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Characterization of a hybrid zone between two chromosomal races of the weta *Hemideina thoracica* following a geologically recent volcanic eruption

MARY MORGAN-RICHARDS*†, STEVEN A. TREWICK† & GRAHAM P. WALLIS

Department of Zoology, University of Otago, PO Box 56, Dunedin, New Zealand

Two chromosomal races ($2n = 17$ and $2n = 15$; XO) of the weta *Hemideina thoracica* meet at the centre of a volcanic region in North Island, New Zealand. Five independent polymorphic genetic markers showed broadly coinciding, steep frequency clines from north to south across this zone beside the flooded crater, Lake Taupo. Three unlinked nuclear gene markers provide estimates of zone width that are at least twice the width of the chromosomal and mitochondrial clines, with cline centres displaced at least 2.5 km. The different zone widths and centres suggest that this hybrid zone is a semipermeable barrier reducing the introgression of the chromosomal markers more than genic markers. We estimate that this species of weta must have a dispersal rate of at least 100 m per generation using the time since the last Taupo eruption (1850 years ago), which covered an area of about 20 000 km^2 with pyroclastic flow.

Keywords: allozymes, chromosomal races, gene flow, genetic structure, hybrid zone, microsatellites, mtDNA, Orthoptera.

Introduction

Hybrid zones are of interest to evolutionary geneticists because they allow us to explore the genetical interactions of partly differentiated populations. Hybrid-zone theory and the development of molecular and analytical techniques have provided the tools and theoretical framework for the development of the study of speciation, reinforcement, gene-flow and integration. Many hybrid zones that have been extensively studied involve the hybridization of cytogenetically differentiated populations (Hewitt, 1988; Searle, 1993). This wealth of information about the nature and consequences of chromosome variation has shed light on the role of chromosome rearrangements in the speciation process. Chromosome rearrangements have the potential to reduce gene flow because heterozygotes frequently have reduced fertility due to the production of chromosomally unbalanced gametes (White, 1978). Where hybridizing populations are found to differ in their karyotypes the potential for the chromosome differences to act as partial or complete barriers to gene flow is of central importance in the study of speciation. The degree to which chromosome rearrangements act as barriers to gene flow varies among taxa and among zones. For example, chromosome rearrangements have been implicated in alterations to recombination patterns which break up 'coadapted gene complexes' resulting in inviable F_2 offspring of the grasshopper *Caledia captiva* and strong barriers to gene flow (Shaw, 1981; Coates & Shaw, 1984). Evidence for chromosomal rearrangements acting in combination with other genetic traits to reduce fertility and thus reduce intergradation of populations has been documented for a hybrid zone in shrews (Lugon Moulin *et al*., 1996). However, not all chromosome rearrangements inhibit gene flow; in a number of taxa chromosome rearrangements are the only marker showing a narrow cline (Searle, 1993; Fel-Clair *et al*., 1996; Wyttenbach *et al*., 1999). Thus cytogeneticists urge us not to extrapolate from one species to another (Rogatcheva *et al*., 1998).

In any hybrid zone study a number of variables will be unknown. One feature of some importance is the age of the contact and in this study an exact maximum age of the contact is known. Lake Taupo was formed following a huge volcanic eruption about 27 000 years

*Correspondence. E-mail: marym@nhm.ac.uk
†Present address: Department of Botany, Natural History Museum, Cromwell Rd, London SW7 5BD.

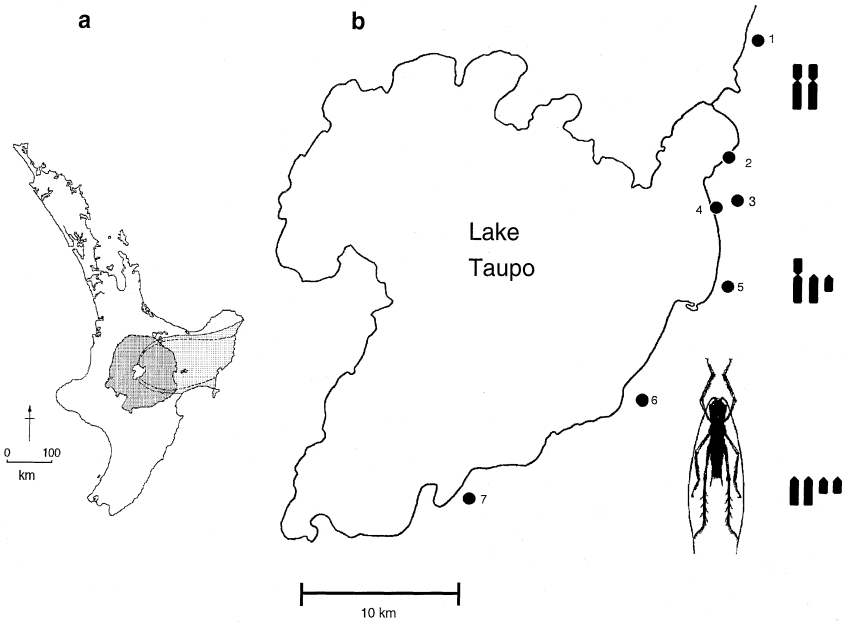

Fig. 1 (a) Area of North Island, New Zealand covered by pyroclastic flow (dark shading) and ash (pale stippling) following the most recent Taupo volcanic eruption (about 1850 years ago). (b) Collecting locations of *Hemideina thoracica* from the shore of Lake Taupo. Diagrams of chromosome markers show the northern race, hybrid, and southern race, from top to bottom, respectively.

ago and the surrounding area has since been subject to sporadic volcanic activity (Healy, 1992). The most recent Taupo eruption occurred about 1850 years ago (estimates range from 1857 to 1813 years ago). This eruption deposited pyroclastic rock over 20 000 km^2 and covered 30 000 km^2 of New Zealand in ash (Fig. 1a) (Wilson & Walker, 1985; Healy, 1992). Thus we know with certainty that plant and animal populations within a radius of about 80 km of Lake Taupo have arrived within the last 1850 years (see also McDowall, 1996).

Tree weta are flightless nocturnal orthopterans (family Anostostomatidae) endemic to New Zealand. The common tree weta species in the northern half of New Zealand (*Hemideina thoracica*) consists of at least seven chromosomal races (Morgan-Richards, 1997). Weta collected from the extreme south of this species' range have a diploid number of 17(XO) in males and 18(XX) in females. North of, and adjacent to this chromosomal race, weta have diploid numbers of 15(XO) and 16(XX). Weta near Taupo have either four pairs of small acrocentric autosomes (17) or two pairs of small acrocentrics and one pair of small metacentric autosomes (15) (Morgan-Richards, 1997). The difference between the karyotypes can most simply be explained as resulting from a single fission/fusion of small autosomes. No morphological characters distinguishing these chromosomal races have been detected. For this study, tree weta were examined from an area where the 17-karyotype race meets the 15-karyotype race in the Central Plateau of the North Island. Lake Taupo forms a barrier to the west and the eastern shoreline forms a natural north–south transect. Tree weta populations karyotypically monomorphic for the two chromosome complements were known to be separated by at most 40 km (Morgan-Richards, 1997). For this study we used a range of molecular markers to address the following questions. 1. Are there molecular genetic differences between these races? 2. Is there evidence of hybridization or introgression? 3. Do frequency clines for independent markers have the same centre (coincident) and width (concordant)?

Materials and methods

Ten sites were searched for tree weta between Huka Falls (site 1) north of Lake Taupo and Parikarangaroa Reserve (site 7) at the southern end of Lake Taupo, forming a transect of 38 km along the eastern shore of the crater lake (Fig. 1b). The land beside Lake Taupo is extensively modified by human activity and searching was successful at only seven sites (Table 1). Nineteen artificial weta hides were made by drilling a hole 9×120 mm in a block of wood and tying to shrubs at site 3. Three months later, six of these weta hides were occupied by subadult male *H. thoracica*. At site 2, night searches were carried out on three sequential nights by scanning branches and trunks of native trees after dusk for 2–3 h. At all other sites weta were collected during the day by extracting them from tree cavities. A total of 87 *H. thoracica* was collected and analysed (Table 1). Cytogenetic analysis and allozyme electrophoresis were performed as described in Morgan-Richards (1997).

Table 1 Collecting locations of *Hemideina thoracica* from the shore of Lake Taupo, New Zealand, and the distribution of genotypes for five polymorphic loci within the population samples. Location is measured as absolute distance from site 1

Site	Distance from site 1 (km)	Sample size	Chromosomes			*Icd*				*Pgd*			Microsatellite (sex-linked)				mtDNA	
			AA	AB	BB	AA	AB	BB	BC	AA	AB	BB	AA + A	AB	BB + B	BC	A	B
1	0	9			9	1	3	5		2	3	4			4	5		9
2	7.6	34			30	3	8	15	1	4	17	7	7	4	21	1		32
3	9.6	12		3	9	2	9	1		12			4	4	2			10
4	9.7	7			6		2	4		4	2		3	2	1		1	5
5	15.3	8	4	3		5	3			4	4		4	1	3			8
6	22.1	15		9		15				15			15				11	
7	38	2	2			2				2			2				2	

mtDNA

DNA was extracted from fresh or frozen muscle tissue using a salting-out method (Sunnucks & Hale, 1996). Universal insect mitochondrial primers SR-J-14233 and SR-N-14588 (Simon *et al*., 1994) were used to amplify a 355-bp fragment of the small ribosomal subunit (12 S) gene. Single Stranded Conformational Polymorphism (SSCP) was used to assign each specimen to one of two haplotypes using a standard protocol (Trewick, 1999). Two representatives of each haplotype were sequenced using Bigdye chemistry (Perkin Elmer) following the manufacturer's protocols.

Microsatellite

Seventeen microsatellite sequences and their flanking regions were isolated and sequenced following Waters *et al*. (1999). One locus was polymorphic within the contact zone, a deformed dimer $(GT)_7$ with three alleles. A breeding experiment between weta from the chromosomal race 15 (from site 2) and the chromosomal race 19 (from Opononi) suggested this locus was sex linked: female offspring were heterozygous ($n = 3$) and male offspring were hemizygous for the maternal allele ($n = 4$). Sex linkage was supported by the absence of male heterozygotes in our study (n males = 42, n females = 40 [16 heterozygotes]); $G_1 = 27.1$, $P < 0.001$). We tested for departure from Hardy–Weinberg equilibrium using the sample from site 2 ($n = 32$). The locus showed significant departure when scored as an autosomal marker ($G_3 = 15.11$, $P < 0.005$) but not when scored as a sex-linked marker ($G_5 = 5.23$, $P > 0.1$).

Genetic analysis

Departures from Hardy–Weinberg equilibrium and linkage disequilibrium within population samples were analysed using exact tests available in GENEPOP version 3.1 (Raymond & Rousset, 1995). Zone widths and centres were estimated with ANALYSE, a software package for the analysis of hybrid zones (Barton & Baird, 1998). Rare alleles detected at site 2 were grouped with the marker characteristic of the northern samples for the cline analysis. Variation in allele frequencies among sites was assumed to be due to a combination of sampling error and a smooth frequency cline and therefore F_{ST} was set to zero. This setting has the effect of giving greater weight to larger samples (N. Barton, personal communication). To assess the sensitivity of our analyses to this parameter setting, we also tried a setting of $F_{ST} = 0.2$. Confidence intervals were based on the points that were 1/7.4 as likely as the maximum likelihood estimates obtained from randomly varying the parameters

(width and centre) using a metropolis algorithm (1000 iterations), following recommendations given with the program.

Results

Cytogenetics

The samples from three northern sites (1, 2, 4; Fig. 1) were monomorphic for the 15-karyotype (coded BB) and samples from the two southern sites (6, 7) were monomorphic for the 17-karyotype (AA) (Table 1). Six chromosomal heterozygotes were found in sites 3 and 5. These six weta all had balanced chromosome complements with five tiny dot chromosomes, one small acrocentric and one slightly larger submetacentric (Fig. 2a); simple heterozygotes (AB) between the 15-karyotype and 17-karyotype. During meiosis in males with normal karyotypes (15 and 17), the 14 and 16 autosomes form 7 and 8 bivalents, respectively, and the X-chromosome forms a univalent. During meiosis in chromosome hybrids, eight chromatid bodies formed in 88% of cells and nine chromatid bodies in 12% of cells ($n = 50$). Thus, three small autosomes (two acrocentric and one metacentric) apparently form a trivalent in the majority of the meiotic cells (Fig. 2b). One male weta from site 3 (homozygous for the 15-karyotype, BB) had only a single testis. This deformed animal was the only weta from the Taupo region observed with a developmental abnormality.

Allozyme and microsatellite analysis

Two of the 25 allozyme loci surveyed were polymorphic: *Pgd* and *Icd*-2. Both of these loci showed a cline in allele frequencies over the chromosome contact zone (Table 1, Fig. 3). None of the samples deviated significantly from Hardy–Weinberg expectations for any of the variable markers. No deviation from linkage disequilibrium was detected in any sample for the seven possible pairwise comparisons of polymorphic autosomal markers. The sex-linked microsatellite locus showed a cline in allele frequencies over the chromosome contact zone remarkably similar to the *Icd*-2 cline (Table 1, Fig. 3).

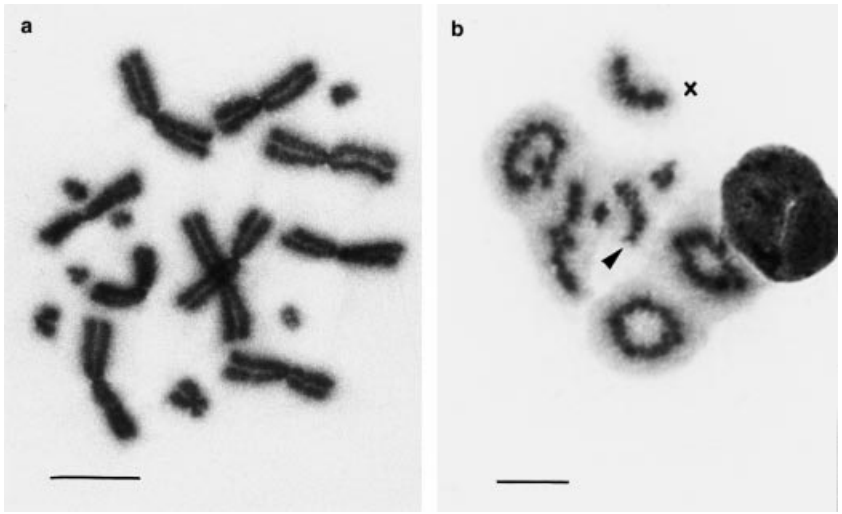

Fig. 2 Cell divisions in chromosomally heterozygous *H. thoracica* from site 3. (a) Mitotic cell from a hybrid female ($2n = 17$, XX) showing four pairs of large autosomes, a pair of large X chromosomes, five dot chromosomes, a small acrocentric and a slightly larger submetacentric (bottom centre). The submetacentric is homologous to the small acrocentric plus one of the five dot chromosomes. (b) Meiotic cell from a hybrid male ($2n = 16$, XO) showing three large autosome ring bivalents, one large autosome rod, an X univalent, two dot bivalents and probable trivalent (indicated by arrowhead). Scale bar equals 10 μm.

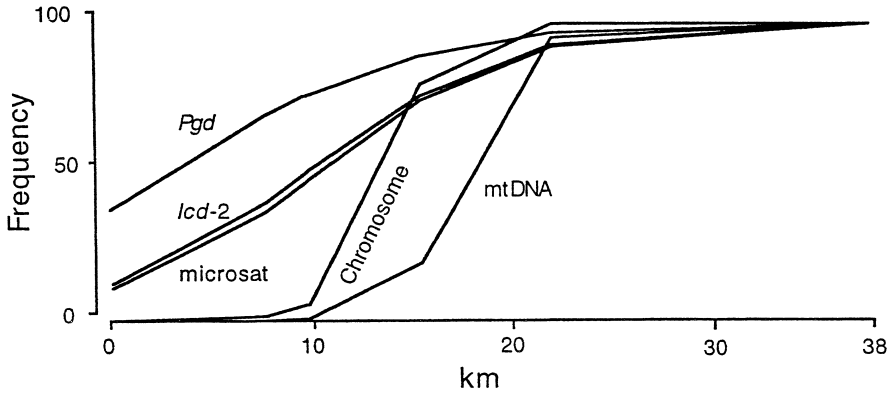

Fig. 3 Fitted tanh curve showing the clinal transition of five genetic markers through the hybrid zone of *Hemideina thoracica* beside Lake Taupo. Location is measured as absolute distance from site 1.

mtDNA

Two haplotypes were identified by single stranded conformational polymorphism (SSCP) of 355 bp of 12S: one found only in the northern sites and one found only in the southern sites (Table 1), with the exception of site 4 which was polymorphic. Sequencing of these mtDNA fragments from four weta (two of each haplotype) revealed a difference of four nucleotide substitutions (three transitions, one transversion).

Cline coincidence and concordance

Two sites contained chromosomal heterozygotes and only one site contained both mtDNA haplotypes. In contrast, four sites were polymorphic for *Pgd* and five polymorphic for *Icd*-2 and the microsatellite. The most northerly samples in our transect were polymorphic for all three nuclear loci, although wider surveying of the species suggested that more northerly populations are monomorphic (Morgan-Richards, 1997). The widths of the clines for *Pgd*, *Icd*-2 and the microsatellite locus do not differ significantly (Table 2). These three clines, however, are two to three times the width of both the chromosome and mtDNA clines (Table 2). The cline for mtDNA is broadly concordant with the chromosome cline, but centred just to the south of the chromosome cline. Both are centred to the south of the three nuclear gene clines (Table 2). Only the microsatellite and *Icd*-2 clines are coincident; all other clines have significantly different centres from each other. When we assessed the sensitivity of our analyses to F_{ST} by setting F_{ST} to 0.2, estimates of cline width and centre (and their associated confidence intervals) changed very little, and no pairwise comparison discussed above changed in its significance.

The frequencies of chromosomal and allozyme markers show concordant changes between sites 3 and 4, although the frequency shift is bigger for chromosomes.

Table 2 Estimations of cline widths and centres for five genetic markers that differentiate populations of *Hemideina thoracica* on the shores of Lake Taupo, New Zealand. A tanh model fitted with maximum likelihood estimates was used to approximate 95% confidence intervals. Centre is measured as absolute distance from site 1

Marker	Width (km)	Confidence interval (95%)	Centre (km)	Confidence interval (95%)
Chromosomes	5.29	4.9–5.8	13.4	13.1–13.7
Icd	17.13	15.6–18.8	10.18	9.7–10.6
Pgd	20.33	18.3–22.8	5.3	4.6–5.8
Microsatellite	19.76	17.9–22.0	9.43	8.9–9.9
mtDNA	6.19	5.4–7.1	17.51	17.0–18.1

Sites 3 and 4 are separated by only 1.1 km yet differ markedly in their allele frequencies. The similarity of the character clines suggests that these two sites, although geographically adjacent, are independent of one another and that our north–south collecting transect was not exactly perpendicular to a linear zone of contact.

Discussion

For the first time a hybrid zone has been characterized between two chromosomal races of the weta *Hemideina thoracica*. Where the 17-karyotype and the 15-karyotype race meet beside Lake Taupo, individuals with a mixture of the two chromosome complements were found. Steep clines in allele frequency were observed for three nuclear loci and a mitochondrial marker over the 38 km surveyed. The approximate broad geographical coincidence of four clines along the eastern shore of Lake Taupo is most likely the result of secondary contact of allopatrically differentiated populations.

Because of the volcanic nature of the region, no weta could have existed on the shores of the lake 1850 years ago and thus secondary contact of the two chromosome races must be recent. The meeting of the two races is unlikely to form a simple east–west line of contact because the area covered by volcanic rock is roughly circular, with Lake Taupo at its centre. Movement of the two races towards the centre would probably create a zone of contact that increased in width and/or age from the centre outwards. The most recent eruption produced a pyroclastic flow that covered a circular area around the lake roughly 160 km in diameter (Fig. 1a; Wilson & Walker, 1985). For the two chromosomal races of *H. thoracica* to have met since the eruption they needed to disperse at least 86 m per generation (generation time of two years (unpublished data)). Taking into account the maximum cline width estimation of about 20 km, a rate of dispersal of at least 100 m per generation is required to explain the current introgression. Naturally the habitat of the weta would need to have spread at a similar or faster rate but we know that revegetation was complete within 200 years of the eruption (Wilmshurst & McGlone, 1996). Although there are no direct measures of dispersal for this species, a related species has been documented travelling 10 m in a single night (Ordish, 1992) so a distance of 100 m in two years is realistic. This is a minimum dispersal rate given that the current zone of contact may act as a barrier to gene flow.

Some of the estimates of cline width provided by the five markers differ significantly. The mitochondrial haplotypes form a cline that is steeper than the *Pgd*, *Icd* or microsatellite cline. If neutral diffusion were operating for all markers the uniparental mode of

inheritance of haploid mtDNA would be expected to result in a narrower cline than that for biparental nuclear markers, as observed. In addition, if female weta did not disperse as far as males this also would result in a narrower mtDNA cline compared to the nuclear markers. However, the cline width estimate for the chromosomal markers is also significantly narrower than that for the three nuclear genes, indeed very similar to mtDNA cline width. The chromosome cline would not be expected to be narrower than the nuclear gene clines unless the chromosomal markers were linked to or causing hybrid disadvantage. The centres of the frequency clines for the five markers vary from 5.3 to 17.5 km south of site 1. Only *Icd* and the microsatellite have clines that are both coincident and concordant. Disparity of the cline centres with respect to various markers may result from differential selection of alleles (e.g. Shaw *et al*., 1993), perhaps exacerbated by differential migration (e.g. Cathey *et al*., 1998) or movement of the tension zone (e.g. Arntzen & Wallis, 1991) resulting in a nonequilibrium situation.

The difference in cline width for nuclear genes vs. chromosomes probably results from a semipermeable barrier that disadvantages only the chromosomes involved in the rearrangements and linked markers. Observations from chromosomally heterozygous weta suggested that the small acrocentric chromosome and a dot chromosome are together homologous with the small submetacentric chromosome, forming a trivalent at meiosis (Fig. 2b). This observation is compatible with the notion that the chromosomal rearrangement that differentiates the two karyotypes is a centric fission or fusion (Morgan-Richards, 1997). Such a change may result in little disadvantage to chromosomal heterozygotes as seen in some taxa (shrews (Rogatcheva *et al*., 1998), mice (Gropp & Winking, 1981; Wallace *et al*., 1998)) although even in these species the genetic background can determine whether such rearrangements reduce fertility (Hauffe & Searle, 1998). Shaw (1981) reviewed five examples of chromosome hybrid zones in orthopteroid insects and concluded that chromosomal rearrangements offer minimal isolation via mechanical impairment of meiosis. In a number of studies where chromosomal markers have been used to identify hybrid zones, selection against hybrids has been explained by a combination of genetical effects rather than purely from selection against chromosomal heterozygotes (Harrison, 1990). However, at this geologically recent contact zone it appears that introgression of nuclear markers is occurring. On reconstitution of parental karyotype (AA or BB) in F_2, nuclear genes are able to introgress more easily. There may be no barrier to the eventual genetic homogenization of these two races, with the exception of the distinct karyotypes, and thus little chance that this hybrid zone will lead to the formation of distinct species. Within the species as a whole, little concordance of allozyme and chromosome markers was found (Morgan-Richards, 1997) supporting the notion that within this species, it is the chromosome heterozygotes themselves that explain most of the reduced fitness of hybrids.

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