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Genetic structure and dispersal patterns of the invasive psocid *Liposcelis decolor* (Pearman) in Australian grain storage systems

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Keywords

storage, structure, genetic, grain, australian, pearman, decolor, liposcelis, psocid, invasive, patterns, systems, dispersal

Disciplines

Life Sciences | Physical Sciences and Mathematics | Social and Behavioral Sciences

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Genetic structure and dispersal patterns of the invasive psocid *Liposcelis decolor* (Pearman) in Australian grain storage systems

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Abstract

Microsatellite markers were used to investigate the genetic structure among invasive *L. decolor* populations from Australia and a single international population from Kansas, USA to determine patterns of dispersal. Six variable microsatellites displayed an average of 2.5–4.2 alleles per locus per population. Observed (H_O) heterozygosity ranged from 0.12–0.65 per locus within populations; but, in 13 of 36 tests, H_O was less than expected. Despite low levels of allelic diversity, genetic structure estimated as θ was significant for all pairwise comparisons between populations ($\theta = 0.05$ –0.23). Due to suspected null alleles at four loci, *ENA* (excluding null alleles) corrected F_{ST} estimates were calculated overall and for pairwise population comparisons. The *ENA*-corrected F_{ST} values (0.02–0.10) revealed significant overall genetic structure, but none of the pairwise values were significantly different from zero. A Mantel test of isolation by distance indicated no relationship between genetic structure and geographic distance among all populations ($r^2 = 0.12$, $P = 0.18$) and for Australian populations only ($r^2 = 0.19$, $P = 0.44$), suggesting that IBD does not describe the pattern of gene flow among populations. This study supports a hypothesis of long distance dispersal by *L. decolor* at moderate to potentially high levels.

Keywords: microsatellites, gene flow, Psocoptera, Liposcelididae, *Liposcelis*, null alleles, Wahlund effect

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Introduction

Liposcelis decolor (Psocoptera: Liposcelididae) is an invasive psocid that is a major pest of stored grain and grain storage structures throughout Australia (Rees, 1998, 2004) and a minor pest of stored products internationally (Turner,

1994). Although sexually reproducing adult *L. decolor* are typically only 1.5 mm in length and apterous, under favourable climatic conditions, infestations are rapid and so severe that they are measured as 'hundreds of thousands of individuals per kilo' (Rees, 1994). *Liposcelis* infestations in Australian grain storage systems once represented less than 1% of invertebrate pest infestations requiring control in 1990, but increased to greater than 40% of infestations in 1996–97 (Rees, 1998). Since then, resistance to chemical control in *L. entomophila* and the severity of *L. decolor* infestations in South Australia has prompted their reclassification as major pests of stored grain in Australia (Nayak *et al.*, 1998).

Long distance dispersal is not uncommon among *Liposcelis* species and can occur either through air currents

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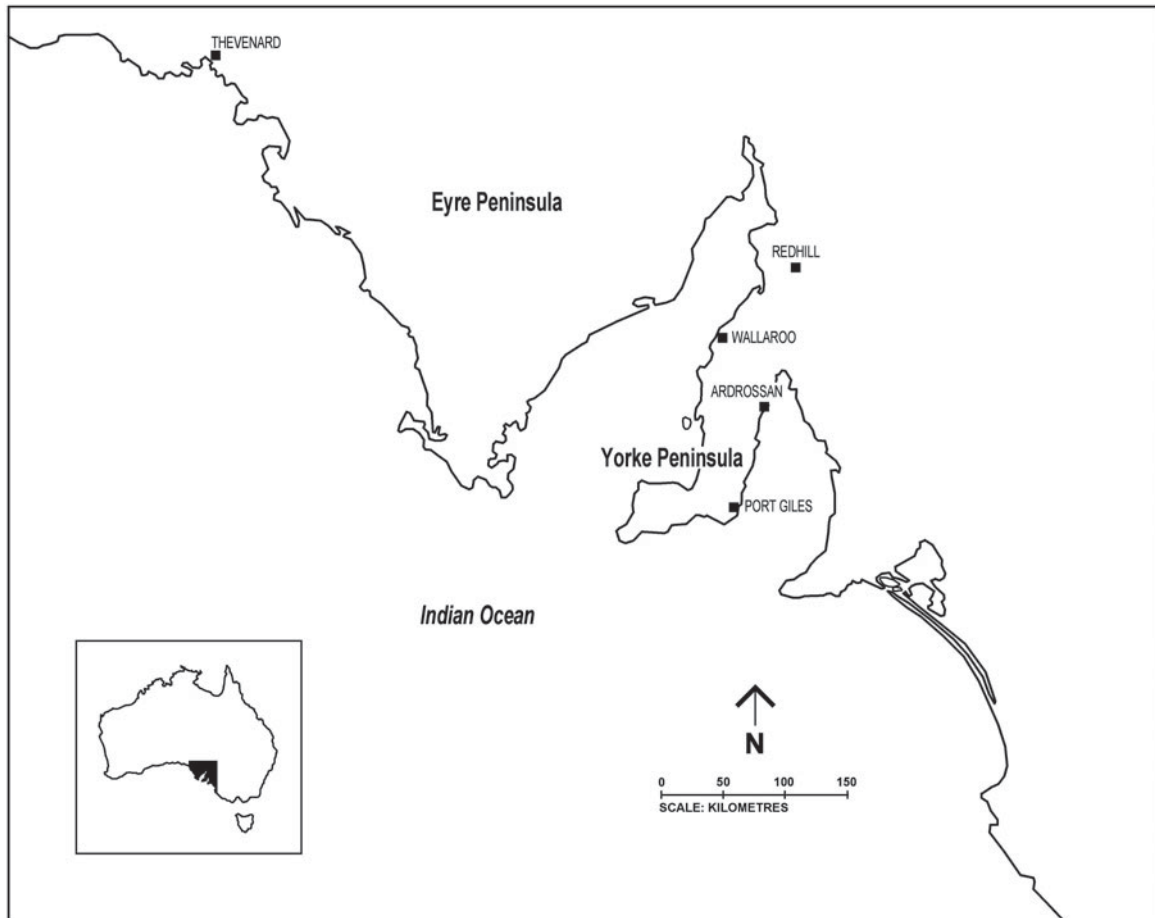


Fig. 1. Locations where *Liposcelis decolor* infestations were sampled within the South Australian export bulk grain storage sites at Thevenard, Wallaroo, Ardrossan and Port Giles and the regional storage site at Redhill.

and drifts (i.e. aerial plankton: Broadhead, 1950) or via the commercial trade of commodities internationally (Broadhead, 1954a,b) and in Australia (Stanaway *et al.*, 2001). It has recently been revealed that the cosmopolitan invasive psocid *L. bostrychophila*, despite also being apterous and small in size, is capable of unrestricted geographic dispersal in excess of 15,000 km through human-facilitated transport (Mikac & Clarke, 2006). The Australian grain storage system can be viewed as a series of networks of suitable habitat patches. The unintentional and unrestricted movement of individuals within these networks (via trucks, trains and ships) may be a key factor in the persistence of *Liposcelis* species there. Artificial dispersal and the resulting gene flow can increase the size and genetic diversity of local populations (e.g. Kolbe *et al.*, 2004) and facilitate the establishment of new populations.

In other invasive insect species, the elucidation of genetic structure and variation within and among geographically distant populations has provided insights into their migration pathways and gene flow (e.g. medfly *Ceratitis capitata*: Bonizzoni *et al.*, 2001). Through the use of microsatellite markers, such genetic insights can aid in the development of integrated approaches to management and control as demonstrated for the diamondback moth *Plutella xylostella*

in Australia (Endersby *et al.*, 2006), and western corn rootworm *Diabrotica virgifera virgifera* in the US (Kim & Sappington, 2005). The aim of this paper is to investigate the genetic structure of Australian *L. decolor* populations (and a single international population for comparison) to better understand dispersal patterns among these populations using microsatellite markers.

Materials and methods

Sample collection and processing

L. decolor infestations were sampled in South Australia at the bulk grain storage sites within the Port facilities of Ardrossan, Port Giles, Thevenard, Wallaroo and at the inland regional storage site Redhill (fig. 1). At each site, 50 crevice traps (150 mm × 150 mm) were systematically placed at 50 m intervals on each level of the facility, such that the whole facility was sampled. *L. decolor* samples were then pooled per location and randomly chosen individuals were subjected to genetic analyses. *L. decolor* were also sampled from a single population in Manhattan, Kansas, USA. A single population from Kansas, USA was included in this study as a representative sample of a possible extreme in

long distance dispersal with the Australian populations. Upon completion of the trapping period, individuals were removed, preserved in 100% ethanol, identified to species using the key of Mockford (1991) and stored at -20°C pending genetic analyses. Total genomic DNA was isolated from whole individual *L. decolor* from each population following methods described by Mikac (2006). Six polymorphic (GATA)_n microsatellite loci that had been identified from *L. decolor* DNA (Mikac, 2006) were used. PCR reactions were carried out in 12.5 μl volumes using 25 ng of DNA, 0.4 μM each primer, 0.2 mM each dNTP, 1 \times PCR buffer, 4 mM Mg^{2+} , 1 M Betaine, 0.50 \times bovine serum albumin (BSA) and 1 unit of *Taq* (New England Biolabs). PCR cycling was performed on a Corbett Research Palm Cycler, using an initial denaturation step of 94°C for 3 min (mins) followed by 40 cycles of 94°C for 30 s, 45°C 30 s and 72°C 30 s, with a final extension temperature of 72°C for 5 min.

The amplification products were run on a Corbett Research laser GelScan 2000 and visualized with CyberSafe using the following quality control practises. PCR assays were carried out using filter tips to eliminate the possibility of aerosol contamination from carryover products. Fragment size was inferred by comparison with a 50 base pair size ladder run in multiple lanes on each gel. A separate negative control was included in each set of PCR reactions as an indication of potential contamination. Multiple individuals from each population were genotyped twice to ensure correct scoring across gels.

Population structure and gene flow analysis in *L. decolor*

Allele sizing was performed using the ONEDScan gel documentation software (Scanalytics). Number of alleles and expected (H_E) and observed (H_O) heterozygosity and Weir & Cockerham's (1984) F_{IS} (inbreeding co-efficient) per locus were estimated using FSTAT 2.9.3 (Goudet, 2001). MICRO-CHECKER (van Oosterhout *et al.*, 2004) was used to test for the presence of null alleles per locus and population. Tests of fit to Hardy-Weinberg equilibrium (HWE) and genotypic linkage disequilibrium were performed using Markov chain methods (10,000 dememorizations, 500 batches, 10,000 iterations) in GENEPOP 3.4 (Raymond & Rousset, 1995a). The same method was used to test for significant differentiation (Fisher exact tests) among populations for all loci and population pairs. This test is considered relatively accurate for small sample sizes and low frequency alleles (Raymond & Rousset, 1995b). Weir & Cockerham's (1984) F_{ST} , estimated as θ , was calculated among population pairs using FSTAT version 2.9.3 (Goudet, 2001). Due to the presence of null alleles, further estimates of F_{ST} were recalculated in FFreeNA using the *ENA* (excluding null alleles) method described by Chapuis & Estoup (2007). The *ENA* method corrects for a positive bias in F_{ST} estimates when null alleles are present, thus providing a more accurate estimate of F_{ST} in the presence of null alleles (Chapuis & Estoup, 2007). Testing for isolation by distance was undertaken in FSTAT version 2.9.3 (Goudet, 2001) using a Mantel test to determine if there was a significant positive correlation between matrices of genetic differentiation as estimated by $F_{ST}(1/F_{ST}-1)$ and the natural logarithm (\ln) of geographic distance in kilometres among populations. Geographic distances between populations were based upon the distance between populations via transport corridors along roads, railroad tracks or across the sea. Evidence of recent bottlenecks was assessed for

populations using BOTTLENECK 1.2 (Cornuet & Luikart, 1996). This analysis incorporated a stepwise mutation model (SMM: Kimura & Ohta, 1978) and a two-phase model (TPM) (Di Rienzo *et al.*, 1994) in which 90% of the mutations follow the SMM, and 10% represent multistep changes (Estoup & Cornuet, 1999). Wilcoxon sign-rank tests (Luikart *et al.*, 1999) were used to determine whether deviations of observed heterozygosity relative to that expected at drift-mutation equilibrium were significant ($P < 0.05$). A mode shift in allele frequency distribution was used as an indicator of a population bottleneck (Luikart *et al.*, 1999).

Results

Genetic diversity

After correction for multiple tests ($n=75$), significant linkage disequilibrium was only detected for the paired loci Lip138/Lip169 and Lip130/Lip197 ($P < 0.05$). However, this only involved one population for the paired loci Lip138/Lip169 and two populations for Lip130/Lip197. Therefore, these loci were retained in all further analyses. The loci Lip73, Lip130, Lip138 and Lip197 displayed significant heterozygote deficiencies in 3–4 populations. After correction for multiple tests ($n=75$), each of these loci were found to be out of HWE. For these same loci, MICRO-CHECKER indicated the possible presence of null alleles in one to five of the five populations for which there were adequate data. Loci Lip117 and Lip169 did not differ from expectations of HWE and no null alleles were indicated.

Among the sampled populations, the number of alleles and allelic richness was low (table 1). The number of observed alleles ranged from one to six per locus with an average of 3.2 alleles across the six loci (table 1). Among populations, the number alleles ranged from one (Ardrossan for Lip117 for which only three of 56 individuals repeatedly PCR amplified) to six alleles (Thevenard and Kansas, USA for Lip73) per locus to produce average values of 2.5–4.2 alleles per locus per population (table 1). Mean F_{IS} values among populations ranged from 0.21 (Ardrossan) to 0.53 (Thevenard) (table 1). However, within populations, the F_{IS} values per locus often varied considerably (e.g. 0–1; Port Giles and Wallaroo). Heterozygosity estimates (H_O and H_E) were low to moderate across most populations (tables 1). Mean H_O per population ranged from 0.26 (Thevenard) to 0.36 (Redhill), while H_E ranged from 0.36 (Ardrossan) to 0.46 (Redhill) (table 1). In most cases (except Ardrossan for Lip73 and Port Giles for Lip130), if F_{IS} values were > 0.50 then H_O values were low and significantly out of HWE (table 1).

Population differentiation

Across all populations, θ estimates per locus ranged from 0.03–0.17, and across all loci θ was significantly different from zero ($\theta=0.12$, 95% CI 0.08–0.15), suggesting overall population differentiation (table 1). For each pairwise combination of populations, θ ranged from 0.05–0.23; and all values were significantly different from zero after correction for multiple tests ($n=15$, $P < 0.05$) (table 2). Likewise, *ENA*-corrected F_{ST} estimates over all loci and populations were significantly different from zero ($F_{ST}=0.11$, 95% CI 0.14–0.07). However, *ENA*-corrected F_{ST} estimates in pairwise population tests were consistently lower than the

Table 1. Number of alleles per locus, allelic richness and observed and expected heterozygosity at six microsatellite loci from six populations of *Liposcelis decolor* investigated: *n*, number of individuals scored per locus; # alleles, total number of alleles; *r*, allelic richness; F_{IS} , Weir & Cockerham's (1984) inbreeding coefficient; H_O , observed heterozygosity; H_E , expected heterozygosity; *, significant deviation from Hardy-Weinberg equilibrium.

Population	Microsatellite Loci						Mean
	Lip73	Lip117	Lip130	Lip138	Lip169	Lip197	
1. Ardrossan	<i>n</i> = 16	<i>n</i> = 3	<i>n</i> = 23	<i>n</i> = 31	<i>n</i> = 24	<i>n</i> = 12	18.16
# alleles	2	1	4	4	3	3	2.83
<i>r</i>	1.74	1.00	2.92	2.30	2.36	2.30	2.10
F_{IS}	0.61	0	0.61	0.18	-0.33	0.01	0.21
H_O	0.13	0.00	0.26	0.42	0.71	0.50	0.34
H_E	0.30	0.00	0.65*	0.50	0.53	0.49	0.36
2. Port Giles	<i>n</i> = 37	<i>n</i> = 12	<i>n</i> = 42	<i>n</i> = 34	<i>n</i> = 46	<i>n</i> = 20	31.80
# alleles	4	2	4	3	3	3	3.17
<i>r</i>	3.22	1.25	2.70	2.65	2.64	1.85	2.38
F_{IS}	1	0	0.84	0.35	-0.21	0.19	0.46
H_O	0.00	0.08	0.10	0.41	0.76	0.25	0.27
H_E	0.72*	0.08	0.58	0.63	0.62	0.30	0.44
3. Thevenard	<i>n</i> = 29	<i>n</i> = 29	<i>n</i> = 22	<i>n</i> = 50	<i>n</i> = 29	<i>n</i> = 23	30.33
# alleles	6	5	4	4	3	3	4.17
<i>r</i>	3.23	2.01	2.75	2.39	2.05	2.45	2.48
F_{IS}	0.85	0.39	0.65	0.58	-0.03	0.52	0.53
H_O	0.10	0.21	0.23	0.24	0.52	0.26	0.26
H_E	0.70*	0.33	0.63*	0.57*	0.49	0.53*	0.43
4. Wallaroo	<i>n</i> = 28	<i>n</i> = 18	<i>n</i> = 40	<i>n</i> = 40	<i>n</i> = 40	<i>n</i> = 23	31.5
# alleles	3	2	2	2	3	3	2.50
<i>r</i>	2.66	1.88	1.43	1.96	2.69	2.23	2.14
F_{IS}	1	0.46	0.53	-0.38	0.04	0.74	0.40
H_O	0.00	0.22	0.08	0.68	0.63	0.13	0.29
H_E	0.63*	0.40	0.16	0.48	0.65	0.49*	0.38
5. Redhill	<i>n</i> = 18	<i>n</i> = 23	<i>n</i> = 32	<i>n</i> = 47	<i>n</i> = 49	<i>n</i> = 20	31.5
# alleles	3	2	4	3	3	3	3.00
<i>r</i>	2.67	1.52	2.71	2.40	2.22	2.36	2.31
F_{IS}	-0.30	0.34	0.75	0.63	-0.35	0.74	0.31
H_O	0.83	0.13	0.16	0.21	0.67	0.15	0.36
H_E	0.63	0.19	0.63*	0.57*	0.49	0.57*	0.46
6. Kansas, USA	<i>n</i> = 23	<i>n</i> = 34	<i>n</i> = 26	<i>n</i> = 32	<i>n</i> = 47	<i>n</i> = 20	30.3
# alleles	6	3	4	3	3	2	3.50
<i>r</i>	2.20	1.48	2.47	2.29	2.48	1.93	2.14
F_{IS}	0.11	0.29	0.86	0.72	-0.16	0.57	0.41
H_O	0.48	0.12	0.08	0.16	0.66	0.20	0.28
H_E	0.53	0.16	0.54*	0.55*	0.56	0.46	0.43
Overall							
<i>n</i>	151	119	185	234	235	118	173.6
# alleles	6	7	4	4	3	3	4.5
H_O	0.25	0.12	0.14	0.35	0.65	0.24	0.29

estimated uncorrected θ , and none were significantly greater than zero (table 2).

A Mantel test of isolation by distance (IBD) revealed no relationship between Slatkin's (1995) linearized F_{ST} ($F_{ST}(1/F_{ST}-1)$) and the ln of geographic distance in kilometres for all populations ($r^2=0.12$, $P=0.18$) and for Australian populations only ($r^2=0.19$, $P=0.44$), suggesting that IBD does not describe the pattern of gene flow among populations. Similarly, *ENA*-corrected F_{ST} data did not indicate an IBD effect for all populations ($r^2=0.06$, $P=0.40$) and for Australian populations only ($r^2=0.005$, $P=0.83$). Additional tests conducted for all populations, but restricted to loci without null alleles (i.e. Lip117 and Lip169) also revealed no IBD relationship ($r^2=0.05$, $P=0.38$).

Tests for population bottlenecks using Wilcoxon tests were significant ($P<0.05$) for the Ardrossan, Port Giles, Wallaroo and Redhill populations. These populations all

displayed mode shifts of allele distribution, a qualitative indication of recent bottleneck events.

Discussion

This study reveals a low to moderate level of genetic structure among distant *L. decolor* populations, thus supporting a hypothesis of long distance dispersal. This likely results from genetic exchange and successful colonisation among established populations within the Australian grain storage network. There was evidence of moderate levels of gene flow across different geographic scales, resulting in a lack of isolation by distance among populations within Australia and in comparison with a distant population (i.e. Kansas, USA). Human-mediated dispersal is the most effective means of dispersal for many insects such as *Liposcelis* species that are preadapted to an invasive lifestyle,

Table 2. Pairwise estimates of Weir & Cockerham's (1984) θ (F_{ST}), ENA-corrected F_{ST} across all loci (Chapuis & Estoup, 2007) and approximate geographic distances (km). Values in bold were significant after corrections for multiple tests ($n=15$, $P<0.05$).

	θ	ENA-corrected F_{ST} across all loci	Distance (km)
Ardrossan			
vs Port Giles	0.07	0.03	73.5
vs Thevenard	0.08	0.05	726
vs Wallaroo	0.23	0.07	68.8
vs Redhill	0.13	0.07	124
vs Kansas, USA	0.13	0.07	15,200
Port Giles			
vs Thevenard	0.05	0.04	800
vs Wallaroo	0.15	0.04	140
vs Redhill	0.10	0.03	197
vs Kansas, USA	0.10	0.03	15,200
Thevenard			
vs Wallaroo	0.21	0.10	670
vs Redhill	0.08	0.04	604
vs Kansas, USA	0.10	0.04	15,400
Wallaroo			
vs Redhill	0.21	0.09	92
vs Kansas, USA	0.14	0.08	15,200
Redhill			
vs Kansas, USA	0.05	0.02	15,100

due to their minute size, ubiquity, polyphagy and tolerance to a wide range of temperature and humidity levels (Broadhead, 1954a,b; Turner, 1994; Rees, 1998; Mikac & Clarke, 2006).

A surprising result was the relatively low level of genetic variation in *L. decolor* (table 1) given that the species reproduces sexually and infestations are known to occur as 'hundreds of thousands of individuals per kilo' (Rees, 1994), thus suggesting very large effective population sizes. This is in contrast to moderate to high levels of genetic variation found in *L. bostrychophila* populations from the UK using allozymes (Ali & Turner, 2001) and Australian and international populations of *L. bostrychophila* using randomly amplified polymorphic DNA (RAPDs) (Mikac & Clarke, 2006). Nevertheless, using microsatellite markers, low levels of genetic variation have been found for other invasive insects with large effective population sizes, including the tephritid fruitflies *Ceritis capitata* (Casey & Burnell, 2001) and *Bactrocera papayae* (Shearman *et al.*, 2006). In *L. decolor* populations, low genetic diversity resulting from repeated chemical control in line with set management practices in individual grain storage facilities is expected as this process removes a significant portion of the individuals in a population (e.g. Pratt & Reuss, 2004); our results suggest that these measures may be strong enough to reduce genetic diversity and induce a bottleneck on a population once control has ceased. It is not surprising, then, that significant bottlenecks were detected in the majority of populations investigated (i.e. Ardrossan, Port Giles, Wallaroo and Redhill). These bottlenecks may have contributed to the relatively low heterozygosity and to the moderate to high F_{IS} values found for most populations (table 1), similar to findings of Colautti *et al.* (2005) for the Eurasian spiny waterflea *Bythotrephes longimanus*. In the Argentine ant

Linepithema humile, bottlenecks were responsible for an increase in their invasion success in their introduced range through the loss of alleles associated with intraspecific aggression (Tsutsui *et al.*, 2000). It is possible that *Liposcelis* invasion success could in part be attributed to the cumulative loss of alleles that may have once hindered their invasion success, leaving individuals that are best able to survive and adapt to life in grain storage environments, as discussed by Ali & Turner (2001) for *L. bostrychophila*.

Alternatively, apparently low levels of genetic variation and significant deviation from HWE in this study could have been caused by the presence of null alleles or a Wahlund effect. Null alleles typically occur through PCR amplification failure of alleles at specific loci, which is thought to be caused by sub-optimal PCR conditions, degraded samples, insufficient DNA quantities or mutations in primer binding sites (Selkoe & Toonen, 2006), and some of these factors could have influenced our results. However, it is unlikely that significant deviation from HWE could have been exclusively caused by null alleles because the microsatellite loci cross-amplified in five other *Liposcelis* species (Mikac, 2006). Although relatively few problems were associated with RAPD PCR amplification of *L. bostrychophila* (Mikac & Clarke, 2006), *L. decolor* proved to be extremely difficult to amplify at microsatellite loci (Mikac, 2006), thus suboptimal PCR conditions or DNA yield may have resulted in a proportion of the null alleles. Additionally, the microsatellite markers were developed (Mikac, 2006) from a single Australian population (i.e. Roseworthy, South Australia) that was not investigated in this study and that does not experience similar infestation levels or population fluctuations as the six populations investigated in this study. It has been noted that large effective population sizes typically result in higher frequencies of null alleles due to flanking sequence mutations (Chapuis & Estoup, 2007). Therefore, the large effective population sizes of the six populations investigated here may have contributed to the high frequency of null alleles detected, in comparison to initial investigations by Mikac (2006) that did not observe null alleles using the same loci. Given that four of six *L. decolor* microsatellite loci were found to be out of HWE and were also shown by MICRO-CHECKER to possibly contain null alleles, we estimated F_{ST} using loci with or without probable null alleles and used corrected ENA- F_{ST} estimates (Chapuis & Estoup, 2007). Overall estimates of F_{ST} did not vary substantially as a result of probable null alleles, but may have lead to an overestimate of F_{ST} values among population estimates of F_{ST} (table 2). Thus, the probable presence of null alleles in the data set would have reduced the estimates of genetic diversity and possibly reduced estimates of gene flow (table 2). However, in the two loci (Lip117 and Lip169) for which there was no evidence of null alleles, all measures of genetic diversity were similarly low. In future studies of *Liposcelis* species using the microsatellites developed by Mikac (2006), sequencing of the microsatellite flanking regions (to investigate possible flanking sequence mutations) should be conducted to further investigate the cause of suspected null alleles.

Tests for IBD were not significant, thus reinforcing the need to analyse the specifics of human-mediated transport of *L. decolor* over short and long distances within the Australian grain storage network. The unintentional movement of *L. bostrychophila* within the Australian grain storage network (via trucks, trains and ships) is a key factor in its persistence

(Mikac & Clarke, 2006) and potentially the persistence of *L. decolor* as well. Some of the estimates of genetic structure among the port storage sites investigated are consistent with the manner in which grain is shipped from South Australia for export. Among South Australian populations, the major port facility for central and western Eyre Peninsula at Thevenard, had one of the lowest levels of differentiation with Port Giles, the major port facility for southern Yorke Peninsula, despite their 800 km geographic separation (fig. 1, table 2). Indeed, these populations were less divergent than Ardrossan and Port Giles, which are 73 km apart, or Wallaroo and Port Giles, 140 km apart (fig. 1, table 2). However, differences in genetic structure between these later two examples were not unexpected since there is very limited transportation of grain between these sites. Port Adelaide (not sampled in this study) is the major grain port for the whole of eastern South Australia, and grain from most of Yorke Peninsula is directly transported to Port Adelaide. Genetic divergence among Australian populations and the single USA population from Kansas was moderate with one pairwise comparison showing little genetic differentiation (Redhill versus Kansas, USA; table 2). Grain commodity trading between the USA and Australia is not uncommon, and gene flow between these countries is possible and has probably occurred historically for *L. decolor*, as demonstrated by RAPDs for *L. bostrychophila* (i.e. gene flow among South Australian and Kansas, USA populations was found by Mikac & Clarke (2006)). Indeed, it has been speculated that the current distribution of *Liposcelis* pest species (i.e. *L. bostrychophila*, *L. decolor* and *L. entomophila*) in Australia was assisted by humans during the movement of grain throughout Australia (Rees, 1994), particularly as the grain storage network is well connected by train, roads and seaports. Broadhead (1950) suggested that long distance dispersal was not uncommon among *Liposcelis* species, as they had been discovered as aerial plankton 300 m above ground. It is more likely, though, that the commercial trade of commodities is a more effective and reliable dispersal mechanism given that *Liposcelis* species were documented five decades previously from the UK in shipped commodities and shipping warehouses (Broadhead, 1954a,b). Recently, *Liposcelis* species have been found in import shipping containers at Port Brisbane, Australia, proving further evidence of their assisted dispersal via human trade routes (Stanaway *et al.*, 2001). Due to a relatively long life span (4–10 months for *L. bostrychophila*: Turner, 1994), *Liposcelis* species can persist within the grain storage system for extended periods. Individuals can lie dormant until a suitable habitat and favourable abiotic conditions trigger heavy infestations, as frequently occurs in South Australia, particularly Thevenard (Rees, 1994). Modern worldwide travel and transport is such that any continent's grain storage system can be reached within a short period of time, thus allowing *Liposcelis* species to disperse and establish populations with ease. This is supported by low to moderate levels of genetic differentiation among global populations of *L. decolor* and *L. bostrychophila* (Mikac & Clarke, 2006) associated with global grain storage systems.

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