favor an increase or a decrease in reproductive isolation depending on the relative fitness advantages to the individual, and the initial allelic variation existing within the populations. Gene flow is likely to reduce genetic distinctiveness and thus increase competitive interactions, while diverging selection would favor traits that reduce competition. However, an equilibrium might develop where different factors have opposing outcomes, resulting

each hind tibia, ere recorded for each individual. Tubercles (small protuberances) in the position usuall occupied b prolateral spine IV in H. crassidens and H. trewicki ere recorded as half spines.

Evidence for the divergence of traits in regions of s mpatr as sought b comparing the si e of adults from allopatric and s mpatric populations. Character displacement theor predicts greater differentiation in s mpatr than in allopatr . Length of the left hind tibia as measured using electronic callipers accurate to 0.01 mm, as an indicator of overall bod si e (Minards et al. 2014). ANOVA as performed ith Tuke 's test to check for signi cant differences bet een population means using Minitab 16 Statistical soft are. The si e comparison used a sample of 65 adult females, because male tree ētā can mature at three different instars hereas females mature onl at the tenth (Kell and Adams 2010; Minards et al. 2014).

Cytogenetics

Wētā ere kar ot ped as previousl described (McKean et al. 2015). Both species pairs contain differences in the relative si es of their chromosomes allo ing differentiation of the three species (McKean et al. 2015). The kar ot pes of F_1 h brids ere predicted based on parental kar ot pes and compared to kar ot pes obtained from putative h brids. For the Mohi species pair (H. thoracica and H. trewicki), total chromosome number is the same, so F_1

		H. crassidens					*H. thoracica*					*H. trewicki*
	174					5	1	6	1			
	176								1			
	177		4			8	16					
	17						3		4	1		
	182							14				
	184						1					
	187			10	2							
35	224		7	6	16	3						
	227			1	6							
	228				2							
	230				3							
	231		3									
	233		2		1	1						1

PCR products ere sequenced using a capillar ABI3730 Genetic Anal er (Applied Bios stems Foster Cit , CA. USA). DNA sequences ere visuali ed and aligned in Geneious v6.1.7 (http:// .geneious.com; Kearse et al. 2012). For mtDNA haplot pes e used the integer neighbor-joining method (French et al. 2013) ith reticulation tolerance set to ero. This allo ed unequivocal assignment of each haplot pe to species clusters. Variation at nuclear loci as visuali ed using minimum spanning net orks (Bandelt et al. 1999). Net- orks ere generated using PopART (Population Anal - sis ith Reticulate Trees; Leigh and Br ant 2015). We used Fisher's e act test to determine hether the h brid mitochondrial haplot pes suggested a species bias of

mothers. Sequences are available at http://evolves.massey.ac.nz/DNA_Toolkit.htm.

Microsatellite loci

Sixteen microsatellite primer pairs developed for South Island species of tree hētā were trialled. Six loci that

indicate backcross h brids. In contrast, putative h brid ētā had the kar ot pe e pected in F_1 h brids bet een their respective parent species (Fig. 3). Female h brids (n = 4) did not provide mitotic cells as the all lacked ovarian material usuall used for c togenetic preparations.

Mitochondrial DNA sequences

Ne mitochondrial COI sequences (645 bp) ere obtained from 43 ētā and 12 haplot pes ere identi ed (Table 2). These data supplemented previousl haplot ped ētā individuals (Bulgarella et al. 2014). Haplot pe clusters corresponded ith the three species and t o distinct H. crassidens lineages (Fig. 4A). There as no evidence of mitochondrial haplot pe sharing among the three species. Eight out of nine putative H. thoracica and H. crassidens h brids had a H. crassidens haplot pe, from hich it can be inferred that the had an H. crassidens mother. Onl one putative h brid had a H. thoracica mtDNA haplot pe. This observation differs from e pectations of equal likelihood of the t o parent ta a being the mother (Fisher's e act test; P = 0.039). Haplot pe data are available http://evolves.masse .ac.n /Te t%20Files/DNA%20Toolkit.htm.

Nuclear loci

We obtained unambiguous sequences for each locus from 105 ēt¯

(Morgan-Richards 1995; Tre ick and Morgan-Richards 2004). At K = 3 (second highest support) the three species separated. The s mpatric populations comprised t o species' genot pe clusters as identi ed b phenot pe ith lo levels of introgression inferred from assignment prob-

e change; F_{ST} = 0.606 (Mohi) and 0.665 (Kahutera a). The distribution of alleles at t o loci provided evidence of potential introgression bet een species in Kahutera a (HR12, HR35; Table 2). For e ample the sample of Kahutera a H. thoracica had t o alleles that ere also found in H. crassidens but ere not observed in allopatric population samples of H. thoracica (alleles 242, 250; HR35 locus; Table 2). Our estimates of gene o bet een the species pairs ere ver lo , and not distinguishable from ero as inferred ith Ba esAss v3.0 (assuming neutralit ; Fig. 5).

Discussion

The tree ētā Hemideina thoracica meets and mates ith t o different related species and the long-term outcome of these t o ones of interspeci c h bridi ation ill be in uenced b the rate of gene o . Our data sho s that at Mohi H. thoracica and H. trewicki differ in si e. Hemideina thoracica adult females have longer hind tibia than H. trewicki, and longer tibia than conspeci cs at Kahutera a. In addition, the absence of adult H. thoracica during sampling at Mohi suggests a difference in developmental timing. Both these traits (si e and maturation timing) have the potential to contribute to reproductive isolation but are unlikel to prevent all mating (G nne and Jamieson 1998). Con rmation of an F_1 h brid collected from the ild demonstrates that these t o

lo , as ed differences ithin our samples ere found at t o nuclear loci, mitochondrial haplot pe and kar ot pe. The parent species appear to be retaining separate identities in s mpatr , so a bimodal h brid one appears to be the best description for the contact of H. thoracica and H. crassidens at Kahutera a. It is likel these species are differentiated enough to maintain their o n evolutionar trajectories in s mpatr , but e change of adaptive alleles cannot be ruled out (Jiggins and Mallet 2000). The similarit of phenot pe of H. thoracica and H. crassidens is likel to result in stronger interspeci c competition than bet een H. thoracica and H. trewicki. This nding is concordant ith the competitive e clusion h pothesis for H thoracica and H. crassidens based on distribution data, environmental modeling and genetic structure (Bulgarella et al. 2014). Hemideina thoracica has probabl displaced H. crassidens during the current interglacial as the range of H. thoracica has e panded south (Tre ick and Morgan-Richards 1995; Bulgarella et al. 2014).

None of the three species of tree ētā appeared to have complete premating barriers to reproduction. Fe F_1 h brids ere detected but this could be due purel to postmating (such as sperm competition) or post gotic selection (failure to hatch). Adults of H. thoracica have been observed in the same da time refuge cavities as adults of both H. crassidens and H. trewick (Tre ick and Morgan-Richards 1995, 2000; pers. obs). Even the difference in the timing of maturit bet een H. thoracica and H. trewicki is not enough to prevent some rst generation h brids being produced. Bimodal h brid ones are t picall associated ith strong pre-mating barriers (Jiggins and Mallet 2000; and references therein), although the bimodal h brid one bet een t o species of chr somelidae beetles is an e ception (Peterson et al. 2005). Further studies involving female mate choice are arranted in order to determine the relative roles of pre- and postmating barriers that result in so fe h brids in natural populations. Given the kar ot pe differences (McKean et al. 2015) chromosomal and other genetic constraints are likel to be involved in limiting F_1 fertilit .

Although the sample of H. thoracica × H. crassidens

Conflict of Interest

None declared.

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