Evolution, 57(4), 2003, pp. 849–861

A COMPARISON OF FIVE HYBRID ZONES OF THE WETA *HEMIDEINA THORACICA* (ORTHOPTERA: ANOSTOSTOMATIDAE): DEGREE OF CYTOGENETIC DIFFERENTIATION FAILS TO PREDICT ZONE WIDTH

MARY MORGAN-RICHARDS[1] AND GRAHAM P. WALLIS
Department of Zoology, University of Otago, P.O. Box 56, Dunedin, New Zealand

Abstract.—Tension zones are maintained by the interaction between selection against hybrids and dispersal of individuals. Investigating multiple hybrid zones within a single species provides the opportunity to examine differences in zone structure on a background of differences in extrinsic factors (e.g., age of the zone, ecology) or intrinsic factors (e.g., chromosomes). The New Zealand tree weta *Hemideina thoracica*

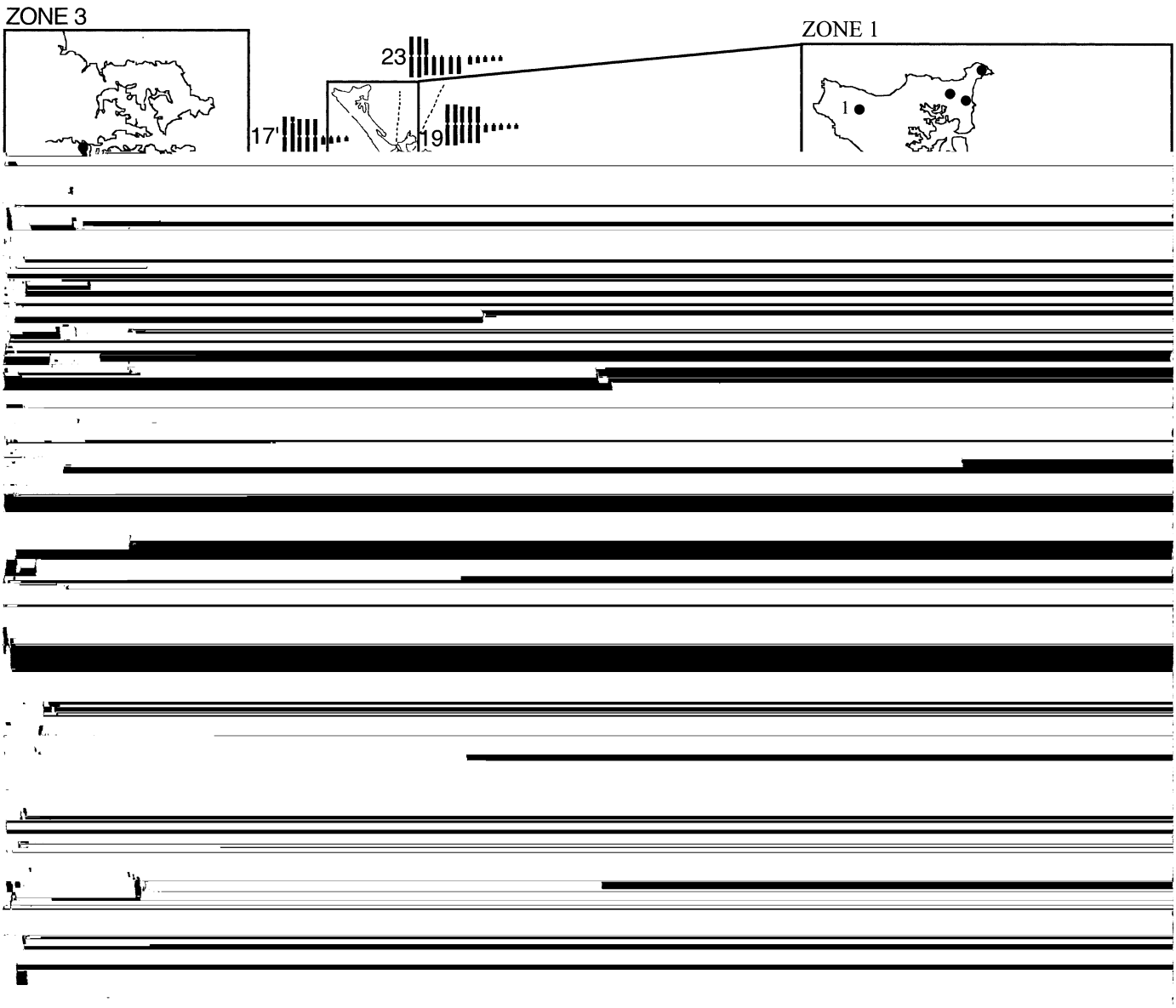

FIG. 1. The distribution of the eight chromosomal races of *Hemideina thoracica* on North Island, New Zealand, showing the haploid karyotype of each race. Dashed lines indicate approximate boundary of each race. Enlargements of five contact zones between these chromosomal races are shown as insets. Sampling locations indicated by spots; only numbered locations were used in cline analyses.

Five hybrid zones involving six different chromosomal races were located and sampled for this comparative study (Fig. 1). *Hemideina thoracica* has greater allozyme and mitochondrial DNA (mtDNA) diversity in the northern third of its range than in its southern two-thirds (Morgan-Richards 1997; Morgan-Richards et al. 2001a). The northern chromosomal races (17, 19, 23) are likely to be of Pliocene origin but southern races are probably much younger (Morgan-Richards et al. 2001a). For Zones 1 and 2 it is likely that the chromosome races first made contact during the early Pleistocene when sandbar formation linked a chain of islands and sea levels fell (Ballance and Williams 1992). Lower levels of mtDNA diversity in the southern compared to the northern races suggest that southern races probably originated during the Pleistocene (Morgan-Richards et al. 2001a). Zone 5 is probably the youngest of the five hybrid zones: it formed following a volcanic eruption less than 2000 years ago (Wilson and Walker 1985; Morgan-Richards et al. 2000).

The hybrid zone between two southern chromosomal races of *H. thoracica* centered in the Taupo volcanic region has been investigated using five genetic markers. Three unlinked nuclear markers (two allozyme, one microsatellite) form clines that are between 15 and 22 km wide but the chromosome marker (a Robertsonian [Rb] translocation) forms a significantly narrower cline approximately 5 km wide. The mitochondrial cline, displaced 4 km to the south, is the same width as the chromosomal cline. The nonconcordant character clines through this hybrid zone suggest that the chromosomal rearrangement that differentiates these two races may limit the introgression of the chromosomes involved in

TABLE 1. Predictions of relative zone width for five chromosomal hybrid zones of *Hemideina thoracica* based on the chromosome characteristics of each zone (hypothesized chromosome rearrangements that differentiate the karyotype pairs at each zone and the percentage of karyotype involved in these rearrangements; see Figure 1 for ideograms).

Zone	Location	Number of Chromosomes (XO)	Characteristic elements	Rearrangements that differentiate the races	% complement in rearrangements	Predicted relative zone width
1	Mt. Camel	17♀ and 19	1 large metacentric (19) or 1 submetacentric (17♀)	1 pericentric inversion or reciprocal translocation		
			1 small acrocentric (19)	1 translocation/duplication	20–35	narrow
2	Karikari	23 and 19	4 medium acrocentrics (23) or 2 large metacentrics (19)	2 Rb translocations	30–35	narrow
3	Waitangi	19 and 17	1 small acrocentric (19)	1 translocation/duplication	1–2	wide
4	Bream Bay	17 and 15♀	2 acrocentrics (17) or 1 metacentric (15♀)	1 Rb translocation	5–7	medium
5	Taupo	15 and 17	2 acrocentrics (17) or 1 submetacentric (15)	1 Rb translocation	6–8	medium

the rearrangements but have little effect on the introgression of unlinked nuclear alleles (Morgan-Richards et al. 2000). The two Taupo races are differentiated by a single Rb translocation involving relatively small autosomes, but at other contact zones larger chromosomes are involved in Rb translocations and other rearrangements (Morgan-Richards 1997). A comparison of hybrid zones could reveal the relative disadvantage conferred by the chromosome rearrangements. In a number of taxa, the more rearrangements that differentiate any two races, the greater the likelihood of disruptions to meiosis resulting in unbalanced gamete formation and reduced fertility (Searle 1993; Searle and Wójcik 1998; Spirito 1998; Gorlov and Tsurusaki 2000). The likelihood of disruptions to meiosis may depend on the type of chromosomal rearrangement, the number of rearrangements, the quantity of chromosome material involved in the rearrangements, and the genetic background on which they occur, or some combination of these effects. A general prediction is that the more rearrangements and the more material involved, the greater the disruption and reduction in fertility (Spirito 1998; Delneri et al. 2003). Rearrangements that involve simple fission/fusions may permit equal disjunction of genetic material and thus have little effect on fertility. If the same chromosome arms are involved in different fusions (e.g., the Monobrachial

The Hybrid Zones and Predictions

The five hybrid zones of *H. thoracica* included in this study and the chromosome differences that characterize them are presented in Table 1. Zones are numbered 1 to 5 from north to south (Fig. 1). Chromosome rearrangements that distinguish the karyotypes are based on studies of plain-stained mitotic and meiotic cells from homozygotes and heterozygotes (Morgan-Richards 1997; this study). We assume that the five hybrid zones in this study arose through secondary contact of populations that differentiated in allopatry. None of the zones are situated in regions in which there exists or has existed in the recent past an identified change in habitat (Newnham 1999), so all five contact zones may be tension zones. All zones are geographically close (Fig. 1) and exist on a homogeneous ecological background of lowland forest. Although some of this forest has been disturbed recently by human activity it is replaced with patchy regenerating scrub that is also suitable habitat for weta.

Based on the number of rearrangements and proportion of the genome involved in the chromosome rearrangements that differentiate the pairs of races, we made predictions of the relative width of the hybrid zone at each of five contact zones between the six chromosomal races (Table 1). In making these predictions we assumed that: (1) the races do not differ for traits that might affect hybrid zone width other than chromosomal rearrangements, and (2) habitat structure is similar in the five zones. Any differences among races that allow ecological or incompatibility selection in the zones could lead

TABLE 2. Frequency distribution of karyotypes and mtDNA markers through five hybrid zones between chromosomal races of *Hemideina thoracica.*

Zone 1, Mt. Camel Sampling site		17♀ contacts 19-karyotype Code	Km from site 1	% 19-karyotype	*n*	% mtDNA	Haplotypes	*n*
Pandora's Track	1	Pnd	0	0	6	0	a(2) b(6)	8
Wahakari	2	Whk	19.5	0	5	0	g(3)	3
Lake Bulrush	3	Bul	29	0	5	0	c(2) g(2)	4
Lake Waihopo	4	Wai	34.5	0	4	0	d, e, f, g	4
Hauhora Heads	5	HhH	47	45.84	12	0	h(13)	13
Motutangi Swamp	6	Mot	52.5	31.25	16	14.29	g(9) l(6) m, n, o, P, R(2)	21
Paparore	7	Papa	65.75	22.73	11	0	k(12)	12
Avocado Stop	8	Avo	68.25	0	7	0	g(8)	8
90-mile beach road	9	NmR	71	100	14	37.5	g, j(9) Q(6)	16
Quarry Road	10	Qry	80	100	8	83.33	i(2) Q(10)	12
Zone 2, Karikari Sampling site		23 contacts 19-karyotype Code	Km from site 1	% 19-karyotype	*n*	% mtDNA	Haplotypes	*n*
Matai Bay	1	Mat	0	0	8	0	a(5) b, d, e(2)	9
Whatuwhiwhi	2	Whw	5.5	9.37	8	0	e(12)	12
Lake Waiporohita	3	Wp	10.5	2.94	17	0	d, e(15)	16
Tahanga Road	4	Tah	20	86.54	13	100	F(13)	13
Pukewhai	5	Pkw	22	81.25	8	100	F(9)	9
Arawhata	6	Arw	25.75	97.92	12	100	F(13)	13
Quarry Road	7	Qry	31	100	8	83.33	c(2) F(10)	12
Zone 3, Waitangi Sampling site		19 contacts 17-karyotype Code	Km from site 1	% 17-karyotype	*n*	% mtDNA	Haplotypes	*n*
KeriKeri Inlet	1	KkI	0	0	4	0	A(5)	5
Mt. Te Puke	2	Puke	3.25	0	13	0	B(11) C, D	13
Haruru Falls	3	Hrr	5.75	11.12	9	0	D(10) E	11
Puketona	4	Ptk	8	100	9	100	h(10)	10
Paihia Walkway	5	Wwy	9.5	100	15	100	h(13) f, g	15
North End Oromahoe	6	ENO	13.75	100	4	100	h(2)	4
Paihia Inlet	7	Pai	17	100	2	100	h(4)	2
Zone 4, Bream Bay Sampling site		17 contacts 15♀-karyotype Code	Km from site 1	% 15♀-karyotype	*n*	% mtDNA 52	Haplotypes	*n*
Otaika Valley	1	Otk	0	0	7	0	a(10)	10
Flyger Road	2	Fly	15	0	6	66.66	b(2) D(2) I, J	6
Prescott Road	3	Prst	19.5	0	17	100	D(17)	17
Uretiti	4	Urt	24	45.46	11	100	D(13)	13
Ahuroa River	5	Ahu	30.75	95.45	11	100	C, D(8) E, G(3)	13
Waipu	6	Wpu	37	95.83	12	100	D(10) G(3)	13
Zone 5, Taupo Sampling site		15 contacts 17-karyotype Code	Km from site 1	% 17-karyotype	*n*	% mtDNA	Haplotypes	*n*
Huka Falls	1	Hk	0	0	9	0	a(9)	9
Rainbow Point	2	Ta	7.6	0	30	0	a(32)	32
Airport	3	Ap	9.6	12.5	12	0	a(10)	10
Five-mile Bay	4	5m	9.7	0	6	16.67	a(5) B	6
Mill Road	5	Mill	15.3	78.57	7	0	a(8)	8
Hinemaiaia River	6	Hin	22.1	100	9	100	B(11)	11
Parikanangaroa	7	Pak	38	100	2	100	B(2)	2

1.30, a software package for the analysis of hybrid zones (Barton and Baird 1998). Cline width is defined as the inverse of the maximum slope and the center is where the cline slope is steepest (Barton and Gale 1993). Variation in allele frequencies among sites was assumed to be caused by a combination of sampling error and a smooth frequency cline and therefore F_{ST} was set to zero. Setting F_{ST} to zero also compensates for variation in sample size. Estimations of cline width and center were also made using F_{ST} . 0, but this parameter had little effect on the confidence intervals and did not alter the conclusions drawn. Confidence intervals were based on the points that were 1/7.4 as likely as the maximum-likelihood estimates obtained by randomly varying the parameters (width and center) using a metropolis

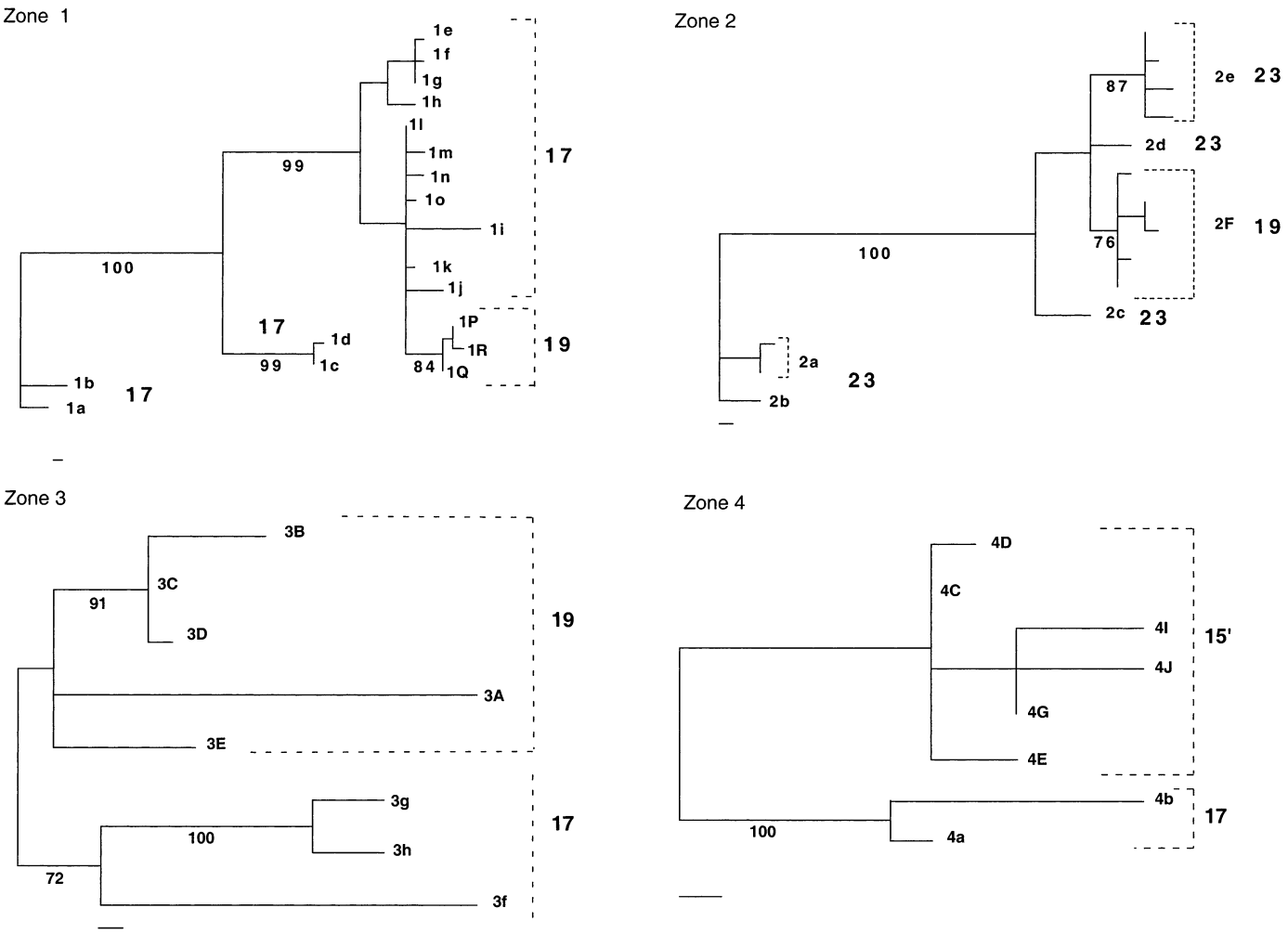

FIG. 2. Maximum parsimony trees for mtDNA sequence data (550 bp of cytochrome oxidase I) from each of four hybrid zones (Zone 5 had only two haplotypes). Terminal branches are labeled according to 12S-SSCP haplotypes. Numbers below branches are bootstrap values (. 70) obtained from 1000 replicates. Scale line 5 1 substitution.

algorithm (1000 iterations), following recommendations given with the program (Barton and Baird 1998).

To assign mtDNA haplotypes to the alternative chromosome races, the COI sequence data was phylogenetically analyzed. PAUP*4.0b (Swofford 1998) was used to implement phylogenetic reconstruction using maximum parsimony (MP). Unweighted and unrooted settings were used. We used 1000 bootstrap iterations and presented the resulting tree. Only bootstrap values that represent good support for branches ($\geq$ 70; Hillis and Bull 1993) are included on the phylograms (Fig. 2). At each of the five zones, one bipartition of the tree divided haplotypes that defined the majority of weta from the two chromosomal races.

RESULTS

Cytogenetics

Chromosome heterozygotes were found at between one and five sites per zone (Table 2). The polymorphic populations did not deviate significantly from Hardy-Weinberg equilibrium (genotypes available on request). All heterozygous weta were chromosomally balanced (without additional or reduced chromosomal material), with the exception of three weta from Zone 4, which all had small additional chromosomes.

TABLE 3. Estimates of cline width and center for chromosome and mtDNA markers through five hybrid zones between chromosomal races of *Hemideina thoracica.* CI, 95% confidence interval approximated with maximum-likelihood estimates.

	Chromosome cline				mtDNA cline			
Zone	Width (km)	CI	Center	CI	Width (km)	CI	Center	CI
1	47.28	(44.0–51.5)	61.81	(60.7–63.0)				
2	10.32	(9.7–11.1)	16.52	(16.1–17.0)				
3	0.53	(0.3–1.3)	6.00	(5.9–6.4)				
4	8.13	(7.4–8.9)	25.32	(24.9–25.7)				
5	5.29	(4.9–5.8)	13.40					

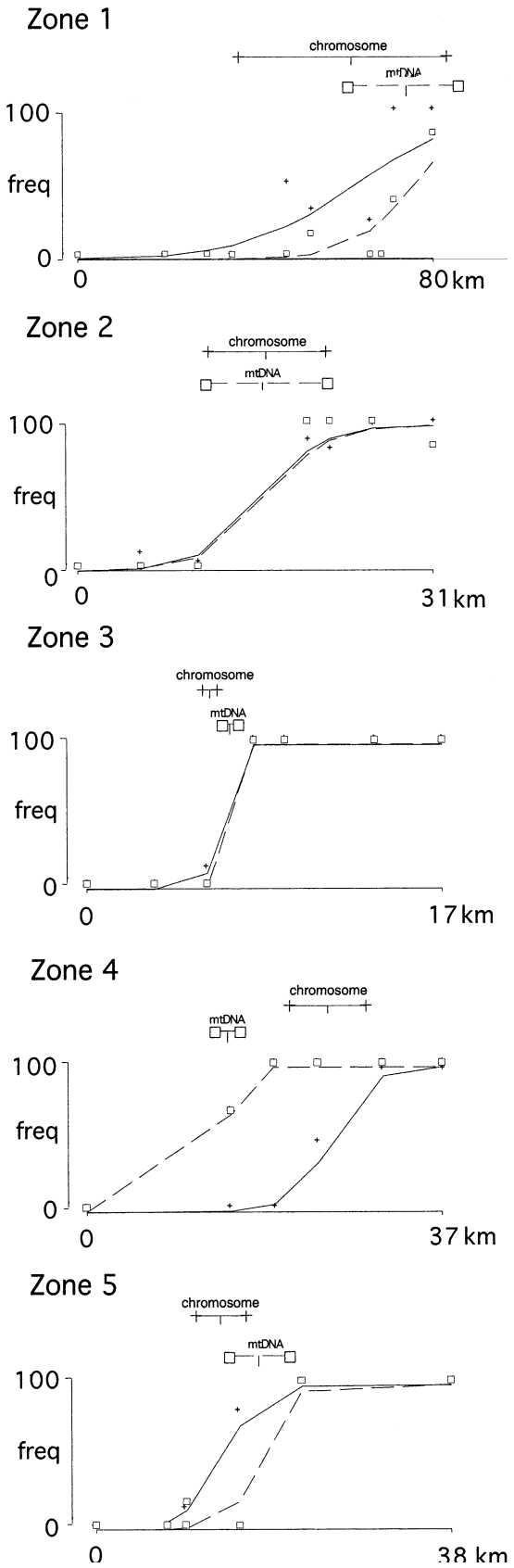

FIG. 3. Character clines across five hybrid zones of the weta *Hemideina thoracica*. Chromosome markers are indicated with crosses, mtDNA markers with open squares. Centers and widths of clines indicated above curves. Note that scales differ for the five zones.

have their widths determined by reduction in fitness of hybrids resulting from chromosome rearrangements (Shaw 1981; Harrison and Rand 1989; Butlin 1998). For example, the width of the hybrid zone between the Moreton and Torresian races of *Caledia captiva* on the eastern coast of Australia does not appear to be determined by the chromosome rearrangements even though evidence for karyotype selection has been found (Groeters and Shaw 1996). Although hybrid zone width may not be determined by the chromosome rearrangements in a number of studies, the chromosome clines themselves do seem to be influenced by chromosome heterozygote disadvantage. For example, in the Mexican lizard *Sceloporus grammicus*, narrow chromosome clines are apparently maintained by genomewide forces, whereas other nuclear markers have much wider clines (Marshall and Sites 2001). The hybrid zone between *Mus domesticus* and *M. musculus* in Denmark is maintained by NORII centromeric incompatibilities; selection detected against Rb fusions does not reduce gene flow, although it may maintain the chromosome cline (Fel-Clair et al. 1998). Within taxa there is some evidence that the width of chromosome clines varies according to the degree of karyotype differences but there are few chromosomally polymorphic taxa in which more than two independent zones have been studied. Both shrews and mice have been studied for multiple hybrid zones and a correlation between zone width and karyotypic differentiation seems to follow for races that belong to the same genetic group (Searle 1993; Searle and Wójcik 1998). In the grasshopper *C. captiva*, three hybrid zones suggest that cline width is determined by the level of genetic divergence rather than chromosome differentiation (Shaw et al. 1993). However, in pocket gophers, hybrid zone width is determined by patchiness of the available habitat rather than genetic (allozyme and chromosomal) or ecological differentiation of the two taxa (Patton 1993). In a comparison of four sunflower hybrid zones, Buerkle and Rieseberg (2001) concluded that intrinsic forces predominate in determining hybrid zone dynamics and boundaries.

The width of the five chromosome clines in five independent hybrid zones of *H. thoracica* varied considerably. As these clines all occur within the same morphological species we argue that their widths differ because of differences in the disadvantage suffered by hybrids rather than variable dispersal abilities of weta. The greater the karyotypic differences distinguishing the races, the lower the predicted fitness of the hybrids (Searle 1993; Spirito 1998) and the narrower the expected cline. This prediction was not met: the zones with the greatest proportion of their genome involved in multiple rearrangements (Zones 1 and 2) had wider clines than Zones 3, 4, and 5, in which single rearrangements involving small chromosomes differentiated the races. Where the least disadvantage due to meiotic disruption was predicted for hybrids, the narrowest clines for chromosome and mtDNA markers were measured (Zone 3; Table 4).

This variation in cline width may be because one or both of our assumptions are wrong: (1) the races differ in traits other than their karyotypes, or (2) there is habitat variation. Any differentiation among chromosomal races that reduces their compatibility (intrinsic), or could allow ecological selection (extrinsic), could affect cline width. Alternatively,

TABLE 4. Predicted relative zone widths based on degree of karyotype differentiation between chromosomal races at each zone and the observed relative cline widths for five independent hybrid zones of *Hemideina thoracica.*

Zone	Chromosomal races	Predicted relative zone width	Width of observed chromosome cline	Width of observed mtDNA cline	Clines	
					Concordant	Coincident
1	17♀ and 19	narrow	very wide	wide	no	no
2	23 and 19	narrow	medium	medium	yes	yes
3	19 and 17	wide	narrow	narrow	yes	yes
4	17 and 15♀	medium	medium	narrow	no	no
5	15 and 17	medium	medium	medium	yes	no

there may be problems with the data. The possible explanations suggested here are not mutually exclusive.

Chromosomes.—(1) Additional undetected chromosome rearrangements might differentiate the races where clines were narrower than expected. At four of the five zones, studies of meiosis in heterozygous males (which can detect rearrangements not visible by plain-staining) were possible and no evidence of such rearrangements was seen. At the narrowest zone (3), no male chromosomal heterozygotes were found. (2) Hybridization might result in an increased chromosomal mutation rate, which could disguise heterozygous weta and reduce the estimates of cline width (Shaw et al. 1983; Naveira and Fontdevila 1985; Morgan-Richards 1995). For example, where karyotypes differ in the number of pairs of small autosomes (Zones 1 and 3), duplication of unpaired autosomes in hybrids could produce parental-type karyotypes. (3) Zones could be wider than expected because of staggering of chromosome clines (Searle 1993; Gorlov and Tsurusaki. 2000). Zones 1 and 2 each involve two chromosome rearrangements in which the clines could be forced apart by selection against double heterozygotes. No evidence was found that the chromosome clines were staggered at Zone 1, in which single heterozygotes were very rare, but this could not be tested for Zone 2 because sampling was not possible in the center of the zone.

Width of zones.—The width of the hybrid zones might be determined by genetic factors not involving chromosome rearrangements (Shaw 1981). For example, shrew hybrid zones between races that belong to different karyotypic groups are much narrower than their degree of chromosome rearrangement would predict, and narrower than zones that involve similar numbers of Rb translocations between races that are genetically and morphologically more similar (Searle and Wójcik 1998). Similar cline estimates for both chromosomal and mitochondrial markers support the idea that the width of the hybrid zones in this species is determined by genomewide forces and not just chromosome heterozygote disadvantage. In addition, genetic changes that cause inviability may have occurred within chromosome rearrangements and could be held together by suppression of recombination (Noor et al. 2001; Rieseberg 2001). This model of chromosome-induced reproductive isolation is more likely to operate where inversions differentiate races because inversions are the only rearrangement commonly associated with crossover suppression. Only the chromosome races at the widest hybrid zone (Zone 1) of *H. thoracica* have been hypothesized to be differentiated by a chromosome inversion.

Age of the zones.—(1) A tension zone is maintained by a balance between hybrid disadvantage and dispersal, and the zone width should be constant once equilibrium is established. Where there is little or no selection against hybrids, shallow clines are expected. In such cases, cline width depends largely on dispersal rate and time since contact. Given enough time, the two populations might be expected to merge. The chromosome races involved in Zones 1 and 2 (17♀-karyotype, 19-karyotype and 23-karyotype) may have been in contact (on and off) since the beginning of the Pleistocene (Morgan-Richards et al. 2001a); sufficient time to completely mix if there were no selection against hybrids. Zones 1 and 2 are thought to have formed at the same time yet they differ in width by 37 km (chromosome cline) and 16 km (mtDNA cline). At Zone 5, on the other hand, the current contact between the two races can be no older than the last Taupo eruption, 2000 years ago (Morgan-Richards et al. 2000). Although chromosome and mitochondrial clines at Zones 1 and 2 are significantly wider than at Zone 5 (42 km, 20 km, 5 km, and 4 km, respectively), weta are able to move at least 80 m per generation (Morgan-Richards et al. 2000), so it would take only 1050 years to close this kind of gap. These results suggest that differential age of zones is unlikely to be a major explanation for the variable cline widths observed. (2) Selection may have resulted in reduced hybrid disadvantage for hybrids (opposite to reinforcement) so that the older zones in northern New Zealand (Zones 1 and 2) have reduced disadvantage compared to younger zones (Howard 1993; Butlin 1995). Selection may be expected to reduce the frequency of alleles that cause karyotypic heterozygotes to suffer a high frequency of meiotic anomalies (Shaw 1981) and select for reproductive compensation traits that counteract reduced output of gametes or embryo loss (Searle 1993). The widest zones (1 and 2) are probably the oldest of the zones studied here (Morgan-Richards et al. 2001a) but they differ signifi-

this study, no evidence of assortative mating was found, because samples that were polymorphic for karyotypes did not deviate from Hardy-Weinberg expectations.

Geographical barriers.—Geographical barriers such as the Waitangi River (Zone 3) may reduce dispersal and narrow the zone. However, rivers also occur at Zone 4, but do not seem to influence cline shape. Shrew chromosome hybrid zones are sometimes affected by rivers and sometimes not (Searle and Wójcik 1998).

Habitat.—Habitat may differ among the zones, which could alter dispersal rate. Pocket gophers form either unimodal or bimodal hybrid zones independent of the degree of genetic (allozymic and chromosomal) and ecological differentiation between parents, but associated with habitat patchiness (Patton 1993). All five zones studied are within 600 km of each other in lowland forest. Although there are no known changes in habitat over the zones it is possible human habitat modification has disturbed ecotones. For example, Zone 1 has something of the appearance of a mosaic hybrid

der stronger selection than the chromosome rearrangement; (2) mitochondrial introgression is prevented by asymmetric assortative mating; (3) there is sex-specific inviability; or (4) there are dispersal differences in the two sexes. The last explanation, that female weta may not disperse as far as males, is not in conflict with the little that is known of weta behavior. Adult male *Hemideina* defend cavities in trees where adult females shelter during the day. A male without a large cavity may travel farther to find one than would a female, and males may travel at night to mate with females that are feeding (Moller 1985, Field and Jarman 2001). However, if males do disperse farther than females, one would expect to see the same lack of nuclear and mitochondrial cline concordance at each weta hybrid zone. It is possible that weta behavior varies with density and/or habitat. None of the four explanations for why mtDNA clines are narrower than chromosome clines can yet be excluded.

Character clines with different centers suggest that there has been asymmetric gene flow, which could be caused by movement of the whole hybrid zone (e.g., *C. captiva*; Shaw et al. 1993) or asymmetric mating (Barton 1993). Nothing is known of the mating success of the various races of *H. thoracica*, so this possibility is worthy of further study. In addition, movement of the zones is possible for those zones without coincidence (Zones 1, 4, and 5), although we have no corroborating evidence for this. In chromosome hybrid zones of pocket gophers, female choice of large males seems to explain the asymmetrical mating between taxa and the introgression of mitochondrial DNA into only one of the two hybridizing taxa (Patton 1993). Tree weta have male-male competition for access to tree cavities and thus access to the females that use these daytime shelters, so there is potential for asymmetric mating if the races differ in body size. A size cline from smaller *H. thoracica* in northern New Zealand to larger weta in the south (M. Morgan-Richards, pers. obs.) has not been studied across the hybrid zones. In two of the three zones in which the clines have different centers (Zones 1 and 5), the mtDNA introgresses into the southern chromosome race, as would be expected if south–north size variation resulted in asymmetrical mating success.

Many hybrid zones have frequency clines that are not much wider than the dispersal ability of the organism involved (Barton and Hewitt 1985). For *H. thoracica*, dispersal has been estimated at a minimum of 80–110 m per generation (Morgan-Richards et al. 2000). At Zone 3, chromosome and mtDNA markers have frequency clines that are as narrow as this measure of dispersal. Zones 2, 4, and 5 have cline widths two orders of magnitude greater than dispersal, but not very different to cline widths given for other species with similar estimates of dispersal ability such as the grasshopper *Chorthippus parallelus* and the toad *Bombina bombina*/*variegata* (Barton and Hewitt 1985; Butlin 1998). However, the widths of chromosome and mtDNA clines at Zone 1 are almost three orders of magnitude greater than dispersal. It seems unlikely that dispersal is in fact much higher for these races in particular. Alternatively, the zone may have once lain on an ecotone that has since been disrupted by human modification, leading to widespread mixing.

Conclusions

We found that the proportion of the chromosome material involved in rearrangements at each zone fails to predict relative chromosome cline width. We also estimated that at five independent hybrid zones within *H. thoracica* mtDNA clines are either narrower or no wider than the chromosome clines. These two observations may be explained by chromosome markers at the widest of zones studied (Zones 1 and 2) being very close to neutral. It is implausible that at the wide zones the chromosome clines are as large as the weta's potential dispersal ability in the time since the races made contact. Cline width would therefore be determined by a variety of other characters not yet measured. In contrast, at one of the narrowest zones (5), clines of nuclear markers were wider than the chromosome clines, suggesting that chromosome markers might be limiting chromosome introgression through this zone (Morgan-Richards et al. 2000). Thus, even within a single species, the type and size of chromosome rearrangements cannot be used to predict fitness of hybrids. The two zones (1 and 2) in the north that we think both formed in the early Pleistocene differ significantly in their width. Loss of habitat may make it impossible to distinguish between possible explanations for their variation confounded by the likely repeated contact and isolation of the races involved during the sea level changes of the Pleistocene. In contrast, younger zones farther south may make excellent sites for future investigations. The narrow, concordant, coincident clines at Waitangi River (Zone 3) suggest that hybrid disadvantage may be limiting gene flow. Whether the karyotype differences that distinguish the races contribute to hybrid disadvantage at this zone remains to be seen.

Most hybrid zone studies involve one, (rarely) two (Flanagan et al. 1999), or four (Buerkle and Rieseberg 2001) transects across a single hybrid zone. A notable exception is a review of 14 well-studied shrew hybrid zones (Searle and Wójcik 1998). Because *H. thoracica* has many chromosomal races it was possible to compare independent zones within a single species. Even with just two markers studied for each of the five hybrid zones, an unexpected level of variation was found among zones. Barton and Hewitt (1985) concluded that most zones are similar in width to the dispersal ability of the animal involved. In our study, with a constant level of dispersal, we found zones that range in width by two orders of magnitude, a similar degree of variation to that observed in shrew hybrid zones. This disparity suggests fitness differences have a much greater role in determining zone width than how far weta and shrews can run, walk, and jump each generation. How true this is for other species may be worth investigation. As is the case with shrew chromosomal hybrid zones, only when the level of genetic divergence between races is similar is it possible to predict the relative fitness disadvantage that chromosome rearrangements will confer on hybrids.

Acknowledgments

The following helped to collect weta: S. Trewick, L. Turner, M. Frank, R. Pierce (New Zealand Department of Conservation), C. Tyrrell, A. Summers, M. Richards, A. Wild, and G. Gibbs. J. Girling, T. Blair and S. Berkeley helped

kill, measure, and dissect weta. The Leigh Marine Department Auckland University and Landcare (Mt. Albert) provided facilities during a collecting trip and the Department of Conservation provided permits to collect on conservation estate. N. H. Barton and S. Baird helped with cline analysis. D. Rowell, S. Trewick, J. Searle, and two anonymous reviewers provided very helpful comments on the manuscript, and J. Richards held the baby. This study was financed by the Marsden Fund administered by the Royal Society of New Zealand (contract PVT 601).

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