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Conservation Genetics: genetic diversity as a goal and a tool in conservation biology

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How is genomics changing conservation biology?

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Thanks to the rapidly increasing efficiency of DNA sequencing, large-scale genomic analyses are now frequently used in hopes of advancing biodiversity conservation. Genomic analyses are advancing several lines of research relevant to conservation, including studies of genetic variation and population structure, demographic history, inbreeding (and inbreeding depression), hybridization (and outbreeding depression), and identifying loci involved with adaptation and phenotypic variation. While genomics clearly has the potential to advance conservation, it remains unclear and controversial when and to what extent genomic analyses can advance conservation substantially more than traditional, smaller-scale genetic approaches. I will discuss the promise and potential pitfalls of conservation genomics, with a focus on identifying conservation problems that are most likely to benefit greatly from large-scale genomic analysis.

Genetic diversity of edge populations: a case study of the eastern spadefoot toad in Israel

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The maintenance of genetic variation within populations and species is a primary concern in conservation biology. Understanding the patterns and processes that shape population genetic structure across the geographical ranges of species is essential in conserving genetic diversity. This field of study is especially important in the face of global climate change, which is expected to cause changes in species distribution range. Populations at the geographic periphery are likely to be most affected by climate change, therefore the genetic structure and diversity of edge populations are the focus of many recent studies. The Coastal Plain of Israel is the southernmost range limit of the eastern spadefoot toad (*Pelobates syriacus*). In a previous study, Munwes et al. (2010) showed that edge populations of *P. syriacus* had greater genetic diversity than core populations. In the present study we further investigate the genetic structure of *P. syriacus* in Israel. We postulate that greater variability in climatic conditions at the edge relative to the core causes fluctuation in selection intensity and trajectory between successive years. Such fluctuating selection could promote an increase in genetic variability at edge population. We collected DNA samples from tadpoles in 24 vernal pools known as breeding sites for *Pelobates syriacus*. Two types of genetic markers were used: eight microsatellite markers, and a 495bp sequence from the mtDNA D-loop. The mtDNA results show gradual decrease in variability from edge to core, the microsatellite results, however, did not show a similar trend. Although allelic richness was similar in edge and core, we did find gradient in allele size from core to edge; alleles in the edge were significantly longer than at the core. Longer microsatellite alleles are prone to higher instability (Legendre et al. 2007), this higher instability can potentially lead to phenotypic diversity, which can give an adaptive advantage to the edge populations. Contrary to our predictions we did not find a clear gradient in the genetic diversity from core to edge in the microsatellites. Nonetheless, the gradients in mtDNA haplotype diversity and in microsatellites allele size can imply that the genetic structure in the edge population is influenced by the fluctuating climatic conditions.

Combining classical population genetics and network analyses for detecting levels of connectivity in a population of *Acacia tortilis*

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Genetic diversity and structure of populations at the edge of the species' spatial distribution are important for potential adaptation to environmental changes and consequently, for the long-term survival of the species. Here, we combined classical population genetic methods with newly developed network analyses to gain complementary insights into the genetic structure and diversity of *Acacia tortilis*, a keystone desert tree, at the northern edge of its global distribution, where the population is under threat from climatic, ecological, and anthropogenic changes. We sampled *A. tortilis* from 14 sites along the Dead Sea region and the Arava Valley in Israel and in Jordan. In addition, we obtained samples from Egypt and Sudan, the hypothesized origin of the species. Samples from all sites were genotyped using six polymorphic microsatellite loci.

A significant genetic structure in *A. tortilis* along the Arava Valley was detected at different hierarchical levels—from the basic unit of the subpopulation, corresponding to groups of trees within ephemeral rivers (wadis), to groups of subpopulations (communities) that are genetically connected relative to others. The latter structure mostly corresponds to the partition of the major drainage basins in the area. Network analyses, combined with classical methods, allowed for the identification of central *A. tortilis* subpopulations in this region, characterized by their relatively high level of genetic diversity and importance in maintaining gene flow in the population. Characterizing central subpopulations may enable conservation managers to focus their efforts on certain subpopulations that might be particularly important for the population's long-term persistence, thus contributing to species conservation within its peripheral range.

Local adaptations in highly connected populations of the Dead Sea Sparrow (*Passer moabiticus*) in Israel

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Populations found at the edge of a species range often display decreased genetic diversity, which together with high gene flow may reduce the ability of populations to adapt to local environmental conditions. The Israeli population of the Dead Sea Sparrow (*Passer moabiticus*), a passerine currently known to occur in a highly disjointed range, is considered peripheral and fragmented, but a recent range expansion has been documented. During peripheral population growth, adaptation depends on whether evolutionary processes (e.g., selection or phenotypic plasticity) can facilitate the prevalence of adaptive traits in the population. In order to elucidate the status of the Israeli population of the Dead Sea Sparrow, in light of the evidence of its recent range expansion, we aimed to describe the genetic and morphological variation of the Israeli populations, and to determine the gene flow between them. We hypothesized that Dead Sea Sparrow populations will show no significant morphological adaptations to local environmental conditions because of a small latitudinal gradient and the recent range expansion. In addition, we expected a high level of gene flow among them. We found evidence of gene flow suggesting high connectivity with no evidence of a recent range expansion, possibly due to insufficient time since expansion. Conversely, latitudinal variation in wing length (male and female) and weight (male) was indicative of local adaptation, in accordance with Bergmann's. This study provides evidence of local adaptation in a small geographic extent despite the presence of gene flow. In a rapidly changing environment, if the rate of environmental change outcompetes the extent of available genetic variation, including that which is introduced by migration, then local adaptation can be impeded. Our results indicate that this phenotypic differentiation may be maintained either via adaptive selection despite gene flow or as a result of phenotypic plasticity, yet further monitoring is required in the face of rapid environmental changes.

Estimating effective population size of the Asiatic wild ass: from theory to decision making

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Effective population size (N_e) is a fundamental evolutionary concept that is highly relevant to conservation biology. N_e is a measure of the strength of genetic drift a population is subject to and can be evaluated in two ways: (1) empirically-estimated from genetic data collected from the population, and (2) theoretically-predicted from demographic, life-history and mating-system data and hypotheses. By comparing the consistency of the empirical estimation based on genetic sampling and the theoretical predictions based on population characteristics, we can identify life history traits that have strong impacts on genetic drift. Such information can assist managers in designing strategies aimed at increasing N_e. We demonstrate this approach with a long-term study of a reintroduced Asiatic wild ass (*Equus hemionus*) population in Israel, which is currently estimated at 300 individuals. We conducted genetic, demographic, and ecological surveys of the wild ass population and evaluated variance effective size (N_{ev}). By contrasting the genetic estimation of N_{ev} with theoretical predictions we revealed that polygyny had the strongest impact on genetic drift: Only when strong polygyny (10-20% mating males per generation) was considered, were the predictions consistent with the genetically-estimated N_{ev}. Strong heritability of female reproductive success ($h_f^2 = 0.91$) was detected within the wild ass population and was also found to strongly affect drift in the system. The low N_{ev} in the wild ass population ($N_{ev} = 24.3$) is of concern. We therefore suggest management actions that will focus on the main factor identified as affecting N_{ev}, namely, increase the number of males contributing to the gene pool. Adding artificial water sources in the wild ass range of distribution will likely increase the number of available territories for dominant males, who are the breeding males, thus, increasing N_{ev}. This approach of contrasting theoretical expectations with empirical genetic estimates to evaluate life-history traits that impact N_e is a general, applicable strategy that can be used for species conservation and management.

Conservation Genetics and Genomics of the fire salamander, *Salamandra infraimmaculata*

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Salamandra infraimmaculata is considered a threatened species in Israel. However, since studying *Salamandra*, we have found in the past 10 years, many more breeding sites than were known previously. In addition, O. Rybak has found that *Salamandra* does well in urban habitats on Mount Carmel. *Salamandra infraimmaculata* has strong pond site fidelity that likely results in differential genetic structure among breeding sites. Strong pond site fidelity has been found by multiple researchers. An exception is that on Mount Carmel, we found dispersal as far as 1280 meters, which is likely to result in overlapping genetic structuring. During our first genetics study, in which 9 breeding sites in Mount Carmel and 11 sites in the Galilee were surveyed, and tissue samples were taken from 475 adults. Microsatellites were used for observing differences in genetic structure in a study that was performed in Prof. Juha Merilä's lab. In this study, we found that there were substantial genetic differences between Mount Carmel and the Galilee. Allelic richness was a lot higher in the Galilee than in Mount Carmel; 40 unique alleles were found in the Galilee and 0 in Mount Carmel. Unrooted neighbor joining tree diagrams resulted in pure separations between Mount Carmel and the Galilee. Structure analysis showed strong differences between the Galilee and Mount Carmel.

A second microsatellite study was conducted and was conducted in Finland. The goal was to consider genetic diversity in peripheral populations compared to populations closer to the core. We collected 692 tissue samples from adult and juvenile fire salamanders from 33 breeding sites (13 from Upper Galilee, 10 from Lower Galilee, 9 from Mount Carmel and 1 from Tel Dan). This study also considered vegetation types, and meteorological aspects such as elevation, average temperature and precipitation. Maximum entropy analysis was also used to score major regions. The Lower Galilee had the lowest stability values of the three regions. Allelic richness increased with maximum entropy scores in the Upper Galilee. Allelic richness also increased with latitude.

A BAPS analysis also demonstrated that Mt Carmel and the Upper Galilee were homogeneous genetically while the Lower Galilee contained genetically differentiated populations.

Lastly, we did transcriptomics/gene expression on fire salamander larvae. We insisted that *Salamandra* tailfins (which do not cause damage to the *Salamandra* larvae) can demonstrate gene expression as opposed to using the whole body. We found that *Salamandra* larvae turns darker when exposed to ultra violet radiation, and they turn darker with increased density. We are currently conducting gene expression studies on *Salamandra* larval development, oxygen ranges, color change, and temperature change.

Cryptic Invaders from the Red Sea: The Dusky Shark in the Mediterranean

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Since the opening of the Suez Canal in 1869, many marine species have passed through from the Red Sea to the Mediterranean. This extensive phenomenon, known as Lessepsian migration, has so far resulted in the migration of over 400 species into the Levant Basin. Unlike other closely monitored marine megafauna such as marine mammals and sea turtles, little is known about shark populations in Israel. The dusky shark (*Carcharhinus obscurus*) is rarely found in most parts of the Mediterranean but is surprisingly common in Israel. Previous work on the dusky shark found the Indo-Pacific population to be genetically separated from the Atlantic one. We collected tissue samples of sharks caught by fishermen off the Israel Mediterranean coast. DNA was extracted and the mitochondrial control region (D-Loop) was sequenced. Results show that samples consisted of haplotypes from both the Atlantic and Indo-Pacific oceans, indicating that Lessepsian migration of the dusky shark has occurred. Albeit rare, the dusky shark is indigenous in the Mediterranean, thus the usual definition of invasion does not apply. We address it as cryptic invasion, a term used for the phenomenon of individuals entering an existing population of the same species from a different biogeographic region. Identifying cryptic invasions is especially important in highly invaded regions such as the Mediterranean Sea, and presents an especially difficult challenge in protecting the species while eradicating invaders and protecting the genetic diversity.

Historical and recent reductions in genetic variation of the *Sarotherodon galilaeus* population in the Sea of Galilee

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The Sea of Galilee has great significance as both a natural habitat and a freshwater source for Israel. Natural changes and anthropogenic impacts have been placing significant pressure on fish communities inhabiting this lake. *Sarotherodon galilaeus* (St. Peter's fish) is an omnivorous fish species with a relatively large population in the lake and with significance for commercial fishing. An alarming decline in annual catch towards 2008 suggested that this unique population might be at risk. With that in mind, we characterized the current genetic variation of this species in Israel with reference to fish from Ghana based on D-loop and microsatellite markers. Genetic variation and differentiation were found mostly among fish from Ghanaian localities and between fish of both countries, whereas fish from all Israeli localities had limited and uniform genetic variation, a signature compatible with historical founder effect followed by local adaptations. Such historical processes could make a population vulnerable and indeed, this was recently reflected in the sudden decline in catch and population size. Comparing genetic variation between archived 30 year-old scales and modern lake fish revealed further reduction in genetic variation coincident with the recent population decline. Thus, a recently occurring genetic bottleneck had placed this unique and isolated population at even higher risk. We carefully discuss the events leading to the current risk status for *S. galilaeus* in Israel and highlight the need for careful monitoring and active management to support a more sustainable future for this and other fish communities in this important habitat.

The mixed genetic origin of Israeli wild boars

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European wild boars (*Sus scrofa*) have had a complex history, which combines post-glacial migrations, local extinctions, introgressions with domestic pigs and translocations. Molecular data have shown that European and Near East boars have different genetic signatures. Interestingly, previous studies have shown that, unlike other Near East populations, extant Israeli boars harbor the European mitochondrial signature. Ancient DNA studies based on mitochondrial control region sequences suggest that human translocations are responsible of the genetic pattern observed in Israel. Indeed, boars/pigs from the Late Bronze Age (until ca. 1150 BCE) in Israel shared haplotypes of modern and ancient Near Eastern boars. European haplotypes became dominant only during the Iron Age (ca. 900 BCE). To better understand the genetic background of Israeli boars and complete previous studies based on control regions, we used Genome-wide SNPs to investigate the nuclear background of ten boar specimens from three populations (Northern Israel, HaSharon, and the Dead Sea). We also sequenced the complete mitochondrial genomes of three individuals, each from a different population. Our results surprisingly show that the nuclear genome of the Israeli boars has a Near Eastern ancestry while the mitochondrial sequence is clearly of European origin. The similarity of the mitochondrial sequence with sequences of a domesticated strain suggests a recent event of mitochondrial introgression. Analyses of both nuclear and mitochondrial data indicate very low levels of genetic variation among Israeli boar populations, in agreement with the view that the Israeli boars went through a severe bottleneck in the 30's. While it has been considered that recent human activities had a limited effect on the wild boar genetic structure, our results indicate that this is not the case in Israel and that phylogeography interpretations based on mitochondrial sequence only should be taken with caution.

Population genetic analysis of the recently rediscovered Hula painted frog (*Latonia nigriventer*) reveals high genetic diversity and low inbreeding

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Since its recent rediscovery in November 2011, the rare Hula painted frog (*Latonia nigriventer*) has remained one of the least understood amphibians worldwide. The low abundance of this species that occupies a highly disturbed habitat is worrying and calls for urgent conservation efforts. However, efficient, long-term management of marginal populations that experienced bottleneck events may require specific measures to prevent the loss of genetic diversity, particularly if the populations are endemic to restricted geographic ranges. We analysed 18 newly developed microsatellite loci in a total of 125 individuals from the only known viable population of Hula painted frogs to examine this population's genetic diversity, genetic structuring as well as investigated the relatedness among individuals. We further combined genetic and capture-recapture data to estimate both the effective population size for this species as well as the number of potentially reproducing adults. Even though both effective population size estimates (~16.6–35.8) as well as estimates of potentially reproducing adults (~236–244) in this population appeared to be very low, we found the population to have yet maintained comparatively high allelic richness (5–12), high genetic diversity ($H_o = 0.771$), and a significantly negative inbreeding coefficient ($F_I = -0.018$). Further population structural analyses revealed strong evidence that these individuals belonged to two genetically different clusters. Given our results, we strongly advocate that apart from habitat restoration, preservation and extension, future studies should urgently focus on detecting possible hidden populations of the Hula painted frog.

Genetic rescue in space: inbreeding depression, ecological fit and the *Iris*

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Genetic rescue is a method to overcome reduced genetic diversity in small and isolated populations. It applies to endangered plant species suffering from fragmentation and reduced gene flow, and requires assisted migration to increase genetic diversity. Despite the appeal of such a simple solution, genetic rescue may risk endangered species if the source of imported genotypes is genetically similar and may cause inbreeding depression. Likewise, genetically distant sources from different ecological backgrounds may create maladapted offspring due to outbreeding. An optimal crossing distance (OCD) was proposed as a compromise between inbreeding and outbreeding depression, where fitness of hybrids between populations is theoretically the highest. We used the endangered *Iris atropurpurea*, an Israeli coastal endemic plant species, to test for the applicability of OCD along an environmental gradient in multiple populations. Plants in Netanya site were pollinated with pollen from populations across the whole distribution of *I. atropurpurea*, and fitness was measured as fruit-set, seed-set, seed viability and offspring survival in the maternal site. We found that while ecological distance between sites had the strongest effect on fruit and seed-sets, suggesting intrinsic outbreeding depression, offspring survival suggest lack of extrinsic outbreeding depression and hint for inbreeding depression. These results suggest that genetic rescue is not as straightforward as it may seem and that for efficient conservation practice the genetic relatedness among populations must be studied, alongside ecological divergence and the extent of local adaptation.

From gene pools to oceans – genetics in the service of conservation of commercially exploited sea urchin species

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Accurate assessment of species diversity is essential to nearly all areas of biology: studies of biodiversity, ecology, policy-making, and conservation all necessitate correct species identification. In particular, identifying cryptic species has far reaching implications on conservation efforts, as threatened endemics may be driven to extinction if left unnoticed. Members of the genus *Tripneustes* are some of the most abundant and ecologically significant tropical echinoids. Highly valued for their gonads, wild populations of *Tripneustes* are commercially exploited for the production of sea urchin roe (gonads) and cultivated stocks are a prime target for the fisheries and aquaculture industry. In addition, cultivated *Tripneustes* are also used as a biological agent to control the growth of alien invasive algae. Over-exploitation of local stocks, escape of urchins from aquacultures, and massive introductions of *Tripneustes* reared in urchin hatcheries to replenish stocks or control algae were considered unproblematic so-far. Novel discovery that *Tripneustes gratilla* is a complex of cryptic species and, in addition, contains highly localized endemic species at the edges of their presumed ranges, calls for a reassessment of protection status and implementation of conservation efforts. Unrecognized endemics within commercially exploited species are at risk of extinction since replenishment of stocks by re-settlement of larvae from other regions is impossible. Anthropogenic re-stocking by individuals harvested in other areas or reared in hatcheries may unwittingly introduce alien species putting further stress on local populations. Here we present results from studies over the past three years to demonstrate the advantages of utilising molecular genetic tools to identify cryptic species and illustrate the importance of such findings for conservation efforts in the oceans.

Restoration Conservation and Characterization of Lost Genetic Diversity of Wheat Landraces to improve crop adaptability and sustainability

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Wheat landraces cultivated in the Fertile Crescent since their domestication thousands of years ago contained considerable genetic diversity in adaptive and agronomically important traits. Although there is a worldwide awareness of the major role of landraces in preserving crop diversity, landraces across all crops are exposed to genetic erosion and extinction due to modernization processes. Wheat landraces in Israel are one extreme example. In the late 19th century, there were hundreds of traditional wheat landraces in Israel. Since the beginning of the 20th century, the genetic diversity of wheat has been sharply eroded by the continual selection for high and stable yields. As a result, the genetically diverse Israeli landraces wheat lines were replaced by a small number of elite “semi-dwarf” cultivars suitable for high-input agrotechnical management and suitability for industrial-based mass food production. While many Israeli wheat landraces have been lost and have become extinct, some representative varieties were sampled and collected at the beginning of the 20th century and were held in Gene Banks and private collections worldwide. The Israel Palestine Landrace (IPLR) Wheat project was initiated to restore, conserve, and study Israel’s traditional Wheat germplasm. Within the project, more than 1000 wheat “accessions” from Israel and Palestine were brought back and restored in the Israeli Gene Bank (IGB). The IPLR is a multi-disciplinary platform which brings together traditional knowledge, historical genetic resources, cutting-edge science, and modern agro-ecological management to increase biodiversity, ecological sustainability, and food security. Our aim is to identify unique varieties and alleles for agronomic and quality traits for research cultivation and breeding. All lines were genotyped based on 84 SNP markers distributed evenly across the wheat A and B genomes. SNP and phenotypic data shows high genetic diversity in the IPLR collection compared to modern cultivars, supporting the high potential of this germplasm. A “core collection” of 96 durum lines was constructed and is currently genotyped using the iSelect 90K bead chip array which will enable comparisons of the diversity of the collection and other regional collections. The IPLR collection will be used for long

term *ex situ* conservation in the IGB. In addition, sub-set samples of landraces were distributed to more than 150 *in situ* sites (botanical gardens, schools and community-based gardens) this season and will contribute greatly in conserving the heterogeneous nature of the different landraces.

Wildlife forensic genetics in Israel: implications on wildlife conservation

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Israel is a biodiversity hotspot. Although a small geographic area, it is a junction of continents representing species from various biogeographical regions, known also as one of the richest places with avian species. Unfortunately, many wildlife species are under threat due to anthropogenic effects and loss of open lands. Despite the fact that the wildlife protection law is extensively enforced in Israel, illegal hunting is one of the biggest threats to the local wildlife. With the aim of supporting conservation of Israeli wildlife, particularly endangered species, we established a genetic database for all wildlife, to be used in conservation genetic and wildlife forensic research. Recently, our focus has been integrating advanced genetic technologies as a wildlife forensic tool to determine new genetic markers, and simultaneously determining multiple known genetic markers. These approaches were addressed to two species often illegally killed in Israel, the mountain gazelle (*Gazella gazella*) and the Indian crested porcupine (*Hystrix indica*). The use of advanced technologies to enforce wildlife protection laws by The Nature and Parks Authority (INPA) has started an "arms race behavior" between poachers and INPA wildlife law enforcement unit. The genetic evidence contributes in the prosecution of crimes against wildlife and helps solve over 55% of the yearly cases. Winning the arms race is essential for the survival of endangered and endemic species in Israel, which are threatened primarily by the illegal hunting.

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