see Appendix 1. Data were available on detailed hand-written records that we computerised.

The statistical estimator

In order to compare within-population levels of diversity across populations using all traits measured, we apply a statistical estimator for within-population morphological diversity. It is estimated in terms of variance, standard deviation (SD) or coefficient of variation (CV) from morphological data of multi-correlated traits. This simple statistic is useful for the calculation of morphological diversity in a population when multiple measurements are taken from each individual and one value for diversity is required for each of the study populations to enable comparison among them. This estimator is especially useful when data from many, often correlated traits are available, or when sample size is too small to detect significant trends across populations if single traits are analyzed.

Table 1. Description of chukar study locations, distance from the range periphery and mean annual rainfall. Rainfall data is from the Israel Meteorological Service (Bitan and Rubin, 1991) and from Nissani (1974). Environment description is based on Danin (1998).

Area - location (abbreviation)	Latitude & longitude	Distance from Periphery* (km)	Environment	Mean annual rainfall (mm)
Upper Galilee - Yiftach (UG)	33°06'N 35°33'E	398	Mediterranean maquis; localised deciduous orchards	700
Jerusalem Mountains - Ness Harim (JM)	31°44'N 35°03'E	240	Mediterranean maquis; localised deciduous orchards	537
Northern Negev - Mishmar Hanegev (NN)	31°23'N 34°41'E	197	Open semi-steppe bathas with croplands	244
Negev Highlands - Sede Boqer (NH)	30°52'N 34°47'E	148	Arid steppes with some orchard oases	91
Southern Sinai Mountains - Saint Catherine (SM)	28°33'N 33°57'E	-145	Desert vegetation of hyper-arid mountains limited to wadis with small orchard oases	73

*See methodology chapter for determination of range periphery.

Table 2. Within-population weighted morphological diversity estimate (EDS) based on coefficient of variation and standard deviation for 35 traits and 23 ratios in males (a) and females (b). Populations are listed from north to south. n = sample size in each population.

a. Males

Area	n	EDS traits		EDS ratios	
		CV	SD	CV	SD
Upper Galilee - Yiftach	12	0.0414	85.946	0.0439	14.919
Jerusalem Mountains - Ness Harim	15	0.0503	94.904	0.0436	14.568
Northern Negev - Mishmar Hanegev	16	0.0590	111.925	0.0537	16.762
Negev Highlands - Sede Boqer	11	0.0478	95.020	0.0475	16.354
Southern Sinai Mountains - Saint Catherine	13	0.0424	83.406	0.0385	11.576

b. Females

Area	n	EDS traits		EDS ratios	
		CV	SD	CV	SD
Upper Galilee - Yiftach	17	0.0379	74.950	0.0394	13.963
Jerusalem Mountains - Ness Harim	16	0.0503	109.686	0.0447	13.926
Northern Negev - Mishmar Hanegev	16	0.0553	116.611	0.0485	15.961
Negev Highlands - Sede Boqer	22	0.0416	82.056	0.0460	14.205
Southern Sinai Mountains - Saint Catherine	12	0.0502	110.349	0.0407	12.891

Calculation of the Estimator in a Dependent Sample (EDS)

When estimating diversity in a dependent sample observations need to be weighted by their degree of independence. As an extreme example, two equivalent traits (100% correlated) should not be counted twice. We here suggest using a weighted average statistic, in which the weighting parameter is the degree of independence of each trait estimated by: $(1 - |r_{ij}|)$ for trait a_j where a is a variability measure (e.g., CV, SD);

and r is the correlation coefficient between traits. The weighted average is then:

$$EDS = \frac{1}{\sum_j (1 - |r_{ij}|)} \sum_j a_j [(1 - |r_{ij}|)] \quad (\text{Equation 1})$$

where EDS stands for Estimator in a Dependent Sample.

Thus the relative weight of each trait in the estimator is determined by its correlation with each of the other traits. This gives an unbiased estimate for within-population diversity, using information based on all individuals and morphological traits measured within a sampled population, and on their correlation matrix. This estimator may be useful in various analyses using multi-correlated phenotypic traits, especially when the required emphasis is not on the absolute numerical values for each trait, but rather on the relative comparison of estimates from different species, populations or groups within a population (e.g. sexes, social classes and age groups) or when testing for spatial and temporal trends in phenotypic variability.

For calculating EDS, various variability measures, including the variance, SD and CV can be used. We prefer the CV when comparing populations, as it is independent of absolute differences in trait means (Soulé & Cuzin-Roudy 1982), commonly detected along climatic and ecological gradients (Begon et al., 1996). We calculated the EDS using both the CV and the SD.

In the case of the chukar presented here, the EDS is separately obtained for adults of each sex within each population, representing the weighted morphological

diversity value over all characters. The EDS was calculated for the 35 traits and for the 23 ratios in each sex using Pearson's correlation coefficient. Males and females were separated in the analysis due to differences in life histories and social structure (Alkon, 1974; Nissani, 1974), which may affect their morphological diversity patterns. Although the analyses in each of the two sexes and for the traits and for the ratios were done separately, these may be dependent so should be treated with caution.

Testing for trends in diversity across the chukar range

Each population was assigned distance from the species range periphery using ArcView (Table 1). This is the south-western global periphery of the species range, determined as the centre of the first grid in which chukar density become zero as determined by Shirihai (1996). It is located in the Eilat Mountains of Israel. All populations except for the one in southern Sinai (see Fig. 1) are found north of here. The Sinai population, being a relict "island" south of this edge was therefore assigned a negative distance value in order to distinguish it from the other populations studied. The relation between distance from range periphery and diversity was tested using both linear and quadratic regression. In addition, EDS values calculated using the CV were arcsine transformed and regressions were calculated between the distance from range periphery and arcsine square root of the EDS.

Results

In all four comparisons, which include traits and ratios in both males and females, the index for within-population morphological diversity (EDS) was the highest in the population of the Northern Negev ecotone (Fig. 2). The probability of obtaining the maximal level at the ecotone in all four cases when five populations are available for comparison is 0.06. In this data base, the study hypothesis predicts a hump-shaped pattern of diversity from core to periphery, with maximum levels of within-

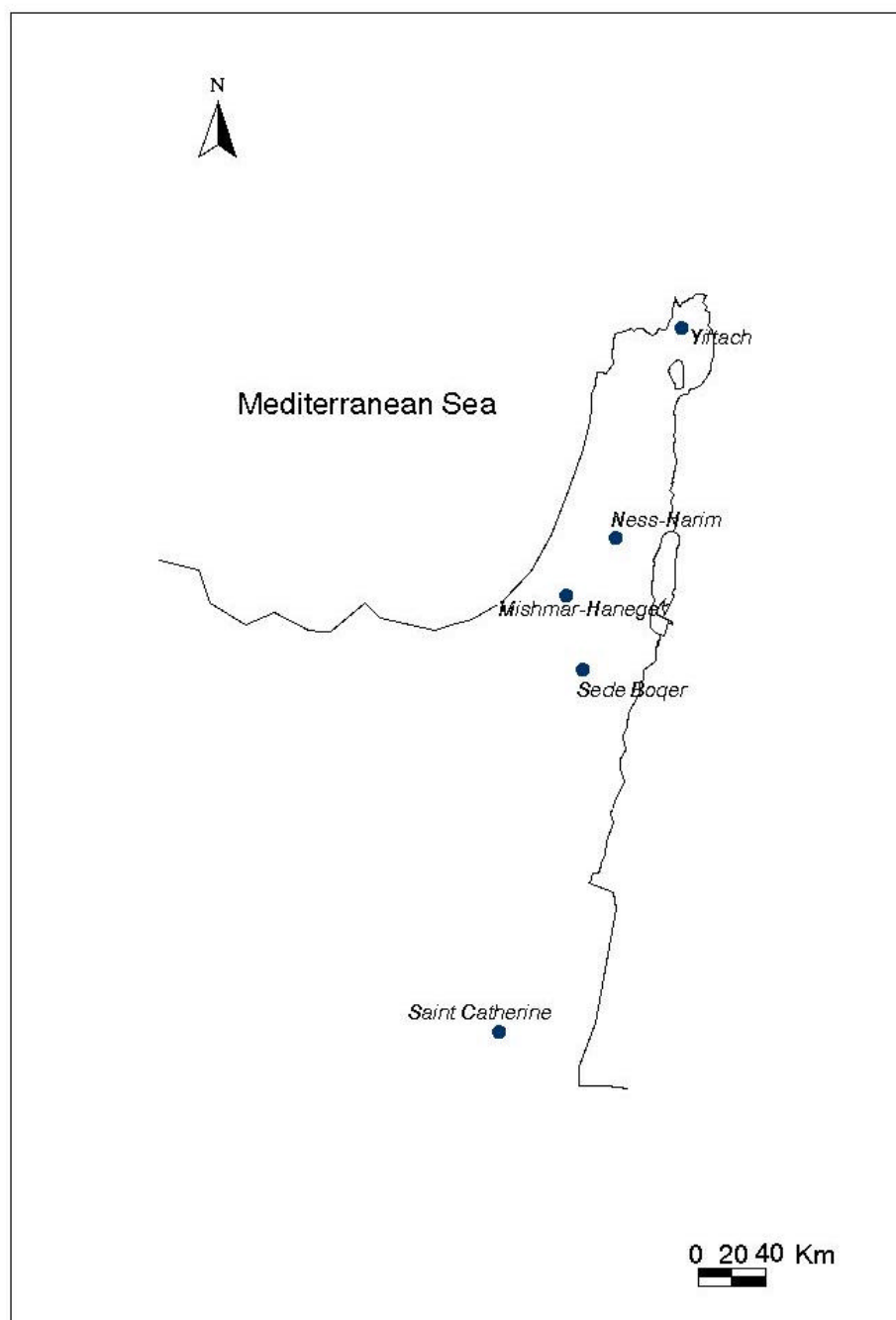
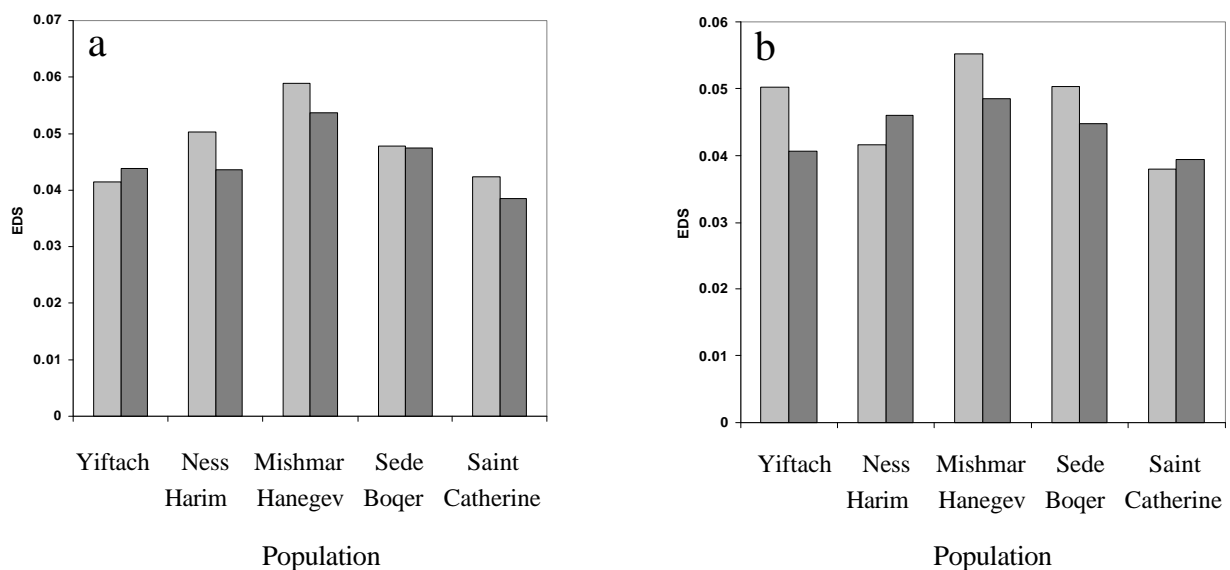


Figure 1. Map of study area and location of populations studied.

population diversity at the Northern Negev (NN) population in the turnover zone. A decline in diversity level from NN towards both the core and the periphery is thus expected. The predicted pattern of diversity, based on the specific site location in our study is therefore $UG < \text{or} = JM$, $UG < NN$, $JM < NN$, $NN > NH$, $NN > SS$ and $NH > \text{or} = SS$ (see Table 1 for abbreviations). For both the traits and the ratios, we have six predicted relationships between sites for males and six for females. In three of these four analyses, based on the CV of the traits and of the ratios in males, as well as that for the ratios in females, agreement with the predicted trend was found (sign test; Sokal and Rohlf, 1995) in 6 of 6 cases ($p=0.0156$ in each case). For female traits, agreement with the predicted trend occurred in 5 of 6 cases and was not statistically significant at the 0.05 level ($p=0.0938$).

Figure 2. Within-population morphological diversity in *Alectoris chukar* populations in Israel and Sinai from north to south. Diversity was estimated based on 35 traits and 23 ratios using the Estimator in a Dependent Sample (EDS) for the coefficient of variation in males (a) and females (b). In each sex, light grey bars are for traits and dark bars for ratios.



When testing relation between distance from the periphery of the range and diversity using a linear vs. quadratic regression, for the linear regression in males and females for both traits and ratios, r^2 square and F values are very low (Table 3). The quadratic regression, in all cases except for that of female traits, shows r^2 square and F ratio values much higher than those of the linear regression (Table 2). Yet the trend is not statistically significant ($P > 0.05$), possibly due to the small sample size and thus low number of degrees of freedom. Trends remained very similar after an arcsine transformation of the EDS. It should be emphasised that only five populations with a total of 150 individuals were available for testing. Given this, a consistent trend seems to appear. Comparison of trends in EDS calculated using the coefficient of variation with those obtained for the standard deviation show very similar trends across populations (Table 3), although slight differences occur, which may be related to the fact that the SD is affected by differences in means amongst populations.

Table 3. Statistics derived from linear vs. quadratic (polynomial) regression between distance of population from range periphery and value of the Estimator in a Dependent Sample (EDS) for the population based on the coefficient of variation. R-square values and F-ratios are given. EDS was calculated using 35 traits and 23 ratios in male and female chukars.

Statistic	Male Traits	Male Ratios	Female Traits	Females Ratios
r^2 linear	0.02	0.18	0.19	0.001
r^2 quadratic	0.64	0.62	0.37	0.90
F ratio linear	0.05	0.66	0.71	0.003
F ratio quadratic	1.75	1.62	0.58	8.58

Discussion

Spatial trends in morphological diversity across the range

Spatial trends in between-species diversity have received wide attention, both theoretically and empirically, in various species and ecosystems (e.g., Ricklefs and Schluter, 1993). Recently, with increasing interest in patterns and processes at the within-species level (Hanski, 1989), and especially at the metapopulation level (Hanski, 1998), genetic and phenotypic studies are being redirected to revealing within-species diversity (Kark et al., in prep; Roy and Foote, 1997; Smith et al., 1997). The advantage of the statistical method we present in this paper is that it is sufficiently powerful to detect differences between populations in their diversity when the sample size for each trait is small, as is often the case when working with vertebrates in natural environments.

Results from the chukar case study seem to support the hypothesis predicting a hump-shaped pattern in within-population diversity across the species range. In accordance with the studied hypothesis, diversity, as estimated here, was maximal in the turnover zone and generally decreased towards both the extreme periphery and the core (Fig. 2). The humpback model tested by a quadratic regression fits the data in most cases much better than the linear monotonous increase or decrease model. Although only five populations were available for testing, a consistent trend in both males and females appears.

While we cannot separate the genetic and environmental components affecting the phenotypic diversity detected in this study, at least some of the traits analyzed show high heritability in birds (Boag and van Noordwijk, 1987; Smith et al., 1997) and are correlated with fitness, flight, movement, and feeding ecology (Nissani, 1974; Smith, 1993; Smith et al., 1997). In addition, our results are consistent with those from analyses of genetic (allozyme) diversity across the chukar range in Israel (without Sinai). These results show a hump-shaped trend with peak diversity at the turnover zone (Chapters 2-4; Kark, 1999; Safriel et al., 1994) and genetic structuring of

populations in spite of substantial levels of gene flow between populations (Kark, 1999).

Trends across the ecotone

Populations located at the margins of species' distribution ranges often experience unfavourable ecological (biotic and/or abiotic) conditions (Brown, 1984; Brown et al., 1995; Gaston, 1990a; Lesica and Allendorf, 1995; Lomolino and Channell, 1995; Wiens, 1989) which lead to reduced population density and fitness (Brown et al., 1995; Caughley et al., 1988; Collins and Glenn, 1991; Gaston, 1990a; Hengeveld and Haeck, 1982; Hoffmann and Blows, 1994; Lesica and Allendorf, 1995; Lomolino and Channell, 1995; Vrijenhoek et al., 1985; Wiens, 1989). These populations eventually fade out, and mark the edge of the species range, a dynamic edge which may move with time while species shift their distributions (Eldredge, 1995). Yet another distribution edge which may exist at the same point in time is the "turnover zone", beyond which populations become ephemeral and less continuous (Brown et al., 1996; Lennon et al., 1997), and populations more isolated and patchily distributed (Boorman and Levitt, 1973; Brown et al., 1996; Carter and Prince, 1988). This is the edge of the species main distribution (Lennon et al., 1997). Thus we suggest that when studying spatial trends in diversity across species ranges there is a need to be more refined, and distinguish between periphery and turnover zone. This latter area of change in the chukar falls within the Mediterranean-desert ecotone an area which is the edge of the continuous distribution for many other animal and plant species (Danin, 1998). It has recently been found in a passerine rainforest species (*Andropadus virens*) that the ecotone sustains increased morphological divergence despite high levels of gene flow (Smith et al., 1997), and may thus be an important centre for speciation, for further survival of the species and for maintenance of biodiversity. We further suggest that the ecotone sustains not only high divergence but also high levels of diversity within its populations in the face of gene flow (Kark et al., 1999), which may confer potential for evolutionary change and speciation processes.

Implications for conservation

Revealing spatial patterns and trends in diversity within species across their distribution range may help determine areas within a species range with especially high levels of within-species diversity. These areas may be worth substantial conservation investment in the face of current human-caused environmental changes (Kark et al., 1999; Safriel et al., 1994). This approach focuses interest on ecotone regions as conservation targets. Much focus has been given to isolated peripheral populations or habitats due to their potential genetic and morphological uniqueness (Lesica and Allendorf, 1995), maintained by especially low levels of gene flow and small population sizes (Da Cunha and Dobzhansky, 1954; Parsons, 1991a; Vrijenhoek et al., 1985). Yet populations located in ecotones may also be worthwhile focusing on, even if they are not genetically isolated, given their potential to maintain high diversity in spite of gene flow (Kark, 1999; Smith et al., 1997). Conserving these ecotone areas, where populations may maintain high levels of diversity within a relatively small geographical area, can be a cost-effective conservation strategy.

We suggest that the study of phenotypic diversity, in addition to genetic diversity, is important for understanding patterns in components of biodiversity which may be related to selection, fitness and speciation processes. Although we usually seek to preserve the species' genetic diversity, the diversity in its morphological traits may well be a mirror to the changing environments where the species is found, and may reflect some important components of diversity related to fitness at the genetic level.

Tools enabling handy and inexpensive but reliable and scientifically sound estimation and monitoring of morphological and genetic diversity should be further developed. The "Estimator in a Dependent Sample" (EDS) presented in this work may be a useful tool for monitoring levels of within-population morphological diversity based on measurements of multiple traits, especially when sample sizes are relatively small. It may be used to compare trends in populations both across time and

space in natural populations as well as collection material, which has recently received increased appreciation in the conservation context.

Acknowledgments

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Appendix 1

The morphological traits used, and their ratios and measurement methods

The traits used for the calculation of the statistical estimator include: body mass, wing length, tarsus length - external measurement, third toe length, culmen length, lower mandible length, tail length, length of gonads, total humerus length, maximal width of humerus distal end, maximal width of humerus proximal end, total ulna length, total carpometacarpus length, width of carpometacarpus proximal end, number of color bands on wing, total coracoid length, dorsal manubrial spine length, maximal sternum labri width, distance between nutrient foramen and top of sternal crest, total femur length, maximal width of femur proximal end, maximal width of femur distal end, total tibia length, maximal width of tibia distal end, distance between the tibia muscular canals, total tarsometatarsus length, maximal width of tarsometatarsus proximal end, maximal width of tarsometatarsus distal end, mandibula (ramus) length, upper jaw: praemaxilla length, maximal upper jaw length (proximal end of praemaxilla to proximal end of nasalia), nasalia length, maximal length of nasal aperture, maximal length of ventral part of praemaxilla and total skull length.

Calculated ratios were usually between traits and total mass and between measured trait and total reference trait length (or width) and include: maximal width of humerus distal end/total humerus length, maximal width of humerus proximal end/total humerus length, width of carpometacarpus proximal end/total carpometacarpus length, maximal sternum labri width/dorsal manubrial spine, distance between nutrient foramen and top of sternal crest/dorsal manubrial spine, maximal width of femur proximal end/total femur length, maximal width of femur distal end/total femur length, maximal width of tibia distal end/total tibia length, distance between the tibia muscular canals/total tibia length, maximal width of

tarsometatarsus proximal end/total tarsometatarsus length, maximal width of tarsometatarsus distal end/total tarsometatarsus length, praemaxilla length/skull length, maximal length of ventral part of praemaxilla/maximal length of nasal aperture, maximal length of nasal aperture/nasalia length, mandibula (ramus) length/skull length, total carpometacarpus length/total humerus length, total ulna length/total humerus length, total tarsometatarsus length/total femur length, total femur length/total tibia, wing length/mass, tarsus length/mass, 3rd toe length/mass, lower mandible length/mass (Nissani, 1974).

Measurements of mass, external measurements and descriptive details were taken soon after sampling, in the field, whereas other measurements were taken in the laboratory. Wing length was measured as the minimal distance between the tip of the longest primary to the carpal joints of the folded wing. Tarsal length was taken from the base of the last complete scale before the divergence of the toes to the angle of the intertarsal joint. The length of the upper beak was measured as a straight line along the cord of the culmen, from its tip to the edge of the feathering at the base of the skull. The length of the lower beak was taken from the articulation of the maxillary to its tip. Length of mandible was taken from the articulation to its tip (Nissani, 1974; Nissani and Tchernov, unpublished ms). Measurements were taken by the same person and using Mitutuyo callipers (Nissani, 1974). For detailed description of traits and measurements see (von den Driesch, 1976).

Preface to Chapter 6

“I believe in no fixed law of development, causing all inhabitants of a country to change...to an equal degree.”

Charles Darwin, 1859

One of the major questions that arose while I was planning the population sampling for testing hypotheses regarding trends in genetic and phenotypic diversity across the distribution range, from core to periphery (Chapters 2-5), was the following: Do individuals from peripheral populations actually perceive a different environment than those further away from the edge of the range? This is highly relevant for understanding the factors underlying diversity patterns to be revealed and differences between populations. A tool which will enable to perceive the ability of individuals to confront stress during development and to compare it across the range would be very valuable. As discussed in the Introduction (Chapter 1), populations located near the edge of the range often have a patchy distribution. In the rich occupied patches, individuals may actually perceive relatively favorable environments. I tested this using a simple yet powerful tool, the measurement of deviation from perfect symmetry, an estimator of the level of developmental instability within a population (see fig. 2 in Chapter 1). I tested trends in asymmetry in a trait common to all individuals across the study gradient, from core to periphery. I selected a range of traits and tested their measurement repeatability on a sample of individuals in the laboratory. Measurement error, similar to fluctuating asymmetry, is normally distributed. Thus in order to avoid a study which actually compares trends in measurement error across the range, it is important to compare traits that have high measurement repeatability. The trait that had by far the highest repeatability

among the pre-measured ones was the length of the third toe. Therefore, and due to the fact that this trait has adaptive value and is being selected in birds (Boag and van Noordwijk, 1987), and especially in chukars, which spend most of their daily foraging activity walking rather than flying (Carmi-Winkler, 1985), I chose this trait and compared asymmetry levels across the chukar range in the same individuals for which the genetic analyses were done. Although evidence at the individual level suggests that in general there is no correlation between the levels of symmetry in different traits of one individual (Clarke, 1998b; but see Lens, 1999b), increasing evidence from various groups shows correlation between asymmetry levels of different traits at the population level (Clarke, 1998b; Lens, 1999), which is the focus of this work. As suggested by Clarke (1998b), Lens (1999) and Lens and van Dongen (1999), if one population is on average more symmetrical than another for one character, it will be more symmetrical also for other characters (Clarke, 1998b; Kat, 1982; Soulé, 1967). The following paper presents a test of the trends and shifts in asymmetry across the distribution range, focusing on the chukar partridge.

Chapter 6

Shifts in bilateral asymmetry within the chukar partridge distribution range in Israel

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Keywords: chukar partridge, core-periphery, developmental stability, directional asymmetry, distribution range, ecotone, environmental stress, fluctuating asymmetry.

Abstract

Three major types of bilateral asymmetry, including fluctuating asymmetry (FA; small random deviations from symmetry), directional asymmetry (DA; where one side is consistently larger than the other) and antisymmetry (handedness, where most individuals deviate from symmetry showing either right or left asymmetry) have been long recognized in the literature. However, little is known about transitions and shifts between asymmetry types, especially across species' distribution ranges. Patterns of asymmetry in the third toe length, a trait with high measurement repeatability, were studied in 11 chukar partridge populations across a steep environmental gradient within ca 400 km within the chukar distribution range in Israel. Several trends were identified, moving from the core towards the very extreme periphery of the range:

1. The frequency of symmetrical individuals in the population significantly decreased, with a steep decline at the steepest part of the environmental gradient studied, within the Mediterranean-desert ecotone.
2. The population mean asymmetry (the absolute value of the difference between the two sides of the body) significantly increased.
3. The expression of the directional asymmetry component significantly increased.
4. The range of asymmetry increased such that the least symmetrical individuals originated from the very edge of the range.

These findings provide primary evidence that substantial shifts in asymmetry patterns and types occur across a species' distribution range within short geographical distances, showing a continuum between asymmetry types and supporting the notion that all three asymmetry types can reflect developmental instability. This reflects sharply changing environments and levels of stress confronted by individuals. Only when the range is widely sampled across a continuum, is the shift in asymmetry types clearly resolved.

Introduction

The study of populations along species' distribution ranges, and especially of peripheral populations, has largely focused on understanding patterns and processes of extinction, population dynamics, fitness, density and genetic diversity across the range (e.g. Andrewartha & Birch 1954; Lawton 1993; Hoffmann & Blows 1994). A more recent focus has been towards the conservation implications of these patterns and the processes underlying them (e.g. Safriel *et al.* 1994, Lomolino and Channell 1995). In this context, a central goal has been to reveal whether the levels of stress, as confronted by individuals, change across the distribution range. Yet it is often difficult to assess stress levels and their changes in long-term field studies of population dynamics, physiology and fitness that span a species' geographic range. An approach that may be useful for comparing the levels of stress confronted by individuals across the range is the estimation of bilateral asymmetry (Leary & Allendorf 1989; Clarke 1992, Møller 1998).

Asymmetry types

Three principal types of bilateral asymmetries in morphological traits (i.e. deviation from perfect symmetry between the right and the left sides of an organism's body) have been described. These include fluctuating asymmetry (FA), directional asymmetry (DA) and antisymmetry (AS; Van Valen 1962; Palmer & Strobeck 1986). The three differ in the distribution of the signed difference between the right and the left (R-L) sides of a trait in a population. Fluctuating asymmetry is defined (based on Ludwig 1932) as the small random non-directional deviations from bilateral symmetry in morphological traits in which symmetry is the normal state. In traits exhibiting FA, signed R-L values in the population are normally distributed around a mean of zero. In traits showing DA, there is a consistent bias towards over development of one specific side relative to the other (Van Valen 1962; Palmer & Strobeck 1986; Møller & Swaddle 1997) and therefore in DA the R-L distribution has a non-zero mean. Antisymmetry (handedness) is similar to DA in the sense that one

side is usually larger than the other, yet the population shows a broad-peaked (platykurtic) or a bimodal distribution of signed R-L about a mean of zero (Palmer & Strobeck 1986).

Fluctuating asymmetry is widely considered an indicator of developmental instability (Clarke & McKenzie 1987; Markow 1995; Møller 1997), reflecting the ability of individuals to buffer themselves during development in the face of stress (Leary & Allendorf 1989; Swaddle *et al.* 1994). Unlike FA, the two other forms of asymmetry, DA and AS, have not been considered as reliable indicators of developmental instability due to their unknown heritable component (e.g. Van Valen 1962; Palmer & Strobeck 1986). While the discussion regarding the assumption that the heritability of FA is lower than that of the two other asymmetry types has not been completely resolved yet (Markow & Clarke 1997), it has led to the recommendation that traits not showing FA (i.e., a normal distribution of signed R-L about a mean of zero) should be excluded from the analysis in studies of developmental stability in favor of traits showing FA only (e.g. see guidelines in Palmer 1994). Such a procedure does not allow potential shifts between asymmetry types to be identified, if they occur.

Graham *et al.* (1993a; 1998) have challenged this conventional thinking and its practical implications for studies of developmental stability. Using a modified reaction-diffusion model, they have suggested that DA and AS may often reflect developmental instability and predicted a continuum between the three asymmetry types. Indeed, several experimental studies involving human-induced stresses (e.g. insecticides) have shown that shifts between asymmetry types can occur within a single population (Leary & Allendorf 1989; Graham *et al.* 1993b).

Developmental stability and asymmetry

Developmental instability and FA are correlated with various components of fitness (Brookes *et al.*, 1997; Clarke, 1995; Møller, 1997) and reflect changes in this crucial characteristic (McKenzie and Clarke, 1988). In humans, FA is negatively

correlated with survival and growth rate and positively correlated with sub-fertility, abortion, child maltreatment by parents and various physical and mental diseases (Thornhill and Møller, 1997). It is negatively correlated with mating success in birds (Møller, 1992; Swaddle and Cuthill, 1994) and humans (Thornhill et al., 1995). More symmetrical men had a larger number of sex partners, started sexual intercourse earlier in their life history, had more extra pair copulations, and their female mates reported a higher proportion of copulation accompanied by orgasm (Thornhill and Gangestad, 1996). Thus individuals with higher levels of FA may have a lower probability of transmitting their genes.

Trends in asymmetry across gradients

Under the prediction that the level and form of asymmetry may shift along changing levels of stress, I studied trends in body symmetry along a natural gradient of changing environmental conditions across a species range in a trait common to all individuals of the species. Developmental stability trends in body symmetry are easily measurable across the distribution range, enabling to distinguish between gradual and abrupt changes within an area of sharp environmental transition. Populations from areas of transition between ecosystems or communities, i.e. ecotones, are particularly attractive for such studies. These populations have recently been shown to maintain increased levels of genetic diversity (Kark et al., 1999) and morphological divergence (Smith et al., 1997), despite high levels of gene flow. A focus on ecotones enables a comparison of natural populations within relatively short geographical distances yet along a steep ecological and climatic gradient. Differences in developmental stability across the ecotone should be reflected in asymmetry levels and/or in shifts to a different asymmetry type. To test whether level and form of asymmetry shift across a species' distribution range, I examined bilateral asymmetry patterns along a steep gradient within the native distribution range of the chukar partridge (*Alectoris chukar*) in Israel, from core to periphery.

Material and Methods

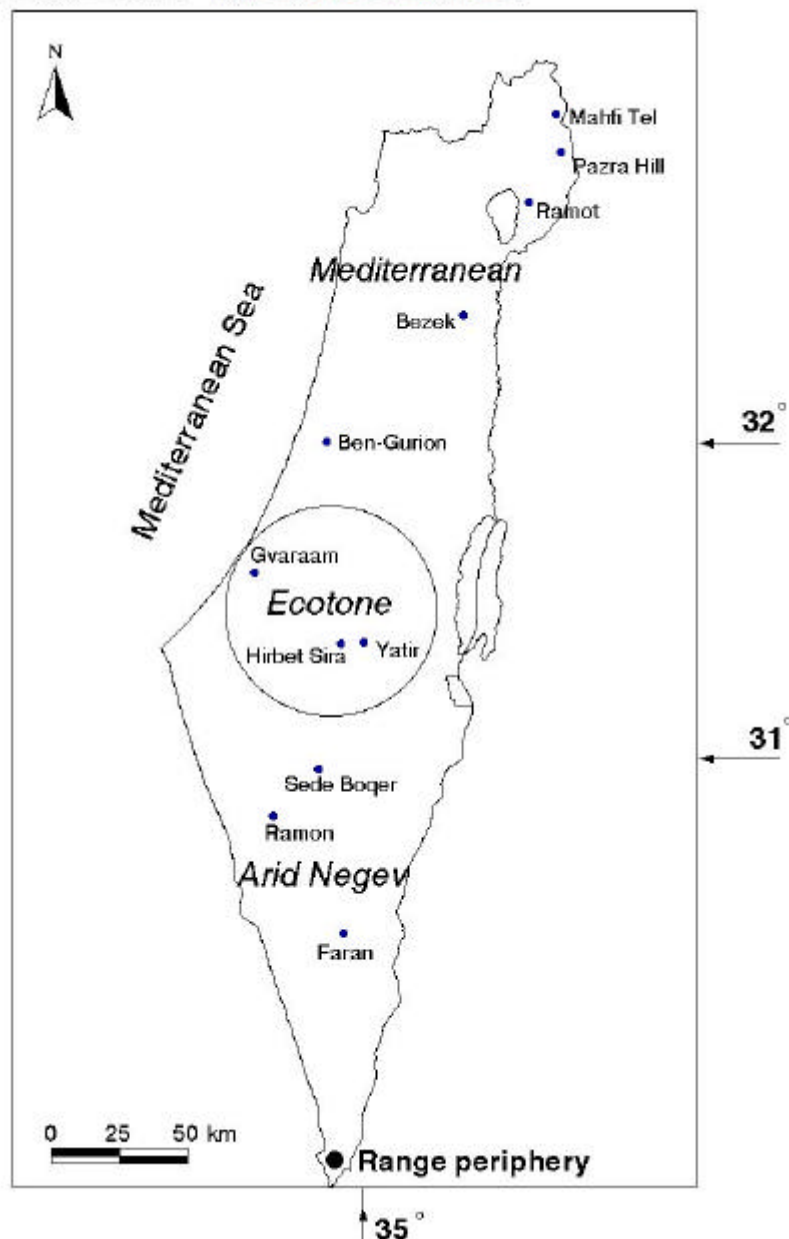
Study area

A steep environmental gradient from Mediterranean to arid climatic regions occurs in Israel across short distances from areas at the northern Golan Heights, where mean annual rainfall is over 900 mm, to areas in the southern Negev desert, where rainfall decreases to less than 50 mm (data from the Israel Meteorological Service, the Hebrew University Geographical Information Systems Center and from Bitan & Rubin 1991; see Kark 1999 for details and maps). An especially steep portion of this environmental gradient occurs along the northern Negev Mediterranean-desert ecotone (Fig. 1), where within a belt of several dozen km mean annual rainfall decreases from over 450 to less than 150 mm and both temporal and spatial variability in rainfall increase (Bitan & Rubin 1991 and the Israel Meteorological Service). This cline is associated with a change in a phytogeographical gradient from largely Mediterranean to largely Saharo-Arabian vegetation, with a combination of both at the ecotone region (Danin & Plitman 1987; Kark, 1999). This gradient coincides with both northern and southern range peripheries of numerous species (Safriel *et al.* 1994).

The chukar partridge

The chukar is continuously distributed and has high population densities in the Mediterranean areas in the north and center of Israel (Shirihai 1996). The species reaches the edge of its continuous distribution in the northern Negev ecotone (Shirihai 1996). The distribution of the species becomes patchy and populations become smaller and more isolated towards the central and southern Negev desert, a region that marks the global periphery of the species' distribution range (Fig. 1; Shirihai 1996). As far as is known, chukars in the study area are sedentary and do not exhibit latitudinal or altitudinal migrations (Shirihai 1996).

Figure 1. Map of study area, population sampling locations and range periphery. The ecotone region is marked with a circle.



Sampling and measurement

Adult birds were collected by the Israel Nature Conservation and National Park Authority rangers and authorized hunters following Kark *et al.* (1999). Sampling took place during the non-breeding season of 1995-6 (August to February). Birds were

measured in the field, except for those from Ben-Gurion Airport, Bezek and Nevatim, which were measured in the laboratory. All measurements were taken by the author, using a metal ruler to an accuracy of 0.1 cm. Locations were sampled in a random order relative to the range periphery to avoid a potentially confounding bias stemming from the increasing experience of the measurer over the course of the study.

A total of 138 males and 114 females in 11 populations were measured (Table 1, Fig. 1). In addition to population based comparisons, populations were pooled into three pre-determined eco-geographical distribution regions (Mediterranean core, ecotone and arid periphery, see Table 1) and analyses were performed across the three regions.

Two measures of third toe length (from joint to claw), including and excluding the claw (long and short measurement, respectively), were obtained for each bird, except for individuals from Pazra Hill and Ramon, for which only the long measurement was taken. The asymmetry pattern across the range was analyzed to test the following hypothesis: if birds tend to dig (e.g. for food) more with one leg, digging may have a different effect in dry vs. mesic areas or in different soil types. Therefore, shifts between asymmetry types could potentially be caused by quicker and uneven erosion of the claws on the two sides of the body in different habitats (P. Taylor, pers. comm.). In such a case, I would predict that the pattern found for the long measure of asymmetry will not be repeated in the short measure, where the claw was excluded. However, this idea was not supported by the results. Similar trends were found for both the short and long measures across the study gradient. The correlation between mean FA for the two measures across populations was 0.91 ($p < 0.0007$). Due to this congruence and given the larger sample size, results are presented here for the long measure.

The length of the third toe had by far the highest measurement repeatability among a range of pre-measured traits that were measured on a sub-sample of individuals and which are often used in studies of asymmetry (including tarsus and wing length) and was therefore selected for comparison across the distribution range

($r=0.99$, $F=76.6$, $p<0.0001$ for the third toe long measurement and $r=0.91$, $F=9.9$, $p<0.0007$ for asymmetry estimation of the difference between the right and the left sides). Measurement repeatability was estimated by measuring 10 individuals on both body sides, and then re-measuring the same set of individuals (giving a total of 40 measurements; see Siikämäki & Lammi 1998). Repeatability of measurements was analysed using a mixed-model ANOVA with Individual (I), Side (S) and Replicate (R) factors following Swaddle et al. (1994). In this model, the ratio between MS (I x S) and the combined MS (I x S x R) and MS (I x R) provides an F test for evaluating whether between-individual variation in estimated asymmetry is significantly greater than can be accounted for by measurement error taking into account session bias (Swaddle & Cuthill 1994; David *et al.* 1999).

Range periphery was taken as the center of the first grid in which chukar density reduces to zero based on the distribution grid system described in Shirihai (1996). Beyond this area, towards the desert, chukars are not currently known to occur, except for an isolated post-glacial relict population located in the southern Sinai Mountain region (Kark *et al.* 1999). Distance from the range periphery was taken from the center of the grid of the population sampling (ca 10 km² in all regions).

Estimation of asymmetry

Distribution of signed R-L values over all individuals ($n= 252$) was drawn and normality of the distribution was tested using the Shapiro-Wilk W test (JMP 3.1.5). Asymmetry was calculated in several ways: First, asymmetry was estimated in each of the populations using mean of R-L absolute values (FA1 of Palmer 1994). Following, the proportion of symmetrical individuals in each population was calculated and compared across the distribution range. An individual was considered symmetrical if the value of its R-L subtraction was zero. This measure does not reflect the size of asymmetry but rather its proportion in a population, and although it may potentially be affected by measurement accuracy, it is useful as a relative measure for comparison among populations.

Comparisons were further done across the three pre-determined areas, to obtain larger sample sizes. Asymmetry was estimated for each of the three regions using FA1 (mean unsigned R-L) and FA4 (variance R-L; Palmer 1994). To test for normality of the distributions, the skewness and kurtosis of the signed R-L were calculated and the distribution was inspected across the three areas following Palmer (1994). In order to test for shifts between asymmetry types across the distribution range, these tests were applied: Directionality in asymmetry was tested in each of the three areas using a Wilcoxon signed-rank test for deviation of the median from zero. This aimed to test whether the median of R-L and the symmetry of the distribution change across the species' range. The significance was estimated following a Sequential Bonferroni Correction (Rice 1989; Palmer 1994).

Results

Trends in asymmetry across the chukar range in Israel

The mixed model ANOVA testing for measurement repeatability retrieved an $F_{9,18}$ of 8.056 ($P < 0.0001$), suggesting high repeatability for the long measurement of the third toe. The proportion of symmetrical individuals in a population was strongly correlated with the distance of the population from the species' range periphery (Spearman $Rho = 0.85$, $p < 0.001$; sexes pooled, Fig. 2). Consistent results were found for the correlation between distance from the range periphery and mean R-L absolute value for both sexes (Spearman $Rho = -0.81$ for males, $p < 0.0026$ and -0.82 , $p < 0.0021$ for females). As males and females exhibited similar trends, the two sexes were pooled for further analysis, except when otherwise indicated. The two ecotonal populations, Yatir and Hirbet Sira, located only several km away from each other (Fig. 1), but occurring within a steep part of the climatic gradient (Yatir having over 50% higher rainfall than Hirbet Sira), showed a sharp change from a mean FA of 0.026 to 0.070 and from 79% to 33% symmetric individuals, respectively (Fig. 2). If body size had increased along the distribution range, from core to periphery, this could potentially

have caused an apparent trend of increasing absolute asymmetry. In such a case, mean absolute R-L may increase even when remaining similar relative to the mean trait size

Table 1

Chukar partridge populations studied in Israel, population code in Figs. 2 and 3, distribution area, distance in km from range periphery (see Fig. 1), sample size, and mean absolute value of right-minus-left length of third toe (R-L) in the population in cm.

Population	Acronym	Distribution area	Distance from periphery (km)	Sample size	Mean R-L (cm)
Mahfi Tel	MT	Mediterranean core	408	23	0.013
Pazra Hill	PH	Mediterranean core	395	16	0.038
Ramot	LR	Mediterranean core	372	22	0.000
Bezek	BR	Mediterranean core	316	19	0.032
Ben-Gurion	BG	Mediterranean core	264	21	0.033
Airport					
Gvaraam	GV	Ecotone	218	24	0.040
Yatir	HY	Ecotone	199	19	0.026
Hirbet Sira	HS	Ecotone	196	30	0.070
Sede Boqer	SN	Arid periphery	148	27	0.100
Ramon	RM	Arid periphery	129	28	0.111
Faran	FR	Arid periphery	86	23	0.094

in the population ($R-L/\text{mean } (R,L)$) when an unweighted estimator, such as FA1 is used. If this had occurred, a weighted estimate of asymmetry, such as FA3 of Palmer (1994) should have been used instead. However, body size in the chukars decreased, while asymmetry increased towards the desert (Kark 1999), and therefore the spatial trends in asymmetry could not have been confounded or created by the use of an unweighted estimator.

When analyzed across the three areas, from the Mediterranean core through the Mediterranean-desert ecotone towards the arid periphery, mean asymmetry increased significantly and was highest in the arid periphery using both the mean (FA1) and the variance (FA4) measures (Table 2). An analysis of variance of mean FA1 (sexes pooled) by area was significant ($F=45.2$, $p<0.0001$). Similar results were obtained when the two sexes were analyzed separately. A Tukey-Kramer multiple comparison test was significant for all area pairs ($p<0.01$). Furthermore, the maximum deviation from symmetry (the absolute size of the $R-L$ difference) increased towards the periphery (Figs. 3,4). Asymmetry, as estimated using the variance, showed a similar trend, increasing from the Mediterranean core to the arid periphery (Table 2).

Table 2

Fluctuating asymmetry, as estimated using mean absolute value (FA1) and variance (FA4) of right-minus-left length of third toe ($R-L$) across three pre-determined areas (Mediterranean, ecotone, arid) in chukars in Israel, sexes pooled

Area	Sample size	Mean $R-L$ (cm)	Variance $R-L$ (cm)
Mediterranean	101	0.022	0.002
Ecotone	73	0.049	0.003
Arid	78	0.103	0.005

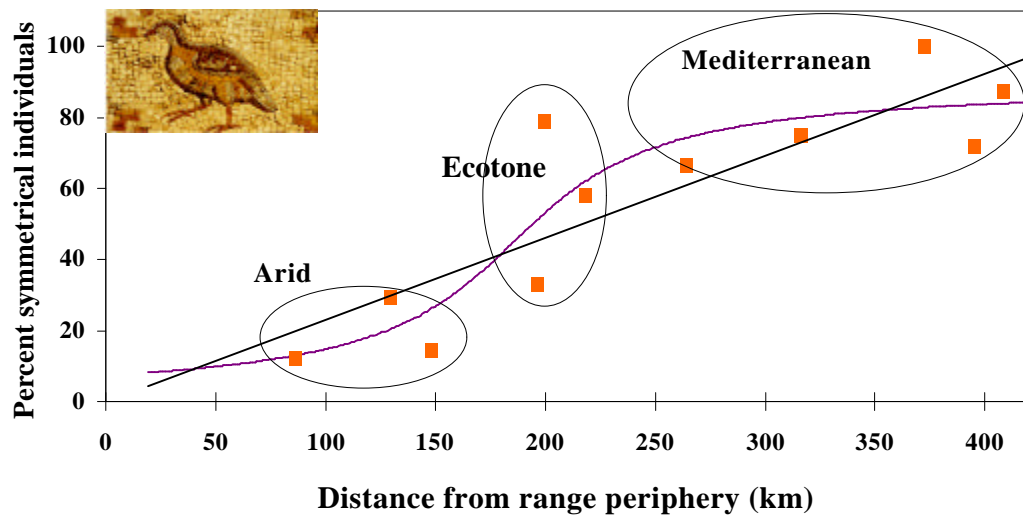


Figure 2. Relation between distance from the range periphery and percentage of symmetrical individuals in the population with linear and arctng (tg^{-1}) regression fits. An individual was considered symmetrical if the value of the right-minus-left subtraction was zero. In the linear regression, 74% of the variance in the percentage of symmetrical individuals among the populations sampled was attributable to their geographic location across the range ($F_{1,9}=25.2$, $p=0.0007$). An arctng regression, which better models the step in the ecotone area (plotted) explained a higher portion of the variance (82%). A logistic regression for distance from periphery vs. proportion of symmetrical individuals was significant with $\chi^2=13.7$, $P<0.0002$, $r^2(U)=0.2602$. Note the abrupt change in the percentage of symmetrical individuals in the ecotone region, especially comparing Yatir (HY with 79% symmetrical individuals) and Hirbet Sira (HS with 33% symmetrical individuals) in the ecotone.

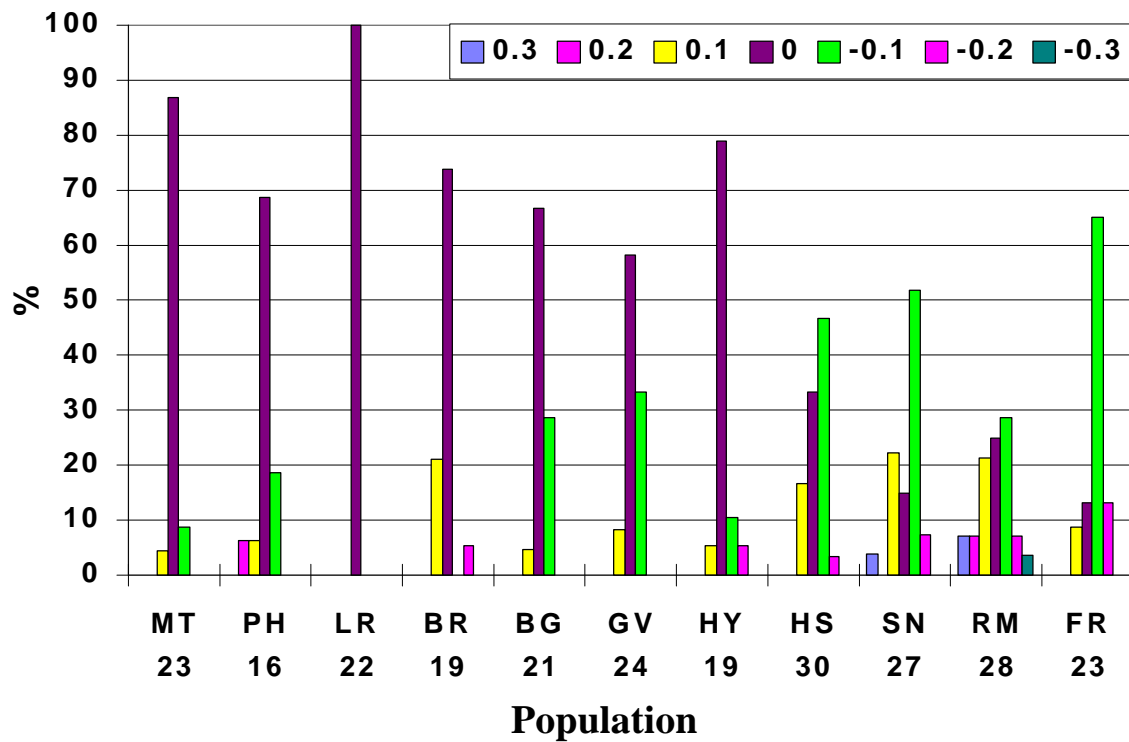


Figure 3. Distribution of percentage of signed right-minus-left values of third toe length in 11 chukar populations shown from core (north) to periphery (south), sexes pooled. Population acronyms are found in Table 1. Sample sizes appear under population codes. Perfect symmetry column is marked for each population. Note the shift between asymmetry types in the ecotone (as apparent when Yatir and Hirbet Sira are compared, with 79% and 33% symmetrical individuals, respectively).

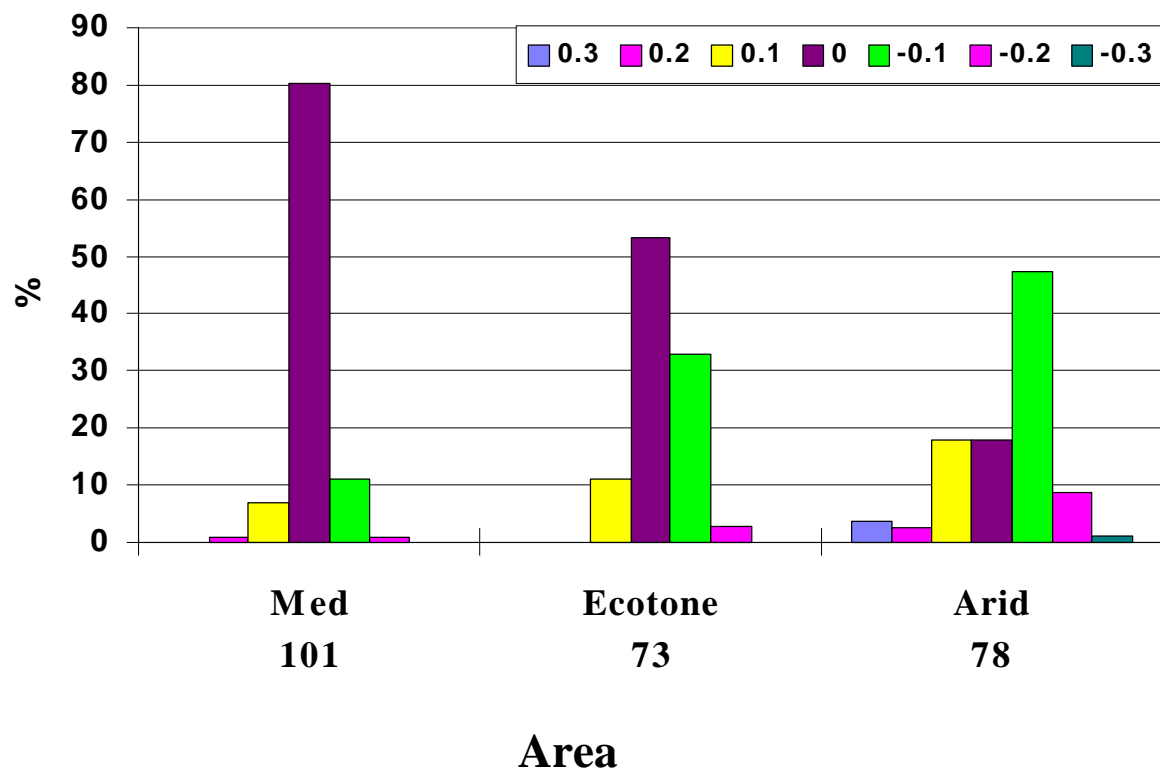


Figure 4. Distribution of percentage of signed right-minus-left values of third toe length in each of three pre-determined regions (Mediterranean, ecotone and arid), sexes pooled.

Shifts in asymmetry

When analyzed for all individuals pooled, the distribution of signed R-L values over all individuals ($n = 252$) showed a unimodal pattern with a median and mode of zero, yet the distribution was not normal. However, when analyzed for each population and area separately, very different patterns of distribution of R-L appeared across the range. While most individuals in the Mediterranean-core were symmetrical, the proportion of symmetrical individuals in the population significantly decreased moving towards the range periphery (Fig. 2). Consequently, a shift in the distribution of asymmetry was observed across the range, from core to periphery. As the degree of asymmetry increased, a directional trend (towards negative R-L) appeared (as seen in Fig. 3 across populations and Fig. 4 across the three areas). While the median of the signed R-L did not significantly deviate from zero in the core, deviation from zero, as tested using the Wilcoxon signed-rank test, was significant in both the ecotone and the arid periphery (Table 3). The skewness of the distribution was significant at the periphery of the range (Table 3). Thus as asymmetry increases, there appears a shift to a directional asymmetry component towards the range periphery.

Along with the decline in the percentage of symmetrical individuals in the population and the increased expression of the directional asymmetry component towards a larger left side (positive R-L) across the range, the proportion of individuals with positive R-L values also increased from core to periphery (Figs. 3, 4). This occurred in both sexes, especially in the males (not shown). The proportion of individuals in the population with a positive R-L increased from 8% in the Mediterranean to 23% in the arid periphery. A Chi Square test of independence between area (for the three areas) and the proportion of individuals with a positive R-L was significant ($\chi^2 = 10.68$, $p < 0.005$), suggesting that the proportion of individuals deviating from symmetry towards a larger right toe significantly differed among the three study areas. Significant leptokurtosis was found in the Mediterranean core

region (Table 3). This may be due to measurement accuracy resulting in a categorical estimate that does not permit the detection of R-L values close to zero.

Table 3

Statistics of the distribution of right minus left side measurements of third toe in chukars across three pre-determined study regions (mean in cm, skewness, kurtosis and Wilcoxon signed-rank test with P values: * - $P < 0.05$, ** - $P < 0.01$, *** - $P < 0.001$ after a sequential Bonferroni procedure).

Area	N	Mean (SE)	Skewness (SE)	Kurtosis (SE)	Wilcoxon signed-rank statistic
Mediterranean	101	-0.0040 (0.0051)	-0.0717 (0.2402)	4.7963 (0.4761)***	-19
Ecotone	73	-0.0274 (0.0081)	-0.0914 (0.2810)	-0.1272 (0.5552)	-165.5 **
Arid	78	-0.0346 (0.0138)	0.8344 (0.2722)**	0.6919 (0.5382)	-376.5 **

Discussion

This study provides evidence for clear changes in the magnitude and patterns of bilateral asymmetry within short geographical distances across the chukar range in Israel, from core to periphery. Mean absolute value of R-L significantly increased from 0-0.04 cm in core populations to 0.09-0.11 cm in the periphery. Variance in R-L increased from core to periphery. The frequency of symmetrical individuals in the population decreased across the core-periphery gradient. The range of individual asymmetry increased so that the most asymmetrical individuals originated from the arid periphery of the range.

The development of a bilateral trait on both sides of an individual is presumably under the influence of the same gene or gene complex (Clarke 1993). Therefore, it has been suggested that deviation from symmetry towards the right or the left sides does not have a significant genetic basis and represents variation of environmental origin (e.g. Palmer & Strobeck 1992), although the tendency to develop in a stable path and to exhibit asymmetry may have a genetic component (Palmer & Strobeck 1986; Møller & Swaddle 1997). While DA in a trait has been argued to have a genetic basis (e.g. Van Valen 1962), recent work suggests that the additive genetic component of DA is often small, comparable to that of FA, and in many cases is actually too small to detect (Graham *et al.* 1998). Based on simulation models and empirical evidence, Graham *et al.* (1998) suggested that the three types of asymmetry are dynamically inter-related and are part of a continuum rather than separate phenomena, with transition between the different forms of asymmetry (Graham *et al.* 1998). Transition from FA to AS and to DA can reflect severe developmental instability (Graham *et al.* 1993a). Indeed, several studies have shown shifts from one type of asymmetry to another under experimental human-induced environmental stress. For example, McKenzie & Clarke (1988) found that during the development of resistance to Diazinon, an Australian blowfly (*Lucilia cuprina*) population shifted from FA to AS. After developing resistance the population shifted back to FA. AS was generated in rainbow trout mandibular pores under stress (Leary & Allendorf 1989). Graham *et al.* (1993b) demonstrated that under stressful conditions of high benzene concentration *Drosophila melanogaster* showed DA in sternopleural bristles compared to unstressed flies, which exhibited FA for the trait. Thus it seems that DA and AS can reflect extreme developmental and/or genetic instability in various cases (McKenzie & Clarke 1988; Graham *et al.* 1993a). This study provides evidence that such a shift between asymmetry types may occur in natural populations.

I assumed in this work that the distribution of the signed R-L in each area is a mixture of three asymmetry components (FA, AS and DA), the first two having a zero mean and median and the latter with a non-zero mean and median (Van Dongen *et al.* 1999). These findings demonstrate that different components are apparent

across the distribution range in a single trait, supporting the notion that the three asymmetry types are inter-related rather than separate phenomena. Levels of asymmetry increase towards the range periphery with a notable addition of a directional component in the ecotone region. Mean R-L deviates from zero with a significant DA component (towards a larger left side) in both the ecotone and the arid periphery of the range. The directional component may be strongly expressed under conditions where perturbations during development are the norm.

It is difficult to explain the findings based only on the genetic-basis approach to DA. It is more likely that the changes in directionality and asymmetry expression in peripheral populations reflect increasing environmental stress with a consequential decrease in developmental stability. Population genetics studies have revealed genetic structuring among populations in the study area despite high levels of gene flow, suggesting that local selection pressures are acting (Kark *et al.* 1999). Yet even in cases where similar genetic diversity and allelic patterns were found in neighboring populations, e.g. the two ecotonal populations from Yatir and Hirbet Sira, they exhibited very different patterns of asymmetry (Table 1, Fig. 3), exhibited (Kark, 1999). This suggests that local chukar populations experience different environmental pressures and stress.

Chukars are not well adapted to desert conditions and in arid and hot environments they are distributed mainly in food- and water-rich patches (Degen *et al.* 1984). The geographical differences in asymmetry suggest that even within these apparently “favorable” arid-zone resource patches, individuals confront higher stress than those from more mesic regions. The increasing levels of asymmetry across the range support recent work showing higher FA in the periphery (Møller 1995; Carbonell & Telleri 1998; Siikämäki & Lammi 1998). Yet unlike previous studies that focused mostly on a core-periphery dichotomy, this work studies asymmetry trends across a more continuous distribution gradient, including the ecotone region, where the edge of the chukar’s continuous distribution occurs, thus enabling to resolve shifts in asymmetry types and characteristics across the species’ range.

This work indicates that the ecotone is an area of transition between lower and higher levels of stress. Beyond the ecotone region, towards the extreme periphery of the range, asymmetry levels significantly increase and change in type. If only part of the range (e.g. the core or the periphery alone) would have been sampled in the study rather than the continuum from core to periphery, completely different conclusions as to the type and extent of asymmetry in the trait would have been drawn. The study suggests that asymmetry can greatly shift across the distribution range, even within short geographical distances and a single trait. I recommend that future studies of asymmetry and of developmental stability do not ignore those traits not showing clear FA, but rather focus on transitions and inter-connections between the various forms of asymmetry.

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D i s c u s s i o n - C h a p t e r 7

Trends in diversity across the range

When I started this work, two major hypotheses regarding trends in genetic diversity across a species range, from periphery to core, were current in the literature. The one, which we termed the “Carson” hypothesis suggested an increase in within-population diversity from periphery to core within a species range. The other, termed the “Fisher” hypothesis suggested that diversity will decrease along this gradient showing maximum diversity at the periphery rather the core of the range (see Safriel et al., 1994 and [Chapter 1](#) for a review of the hypotheses). A literature review of the classical and more recent studies testing these hypotheses revealed a rather confused situation and apparent contradictions. Revealing the factors underlying this dichotomy and, if possible, a partial resolution of these apparent contradictions seemed an important goal, especially in the face of the recent recognition of the importance of spatial distribution patterns in conservation and environmental biology and pure ecological and evolutionary scientific thinking. It appeared from the literature that some of the factors underlying these discrepancies may reflect real differences between the patterns of various species studied. Yet, as discussed in detail in [Chapter 1](#) and in the [Preface to Chapters 3 and 4](#), it appeared to me that methodological factors, such as partial sampling of species’ ranges and comparison of distinct sections of ranges in different studies are contributing to the dichotomy in the literature. It also seemed that a focus on methodological and conceptual factors and emphasis on sampling design and knowledge of the study species’ distribution, behavioral and physiological characteristics, may be crucial in resolving the spatial patterns in diversity across the range. Following the literature review, I developed an integrating hypothesis, which may partly resolve some of the contradictions. This hypothesis, presented in [Chapter 1](#) and discussed below, proposes that within-

population diversity will show a hump-shaped pattern across the species range and will peak at an intermediate area of the range where the species reaches the edge of its more continuous distribution, termed turnover zones. This area may often fall within areas of ecological transition, termed ecotones. I tested the hypothesis in a model species, the chukar partridge (*Alectoris chukar*), for which extensive scientific knowledge, especially regarding its distribution patterns, limiting factors, density, evolutionary history, behavior and physiology, is available (details in [Chapter 1](#)). I focused the study on the steep climatic and ecological gradient in Israel, for which we have substantial climatic, geographical, ecological, historical, and paleontological information.

Trends in genetic and morphological diversity were tested in chukar populations separated by relatively short geographical distances, but subjected to a steep environmental gradient across the species range. As presented in [Chapters 2-4](#), the results supported the proposed hypothesis: genetic diversity showed a hump-shaped pattern across the species range, with peak diversity in turnover zone populations, which were located in the Mediterranean-desert ecotone. Genetic diversity was significantly correlated with location along the distribution gradient moving from the core towards the periphery of the range. Levels of within-population genetic diversity, as estimated by various measures, including observed and Hardy-Weinberg expected heterozygosity, showed a unimodal hump-shaped pattern across the chukar range with peak diversity at the Northern Negev ecotone, where the edge of the species' continuous range occurs. A quadratic regression between distance from range periphery as the independent variable and each of the genetic diversity estimates, especially mean observed and Hardy-Weinberg expected heterozygosity, explained 73 and 80 percent of the total variance, respectively, and was highly significant (see [Chapter 4](#)). The quadratic model explained a significantly higher proportion of the variance than a linear regression (increasing or decreasing) model. In spite of the short distances between the study populations genetic diversity within populations along this gradient shows significant trends ([Chapters 2 and 3-4](#)).

Local populations maintained distinct genetic characteristics even though population genetic data indicated likelihood of substantial gene flow among populations, supporting the “divergence with gene flow model” of speciation (Rice and Hostert, 1993; Smith et al., 1999; Smith et al., 1997), as discussed in [Chapter 2](#). Study populations showed instances of isolation by distance effects in the face of both short distances between populations and the absence of significant geographical barriers ([Chapter 2](#)). The highly diverse genetic structure of different chukar populations across the short geographical gradient given relatively high levels of gene flow could be maintained by a combination of stochastic population dynamics factors and natural selection acting on morpho-physiological traits and on their linked allozyme loci ([Chapter 2](#)).

When the range was partly sampled for the part from the Mediterranean-core to the ecotone only and the extreme periphery was not included, a significant trend of increasing diversity was found for two separate years of study ([Chapter 2](#)). As in many other studies dealing with trends in diversity across the range, the extreme periphery was not included in these first two years of sampling (1990, 1993). The most peripheral populations were taken from areas with high human-related disturbance due to the fact that in this more natural area population density is very low and sampling is very difficult. Therefore, these need not reflect the natural environment near the periphery (see discussion in [Preface to Chapters 3 and 4](#)). Conclusion of the study at that early stage would have most probably resulted in support for the Fisher hypothesis presented in [Chapter 1](#). Yet I was interested to further reveal the trends in diversity as the extreme periphery of the range is approached. Does diversity increase, stabilize or decline again, as predicted by the hump-shaped hypothesis? In order to test the latter hypothesis, a major study was undertaken during the non-breeding season of 1995-6 where 13 chukar populations from ‘natural’ environments and four populations from modern human-related environments were studied across the range (see [Chapters 3 and 4](#) for details). As mentioned in the [Preface to Chapters 3 and 4](#), these populations were carefully selected and sampled following a detailed pre-determined sampling design. Results

were consistent with the two previous years of study for the part of the range from the core to turnover ecotone region. When the extreme periphery was added to the study, a hump-shaped pattern of within-population diversity appeared across the range, supporting the proposed hypothesis. As discussed in [Chapter 3](#), partial sampling of the range would have led to opposite conclusions for each of the different sections studied. If the part from the core towards the turnover zone alone had been studied, without including the extreme periphery, I would have concluded that the data supports the “Fisher” hypothesis. If the part from the turnover zone to the periphery alone would have been sampled, I would have concluded that a trend of decrease

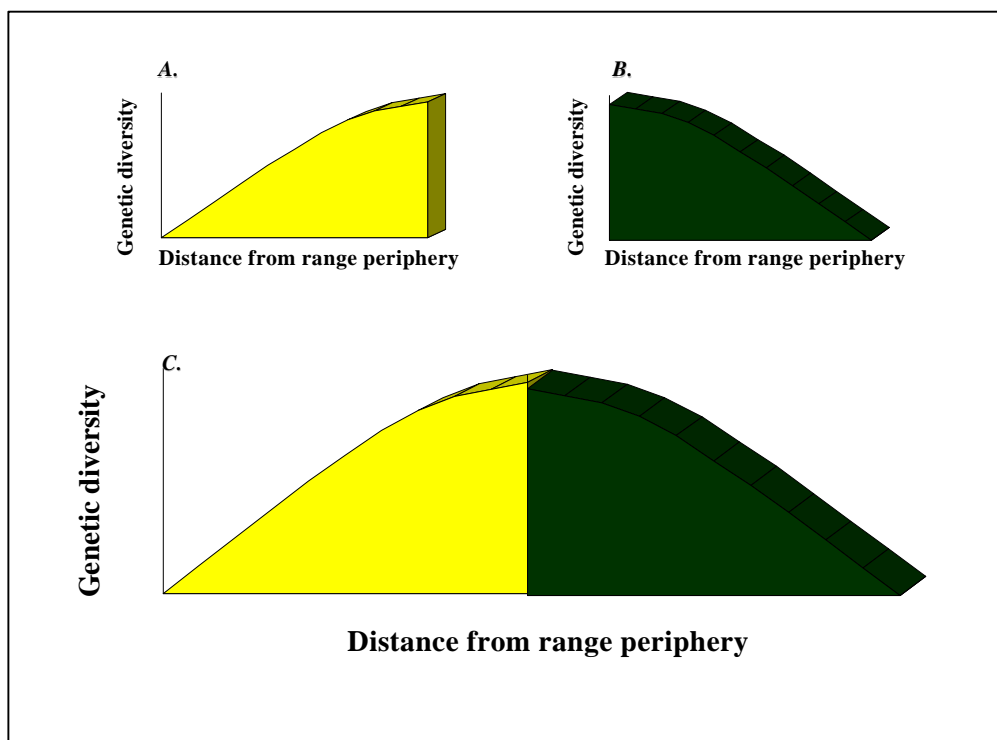


Figure 1. Trends in within-population genetic diversity vs. distance from a species' range periphery, located at the origin, according to the Carson hypothesis (A), predicting an increase in diversity with distance from the range periphery, the Fisher hypothesis (B), predicting a decrease in diversity across the range, from periphery to core, and the integrating hump-shaped hypothesis (C), which combines the two earlier theories.

in diversity occurs towards the periphery, or that there is no clear trend, because it was not statistically significant. If I had not sampled the turnover zone ecotonal populations at all, I would have probably concluded that no clear trend occurs across the range. Only when the full gradient is sampled and the ecotone is included in the study, is the hump-shaped pattern revealed, resolving the contradiction between the two hypotheses, (see Fig. 1).

Trends in phenotypic diversity

Similar results were obtained when trends in diversity were tested at the morphological level based on 35 traits and 23 ratios across five chukar populations, as discussed in [Chapter 5](#). In order to enable a comparison of within-population diversity across populations taking into account data from all traits studied, I used a statistic which was especially developed for this work, termed the “Estimator in a Dependent Sample” (EDS). This estimator calculates a weighted coefficient of variation value for each population which is based on all individuals, traits (or ratios between traits taking into account allometry) and the correlation between each two traits. This estimator is conceptually somewhat equivalent to statistics used in population genetic studies where a mean diversity estimate is required for each population to enable comparison of populations. It is especially useful when data from many, often correlated traits are available, or when sample size is too small to detect significant trends across populations if single traits are analysed. These findings point towards similar trends as those revealed at the genetic level, presented in [Chapters 2-4](#).

Possible factors contributing to the hump-shaped trend

Historical factors

One could reason that the high diversity found in chukar partridges at the Mediterranean-desert ecotone is simply a result of isolation of populations of these two areas during their evolutionary history, and their renewed contact today in a

“hybrid zone” (Barton and Hewitt, 1989). However, paleontological findings of chukars from Israel and Sinai suggest that the distribution of chukars in the region during the Pleistocene glacial periods, when the climate was colder, was more continuous than it is today. While chukars are currently not found in the very arid parts of the Negev and Sinai deserts, there is evidence that chukar distribution in the Late Pleistocene extended into what is now extreme desert, showing a more continuous distribution (see discussion in [Chapter 2](#), Kark et al., 1999). Thus the argument that high levels of diversity are caused by historical re-contact of chukar populations in the Mediterranean-desert ecotone following their historical isolation currently seems improbable. In addition, an examination of allele distribution across the gradient suggests that the higher levels of diversity in the turnover zone are not generated by the combination of two different sets of alleles from the core and the periphery, but rather by the appearance of new alleles and an increase in the frequency of rare alleles. Populations at the Mediterranean-core and arid periphery are more similar to each other for many of the loci studied than to those of the ecotone region. Therefore, these results may be related more strongly to ecological time scale processes. We are currently testing this explanation as part of an ongoing study of trends at the non-coding DNA level done in collaboration with E. Randi (see “Future directions” sub-chapter below).

Ecological factors

Local populations at the extreme periphery exist in isolated and infrequent patches of suitable environment. From a demographic perspective, their persistence is highly dependent on dispersal from other populations (Boorman and Levitt, 1973; Harrison et al., 1988; Pulliam, 1988). These local populations, sometimes termed sub-populations (Hanski and Simberloff, 1997), which may comprise part of a larger metapopulation (Hanski, 1998; Hanski and Gilpin, 1997; Harrison, 1994; Harrison and Taylor, 1997), have traditionally been compared with blinking lights which turn on and off frequently (Boorman and Levitt, 1973; Harrison and Taylor, 1997). In the periphery, occupancy of suitable patches over time is dynamic, potentially leaving

suitable habitats unoccupied (Lennon et al., 1997; Thomas and Hanski, 1997). In these extreme areas of the distribution range, within a local population, population growth rate (r) can be negative, and in this case these populations are usually termed "sink" populations (Hanski and Simberloff, 1997; Holt, 1985; Holt, 1993; Pulliam, 1988). Populations in the periphery often experience low rates of gene flow and large fluctuations in population size, leading to repeated bottlenecks, random genetic drift (Hoffmann and Blows, 1994) and reduced genetic diversity (Hoffmann and Parsons, 1991; Lacy and Lindenmayer, 1995; Lesica and Allendorf, 1995; Vrijenhoek et al., 1985). As population persistence time is low (Lacy and Lindenmayer, 1995), new genotypes may not have enough time to establish themselves within the population, before the local population in which they are found experiences genetic drift or goes extinct (Lesica and Allendorf, 1995). Founder effects, caused by the founding or recolonization of these sink populations by a small number of individuals from an adjacent (Wiens, 1989), possibly self-sustaining source population (Holt et al., 1997), may consequently reduce genetic diversity (Lesica and Allendorf, 1995) and persistence (Kirkpatrick and Barton, 1997). When dealing with adaptive genes under selection, only those few genotypes that can cope and survive in these extreme conditions can persist, whereas others will perish (Hoffmann and Parsons, 1991; Parsons, 1991a). All these factors, based on both selection and population dynamics considerations, suggest that local populations located at the extreme periphery of the species range will maintain low levels of within-population diversity. Nevertheless, it is worthwhile mentioning that when combining diversity in many local peripheral sub-populations across a wider geographical area, genetic diversity at the periphery may be higher. Yet local extinctions and low levels of gene flow may prevent the persistence of unique local genotypes through time.

In the central, relatively favorable areas of the range, where the environmental conditions are near optimal for the species, low within-population diversity levels are again expected. Populations here tend to be large and continuous (Brown, 1984; Brown et al., 1995; Brussard, 1984; Collins and Glenn, 1991; Hengeveld and Haeck, 1981; Hoffmann and Blows, 1994; Lomolino and Channell, 1995; Wiens, 1989;

Chapter 1). Populations here do not necessarily form a metapopulation structure (Stacey et al., 1997). Although the large population size will contribute to the maintenance of some within-population diversity, relatively high rates of gene flow may result in uniformity of allele frequencies (Mills and Allendorf, 1996), and may again prevent the persistence of unique local genotypes through time. When adaptive or strongly selected traits (or genes linked to them) are considered, only the best competing genotypes, most fit to the ecological conditions in the core, will prevail (Karlin, 1982). New genotypes, added into the population by dispersal (see footnote on pg. 48 in Wiens, 1989 for comment on dispersal and migration) or by mutation will have low chances of competing with the more established, relatively fit genotypes which persist for longer periods of time in the favorable and less perturbed environment and in stable, long-lived populations (Lennon et al., 1997). Thus, from both population structure and adaptive trait considerations, levels of within-population diversity are expected to be relatively low in the core.

In the turnover zone of the species range, where environmentally induced fluctuations in population performance and density are intermediate, within-population diversity will be maximal, compared with both the core and the periphery. This area comprises the edge of the continuous distribution of the species in terms of spatial distribution of local populations. Connection and gene flow among local populations within the turnover zone, intermediate relative to that in the continuous core or at the isolated periphery of the range, will enable new individuals and genotypes to enter local populations and establish themselves, and thus will prevent genetic drift. Yet the larger effect of environmental variability on performance relative to the core will prevent few genotypes from dominating over time. This will enable various alleles to coexist in fluctuating frequencies. From adaptive considerations, different genotypes will be the fittest at different times, but may have a chance to maintain themselves also in periods less optimal for them because conditions do not go to extremes, as in the periphery of the range. When the turnover zone falls in the ecotonal areas and is congruent with areas of steep climatic and environmental gradients, selection is expected to be disruptive rather than

directional, being affected by diverse environments. This may also lead to higher levels of diversity at the ecotone.

The proposed “hump-shaped” model

Thus, considerations of the effects of selection as well as metapopulation dynamics (Hanski and Gilpin, 1997; Lesica and Allendorf, 1995) predict that within-population diversity will show a hump-shaped pattern along a species range from core to periphery, and will peak at the turnover parts of the range. Diversity may eventually reach a plateau as distance from the intermediate area increases. The model for humped diversity across the range, when developed and thereafter tested in a model species, the chukar partridge, did not strive to quantify the expected trend, nor did it attempt to specify for ‘neutral’ vs. adaptive directly selected genes (or genes linked to them). However, it predicted a testable trend and patterns that may be explained by population structure and dynamics, as well as adaptive considerations. While the chukar case study supports the model predicting a unimodal pattern of diversity across the range, the precise pattern in each species will depend on the interaction between gene flow, metapopulation dynamics and local selection. For example, when the edge of the continuous range is close to the area where the extreme periphery is located, the distribution of diversity vs. distance from periphery is predicted to be unimodal yet left-skewed, as found at the community level (Abramsky and Rosenzweig, 1984).

Parsons (1989; 1991a) proposed that populations occupying moderately stressful environments will exhibit higher variability and phenotypic plasticity than those from more benign environments, and their metabolic costs will not be constraining (Parsons, 1991a; Parsons, 1991b). Parson's idea is based on physiological considerations, yet leads to similar predictions as the presented model.

Analogy to the community level

Theoretical considerations (Tilman, 1982) and empirical results at the community level show a hump-shaped pattern in species diversity along a productivity gradient (Abramsky and Rosenzweig, 1984), resolving a long-lasting debate between

conflicting approaches. Rosenzweig and Abramsky (1993) suggest that the reason for the discrepancies may have been the fact that investigators were looking at different phases of the gradient, namely, at either the increase or decrease phases, rather than the two combined, which then show the hump-shaped trend. Tilman and Pacala (1993) reason that this prediction of peak species diversity at intermediate productivity is qualitatively rather similar to that of peak species diversity at intermediate rates of disturbance, also known as the intermediate disturbance hypothesis. The latter predicts maximum species diversity at intermediate levels of disturbance (Connell, 1978).

The suggested model regarding patterns of within-population diversity is analogous in many respects to the intermediate disturbance hypothesis. Some of the mechanisms suggested to support each of the two models are similar. For example, the effect of biotic factors (e.g., competition among species) in conditions of low disturbance at the between-species level is somewhat equivalent to the effect between genotypes in the core at the within-species level. At the other extreme of environmental conditions, the effect of environmental abiotic factors may be a central factor at both the community and population level.

The classical hypotheses as special cases

The proposed model encompasses the two classical hypotheses concerning genetic diversity in peripheral vs. core populations, which become special cases, and allows also for more complex situations. Under the model, the apparently contradictory and controversial earlier hypotheses are accommodated and become complementary. They can each explain a portion of the general picture: The case of higher diversity in what appears in the literature as “peripheral” populations, may be observed when populations from the ecotone/turnover zone (rather than extreme isolated periphery) are compared with those from the core. The case of lower within-population diversity at the periphery may be observed when populations from the most extreme periphery of the range, often small isolates, are compared with populations from the turnover zone. As in the case of productivity and species diversity patterns (Rosenzweig and

Abramsky, 1993), when sampling of the range is incomplete and includes only the increase or decrease phase, especially closer to the periphery (Carter and Prince, 1988), or when the ecotone is not sampled or is not separately analyzed, confused patterns and apparent discrepancies may appear. Lennon et al. (1997) suggest that when the scale of the study is too robust and the sampling scale is larger than the space which individual populations occupy, an apparently sharp (observed) trend may be indicated, rather than the existing diffuse distribution edge. This may similarly affect conclusions as to spatial patterns of diversity within populations.

Conflicting results may also result from differing patterns of local spatial distribution of different species. For example, the spatial distribution of some species does not include isolated peripheral populations (see for example marsupial species studied by Caughley et al., 1988) due to an abrupt step-shaped distribution edge caused by an environment change which creates a sharp distribution barrier (Brown et al., 1996; Kirkpatrick and Barton, 1997; Lennon et al., 1997). This effect may also be related to recent changes in natural distribution dynamics and reduction of the range resulting from human-induced factors. In these cases the most peripheral populations observed and sampled may actually be those typical of what is here termed the turnover zone. Yet in many cases a finer differentiation of the range into core, turnover zone and periphery is possible, and may be helpful in revealing patterns in within-population diversity across species ranges. In addition, it may be advised to search for non-linear and non-monotonous trends in order to test for a hump-shaped pattern, which will not be revealed by a linear regression or correlation analysis.

For example, analysis of a study on allozyme diversity in wild barley (*Hordeum spontaneum*) comparing populations from the Mediterranean vs. arid regions of Israel, the latter being near the periphery of the species range, did not show clear trends across the species' range in Israel (Volis et al., 1998; S. Volis, unpublished data). The authors were testing the Carson (1959) and the Fisher (1930) hypotheses presented in [Chapter 1](#), and were therefore searching for monotonous trends. Following the suggestions arising from this work, this data set has recently been

re-examined. A search for non-linear trends and plotting of the data along a continuum rather than pooling populations into two dichotomous regions, as previously done, revealed a different pattern: the results of this re-analysis suggest that a quadratic model explains a much larger portion of the variance compared with a linear one (Kark et al., ms in preparation). The ecotone region was not sampled in their original work and therefore, the complete hump-shaped trend could not be tested, yet it appears that genetic diversity increases from both the Mediterranean-core and the arid-periphery towards the ecotone, which should be further examined to test for the full pattern. I suggest that re-analysis of existing data sets may further reveal trends that were not detected in earlier work and may resolve some of the apparent discrepancies between the current theories in the literature.

Ecological and distribution gradients

In this work, I sampled populations across a distribution gradient, from the core through the turnover zone to the periphery studying the chukar partridge in Israel. This cline is partly congruent with a latitudinal, climatic and floristic gradient from Mediterranean to arid ecosystems, along which rainfall, temperature, plant and animal composition, phytogeography, competition, species diversity, richness and many other climatic and environmental variables change (see [Chapter 1](#)). Following the goals of the work, I tested the relation between diversity (or developmental stability) and location along the distribution gradient, as estimated by the distance from the chukar range periphery. Climatic (e.g. rainfall) and distribution variables are often correlated, the first partly determining the latter. A multiple regression analysis between mean annual rainfall, mean summer and winter temperature and distance from the sea (taken from the Hebrew University Geographical Information Systems computerized data base) vs. distance from range periphery was highly significant with very high r-square. The relationship between these factors is causal: the distribution reflects the ways in which the environment has influenced the species and shows the environment as perceived by the chukars. The edge of the range reflects a location from which on the species does not exist at all. A combination of

biotic, abiotic and historical variables reach a threshold that does not permit the persistence of the species and from there on density decreases to zero. Therefore, these factors go hand in hand, the integration of numerous environmental factors determining the distribution. The distribution is a summary of how the species actually responds to the changes in environmental factors. This is somewhat comparable to a study of diversity patterns across a latitudinal gradient along which rainfall and other climatic variables change. The latitude often “summarizes” the diverse variables that affect the persistence of a species in space, including abiotic, biotic, evolutionary and historical factors. A species’ distribution pattern reflects the response of the species to *its* environment. In the context of my research questions and goals, studying this gradient, with reference to environmental shifts along it, is, I argue, a more conclusive approach for revealing spatial trends and comparing populations within species, especially in the context of biodiversity conservation.

Trends in developmental stability across the range

While three major types of bilateral asymmetry are long known in the literature, including fluctuating asymmetry, directional asymmetry and antisymmetry (reviewed in Chapters 1 and 6), little is currently known about the transitions and shifts between the three types of asymmetry (Graham et al., 1998; Chapter 6). Historically, fluctuating asymmetry has been used as an estimator of developmental instability and environmental stress, yet the two other asymmetry types were not considered useful in this context due to their unknown genetic basis. Workers on developmental instability have often excluded traits showing directional asymmetry and antisymmetrical components in the analysis (Palmer, 1994). An implicit assumption when following this logic is that within a single species, all populations, although may differ in levels of asymmetry will show one type of asymmetry for a similar trait. Yet, as far as I know, this assumption has not been directly examined. This has most likely caused a bias in the study and the understanding of factors affecting asymmetry. While comparing trends in asymmetry across populations, I plotted the distribution of asymmetry in all study populations. Although the distribution did not

show a typical normal bell, expected in the case of fluctuating asymmetry (which I was originally looking for), I decided to continue with the analysis of the trait asymmetry patterns. I further tried to test both trends in fluctuating asymmetry and shifts between different asymmetry types across the range. I followed the rationale presented by Graham et al. (1993), which suggested, based on theoretical and some experimental work, that the three asymmetry types are dynamically inter-related with a continuum between them. Asymmetry, as measured in chukar partridges across the distribution range in the selected trait, changed from more fluctuating in the core to more directional and antisymmetrical towards the periphery. The main shift occurred in the ecotone between Mediterranean and desert regions (see fig. 2 in [Chapter 6](#)). The findings of this study provide primary empirical evidence for shifts in levels and type of asymmetry across a species partridge natural distribution range, showing a continuum between asymmetry types and supporting the notion that all three asymmetry types can reflect developmental instability ([Chapter 6](#)). An important implication of this work relates to the interpretation of the type of asymmetry revealed at a certain trait. As in the study of trends in diversity across the range, if only part of the range (e.g. core to turnover zone or turnover zone to periphery) were sampled in the study rather than the full continuum from core to periphery, completely different conclusions as to the type of asymmetry would have been drawn for each section. Only when the range is widely sampled is the shift in asymmetry types resolved.

As presented in [Chapter 6](#) in detail, fluctuating asymmetry increases in the examined trait in natural populations of chukar partridges across the range, from core through turnover zone to extreme periphery, with a notable shift from fluctuating towards directional asymmetry. It is difficult to explain the findings based only on the genetic-based approach to directional asymmetry. It is more likely that the changes in directionality and asymmetry expression in peripheral populations reflect increasing environmental stress with a consequential decrease in developmental stability. The directional component seems to be strongly expressed under conditions where perturbations during development are the norm. This supports the hypothesis

that local chukar populations experience differing selection pressures. The results presented in [Chapters 2-4](#) suggest that genetic structuring among chukar populations in the study area is maintained even though high levels of gene flow exist among populations. Chukars are not well adapted to desert conditions. In arid and hot environments they are distributed mainly in food and water-rich patches (Degen et al., 1984). The asymmetry work reveals that although chukars near the edge of their range may be located in “favorable” and resource-rich patches relative to the surrounding desert environment, individuals confront higher stress relative to those from other areas across the range. Higher levels of environmental stress are confronted at the periphery of the distribution range, possibly leading to reduced developmental stability ([Chapter 6](#)).

Types of range edges

Following the results of both the genetic diversity and asymmetry chapters of this work, I suggest that instead of a single type of range periphery at least two types of range edges should be accounted for:

1. The edge of the species continuous range, also termed the “turnover zone”, beyond which populations often become small, fluctuating and isolated (see [Chapter 1](#)).
2. The "decay zone" (which I also term the extreme periphery), beyond which the species does not occur at all and population density reduces to zero. Marked on a map, this is the outermost margin of the range.

These two types of thresholds are expected along a species' range, the first delimits the extreme periphery from the area where the species does not occur at all. This area may extend across relatively large geographical regions. The second marks the area (turnover zone) where the species' spatial distribution pattern rapidly changes and beyond which the extreme periphery occurs. The turnover zone is expected to be located in relatively small geographical regions, where rapid climatic and ecological shifts occur (ecotones), as in the case of the Mediterranean-desert

ecotone in Israel (Danin, 1998; Chapters 1-6), the Savanna-rainforest ecotone in Cameroon in West Africa (Smith et al., 1997), and the dry-wet rainforest in Queensland, Australia (Smith et al., 1999). These areas and thresholds are expected to be dynamic through time (Kirkpatrick and Barton, 1997). The empirical study and theory presented in this work support these ideas. Further studies should test the generality of these ideas focusing on ecotone regions and on distribution gradients, which seem to teach us much more than previously acknowledged on patterns and processes in biodiversity.

Conservation implications

Diversity and asymmetry in conservation biology

The field of conservation biology has developed and gained momentum in the past two decades, especially in the context of biodiversity conservation (see Chapter 1). Together with the increased interest in this field, the necessity to develop scientific tools which enable characterization of the dynamics of animal and plant populations in time and space is crucial. This is becoming one of the major goals in conservation biology research. Furthermore, in the face of wide-ranging environmental and climatic changes (Peters, 1991; Wyman, 1991), the need to use these scientific tools which enable estimation of the environmental conditions and their changes is increasing. Especially relevant are tools which allow us to follow and predict the effect of local and global changes on the survival and performance of animal and plant species. One of the most attractive tools, which is receiving substantial interest in recent years, is the estimation of fluctuating asymmetry. As discussed in detail in Chapters 1 and 6, it is an estimator of developmental instability. Comparison of asymmetry levels in different individuals, and especially in different populations, enables the estimation of the degree of stress confronted during development (Clarke,

1998b). Therefore, it has been suggested that asymmetry can be used as a valuable tool for following and monitoring changes in the environment, and in the ability of individuals to develop in a stable path. Lens et al. (1999a) suggest that this technique will be the most efficient in peripheries of species ranges, and in marginal and disturbed habitats (Lens et al., 1999a). Results of this work show that fluctuating asymmetry indeed increases from core to periphery, with shifts in asymmetry types occurring along this cline (Chapter 6). This work also indicates that the chukar turnover zone, located in the ecotone region, as perceived by the birds, is an area of transition between low and high levels of environmental stress confronted, as reflected in increasing developmental instability (estimated by asymmetry). The high variance in asymmetry within the small geographical bounds of the ecotone bodes well for molecular studies directed to eliciting modes of gene regulation in response to chronic environmental stimuli. A valuable extension to this work may be to follow trends in asymmetry in populations through time in changing environments and to test whether these changes cause shifts in the degree and type of asymmetry. Evidence from recent work (R. Alford, personal communication) shows a rapid increase in asymmetry levels just before a steep decline and extinction of amphibian species in Australia occurred. Following these changes may thus provide us with an invaluable tool as a warning signal and allow action for prevention of further decline of natural populations of species, when possible. I suggest that this tool should further be tested for its feasibility and applicability in monitoring of natural populations. Setting a system of population monitoring stations, where levels of environmental stress, as estimated by the developmental instability, are monitored at different locations across species ranges may be a useful first step in prevention. In cases where rapid changes in stress are observed, a further and wider investigation and actions may be directed to those populations and regions.

Conservation implications to Global Environmental Change

Global Environmental changes, and especially Global Climatic Changes are rapidly occurring (Dobson, 1993) and are changing the challenges confronting

conservation biologists and decision-makers (Wyman, 1991). These changes are affecting ecosystems, species, populations and individuals from the global to the more local scales (Vitousek, 1994). The classical conservation approach of creating static nature reserves and protected areas may not suffice in the face of rapid changes to the environment. These changes are causing shifts in species distribution patterns, population dynamics and extinction processes, yet are probably too fast to enable most species to adapt (Dobson, 1993). It seems more reasonable that the species and populations that will survive through these changes will be those with high levels of genetic diversity (Safriel et al., 1994), which enable adaptation to various environments, will be those with wide distribution ranges or species with high mobility which will be able to follow, “track” the changing environment (habitat tracking, see Eldredge 1995). Therefore, concentrating efforts towards the conservation of populations that are currently rich in genetic diversity, having unique, as well as common alleles, and adapted to changing environments may enable the species’ long-term survival. Ecotone regions and populations occupying them, if rich in diversity and originating from areas where change and transition between different environments (e.g. mesic and arid, warm and cold etc) is the norm, may be good candidates.

I believe that a dynamic conservation approach should be developed. This will emphasize continuity of nature reserves and natural areas, to enable movement of animal and plant species in the changing environments. Directing attention towards dynamic conservation efforts may be a key to the conservation in a dynamic and rapidly changing environment. This will include maintaining the flexibility to dynamically prioritize and change the areas receiving higher vs. lower conservation priority, conservation outside nature reserves (e.g., in open areas, large urban parks and set-aside arable land (Wilby, 1996), and establishing a reliable monitoring system for following and detecting the effects of the changes on natural populations. This approach will enable to conserve dynamic ecological and evolutionary processes, rather than static spatial and temporal patterns alone.

Conservation goals and prioritizing for biodiversity conservation

Attempts to reveal related spatial and temporal dynamics, patterns and processes at various levels - from individual through species up to ecosystems - are becoming more important than ever (Mangel et al., 1996; Ginsberg, 1999; Lawton, 1995; Mittermeier et al., 1998; Pimm et al., 1995; Smith et al., 1997). Revealing spatial trends in diversity can facilitate conservation planning, prioritizing and the identification of populations and areas that may warrant special attention for present and future conservation (Lomolino and Channell, 1995; Mittermeier et al., 1998; Safriel et al., 1994).

Because we cannot resolve levels of diversity across all species' ranges, we should try to reveal general spatially-based patterns in biodiversity that may be repeated in many species. If these are shown to be more general, we can try to set conservation priorities upon spatially-based considerations, using modern available tools, and especially Geographical Information Systems. This was the approach taken in this work. Conservation recommendations and prioritization may largely depend on the goals of the decision-maker (e.g. the Nature Conservation and National Park Authority in Israel). For example, if the goal is to conserve the highest levels of diversity within natural populations, the emphasis should be directed to the ecotone region, which was shown to harbor the highest levels of genetic diversity across the chukar range in Israel. If the goal is to prevent populations with especially, or relatively low levels of diversity from going extinct due to genetic or demographic processes, it may be recommended to give high priority to the conservation of the most peripheral and core populations.

In addition, the decision-maker should set priorities as to the time scale of the processes it is interested in conserving. This may largely affect the practical decision as to what to conserve and how to do it. In some cases the different levels may actually be congruent, making conservation decisions easier. For example, if the highest priority is towards enabling future evolutionary processes, such as speciation (see Orr and Smith, 1998), in the chukar case study, we may decide to conserve the

ecotone area. Evidence from this work (Chapters 2-5) and from Smith et al. (1997) suggests that ecotones sustain especially high divergence and diversity following a “divergence-with-gene-flow” model of speciation (Smith et al., 1999). If the priority is towards preventing current declines towards extinction of the species or to conserving high diversity for purposes of re-introduction etc., in the case of the chukar we will probably recommend to conserve the ecotone region as well.

Another question that has received much attention at the community and ecosystem levels is what should actually be conserved. Three of the major conservation strategies (see Chapter 1) appearing in the literature suggest:

1. A focus on areas especially rich in diversity and identification of areas which are relatively small in size yet harbor large numbers of species (the “diversity hotspots approach”; Ginsberg, 1999; Mittermeier et al., 1998).
2. A focus on areas especially rich in endemic species (the “endemism approach”; Mittermeier et al., 1998; Pimm et al., 1995). This may, in some cases, partly overlap with areas comprising diversity hotspots, as discussed by Mittermeier et al. (1998).
3. A focus on a representation of all ecosystem and habitat types within regional conservation strategies (e.g. the Global 200 program summarized in Olson and Dinerstein (1998; the “representation approach”; see also Chapter 1).

I suggest that it may well be possible to adopt equivalent approaches at the level of within-species diversity. In the case of the research model I chose, the chukar partridge, conserving the turnover zone of the species range, located in the Mediterranean-desert ecotone region will enable to maximize all three criteria:

1. It was shown to be especially rich in diversity, comprising a “within-species diversity hotspot” (see Chapters 2-5);
2. It was rich in unique (“endemic”) alleles, not found in other populations (Chapters 2-5).
3. It represented all other distribution areas included in this study in genetic composition. Populations from this intermediate area of the range not only had nearly

all alleles found in all other populations, both core and peripheral, but they also had additional alleles, not found in other populations (Kark et al, 1999).

As mentioned, this has implications in understanding speciation and extinction processes at areas of transition and across species ranges (Endler, 1977; Orr and Smith, 1998), which are highly important in the study of biodiversity conservation.

Conservation recommendations

Several conservation recommendations may thus be derived from the findings of this work. I will divide these into (a) general recommendations deriving from this work on the chukar as a model species, which apply for other species and (b) specific recommendations for the chukar in Israel, which were not the primary goal of this work yet derive from the findings.

General recommendations

The chukar partridge was selected as a model species for various reasons which are discussed in Chapter 1. One of the basic reasons was the distribution pattern of this species. Chukars in Israel and the region have diverse distribution patterns, from continuous and large core populations through turnover zone populations at the edge of the continuous range to small and isolated populations at the “decay zone” (see above) towards the very edge of the range. Therefore, this enabled to compare diversity pattern for populations which may represent various other species and situations. As discussed in Chapters 3 and 4, this case study may be more general also for species which have only small and isolated populations or only continuous ones up to the very edge of the range, where density rapidly declines.

The approach taken in this study in the conservation context was a spatial one. I proposed a hypothesis that focuses attention towards areas of transition, which were predicted to maintain high diversity. This hypothesis was supported following a wide and carefully planned sampling of the range in Israel, resolving trends that were previously undetected. Sampling and research plan across the range may be crucial in resolving previously un-detected patterns, and in setting conservation priorities. This

may apply to other animal, as well as plant species, as demonstrated following the re-analysis of the data in the study of the wild barley (see above).

Ecotones harbor many species (Holland et al., 1991), many of which have turnover zones in these areas of environmental change. Hence by conserving the ecotone region, which is relatively small in size yet rich in diversity, we may manage to conserve high diversity at both the within and between species scales. This is a cost-effective strategy. I recommend that turnover zone populations in Israel within the ecotone area of the northern Negev receive high research attention and conservation priority because they potentially guarantee the maintenance of high within-species diversity and future processes. These ecotone populations may well function as sources of genetic variability for other populations, some of which may be sink populations (Pulliam 1988, Dias 1996, Hanski & Simberloff 1997) whose persistence may depend on dispersing individuals and genotypes originating from these regions. Management should ensure that dynamic populations and adaptive processes (Lacy 1997) in ecotone populations be maintained.

The chukar is typical of open areas, an environment which is rapidly being developed in many countries. Therefore, it may be a good model and monitoring species for the degree to which these changes are causing a decline in natural populations and are changing their levels of diversity. As discussed in [Chapter 2](#), and as suggested for the chukar case study, conservation of populations and metapopulation processes must contend with continued development and rapid urbanization of wide areas in Israel and other regions. Habitat fragmentation appears to be especially severe in the densely populated areas in the north and center of Israel. However, even the ecotone area of the northern Negev is being rapidly developed and fragmented, with ever diminishing likelihood of gene flow among local populations. Therefore, an important management priority may be to create or identify existing habitat corridors that are essential links among populations. Enabling connection between suitable habitat areas in the face of fragmentation may be required for conserving connectivity, gene flow and diversity within populations and preventing genetic and demographic stochastic processes that may lead to loss of diversity and

local population extinction (Thomas and Hanski, 1997). Landscape-level (Wiens, 1989) assessments and monitoring are probably required as first steps to prevent isolation of local populations and conserve essential links among them. Large-scale conservation programs, such as a plan for a biosphere reserve in the southern Shefela at the margins of the ecotone region in Israel is a promising direction (Y. Shkedy, personal communication).

A different landscape dynamic applies to marginal areas (e.g. those of the central and southern Negev desert in the chukar case study), where irrigation-based agriculture and settlement are creating rich habitat patches in areas that formerly supported only sparse chukar populations, and are changing patterns of distribution (Shirihai, 1996). Recent changes have already affected patterns of dispersal and genetic diversity in some environments. This work revealed that genetic characteristics of desert chukar populations may differ in natural and neighboring irrigated agricultural environments with relation to their location across the range (Chapter 4). Thus it is essential to maintain a delicate balance between reduced rates of gene flow, which may result in deterioration of diversity in local populations, and increased gene flow which may result in uniformity of allele frequencies between local populations. The latter may prevent populations from responding to local selection pressures which is essential for the preservation of the genetic structuring along the gradient and maintenance of unique local population genetic attributes (Mills and Allendorf, 1996).

Specific recommendations for the chukar

Chukars are a game species in various parts of northern and central Israel and in many other parts of the species' global distribution. Game hunting and habitat loss have been contributing to the extinction of local chukar populations. Hunting programs, such as that recently set by the Scientific Division of the Israel Nature Reserves Authority (S. Nemtsov, pers. comm.) should refer to priorities set for the species' conservation. Future efforts to restore chukars to former range may depend on identifying and preserving areas with extant populations rich in genetic diversity.

These should take into account local uniqueness of chukar populations and the fact that substantial genetic structuring was revealed across short distances. Chukars have large natural Eurasian distributions and were successfully introduced to western North America, New Zealand and elsewhere (Cramp and Simmons, 1980; Shirihai, 1996; Snow and Perrins, 1998). Although the species has not acquired threatened status at the global level, many local vulnerable populations exist within the species range, mainly due to habitat loss and hunting, which may warrant special attention for conservation (Snow and Perrins, 1998). I suggest that ecotone populations in Israel comprise such a valuable genetic resource for biodiversity conservation.

The findings of this work have revealed a substantial measure of genetic and morphological structuring among Israeli chukar populations, and suggest that the genetic structure of populations along the gradient may depend on the fine balance between isolation from and connectivity with neighboring populations (Kark et al., 1999; Mills and Allendorf, 1996). While connection between populations is important, I suggest, based on the findings of this work, that release of chukars from one part of the range to another for hunting purposes, as done for various phasianid species in Europe (e.g. in Italy; Snow and Perrins, 1998) should be avoided, if possible, to enable the maintenance of local unique genotypes and structures.

Accordingly, the increasing human-induced changes to the environment and to the rates of gene flow among populations should be counteracted so as to restore this balance. This may apply for many other animal and plant species as well.

F u t u r e d i r e c t i o n s

Various questions and research directions arise from this work. Some are currently being investigated and others may be applied in future work. I will shortly discuss some of the central directions:

1. Comparison of trends revealed along the core-periphery distribution gradient in Israel with other areas of distribution for the chukar partridge. This direction is being developed today in a study which I have started in Gansu Province, China in collaboration with Profs. Uriel Safriel, Ettore Randi, Liu Naifa, Chen Qiang and Zhou Tianlin. In this work, we are comparing genetic diversity at the DNA level (mDNA control region sequence diversity and microsatellite polymorphism) of five chukar populations sampled across a similar gradient. We selected an area where, in similarity to Israel, a steep environmental change occurs across relatively short geographical distances. In this area of eastern Gansu, Qingyang Region, mean annual rainfall decreases rapidly from approximately 650-700 mm in the south to ~ 200 mm in the north on the fringes of the Gobi Desert along ~250 km, where chukar distribution reaches its northern periphery. Results of this work will be compared with those from Israel. These results will also be compared with those from the hybrid zone between the chukar and the European *Alectoris graeca* species in the Turkey-Bulgaria region.

2. Comparison of trends in within-population genetic diversity at the DNA non-coding level. Trends across populations in the mDNA D-Loop hyper-variable region (2nd domain) are being compared with those revealed at the protein and morphological levels. This will enable a comparison of trends, from DNA to phenotypic diversity. These comparisons of coding vs. non-coding genetic diversity will help reveal the role of population dynamics stochastic factors such as genetic drift and those of natural selection in determining the hump-shaped pattern of diversity revealed across the chukar range in Israel at the morphological and protein levels.

3. Comparison of trends in diversity and in developmental instability, as estimated by fluctuating asymmetry across the range and the role of ecotones in additional species from different groups. A study focusing on a tree (*Pistacia Atlantica*) species has been initiated in collaboration with Dr. Moshe Inbar testing asymmetry in the species' compound leaves across the range in Israel and the region. In addition, I am currently analyzing the data from a succeeding study, focusing on two Lepidopteran (butterfly) species. These Pierid species are currently being studied across their distribution gradients in Israel to reveal trends in asymmetry and in diversity and to compare with the chukar findings. One of these species, (*Euchloe Belemia*) has a distribution rather similar to that of the chukar in Israel and the other species, which is very similar to it in appearance (*Euchloe falloui*) is a north African and Saharan species and reaches the edge of its range in Israel, yet this is a northern rather than southern distribution periphery. Both species are being studied for asymmetry in six traits and for diversity at different levels to test the hump-shaped model presented in this work.

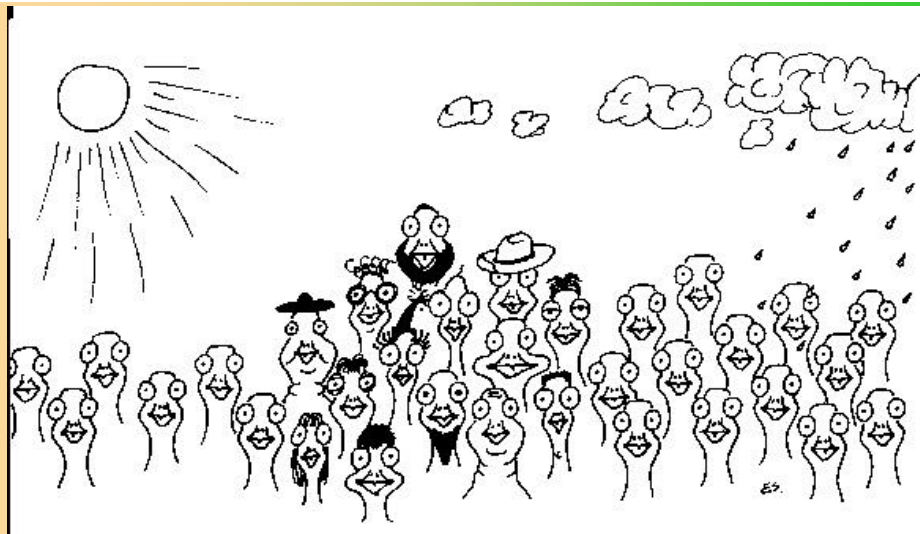
S u m m a r y

I will summarize this study with reference to the research goals presented in the introduction (Chapter 1):

1. In this work, I critically tested the classical hypotheses regarding trends in genetic diversity within populations across a species range developed earlier in this century. I showed that some of the discrepancies between the hypotheses and their empirical evidence may be due to incomplete and inconsistent sampling of the range. The Carson and Fisher hypotheses may be somewhat resolved under the integrating hypothesis presented below.
2. I tested a novel hypothesis regarding trends in within-population diversity, looking at the chukar partridge as a research model. The theory predicts a hump-shaped pattern of diversity across the range with peak levels in turnover zone populations located at the edge of the species continuous range, which occurs at the Mediterranean-desert ecotone. Populations in this area harbor especially high levels of genetic diversity, comprising of “diversity hotspots” and especially high levels of unique and rare alleles, not found in other populations. Partial sampling of the range would have probably led to contradicting conclusions for different sections.
3. Morphological asymmetry in the trait examined significantly increased across the chukar range, from core to periphery, with an abrupt step at the Mediterranean-desert ecotone. The ecotone region delimits a real periphery for the species in terms of the environment it perceives. I suggest that at least two (rather than one) types of range edges should be accounted for: the extreme periphery, beyond which the species does not occur any longer and the edge of the species continuous range, beyond which populations become small, fluctuating and isolated. Both are dynamic through time. A shift between asymmetry types was revealed across this gradient from largely fluctuating to directional and

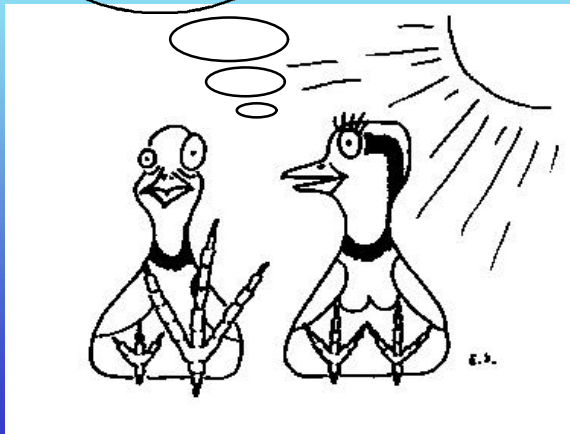
antisymmetrical. As far as I know, this is first evidence for a shift in asymmetry across a species natural distribution range. Thus I conclude that developmental instability increases across the species' range, from core to periphery.

4. An increased focus on the study and conservation of areas of ecological transition (ecotones) seems highly important for biodiversity conservation. These areas may well deserve further research attention as a reservoir of genetic and morphological diversity. I suggest that the highest conservation priority be given to this area, in which peak levels of diversity occur, comprising a diversity hotspot.

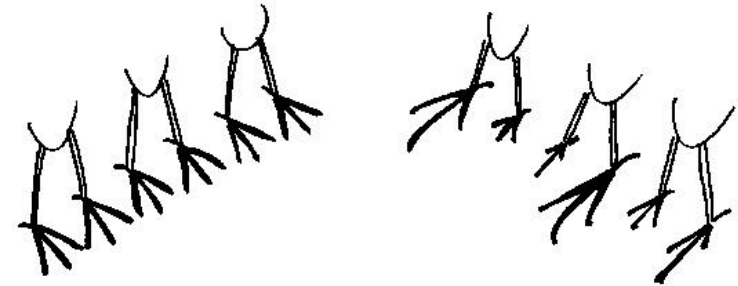


...Ecologists are starting to suspect there is something even more special about the ecotone...

I really like you Chuck,
but life looks too stressful
down at the periphery
where you live...



core meets periphery



...Does he look stressed
to you, dear?



P r e f a c e t o C h a p t e r 8 (a p p e n d i x)

The genetic basis of developmental stability, as estimated by fluctuating asymmetry, has been debated for over fifty years among developmental and evolutionary biologists. One of the central theories, sometimes termed the “heterozygosity theory” suggests that higher levels of genetic diversity, as reflected in heterozygosity, will result in increased stability during development and thus in lower asymmetry. While in many cases this relationship is tested for separate data sets, this work provides a unique opportunity to estimate the correlation between asymmetry at the studied trait and heterozygosity at two levels: (1) Population level: where mean heterozygosity within a population is predicted to be negatively correlated with mean population FA; and (2) Individual level: where the proportion of heterozygous loci of an individual and its degree of asymmetry are predicted to be negatively correlated. Because the same individuals were estimated for asymmetry and genetic diversity, the chukar data set of this study provides an opportunity to directly test the two hypotheses across the distribution gradient in Israel. It shows that partial sampling of the range would have led to different, possibly opposite conclusions regarding the association between asymmetry and diversity. This chapter presents the test of the relationship between the two factors.

Chapter 8 - Appendix

RELATIONSHIP BETWEEN ALLOZYME HETEROZYGOSITY AND ASYMMETRY ACROSS THE CHUKAR PARTRIDGE RANGE IN ISRAEL

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Key words: *Alectoris chukar*, allozyme heterozygosity, core and peripheral populations, developmental instability, ecotone, fluctuating asymmetry.

Abstract

The genetic basis of developmental stability, as measured by fluctuating asymmetry (FA), has been debated for over 50 years among developmental and evolutionary biologists. One of the central theories regarding this topic, sometimes termed the “heterozygosity theory”, suggests that higher levels of genetic diversity, as reflected in heterozygosity, will result in increased stability during development and thus in lower asymmetry. In this study, using a single data set, we aimed to test the correlation between asymmetry and heterozygosity at two levels: (1) The population level: where mean heterozygosity within a population is predicted to be negatively correlated with mean population FA; and (2) The individual level: where the proportion of heterozygous loci of an individual and its degree of asymmetry are predicted to be negatively correlated. We here test the two hypotheses across a steep distribution gradient in Israel. While previous work has focused mainly on testing this association within single populations, we suggest that study across species ranges may help in resolving the generality of the association. Focusing on the chukar partridge as a research model, we resolved mean heterozygosity levels in 26 loci and FA in third toe length of 11 populations across a steep distribution gradient from the very extreme arid periphery, through the Mediterranean-desert ecotone towards the Mediterranean core areas further away from the range boundaries. Genetic diversity, as estimated using both observed and expected heterozygosity and as tested across the range from core to periphery was not associated with FA at either the population or at the individual level. Partial sampling of the species range, from core to ecotone only or from ecotone to periphery exclusively reveals opposing trends in the association between asymmetry and observed heterozygosity. We argue that a thorough sampling of the distribution range is essential for understanding the relationship and trends in genetic diversity and in developmental stability.

Introduction

Relationship between heterozygosity and developmental stability

The relationship between heterozygosity and developmental stability, as estimated by fluctuating asymmetry, has been debated for over 50 years (Clarke, 1993; Markow, 1995). Fluctuating asymmetry (FA) is the unsigned difference between the two sides of a bilaterally symmetrical morphological trait where symmetry is the normal state (Ludwig, 1932). FA is considered a useful indicator of developmental instability and environmental stress (Leary and Allendorf, 1989; Van Valen, 1962) and has been shown to be correlated with fitness components in various cases (Brookes et al., 1997; Clarke, 1995; Møller and Swaddle, 1997). FA reflects the ability to carry out identical development of bilateral traits in the face of environmental and genetic stress. Genetic stress may include, for example, loss of genetic diversity due to inbreeding and genetic drift as well as disruption of co-adapted gene complexes (see Brookes et al., 1997; Clarke, 1995; Møller and Swaddle, 1997 for discussion). As the development of both sides of a symmetrically bilateral trait is presumably under the influence of an identical set of genes (Clarke, 1993; Markow, 1995; Møller and Swaddle, 1997), differences in asymmetry between the two sides of the body represent in many cases variation of environmental origin (Clarke, 1993; Palmer and Strobeck, 1986). Yet the tendency to develop in a stable path and to exhibit asymmetry (to either side) may be affected by genetic factors (Møller and Swaddle, 1997; Palmer and Strobeck, 1986). Two other major forms of asymmetry, antisymmetry and directional asymmetry (see Leary and Allendorf, 1989; Palmer and Strobeck, 1986 for definitions), have been suggested as having a genetic component and thus as not useful for estimating developmental instability. Yet increasing evidence suggests that various forms of asymmetry, rather than FA exclusively, may reflect the ability to carry out identical development of bilateral traits in the face of environmental and genetic stress (Graham et al., 1998; Graham et al., 1993; Møller and Swaddle, 1997). As recently argued by Graham et al. (1998): “Numerous studies

have shown that directional asymmetry has a very small additive genetic component, often too small to detect and comparable to that of fluctuating asymmetry”.

The two major mechanisms for explaining maintenance of developmental stability both have a genome-wide basis (Clarke, 1998). These include the “heterozygosity theory”, predicting that levels of protein heterozygosity will be inversely correlated with FA (Lerner, 1954) and the “genomic coadaptation theory”, predicting that more balanced coadapted gene complexes (i.e. groups of interacting loci) will show higher stability in development; reviewed in Clarke, 1993; Markow, (1995). There is also evidence that instability is related to changes in specific genes (McKenzie and Clarke, 1988). However, the empirical evidence is conflicting and insufficient, especially at the individual rather than the population level (Clarke, 1993; Markow, 1995). While much work focusing on the relationship between heterozygosity and asymmetry has concentrated on single or few populations (but see Hartl et al., 1995; Kat, 1982; Leary et al., 1985; Siikämäki and Lammi, 1998), it is compelling to compare a larger number of populations and to try to reveal trends in this relationship across a species range.

The heterozygosity theory

The heterozygosity theory is attractive mainly due to its testability and intuitiveness, especially as compared to the gene balance theory. Lerner (1954) suggested that developmental homeostasis, as estimated by FA and phenotypic variation will be inversely related to heterozygosity (Livshits and Smouse, 1993a). The major rationale of the theory is that heterozygosity has a buffering role, as it increases biochemical diversity and thus enables a dynamic stable developmental pathway in changing environments (Livshits and Smouse, 1993b; Mayr, 1970). While there are studies supporting the theory (e.g. Kat, 1982; Leary et al., 1985; Siikämäki and Lammi, 1998), there is also work opposing it (Britten, 1996; Livshits and Smouse, 1993a; Møller, 1998; Woolf, 1993), particularly at the population level (Clarke, 1993). A critical literature review of the evidence for the theory can be found in Clarke (1993).

A negative correlation between heterozygosity and FA has been found in the European subspecies of the honeybee (*Apis mellifera*). Yet Clarke (1997) has recently reviewed earlier studies and has suggested that this relationship is not general. In other areas of the *Apis mellifera* distribution range and in several other hemipteran species FA is not significantly correlated with genetic diversity (heterozygosity levels). Thus, as in the case of the honeybee, the relationship between asymmetry and genetic diversity, as estimated by heterozygosity levels, seems more complex than previously appreciated (Clarke, 1997). This relationship deserves further direct testing, especially given the fact that empirical evidence is inconsistent (Møller and Swaddle, 1997) and is sometimes derived from separate data sets for each of the two variables tested, genetic diversity and asymmetry. A study on *Gambusia holbrooki* showed that the significance and strength of the correlation between FA and genetic diversity may depend on the environmental conditions which are tested (Mulvey et al., 1994). We suggest that a comparison of the relationship between genetic diversity and asymmetry across populations within a species range from core to periphery is strongly needed, and may help resolve some of the apparent contradictions appearing in the literature.

The heterozygosity theory may be tested at two main levels: (1) Population level: where mean population heterozygosity is predicted to correlate with mean FA in the population; and (2) Individual level: where the proportion of heterozygous loci of an individual and its degree of asymmetry are predicted to be correlated. In this work, we aim to test the two hypotheses focusing on the chukar partridge in Israel across a steep climatic and distributional gradient. Work across a species range provides a unique opportunity to test these associations in relation to ecological and environmental changes and is important for resolving the generality of the association between asymmetry and heterozygosity.

The chukar partridge

The chukar (*Alectoris chukar*), a bird of the phasianid family is naturally distributed in eastern Euro-Asia (Shirihai, 1996; Snow and Perrins, 1998). In Israel, the species is

found across a sharp climatic cline from Mediterranean regions in the north where mean annual rainfall is over 500 (up to 1000 mm) to extremely arid areas only ca 200 km away in the Negev Desert, where mean annual rainfall is less than 50 mm (Bitan and Rubin, 1991). In this arid area, the chukar reaches the limits of its distribution range (see range periphery marked in Fig. 1) (Shirihai, 1996). An exception to this is a single isolated population found in the Mount Sinai region (Kark et al., 1999). An especially steep part of this gradient occurs at the northern Negev ecotone (i.e. area of transition) between Mediterranean and desert ecosystems, where within a belt of less than 60 km, rainfall decreases several fold. This area is the edge of the continuous distribution of the chukar, and from here on towards the desert, distribution becomes patchy and populations small and non-continuous (Kark et al., 1999; Shirihai, 1996). The chukar is sedentary across its Eurasian range and does not exhibit known latitudinal or altitudinal migration (Shirihai, 1996).

In this study, we aim to test the association between heterozygosity and developmental stability (as measured by FA) at both the individual and population levels across the chukar range in Israel, from the Mediterranean core through the ecotone to the extreme arid periphery.

Materials and Methods

Population sampling

Eleven chukar populations were sampled across Israel from the northern Golan to the southern Negev desert (Fig. 1). Locations were carefully selected as “natural” or semi-natural open areas with minimum or no hunting during the past decades, and without agriculture, irrigation, roads or settlements within a radius of 10 km from the center of the population sampling area, in most cases much more. Population was defined based on areas size (ca 10 sq. km). The two most distant populations were located 322 km away from one another (Fig 1). Populations were preliminarily divided into three distribution regions in Israel, which included Mediterranean core, ecotone and arid periphery (see Table 1 for population areas),

Birds were hunted by Israel Nature Reserves Authority rangers and authorized hunters during the non-breeding season of autumn-winter 1995-6. 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 . Samples were taken in dry ice to E.R.'s laboratory for further analyses.

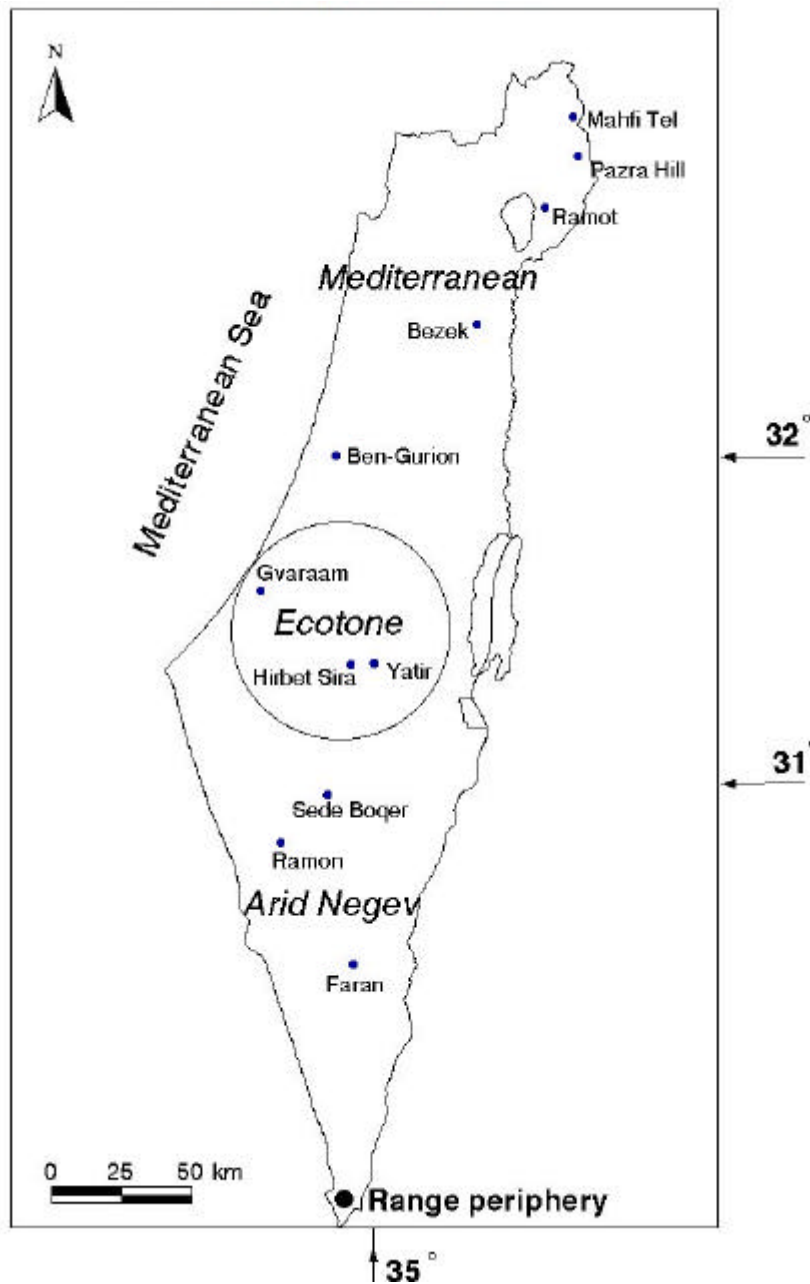


Figure 1. Map of study area, population sampling locations and chukar range periphery. The ecotone region is marked in a circle.

Genetic analysis

Samples of each tissue were separately homogenated 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, of which nine were polymorphic (see Randi and Alkon (1994) for list of loci, except PEP-2, LDH, SOD-2, mGOT, mIDH, 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).

Fluctuating asymmetry

For each individual, the length of the right and left third toe, from joint to digital tip was measured in the field, except for individuals from Bezek and Ben-Gurion Airport (Table 1) which were measured in the laboratory. This measurement was selected as having the highest repeatability from a collection of traits preliminarily measured in the laboratory on a sample of individuals from Ben-Gurion Airport. Measurement repeatability was estimated by measuring 10 individuals on both sides of the body (giving a total of 20 measurement in each replication round), and then remeasuring the same individuals (see also Møller and Swaddle, 1997; Siikämäki and Lammi, 1998). We further analyzed the repeated measurement data using a mixed-model ANOVA with factors Individual (I), Side (S) and Replicate (R) following Swaddle et al. (1994). In this model, the ratio between MS (I x S) and the combined MS (I x S x R) and MS (I x R) provides an F test for evaluating whether between-individual variation in the estimated asymmetry is significantly larger than can

were symmetrical in the population and sample sizes for FA calculations. See Fig. 1 for population locations.

Population	Area	Mean observed heterozygosity	Mean expected heterozygosity	Mean sample size per locus	Mean FA	% symmetrical individuals	S _i F _i
Tel Mahfi	Mediterranean core	0.052	0.069	27	0.013	87.5	
Pazra Hill	Mediterranean core	0.063	0.076	24.7	0.038	72.22	
Ramot	Mediterranean core	0.079	0.080	24.1	0	100	
Bezek	Mediterranean core	0.086	0.094	17.5	0.032	75	
BG Airport	Mediterranean core	0.093	0.105	24.7	0.033	66.66	
Gvaraam	Ecotone	0.120	0.115	25.9	0.040	58.33	
Yatir	Ecotone	0.106	0.107	19.8	0.026	78.95	
Hirbet Sira	Ecotone	0.103	0.107	28.7	0.070	33.33	
Sede Boqer	Arid periphery	0.073	0.096	27.6	0.100	14.81	
Ramon	Arid periphery	0.096	0.100	31.7	0.111	29.63	
Faran	Arid periphery	0.094	0.105	25.8	0.094	12.5	

be accounted for by measurement error taking into account session bias (David et al., 1999; Swaddle and Cuthill, 1994). All measurements were taken by the same observer (S.K.) using a metal ruler to an accuracy of 0.1 cm. Sampling and measurement order of populations were both random across the north-south distribution gradient.

Only adult (non-juvenile) birds were included in the analyses. Juveniles were identified based on feather color patterning (Alkon, 1979). Positive correlation between mean trait size and mean FA may potentially confound data interpretation. However, Pearson correlation coefficient between mean trait size and mean asymmetry across all populations was a negative -0.50 in males and -0.34 in females. Therefore, we present results using the most simple index for FA, which is the absolute value of the right-minus-left measurement (R-L; reviewed in Palmer and Strobeck, 1986). In addition, a second index of FA, variance R-L (FA4 of Palmer and Strobeck, 1986) was calculated in all populations. This index is less sensitive to directional asymmetry (Palmer and Strobeck, 1986). Antisymmetry and directional asymmetry (Palmer and Strobeck, 1986; Van Valen, 1962) were tested for by examining the distribution of signed right-minus-left values (Leary and Allendorf, 1989) in each population and over all populations combined.

Relation between genetic diversity and asymmetry

Population level

A linear regression was performed between mean observed heterozygosity and mean FA calculated for the two sexes pooled weighed by their frequency, and between mean heterozygosity and the percentage of individuals within each population that were asymmetrical (i.e., had R-L values different than zero). Regression was also performed following an arcsine square root transformation for the percentage of symmetrical individuals and for heterozygosity. In these calculations, all individuals

for which either FA or genetic diversity estimates were available were included (n=252).

Individual level

Regression between the proportion of the loci analyzed in which the individual was heterozygous and the asymmetry estimate (absolute R-L) for the same individual was obtained. This association was only examined in individuals for which both estimates were available (n=247). This regression was also calculated following an arcsine transformation for the percentage of heterozygous loci for each individual. In addition, within each of the 11 study populations separately, association between the proportion of heterozygous loci and the absolute R-L value was calculated.

Results

Measurement repeatability

A similar measurement was retrieved in 19 of the 20 repeated measurements. The correlation between the two repeated measurements was 0.99 ($P < 0.00001$). Correlation for the absolute R-L estimate of each individual was 0.82 ($P < 0.004$). A mixed-model ANOVA with factors Individual (I), Side (S) and Replicate (R) retrieved an $F_{9,18} = 8.056$ ($P < 0.0001$) suggesting high repeatability for this trait.

Population level

Mean observed heterozygosity (H) was not associated with mean asymmetry when tested across all 11 study populations (Table 1). Similar trends were found in males and females. Therefore, in order to enlarge sample sizes, the two sexes were pooled for further analyses. R square was low and was not significant ($r^2 = 0.046$, $p = 0.52$; Fig. 2a), Spearman Rho was 0.025, $p = 0.7$. In addition, the regression between mean H and the percentage of symmetrical individuals was not significant

and showed an r^2 of 0.074 ($p=0.42$). These relationships were maintained after an arcsine transformation of the data ($r^2=0.056$, $p=0.49$ for H vs. mean FA and $r^2=0.083$, $p=0.39$ for H vs. the percentage of symmetrical individuals). Regression between mean expected heterozygosity and mean FA was not significant and showed similar trends to those revealed between mean observed H and mean FA ($r^2 = 0.18$, $p=0.19$, Spearman Rho was 0.36; $p=0.28$). This was maintained after an arcsine transformation of heterozygosity means.

Individual level

At the individual level, again, a non-significant and very low correlation was found between the proportion of heterozygous loci in each individual and its R-L value showing a non-significant r^2 of 0.0029, $p=0.40$ and a Spearman Rho of 0.0055, $p= 0.93$. Similarly, this regression did not show significant deviation from a slope of zero after an arcsine transformation of the data ($r^2=0.004$, $p=0.32$). A non-significant low r^2 value was resolved when each population was analyzed separately. The association between the proportion of heterozygous loci in an individual and its R-L value showed in all 11 study populations an r square lower than 0.1 and p value higher than 0.1.

Trends across the chukar range

At the population level, the relationship between H and mean FA showed inconsistent trends for different parts of the range (core to ecotone (Fig. 2b) vs. ecotone to periphery (Fig. 2c)). Plotted for the part of the range from the core to the ecotone (8 populations), without including the arid peripheral populations, a non-significant positive relation between H and mean FA appeared, with a Pearson correlation coefficient of 0.476 ($r^2=0.226$, $p=0.234$). For the part of the range from the ecotone to the periphery (6 populations) Pearson correlation coefficient was a negative -0.732 ($r^2=0.536$, $p=0.098$).

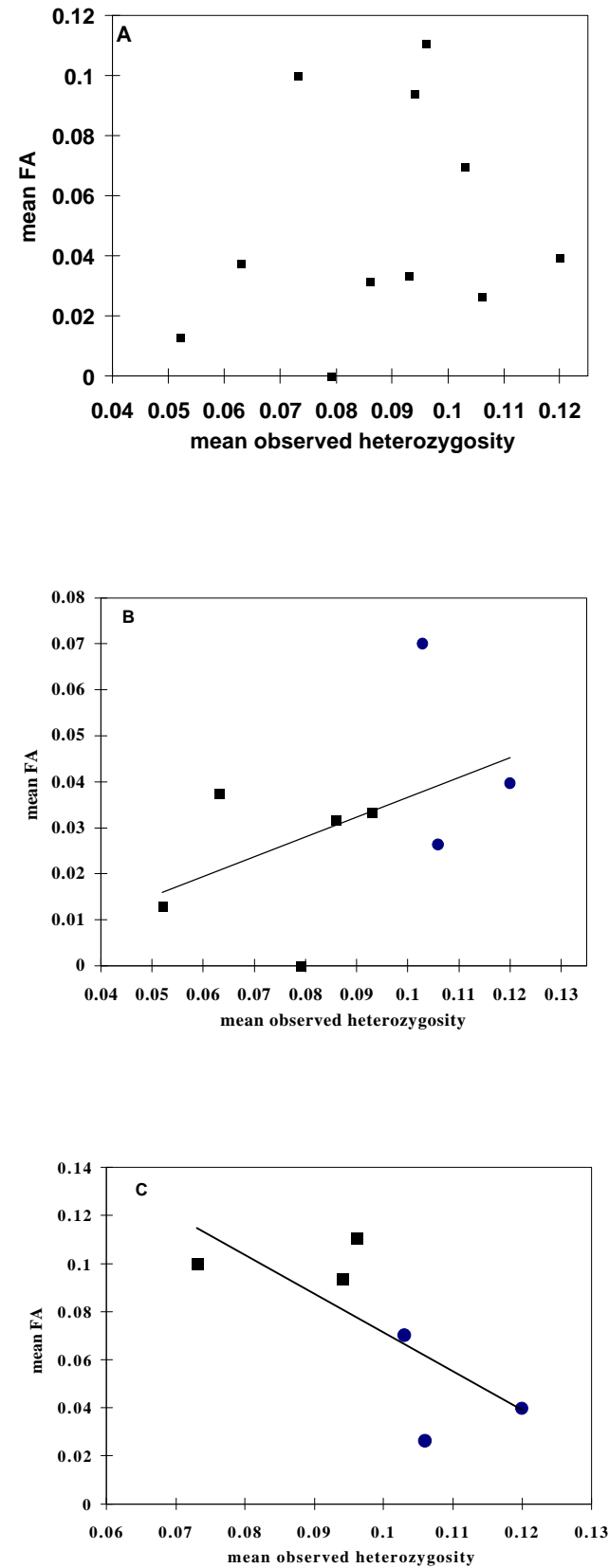


Figure 2. Relation between mean observed heterozygosity (H) and mean fluctuating asymmetry (FA) in 11 study populations across the chukar partridge range in Israel from core through ecotone to periphery (A); core (squares) and ecotone (circles) only (B); ecotone (circles) and periphery (squares) only (C).

Mean observed heterozygosity showed a unimodal pattern across the range. Diversity peaked at the Mediterranean-desert ecotone, and decreased monotonously towards the core and non-monotonously towards the extreme periphery of the chukar range, as seen in Fig. 3. Populations sampled at the ecotone had the highest diversity levels compared to all other populations studied across the range in Israel, from core to periphery. Asymmetry, as estimated by both mean absolute R-L and variance R-L, increased from core to periphery with a leap at the ecotone (Fig. 3). Equivalently, the percentage of symmetrical individuals in the population decreased towards the periphery (Table 1).

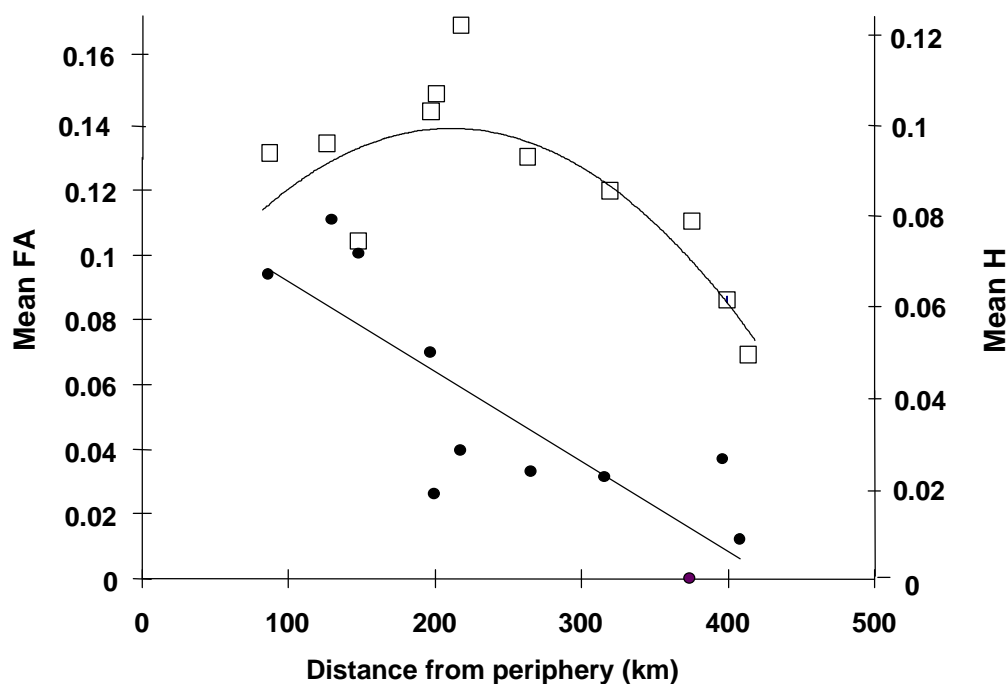


Figure 3. Trends in mean observed heterozygosity (squares) and in mean fluctuating asymmetry (circles) vs. distance from chukar range periphery in Israel given in km. A linear regression mean least squares line is fitted to the fluctuating asymmetry vs. distance plot and a quadratic regression to the heterozygosity vs. distance plot.

Distribution of signed R-L values showed a unimodal pattern, with a median and mode of zero in all populations pooled, yet was not normally distributed (both sexes separated and pooled) using the Shapiro-Wilk W test (JMP 3.1.5). The deviation from normality was mainly due to left skewness of the distribution, pointing towards a directional asymmetry component. A shift in the distribution and asymmetry pattern was observed across the range, from core to periphery (Kark S., submitted for publication). As the degree of asymmetry increased from core to periphery, a trend of dirasymmetry (with negative R-L) appeared. Yet together with this increasing expression of the directional component, the fluctuating asymmetry component, as reflected in the levels of variance R-L (sexes pooled), an estimate less affected by DA, also increased across the gradient from core through ecotone towards the chukar range periphery (S. Kark et al, ms submitted for publication; see [Chapter 6](#)).

Discussion

Genetic diversity, as estimated by observed and expected heterozygosity based on 9 polymorphic loci of 26 loci analyzed, was not associated with asymmetry at either the individual nor population levels when tested along a steep gradient across the chukar range in Israel from core to periphery. Moreover, this trend was consistent when tested within each population separately from core to periphery and for all populations across the range combined. These results do not support the “heterozygosity theory”. Different spatial patterns were revealed in each of these two variables, FA and H, across the chukar range in Israel. While mean observed heterozygosity showed a hump-shaped pattern along the range from core to periphery, peaking at the Mediterranean-desert ecotone, asymmetry, as estimated by both mean absolute R-L and variance R-L, increased monotonously from the core towards the periphery with a rather abrupt step at the ecotone (see Fig. 3). The two most geographically proximate populations in the sample, located only several km away from each other and originating from the northern Negev, where the sharp transition between Mediterranean and desert ecosystems occurs, showed a steep decline in the

percent of symmetric individuals in the population from 79% in Yatir, where mean annual rainfall reaches ~300 mm to 33% in Hirbet Sira (with ~200 mm; see Figs. 1 and 2). Yet the two had a rather similar genetic structure and diversity levels (Table 1, Kark, unpublished data; see [Chapter 4](#)).

If we were to sample only part of the distribution range studied, e.g. from the core towards the ecotone only, or alternatively from the ecotone towards the periphery exclusively, we may have concluded that a positive or no clear relationship exists between heterozygosity and asymmetry for the prior and a negative for the latter part of the range (see Fig. 2b,c). Thus sampling of only one of these two parts of the range may have possibly led to different conclusions for the species in Israel. Siikämäki and Lammi (1998) have found that asymmetry in the flowers of an annual plant species (*Lychnis viscaria*) in Finland was higher in marginal populations compared with core populations, which had higher levels of heterozygosity. Thus a significant correlation was shown between allozyme diversity and FA. When controlled for population size in a partial correlation analysis, the association between expected heterozygosity and FA remained significant. Yet when the plants were grown in a common-garden conditions rather than their original environment, the differences in FA between margin and core and the association between asymmetry and FA both disappeared, suggesting that environmental factors are mainly responsible for the difference in asymmetry levels between marginal and core populations (Siikämäki and Lammi, 1998). The authors suggest that due to interactions between genetic and environmental stresses, the effect of genetic variability on FA is apparent only when some other environmental stress is acting. We suggest that there may be various factors, including population size, which are affecting both symmetry and genetic diversity, yet do not necessarily lead to a direct and causal relationship between the two, where higher levels of heterozygosity predict higher developmental stability, as reflected in high symmetry.

Although empirical evidence for correlation between asymmetry levels of different traits of a single individual level appears to be inconsistent, at the population level increasing evidence suggests that FA levels are correlated among different traits

(Clarke, 1998, but see Hartl et al., 1995). Thus trends observed across populations at a specific trait may somewhat reflect trends in other traits, yet this should be further studied. The trait we examined, third toe length, is related with locomotion, highly important for this phasianid species that spends much of its time walking (Alkon, 1974). Thus, it seems reasonable to suggest that this is an adaptive trait under selection pressures (Boag and van Noordwijk, 1987).

FA and other types of asymmetry are proving as strong tools in evaluating the environments as confronted by individuals and should be further tested for applicability to wider conservation biology needs (Leary and Allendorf, 1989; Sarre et al., 1994). Yet, even within a single species range and across relatively short distances, there may be different relations between asymmetry and levels of genetic diversity, and specifically heterozygosity within populations. In the chukar case, partial sampling of the range, as mentioned, may have revealed completely different trends for the different sections studied. Although in both cases the correlation between asymmetry and heterozygosity was not statistically significant, the direction of the correlation was opposite. Pearson correlation coefficient for the part from the core to the ecotone was positive ($p=0.234$), while for the part of the range from the ecotone to the periphery r was negative ($p=0.098$). A different picture is revealed in a more continuous and detailed sampling of the range.

Mulvey et al. (1994) studied asymmetry levels and fitness in relation to heterozygosity classes in *Gambusia holdobrooki* reared at normal vs. hot and stressful temperatures. They showed that a strong and significant correlation between FA and heterozygosity occurred only under stressful conditions. In the non-stressful environment this relationship, though negative, was weak and non-significant. Thus performance differences among genotypes may occur only under environmentally stressful conditions (see Mulvey et al., 1994 and references therein). Based on these lines, one causal explanation for the different findings of this work may be that a negative relationship between genetic diversity and asymmetry is apparent only under more stressful conditions in peripheral parts of the range and disappears (or flips) under more favorable conditions. Thus symmetry increases with diversity only under

a certain threshold of stress. Another explanation may be that factors affecting both heterozygosity levels and developmental stability in similar directions, such as genetic drift, are dominant near the periphery where abiotic factors may be stronger (Kark, 1999). These factors may be less important further away from the range boundaries where biotic factors may be more important (Brown et al., 1996; Kark, 1999). The difference in the relationships between asymmetry and heterozygosity in the different parts of the range may also be related to the fact that directional asymmetry is expressed in an increasing fashion as we approach the chukar range periphery. The directional asymmetry component may be related to levels of heterozygosity in a different way and may thus show a different trend when compared with the populations where it is not expressed. Yet increasing evidence suggests that both directional asymmetry and antisymmetry, in addition to fluctuating asymmetry, often reflect severe developmental instability (Graham et al., 1998; Graham et al., 1993; Møller and Swaddle, 1997) and that all three asymmetry forms can arise from non-linear processes of development (Graham et al., 1993). Yet a more detailed analysis of the data suggests that even within each of the populations studied there is no significant correlation between allozyme diversity and asymmetry levels. It may well be that different factors are shaping the spatial trends of genetic diversity as estimated by allozyme heterozygosity and of fluctuating asymmetry.

Detailed planning of sampling across a species range with emphasis on the distribution patterns and the ecology of the study species are crucial in revealing real patterns and relations among genetic diversity and asymmetry. This is especially important if we aim to derive recommendations for conservation planning and management of the species based on scientific knowledge. We suggest that detailed sampling of the range, which includes a more complete and continuous gradient, from the very extreme peripheral populations through the ecotone to populations at the core, can reveal spatial patterns along the range and lead to a better understanding of the relationships between different factors studied.

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