Department of Defense
Legacy Resource Management Program

05-112

Conserving Integral Units of Chihuahuan Desert Biodiversity:
High allelic richness and population divergence for an expressed nuclear gene in an imperiled fish

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February 2006

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Submitted to Department of Defense Legacy

February 2006

INTRODUCTION

The majority of conservation genetics studies rely on neutral markers to examine the population structure of imperiled species. Neutral, or unexpressed, markers may be more sensitive to changes in population structure; however, they do not necessarily indicate biologically relevant differences between populations. By using expressed markers, the effects of selection can be taken into account, something that is not possible with neutral markers.

Many of the conservation studies focusing on expressed genes draw conclusions based solely on mitochondrial genes. Mitochondrial genes are easier with which to work from a technical stand-point; however, they have two major disadvantages. The first disadvantage is that mitochondrial genes are haploid, reducing the amount of information gleaned from each individual sampled. The other major disadvantage is that the mitochondrial genome is maternally inherited, eliminating the contribution of males to genetic diversity. Ideally, conservation genetics studies would examine expressed nuclear genes.

One well-studied nuclear gene complex, the major histocompatibility complex (*Mhc*), is responsible for cellular and humoral antigen recognition in vertebrates. The complex is composed of 3 classes of genes, though most research has focused on the class I and class II genes. The class I *Mhc* genes allow for cellular antigen recognition. The class II *Mhc* genes are responsible for humoral response and are highly variable, with up to 30 loci in great reed warblers (although some may be pseudogenes; Westerdahl *et al.* 2000), and over 100 alleles in humans (Apple and Erlich 1996). Structurally, *Mhc* class II proteins are heterodimers; the alpha helix forming the backbone of the protein and the beta sheet forming a “trough” in the protein structure where antigens are bound (Madden 1995). The amino acids coded for by the DNA sequence in exon 2 of the *Mhc* class II β gene sequence determine which specific antigens can be recognized by the protein.

The high variability of *Mhc* class II β gene sequence is hypothesized to be maintained by balancing selection, where individuals with homozygous genotypes are theoretically at a selective disadvantage (Doherty and Zinkernagel 1975); with a limited range of unique antigens that can be recognized. Empirical evidence appears to support this hypothesis (*e.g.* Patterson *et al*. 1998, Hedrick *et al.* 2001, Schad *et al.* 2005, but see Potts *et al*. 1994), and environmental contaminants may further complicate the phenomenon (*e.g.* Cohen 2002). *Mhc* Class II β genes have been shown to be highly variable in teleost fish with as many as 17 loci in cichlids (*e.g.* Málaga-Trillo *et al*. 1998).

The extremely variable nature of *Mhc* class II β DNA sequence makes it an ideal marker, especially for organisms that display little genetic diversity at other markers; such as *Cyprinodon tularosa* Miller and Echelle (Cyprinodontidae), the White Sands pupfish. This New Mexico state-endangered fish has been shown to exhibit extremely low allozyme diversity (Stockwell and Mulvey 1998), and comparatively low diversity in microsatellite markers (Stockwell *et al.* 1998). Previous work on *C. tularosa* using unexpressed markers has shown that significant genetic differentiation exists between the two native populations (Salt Creek and Malpais Springs) located on the White Sands Missile Range in New Mexico (Stockwell *et al.* 1998). The two populations, which have been historically isolated, differ in parasite communities (Collyer and Stockwell 2004), suggesting that functional differences may have evolved in immunity-related genes.

Currently, we are examining variation in *Mhc* to determine whether such functional differences exist.

Materials and Methods

C. tularosa were collected from Salt Creek and Malpais Spring in 2003 by seining and minnow-trapping. DNA was extracted from the fin clips of 30 adults, as well as unfertilized eggs from 3 representative females, using DNeasy kits (Qiagen®) and stored at -20°C for later use.

Exon 2 of the *Mhc* class IIβ gene was initially amplified from egg DNA using the degenerate primers XIS and MRS of Cohen (2002). Amplification reactions were prepared using the following protocol: 10.825 µl double processed tissue culture water (Sigma), 2.5µl 10X PCR buffer (ABI), 2.5 µl 2mM dNTPs, 0.5 µl each 20mM primer, 0.175 µl AmpliTaq® Gold enzyme (ABI), and 8 µl template DNA. The initial amplifications followed the thermocycler protocol of Cohen (2002). PCR products were purified using Qiagen® QuickSpin™ kits as per manufacturer's specifications.

The following sequencing reaction was prepared using the purified DNA: 11.64 µl DNA, 0.64 µl 5mM primer, and 8 µl QuickStart (Beckman Coulter) and subjected to the manufacturer recommended thermocycler protocol. Subsequent ethanol precipitation of the DNA was performed as per manufacturer's instructions and DNA sequencing was performed on a CEQ 8000 (Beckman Coulter).

Sequence chromatograms were verified and sequences were manually aligned, as no gaps were present in the sequences. DNA sequences were trimmed to include only exon 2, in order to focus on expressed differences in gene sequence. DNA polymorphisms were evaluated in DNASP (ver. 4.0, Rozas and Rozas 1995). Species-specific primers were designed by hand, and putative primers were checked using Amplify (ver. 3.1.4, Engels 2005).

Two internal primers, CtINT457F (5'-CTCTGCAGGTAGGAGCGATAATCT-3') and CtINT511R (5'-ACCTCACAGCGATCTCTGATCTATC-3') were designed to remove part of the intron sequence, and to increase successful sequencing of the reverse strand, respectively. These primers were tested as above, with the following change: amplification was performed using the SALS2 protocol: 5 min denaturation at 94C, followed by 34 cycles of 1 min at 94C, 1 min at 55C, and 1 min at 72C, with a final elongation step of 10 min at 72C. Primers CtINT457F and CtINT511R were then used to amplify DNA from whole fish extractions for 30 individuals from each of the two *C. tularosa* populations as previously described, with the following change: 17.825 µl double processed tissue culture water (Sigma) and 1 µl DNA template were used in each reaction to maintain a final volume of 25 µl.

During screening of fin-clip DNA, a product that was 200 bases longer than expected was amplified from a single individual. Subsequent sequencing showed this product to be a second *Mhc* locus. Therefore, the locus 2-specific primer *Mhc*2aF (5'-CTCCTCTATGGTCCTCAGAGATCG-3') was designed, taking advantages of differences in the intron sequence of locus 1 and 2. This primer, in conjunction with the MRS primer (Cohen 2002), amplified a 400-base band from both *C. tularosa* and *C. variegatus*.

In order to verify putative heterozygotes, cloning was performed on 18 Malpais and 15 Salt Creek individuals using the PCR-Script Amp Cloning Kit (Stratagene) as per the manufacturer's instructions. After blue-white screening, clones containing plasmids with inserts were isolated and grown overnight at 37° C. Isolated clones were further screened for the appropriate insert by boiling a sample of each colony in 100µl double-processed tissue culture water (Sigma) for 15 minutes and centrifuging at 4000RPM for 10 min. Amplification reactions were prepared using 5 µl of the supernatant, 2.5 µl AmpliTaq Gold buffer, 1µl 5mM dNTPs, 0.5 µl each 20mM T7-pblue (5'-TACGACTCACTATAGGGCGAAT-3') and M17-pblue (5'-TCACACAGGAAACAGCTATGAC-3'), 0.175 µl Amplitaq Gold, and 15.325 µl double-processed tissue culture water (Sigma), and reactions were amplified using the SALS2 protocol. Three ml overnight cultures were grown at 37° C and plasmids were purified using QiaSpin Plasmid Minikits (Qiagen) as per manufacturer's instructions, for up to seven colonies from each individual that contained an insert of the appropriate length.

Purified plasmids were sequenced, using the following ingredients: 9.36µl double-processed tissue culture water (Sigma), 0.64 µl 5mM PCR primer, 2 µl purified plasmid, and 8 µl QTS quick start (Beckman Coulter) and were subjected to 40 cycles of PCR using the manufacturer's recommended conditions. DNA sequencing was performed as previously described. DNA sequences for clones were analyzed as previously described.

During the initial screening of clones, a third *Mhc* locus was discovered, differing significantly in exon sequence from locus 2. The locus 3-specific primers Ct*Mhc*3F (5'-GGTTCTGTTCTGGTTCTGTTTCTC-3') and CtMRS+2 (5'-

ACTCACCTGATTTATCCAGAGC-3') were designed and amplified on the SALS2 protocol as previously described.

In screening clones for locus 2, it became apparent that at least two loci were co-amplifying. To analyze the data, a chi-squared test was performed on the counts of shared alleles to determine whether allele occurrence differed between populations.

Results

No verifiable polymorphisms were found in the exon 2 sequence of *C. tularosa* for either locus 1 or locus 3; however, a significant amount of genetic diversity was found in locus 2. A total of 46 unique alleles were recovered; however, on some occasions more than two alleles were recovered multiple times from a single individual, suggesting that at least one additional locus exists that we were not able to separate from locus 2. At no time were more than four alleles recovered from a single individual, however, so it is likely that only two loci were co-amplified. Of the 46 unique alleles recovered from the 33 fish examined, with only 4 alleles found in both populations (Fig.1). Twenty alleles were private to the Salt Creek population and 22 private alleles were recovered from the Malpais Spring population. A chi-squared test of the four shared alleles revealed that significant differences exist between Malpais Spring and Salt Creek ($p < 0.002$).

Discussion

While four or more *Mhc* class IIβ loci have been found in more distantly related families of fish (Gasterosteidae, Reusch *et al*. 2001; Cichlidae, Málaga-Trillo *et al*. 1998; Cyprinidae, Sultmann *et al*. 2000), only one or two loci have been reported in the studied fishes most closely related to *C. tularosa* (Poecilidae, Roney *et al*. 2004; Fundulidae, Cohen 2002). Here we report the presence of at least three or four loci in *Cyprinidon tularosa*.

Previous work on *C. tularosa* has shown that little genetic variation exists for allozyme markers and that there is comparatively little diversity in microsatellite markers. In contrast, the species shows a high level of diversity in the exon 2 sequence for this important expressed gene. The allelic richness discovered when surveying locus 2 is more than half that of the combined richness for the 14 microsatellite markers previously studied.

Both of the natural populations, Salt Creek and Malpais Spring, had high levels of allelic diversity, with large numbers of private alleles occurring at low frequency in each population. The highly significant difference in allele occurrence, conservatively determined only from shared alleles (Fig. 2), further supports the ESU designations of Stockwell *et al*. (1998). The two populations differ ecologically in a number of attributes, including parasite communities (Collyer and Stockwell 2004), which may contribute to the differences seen in this important immune system gene.

The high level of genetic diversity seen in *C. tularosa* is consistent with expectations based on other fish species (Table 1), that range from 13 DNA sequence alleles (Málaga-Trillo *et al*. 1998) to 41 alleles at the amino acid-level (Cohen 2002). Regardless of whether genetic diversity is parasite-driven (Hedrick *et al*. 2001), or being maintained by mate selection (Potts *et al*. 1994), it is clear that the importance of studying expressed nuclear genes in imperiled species cannot be overstated.

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Acknowledgements

The authors would also like to thank Robert Myers (Environmental Stewardship, Environmental Division in the Directorate of Public Works, WSMR), for arrangement of range visitation. Janice Terfehr assisted with collecting fish. This research was funded by DoD Legacy Resource Program (no. DACA87-00-H-0014) administered by H. Reiser and J. Dye, (CES/CEV, Holloman AFB) to CAS. Pupfish were collected on White Sands Missile Range under New Mexico State collecting permit 2887. This paper was approved for public release by White Sands Missile Range, distribution unlimited.

Figure 1

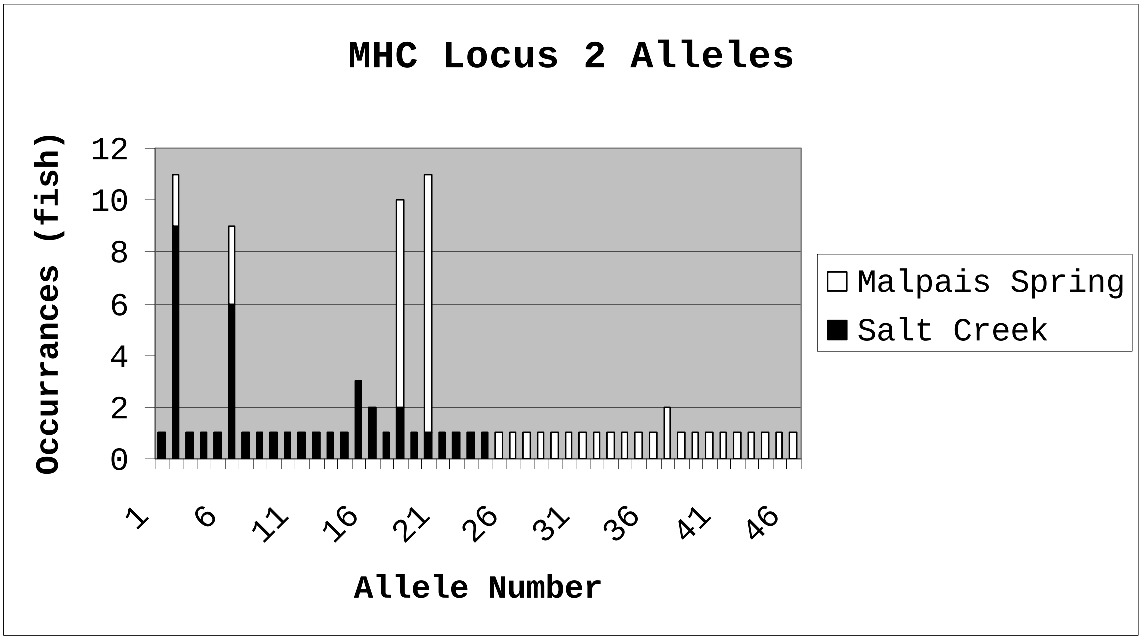
MHC Locus 2 Alleles
Occurrances (fish)
0
2
4
6
8
10
12
1
6
11
16
21
26
31
36
41
46
Allele Number
☐ Malpais Spring
■ Salt Creek

Figure 2

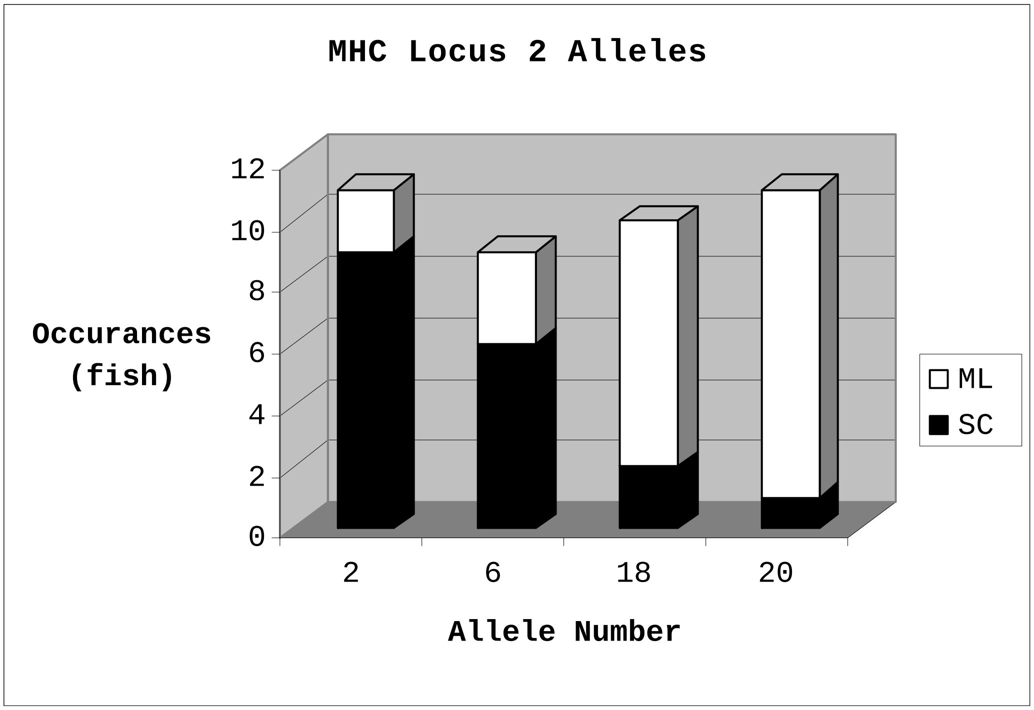
MHC Locus 2 Alleles
Occurances (fish)
0
2
4
6
8
10
12
2
6
18
20
Allele Number
☐ ML
■ SC

Table 1

Table 1. Allelic richness of *Mhc* class II genes as reported in the literature for other teleost fish species.

Family	Genus	Species	#alleles	citation
Gasterosteidae	Gasterosteus	aculeatus	24	Reusch *et al* . 2001
Gasterosteidae	Gasterosteus	aculeatus	28	Wegner *et al* . 2003
Cichlidae	multiple	multiple	13	Malaga-Trillo *et al* . 1998
Salmonidae	Salmo	salar	23	Langefors *et al* . 2000
Fundulidae	Fundulus	heteroclitus	41	Cohen *et al* . 2002

Appendix A: DNA sequences

Locus 1:
Monomorphic, sample from Salt Creek Upper fish # 15
TTCAGTCTGGATTACTCTGATTAGCAGATATAATCTGCTTCTGTTGATCAGGA
AGGGTCAATGACTGATCAGTTTAAATTGTTTTAAGTGTCATTTTCTGTCCAGC
CGCTCCATTCATCAAACTGGTCAGTGTATTGATCCTTCATGTGCCTCAGAGTT
TAAATCAGCTGATATCAGATCAATAATGTTCTGATTATTGATGCTGATCTTCT
GTTCTGGTTCCCAGATGGATATGAGTATTATGCACTGAATCGTTGTGTGTTTA
ACTCCACTGAGCCGAAGGACATCGAGTACATCTTCTCCTACTATTACAACAA
GAAGGAGTTCCTCAGGTTTGACACCAGTGTGGGGCACTATGTTGGATACACG
GAGCTGGGAGTGAAGAACGCAGAACAATGGAACAAAGATAGATCAGAGATC
GCTGTGAG

Locus 3:
Monomorphic, sample taken from Malpais Spring Upper fish #2
TCTTTGTGAGTTTACCTCCCCTGAGCTGAAGGACATCGAGTACATTCGCTCAG
AGTTTTATAACAAAGAGGAGCTCTTCAGGTTCACCAGCAGTTTGGGGAAGTT
TGTTGGATTCACAGATTACGGCATCTTCCAGGCAGAATACCGAAACAATGAT
ACTGTATTAATTCAGGCACTGAGAGCTGAGAAGGAGAGATACTGCCAACACA
ACATTGGTATCTTCTACTCCAATGCTCTGGATAAATCAGGTGAG

Locus 2: (SCUP = Salt Creek Upper, MLUP = Malpais Spring Upper)
>SCUP1-2
AATAATGTTCTGATTATTGATGCTGAGCTTCTGTTCCGGTTCCCAGATGGATT
CATGGAATATGTACTGGATCGTTGTGTGTTTAACTCCACTGAGCTGAAGGACA
TCCAGTACATCTACTCTGAATATTACAACAAGAAGGAGATCCTCAGGTTTGA
CAGCAATGTGGGGAAATATGTTGGATACACGGATCTGGGAGTGAAGAACGC
AGGACGATTCAACAAAGATCCGTCAGAGATAGCTAGGAGGAAGGGTGAGAG
GGAGAGATACTGCCAGCATAACATTGGTATCTGGTACTCCAATCCTCTGTCTA
AATCAGGT
>SCUP1-3
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ACAGCAATGTGGGGAAATATGTTGGATACACGGATCTGGGAGTGAAGAACG
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GGGAGAGATACTGCCAGCACAACATTGGTAATGAGTACCAGGCTGCTCTGTC
TAAATCAGGT
>SCUP1-08
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TCCAGTACATCTACTCTGAATATTACAACAAGAAGGAGATCCTCAGGTTTGA
CAGCAATGTGGGGAAATATGTCGGATACACGGATCTGGGAGTGAAGAACGC
AGAACGATTCAACAAAGATCCGTCAGAGATAGCTAGGAGGAAGGGTGAAAG

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CAGAACGATTGAACAAAGATCCGTCAGAGATAGCTATGAGGATGGGTGAGA
GGGAGAGATACTGCCAGCACAACATTGGTAATGAGTACCAGGCTGCTCTGTC
TAAATCAGGT
>SCUP2-02
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TCCAGTACATCTACTCTGAATATTACAACAAGAAGGAGATCCTCAGGTTTGA
CAGCAATGTGGGGAAATATGTTGGGTACACGGATCTGGGAGTGAAGAACAC
AGAACGATTCAACAAAGATCCGTCAGAGATAGCTAGGAGGAAGGGTGAGAG
GGAGAGATACTGCCAGCATAACATTGGTATCTGGTACTCCAATCCTCTGTCTA
AATCAGGT