

Table 4.8: Genotype-environment interaction in early life-history traits (DT, BWT and GR) measured on males. The genetic correlations across each pairing of laboratory temperatures are given for the Standard Family Mean, Spearman's Rank, Robertson's and Yamada's methods. Significant F-ratios from the ANOVAs are also presented.

Trait	Temps (°C)	Standard Family Mean	Spearman's Rank	Method of Robertson	Method of Yamada	ANOVA
DT	21 - 25	0.181	0.166	0.200	-0.821	***
	21 - 29	0.150	0.011	0.325	-0.352	***
	21 - 33	0.286	0.243	0.347	-0.287	***
	21 - 37	0.034	0.052	0.119	-1.000	***
	25 - 29	0.664	0.625	0.762	0.727	***
	25 - 33	0.792	0.812	0.900	0.894	**
	25 - 37	0.661	0.675	0.762	0.729	***
	29 - 33	0.727	0.682	0.838	0.821	***
	29 - 37	0.634	0.650	0.735	0.693	***
	33 - 37	0.723	0.736	0.826	0.808	***
BWT	21 - 25	0.656	0.605	0.929	0.911	NS
	21 - 29	0.667	0.649	0.861	0.820	***
	21 - 33	0.631	0.576	0.789	0.710	***
	21 - 37	0.637	0.559	0.789	0.712	***
	25 - 29	0.889	0.883	1.002	1.000	NS
	25 - 33	0.860	0.828	0.946	0.944	*
	25 - 37	0.880	0.824	0.974	0.974	NS
	29 - 33	0.907	0.888	0.969	0.968	NS
	29 - 37	0.865	0.837	0.934	0.932	**
	33 - 37	0.915	0.880	0.995	0.995	NS
GR	21 - 25	0.515	0.468	0.595	0.363	***
	21 - 29	0.596	0.500	0.679	0.525	***
	21 - 33	0.524	0.464	0.549	0.260	***
	21 - 37	0.371	0.315	0.377	-0.181	***
	25 - 29	0.853	0.858	0.934	0.931	*
	25 - 33	0.869	0.872	0.938	0.936	*
	25 - 37	0.847	0.835	0.909	0.905	**
	29 - 33	0.904	0.896	0.962	0.961	*
	29 - 37	0.871	0.826	0.925	0.921	**
	33 - 37	0.911	0.894	0.969	0.968	NS

* $P < 0.05$, ** $P < 0.01$, *** $P < 0.001$, NS = non-significant

Note: For the ANOVAs DT, BWT and GR were \log_{10} transformed. For

Robertson's and Yamada's methods, the transformed data were also converted into standard measure.

Table 4.9: Genotype-environment interaction in early life-history traits (DT, BWT, GR and EPEAK) measured on females. The genetic correlations across each pairing of laboratory temperatures are given for the Standard Family Mean, Spearman's Rank, Robertson's and Yamada's methods. Significant F-ratios from the ANOVAs are also presented.

Trait	Temps (°C)	Standard Family Mean	Spearman's Rank	Method of Robertson	Method of Yamada	ANOVA
DT	21 - 25	0.066	0.027	0.130	-1.000	***
	21 - 29	0.046	-0.026	0.171	-0.955	***
	21 - 33	0.279	0.223	0.339	0.601	***
	21 - 37	0.189	0.141	0.241	-0.586	***
	25 - 29	0.628	0.660	0.728	0.683	***
	25 - 33	0.833	0.846	0.931	0.928	**
	25 - 37	0.800	0.795	0.880	0.871	***
	29 - 33	0.601	0.570	0.719	0.671	***
	29 - 37	0.714	0.712	0.825	0.806	***
33 - 37	0.840	0.822	0.949	0.947	NS	
BWT	21 - 25	0.856	0.809	1.016	1.000	NS
	21 - 29	0.777	0.706	0.918	0.897	*
	21 - 33	0.765	0.762	0.855	0.813	***
	21 - 37	0.793	0.776	0.985	0.983	NS
	25 - 29	0.899	0.858	1.009	1.000	NS
	25 - 33	0.895	0.866	0.997	0.997	NS
	25 - 37	0.883	0.883	1.025	1.000	NS
	29 - 33	0.890	0.841	0.968	0.967	NS
	29 - 37	0.771	0.744	0.889	0.882	**
33 - 37	0.788	0.752	0.892	0.885	**	
GR	21 - 25	0.579	0.473	0.601	0.379	***
	21 - 29	0.494	0.360	0.529	0.217	***
	21 - 33	0.548	0.492	0.536	0.242	***
	21 - 37	0.454	0.354	0.458	0.076	***
	25 - 29	0.895	0.845	0.979	0.979	NS
	25 - 33	0.937	0.923	1.014	1.000	NS
	25 - 37	0.920	0.909	1.024	1.000	NS
	29 - 33	0.870	0.815	0.932	0.929	**
	29 - 37	0.819	0.784	0.904	0.898	**
33 - 37	0.882	0.832	0.952	0.951	*	
EPEAK	21 - 25	0.253	0.323	0.399	-0.179	***
	21 - 29	0.143	0.190	0.195	-0.968	***
	21 - 33	0.186	0.252	0.364	-0.285	***
	21 - 37	-0.045	-0.032	0.365	-0.276	*
	25 - 29	0.790	0.850	0.922	0.919	NS
	25 - 33	0.694	0.653	0.870	0.861	NS
	25 - 37	0.541	0.545	0.794	0.770	NS
	29 - 33	0.665	0.689	0.840	0.827	NS
	29 - 37	0.420	0.482	0.506	0.343	**
33 - 37	0.618	0.606	0.931	0.928	NS	

* $P < 0.05$, ** $P < 0.01$, *** $P < 0.001$, NS = non-significant

Note: For the ANOVAs DT, BWT and GR were \log_{10} transformed and EPEAK square root transformed. For Robertson's and Yamada's methods, the transformed data were also converted into standard measure.

Table 4.10: Genotype-environment interaction in early life-history traits (DT, BWT, GR and EPEAK) for males and or females. The genetic correlation across five laboratory temperatures (21°, 25°, 29°, 33° and 37°C) using the methods of Robertson and Yamada are given. Significant interactions from the ANOVAs are also presented.

	Method of Robertson	Method of Yamada	ANOVA
Males			
DT	0.645	0.610	***
BWT	0.933	0.931	***
GR	0.830	0.820	***
Females			
DT	0.657	0.625	***
BWT	0.957	0.956	**
GR	0.844	0.835	***
EPEAK	0.676	0.646	***

* $P < 0.05$. ** $P < 0.01$. *** $P < 0.001$

Note: For the ANOVAs DT, BWT and GR were \log_{10} transformed and EPEAK square root transformed. For Robertson's and Yamada's methods the transformed data were also converted into standard measure.

Table 4.11: Genotype-environment interaction in early life-history traits (DT, BWT, GR and EPEAK) for males and/or females. The genetic correlation across four laboratory temperatures (25°, 29°, 33° and 37°C) using the methods of Robertson and Yamada are given. Significant interactions from the ANOVAs are also presented.

	Method of Robertson	Method of Yamada	ANOVA
Males			
DT	0.806	0.795	***
BWT	0.970	0.969	**
GR	0.940	0.939	***
Females			
DT	0.837	0.830	***
BWT	0.966	0.965	**
GR	0.969	0.969	**
EPEAK	0.812	0.802	**

* $P < 0.05$. ** $P < 0.01$. *** $P < 0.001$

Note: For the ANOVAs DT, BWT and GR were \log_{10} transformed and EPEAK square root transformed. For Robertson's and Yamada's methods the transformed data were also converted into standard measure.

Table 4.12: The intra-locality product-moment correlation coefficients (r) between DT and BWT in males measured at five laboratory temperatures. Sample sizes are given in parentheses.

Popn	Temperature									
	21°C		25°C		29°C		33°C		37°C	
CLER	0.90	(3)	0.36**	(57)	0.30*	(44)	0.38**	(46)	0.47***	(47)
EM		(2)	0.23	(45)	0.05	(29)	0.00	(42)	0.57***	(38)
ROLL	0.62	(8)	0.18	(40)	0.23	(42)	0.11	(45)	0.30	(43)
BIL	0.49*	(19)	0.17	(48)	0.11	(36)	0.21	(26)	0.27	(45)
MONT	0.22	(26)	0.37*	(38)	0.34*	(40)	0.36*	(34)	0.57***	(39)
MUND	0.83**	(10)	0.21	(41)	0.09	(45)	0.24	(43)	0.58***	(33)
C.L.	0.68**	(14)	0.46**	(40)	0.17	(55)	0.03	(32)	0.19	(44)
GAY	-0.07	(15)	0.57***	(41)	-0.02	(39)	-0.28	(44)	0.49***	(43)
TANS	-0.16	(19)	0.68***	(36)	0.13	(30)	-0.20	(24)	0.51**	(31)
GOOM	0.48*	(25)	0.48***	(44)	0.20	(47)	-0.04	(45)	0.16	(32)
KING	0.33	(10)	0.30	(42)	0.20	(40)	0.25	(43)	0.40**	(43)
DALB	0.02	(14)	0.06	(40)	0.17	(39)	-0.02	(48)	0.19	(47)
C.P.	-0.13	(31)	0.39**	(44)	0.24	(52)	0.47**	(43)	0.40**	(43)
LEYB	0.47*	(28)	0.25	(41)	0.19	(44)	-0.11	(53)	0.55***	(45)
GOON	0.12	(32)	0.61***	(42)	0.06	(43)	0.12	(34)	0.35*	(36)
WAR	0.21	(15)	0.41*	(36)	0.45**	(44)	0.21	(41)	0.20	(43)
INV	-0.28	(26)	-0.21	(39)	0.22	(41)	0.03	(43)	0.50**	(33)
TAM	0.67***	(25)	0.28	(36)	0.14	(34)	-0.12	(39)	0.29	(32)
CAR	0.55***	(34)	0.18	(47)	-0.43**	(43)	-0.00	(44)	0.31	(38)
COOL	0.55***	(37)	0.13	(45)	0.43**	(43)	0.07	(51)	0.16	(51)
DUN	0.08	(14)	-0.09	(39)	0.20	(41)	-0.14	(42)	0.13	(42)
WELL	0.27	(9)	0.44**	(43)	0.59***	(39)	0.41**	(42)	0.35*	(39)
OR	-0.07	(23)	0.34	(34)	0.04	(51)	-0.45***	(56)	-0.09	(40)
COW	0.17	(15)	-0.13	(41)	-0.43**	(42)	-0.05	(42)	0.18	(42)
BARM	0.42	(18)	0.48**	(41)	-0.23	(36)	-0.26	(38)	0.60***	(40)
TEM	0.43	(17)	0.49**	(33)	-0.34*	(50)	-0.09	(38)	-0.37**	(50)
MANG	-0.06	(16)	0.01	(46)	-0.24	(40)	-0.36**	(55)	0.03	(45)
Y.C.	0.15	(35)	0.01	(49)	-0.39*	(42)	0.38*	(39)	-0.37**	(41)
COOK	0.11	(41)	0.25	(42)	0.13	(52)	-0.23	(39)	0.11	(43)
HOLB	0.15	(19)	0.38*	(44)	-0.08	(54)	0.26	(35)	0.34*	(42)
MULL	0.37	(17)	0.13	(41)	0.12	(46)	-0.16	(45)	0.57***	(44)
BEN	0.67***	(26)	0.54***	(42)	0.03	(40)	0.11	(40)	0.26	(50)
MANS	0.18	(26)	-0.35*	(41)	0.23	(50)	-0.09	(52)	0.66***	(41)
DROM	0.17	(36)	-0.27	(36)	0.32*	(44)	0.14	(46)	0.17	(37)

* $P < 0.05$. ** $P < 0.01$. *** $P < 0.001$

Table 4.13: The intra-locality product-moment correlation coefficients (r) between DT and BWT in females measured at five laboratory temperatures. Sample sizes are given in parentheses.

Popn	Temperature									
	21°C		25°C		29°C		33°C		37°C	
CLER	0.75	(3)	0.27	(36)	0.44**	(45)	0.35*	(37)	0.33*	(40)
EM	0.13	(4)	0.28	(35)	0.35*	(43)	0.50***	(41)	0.40**	(44)
ROLL	0.20	(9)	0.43**	(42)	-0.08	(44)	0.12	(36)	0.61***	(37)
BIL	0.20	(20)	0.18	(37)	0.11	(50)	0.18	(57)	0.62***	(40)
MONT	0.41*	(27)	0.27	(50)	-0.14	(47)	0.42**	(48)	0.63***	(40)
MUND	0.58	(11)	0.12	(42)	-0.02	(35)	0.40*	(29)	0.44**	(43)
C.L.	0.29	(18)	0.60***	(46)	-0.09	(42)	0.16	(50)	0.55***	(46)
GAY	0.35	(26)	0.31*	(41)	0.11	(43)	0.58***	(33)	0.44*	(34)
TANS	0.23	(22)	0.63***	(41)	-0.12	(41)	0.26	(49)	0.32	(36)
GOOM	-0.26	(30)	0.16	(42)	-0.06	(40)	0.36*	(40)	0.42**	(39)
KING	0.17	(12)	0.55***	(44)	0.25	(43)	0.00	(43)	0.53**	(36)
DALB	0.14	(25)	0.32*	(42)	-0.04	(47)	0.21	(36)	-0.03	(37)
C.P.	-0.12	(29)	0.23	(47)	0.21	(39)	0.21	(44)	0.45**	(41)
LEYB	0.15	(37)	0.45**	(39)	-0.13	(46)	0.44**	(39)	0.70***	(46)
GOON	0.36*	(34)	0.24	(42)	0.08	(40)	0.35*	(39)	0.66***	(30)
WAR	0.06	(18)	0.34*	(41)	0.29	(38)	0.30	(30)	0.54**	(27)
INV	0.11	(21)	0.18	(41)	0.24	(44)	0.18	(40)	0.57***	(38)
TAM	0.47*	(27)	0.19	(32)	0.13	(27)	0.33	(35)	0.61***	(31)
CAR	0.36	(28)	0.50**	(38)	0.33*	(46)	0.45**	(41)	0.61***	(38)
COOL	0.34*	(34)	-0.14	(37)	0.15	(54)	0.17	(41)	0.45**	(39)
DUN	0.54	(8)	-0.04	(44)	-0.02	(54)	-0.30*	(43)	-0.06	(45)
WELL	0.03	(10)	-0.02	(44)	0.23	(48)	0.26	(44)	0.33*	(44)
OR	-0.02	(19)	0.07	(51)	0.01	(38)	0.15	(38)	0.15	(42)
COW	0.56*	(17)	0.24	(37)	-0.20	(42)	0.17	(44)	0.44**	(35)
BARM	0.44*	(29)	0.40*	(38)	0.19	(32)	-0.07	(45)	0.52***	(37)
TEM	0.41	(11)	0.30*	(52)	0.34*	(38)	0.05	(48)	0.07	(36)
MANG	0.38	(22)	-0.21	(37)	0.04	(44)	-0.08	(37)	-0.17	(44)
Y.C.	0.13	(31)	0.24	(45)	-0.03	(49)	-0.03	(44)	-0.25	(36)
COOK	0.64**	(18)	0.27	(42)	0.01	(34)	0.18	(48)	0.42**	(47)
HOLB	0.11	(27)	0.45**	(41)	-0.10	(40)	0.16	(53)	0.50***	(49)
MULL	0.39	(21)	0.15	(44)	0.05	(47)	-0.03	(47)	0.67***	(39)
BEN	0.33	(14)	0.50***	(46)	-0.17	(51)	0.00	(49)	0.39*	(40)
MANS	0.14	(22)	0.31*	(51)	0.30	(37)	0.10	(35)	-0.11	(41)
DROM	0.44	(19)	-0.01	(47)	0.02	(37)	0.27	(38)	0.43**	(37)

* $P < 0.05$. ** $P < 0.01$. *** $P < 0.001$

Table 4.14: The intra-locality product-moment correlation coefficients (r) between DT and EPEAK in females measured at five laboratory temperatures. Sample sizes are given in parentheses.

Popn	Temperature									
	21°C		25°C		29°C		33°C		37°C	
CLER		(2)	0.03	(30)	0.18	(29)	0.18	(29)	0.22	(30)
EM		(2)	-0.02	(30)	-0.18	(30)	-0.19	(30)	0.23	(30)
ROLL	0.12	(6)	0.27	(30)	0.06	(30)	0.38	(27)	0.40*	(30)
BIL	-0.66*	(14)	-0.28	(29)	-0.41*	(30)	-0.17	(30)	0.09	(30)
MONT	-0.19	(23)	0.12	(30)	-0.13	(30)	0.19	(30)	0.22	(30)
MUND	-0.84**	(8)	-0.10	(29)	0.11	(30)	0.07	(28)	0.00	(29)
C.L.	-0.54*	(14)	0.13	(30)	-0.23	(30)	-0.12	(30)	0.33	(30)
GAY	-0.24	(23)	-0.40*	(29)	-0.45*	(30)	0.19	(30)	-0.28	(30)
TANS	-0.08	(15)	0.34	(30)	0.04	(30)	-0.03	(30)	0.41*	(30)
GOOM	-0.40	(24)	-0.03	(30)	-0.36	(30)	0.11	(30)	0.17	(30)
KING	-0.28	(10)	0.21	(29)	-0.26	(29)	-0.05	(30)	0.06	(30)
DALB	0.38	(12)	0.15	(30)	0.14	(30)	0.41*	(29)	-0.26	(28)
C.P.	-0.64**	(18)	-0.43*	(30)	0.12	(29)	-0.15	(30)	0.11	(30)
LEYB	-0.03	(26)	0.09	(30)	-0.09	(30)	0.01	(30)	0.34	(30)
GOON	-0.30	(23)	0.25	(30)	0.03	(30)	0.17	(30)	0.13	(30)
WAR	-0.39	(9)	-0.26	(30)	0.13	(29)	-0.27	(30)	-0.01	(27)
INV	-0.24	(15)	-0.27	(30)	-0.03	(30)	-0.23	(30)	-0.26	(30)
TAM	-0.43	(18)	-0.32	(30)	0.08	(27)	-0.22	(30)	-0.06	(30)
CAR	-0.46	(16)	0.03	(30)	0.04	(30)	0.39*	(30)	0.19	(30)
COOL	0.35	(21)	-0.21	(30)	-0.34	(29)	0.05	(30)	0.07	(30)
DUN	-0.16	(4)	0.04	(30)	0.08	(30)	-0.37**	(30)	-0.44*	(28)
WELL	-0.63	(8)	-0.15	(30)	0.09	(30)	0.08	(30)	-0.03	(30)
OR	-0.54	(13)	-0.16	(29)	-0.30	(29)	-0.22	(30)	-0.16	(30)
COW	-0.02	(8)	-0.32	(30)	0.33	(30)	-0.58***	(30)	0.08	(29)
BARM	-0.67**	(19)	0.00	(29)	0.08	(29)	-0.32	(30)	0.11	(29)
TEM	0.08	(5)	-0.04	(29)	-0.27	(30)	0.34	(30)	0.09	(29)
MANG	0.02	(9)	0.03	(30)	-0.19	(30)	-0.14	(29)	-0.21	(29)
Y.C.	-0.33	(20)	0.12	(30)	-0.10	(30)	0.21	(29)	0.01	(29)
COOK	-0.13	(14)	-0.01	(30)	-0.18	(30)	0.09	(29)	0.09	(30)
HOLB	0.00	(18)	-0.07	(29)	0.04	(30)	-0.29	(30)	-0.12	(28)
MULL	-0.65*	(13)	0.18	(30)	-0.02	(30)	-0.14	(30)	0.38*	(28)
BEN	-0.23	(5)	0.37*	(30)	-0.28	(30)	-0.02	(29)	0.36	(30)
MANS	-0.34	(11)	-0.36	(30)	0.20	(30)	0.02	(30)	-0.15	(28)
DROM	-0.51	(11)	-0.30	(30)	-0.27	(29)	0.12	(30)	-0.21	(29)

* $P < 0.05$. ** $P < 0.01$. *** $P < 0.001$

Table 4.15: The intra-locality product-moment correlation coefficients (r) between BWT and EPEAK in females measured at five laboratory temperatures. Sample sizes are given in parentheses.

Popn	Temperature									
	21°C		25°C		29°C		33°C		37°C	
CLER		(2)	0.30	(30)	0.14	(29)	0.51**	(29)	0.41*	(30)
EM		(2)	0.47**	(30)	0.37*	(30)	0.12	(30)	0.43*	(30)
ROLL	-0.46	(6)	0.11	(30)	0.56**	(30)	0.58**	(27)	0.40*	(30)
BIL	0.07	(14)	0.30	(29)	0.43*	(30)	0.48**	(30)	0.24	(30)
MONT	0.02	(23)	0.52**	(30)	0.17	(30)	0.16	(30)	0.42*	(30)
MUND	-0.86**	(8)	0.61***	(29)	0.29	(30)	0.07	(28)	0.15	(29)
C.L.	-0.36	(14)	0.30	(30)	0.18	(30)	0.57***	(30)	0.59***	(30)
GAY	0.18	(23)	0.06	(29)	0.02	(30)	0.36*	(30)	0.32	(30)
TANS	0.04	(15)	0.41*	(30)	0.34	(30)	0.28	(30)	0.42*	(30)
GOOM	0.35	(24)	0.02	(30)	0.29	(30)	0.36*	(30)	0.69***	(30)
KING	0.45	(10)	0.24	(29)	-0.02	(29)	0.44*	(30)	0.13	(30)
DALB	0.02	(12)	0.27	(30)	0.23	(30)	0.30	(29)	0.50**	(28)
C.P.	-0.10	(18)	0.25	(30)	0.15	(29)	0.33	(30)	0.42*	(30)
LEYB	0.34	(26)	0.30	(30)	0.20	(30)	0.29	(30)	0.62***	(30)
GOON	-0.08	(23)	0.35	(30)	0.39*	(30)	0.35	(30)	0.44*	(30)
WAR	0.46	(9)	0.25	(30)	0.35	(29)	0.24	(30)	0.33	(27)
INV	-0.02	(15)	0.24	(30)	0.51**	(30)	0.25	(30)	0.07	(30)
TAM	0.08	(18)	0.19	(30)	0.40*	(27)	0.23	(30)	0.23	(30)
CAR	-0.23	(16)	0.40*	(30)	0.26	(30)	0.40*	(30)	0.43*	(30)
COOL	0.49*	(21)	0.47**	(30)	0.22	(29)	0.44*	(30)	0.38*	(30)
DUN	-0.77	(4)	0.37*	(30)	0.16	(30)	0.23	(30)	0.46*	(28)
WELL	0.13	(8)	-0.02	(30)	0.56**	(30)	0.52**	(30)	0.46*	(30)
OR	0.33	(13)	0.07	(29)	0.50**	(29)	0.02	(30)	0.82***	(30)
COW	0.45	(8)	0.15	(30)	0.22	(30)	0.02	(30)	0.31	(29)
BARM	-0.08	(19)	0.28	(29)	0.22	(29)	0.26	(30)	0.56**	(29)
TEM	-0.28	(5)	0.31	(29)	0.43*	(30)	0.44*	(30)	0.28	(29)
MANG	0.30	(9)	0.38*	(30)	0.25	(30)	0.00	(29)	0.70***	(29)
Y.C.	-0.20	(20)	0.47**	(30)	0.15	(30)	0.32	(29)	0.36	(29)
COOK	0.01	(14)	0.27	(30)	0.54**	(30)	0.56**	(29)	0.41*	(30)
HOLB	0.14	(18)	0.15	(29)	0.34	(30)	0.50**	(30)	0.34	(28)
MULL	-0.17	(13)	0.41*	(30)	0.30	(30)	0.34	(30)	0.39*	(28)
BEN	-0.61	(5)	0.46*	(30)	0.32	(30)	0.24	(29)	0.39*	(30)
MANS	-0.31	(11)	-0.08	(30)	0.44*	(30)	0.22	(30)	0.25	(28)
DROM	-0.19	(11)	0.20	(30)	-0.01	(29)	0.27	(30)	0.11	(29)

* $P < 0.05$. ** $P < 0.01$. *** $P < 0.001$

Table 4.16: The intra-locality product-moment correlation coefficients (r) between GR and EPEAK in females measured at five laboratory temperatures. Sample sizes are given in parentheses.

Popn	Temperature									
	21°C		25°C		29°C		33°C		37°C	
CLER		(2)	0.27	(30)	0.06	(29)	0.50**	(29)	0.31	(30)
EM		(2)	0.59***	(30)	0.45*	(30)	0.21	(30)	0.41*	(30)
ROLL	-0.36	(6)	0.02	(30)	0.51**	(30)	0.38*	(27)	0.31	(30)
BIL	0.51	(14)	0.49**	(29)	0.61***	(30)	0.56**	(30)	0.26	(30)
MONT	0.17	(23)	0.54**	(30)	0.20	(30)	0.09	(30)	0.42*	(30)
MUND	-0.25	(8)	0.63***	(29)	0.26	(30)	0.05	(28)	0.15	(29)
C.L.	-0.05	(14)	0.28	(30)	0.24	(30)	0.59***	(30)	0.57***	(30)
GAY	0.33	(23)	0.20	(29)	0.27	(30)	0.36	(30)	0.48**	(30)
TANS	0.05	(15)	0.37*	(30)	0.28	(30)	0.31	(30)	0.29	(30)
GOOM	0.47*	(24)	0.02	(30)	0.47**	(30)	0.39*	(30)	0.69***	(30)
KING	0.55	(10)	0.21	(29)	0.11	(29)	0.47***	(30)	0.13	(30)
DALB	-0.23	(12)	0.22	(30)	0.13	(30)	0.08	(29)	0.58**	(28)
C.P.	0.47	(18)	0.44*	(30)	0.10	(29)	0.42*	(30)	0.44*	(30)
LEYB	0.29	(26)	0.30	(30)	0.20	(30)	0.33	(30)	0.64***	(30)
GOON	0.18	(23)	0.31	(30)	0.38*	(30)	0.30	(30)	0.49**	(30)
WAR	0.67*	(9)	0.43*	(30)	0.30	(29)	0.36	(30)	0.38*	(27)
INV	0.10	(15)	0.31	(30)	0.52**	(30)	0.34	(30)	0.20	(30)
TAM	0.38	(18)	0.30	(30)	0.29	(28)	0.35	(30)	0.30	(30)
CAR	0.15	(16)	0.42*	(30)	0.27	(30)	0.26	(30)	0.43*	(30)
COOL	0.21	(21)	0.49**	(30)	0.36	(29)	0.42*	(30)	0.39*	(30)
DUN	-0.30	(4)	0.36	(30)	0.12	(30)	0.29	(30)	0.57**	(28)
WELL	0.59	(8)	0.03	(30)	0.54**	(30)	0.56**	(30)	0.52**	(30)
OR	0.50	(13)	0.13	(29)	0.54**	(29)	0.13	(30)	0.80***	(30)
COW	0.55	(8)	0.36*	(30)	0.01	(30)	0.27	(30)	0.32	(29)
BARM	0.37	(19)	0.32	(29)	0.17	(29)	0.35	(30)	0.58***	(29)
TEM	-0.56	(5)	0.36	(29)	0.60***	(30)	0.33	(30)	0.25	(29)
MANG	0.14	(9)	0.36	(30)	0.29	(30)	0.06	(29)	0.70***	(29)
Y.C.	0.09	(20)	0.49**	(30)	0.16	(30)	0.22	(29)	0.35	(29)
COOK	0.11	(14)	0.32	(30)	0.56**	(30)	0.55***	(29)	0.43*	(30)
HOLB	0.09	(18)	0.20	(29)	0.29	(30)	0.58***	(30)	0.46*	(28)
MULL	0.55	(13)	0.34	(30)	0.31	(30)	0.46*	(30)	0.27	(28)
BEN	-0.83	(5)	0.39*	(30)	0.37*	(30)	0.27	(29)	0.33	(30)
MANS	-0.10	(11)	0.10	(30)	0.39*	(30)	0.21	(30)	0.26	(28)
DROM	0.10	(11)	0.29	(30)	0.13	(29)	0.23	(30)	0.22	(29)

* $P < 0.05$, ** $P < 0.01$, *** $P < 0.001$

Table 4.17: The inter-locality product-moment correlation coefficient (r) based on 34 population means weighted for sample size.

Traits	Temperature				
	21°C	25°C	29°C	33°C	37°C
Males					
DT - BWT	0.493**	0.049	-0.068	-0.202	0.082
Females					
DT - BWT	0.304	-0.007	-0.075	-0.293	0.075
DT - EPEAK	-0.442**	0.559***	0.026	0.370*	-0.022
BWT - EPEAK	0.257	0.506**	0.551***	0.370*	0.656***
GR - EPEAK	0.570***	0.214	0.509**	0.217	0.604***

* $P < 0.05$, ** $P < 0.01$, *** $P < 0.001$

Table 4.18: ANOVAs testing for the presence of genotype-sex interaction in early life-history traits (DT, BWT and GR) measured on both sexes. Mean squares for each effect, with significant F-ratios, are given within each laboratory temperature.

Temp	Source	df	DT	BWT	GR
21°C	POP	33	1613.162***	482304.416***	55.184***
	SEX	1	1720.322***	334335.290*	172.311***
	PxS	33	126.212	78689.366	7.188
	ERROR	1340	98.574	54971.194	6.718
25°C	POP	33	143.442***	671056.762***	350.983***
	SEX	1	36.557*	3944782.467***	2084.408***
	PxS	33	6.792	29723.745	15.428
	ERROR	2780	6.378	45162.030	17.688
29°C	POP	33	36.800***	893949.577***	965.214***
	SEX	1	8.531	7347575.980***	6160.108***
	PxS	33	3.537	35268.826	32.025
	ERROR	2834	3.002	38431.162	38.248
33°C	POP	33	25.757***	1025093.281***	2272.587***
	SEX	1	4.936	4368097.835***	6389.374***
	PxS	33	0.810	46136.604	88.603
	ERROR	2782	1.583	38084.168	67.950
37°C	POP	33	34.555***	755678.307***	1845.255***
	SEX	1	1.146	6307355.874***	12078.068***
	PxS	33	1.681	55577.723	107.411
	ERROR	2668	1.934	45545.572	80.827

* P < 0.05, ** P < 0.01, *** P < 0.001

4.3 Discussion

The significant F-ratios from the oneway analyses of variance (Tables 4.2 and 4.3) indicate that these natural populations of *T. castaneum* originating from 34 different geographical locations in Eastern Australia are differentiated with respect to developmental period (DT), adult body weight (BWT), and growth rate (GR) in both sexes, and peak fecundity (EPEAK) in females, when measured in each of five laboratory temperatures. All but one of the F-ratios were highly significant ($P < 0.001$). The one exception, EPEAK in females at 21°C, was still significantly differentiated, but at a lower level ($P < 0.05$). These differences must be genetically based since the beetles, which were two generations removed from the wild, were reared under uniform laboratory conditions.

Having established the presence of significant life-history variation among populations it was then appropriate to investigate any linear relationships between this genotypic (population) variation and corresponding variation in the environment. For this purpose, the natural populations had been deliberately sampled at approximately regular distances along a latitudinal gradient extending from Clermont in Queensland to Dromana in southern Victoria, a distance covering more than 15 latitudinal degrees.

Significant latitudinal clines were found for egg to adult developmental period (DT) in both sexes at four of the five laboratory temperatures studied (see Tables 4.4 and 4.5). Clearly, latitude explains a significant proportion of the observed genetic variation underlying developmental rate, such that populations originating from higher latitudes display faster rates of development than those from lower latitudes. Significant clinal patterns were not found in DT at 21°C, a temperature close to the lower biological limit of this species (Howe 1956). Significant latitudinal clines also were found for peak fecundity (EPEAK) when measured on females at 25°, 29° and 33°C, such that populations from higher latitudes produced less eggs than those from lower latitudes. At the more stressful temperatures (21° and 37°C) significant latitudinal clines in EPEAK were not found. No significant latitudinal clines in adult body weight (BWT) or growth rate (GR) were detected at any of the five laboratory temperatures in either males or females.

For describing the dependence of the early life-history traits on latitude the means for each population were based on data from numerous individuals. When there is more than one value of the dependent variable Y for each value of the independent variable X, two sources of error can be separated in an analysis of variance, error associated with deviations

from linear regression and the within groups error (see Sokal and Rohlf 1981). Significance of the mean square for deviations from regression (when tested against the within groups error) could mean either that the dependent variable Y is a curvilinear function of X or that there is a large amount of random heterogeneity around the regression line, or both.

Since the deviations from regression were significant for all the simple linear regressions describing the dependence of DT, BWT and GR in both sexes, and EPEAK in females, on the independent variable LAT at all five laboratory temperatures, curvilinearity was investigated. Polynomial equations were significantly better at describing the relationships in most cases than were the simple linear regressions. Although these equations (which are not given) in themselves do not identify the important selective pressures influencing the life-history of these natural populations they do suggest that some environmental factors which are not linearly related to latitude, either singly or in combination, are producing regular (systematic) patterns in life-history traits.

Temperature and relative humidity are known to affect the biological characteristics of *T. castaneum* (Howe 1956, 1962; Sokoloff 1974) and since these climatic elements are known to vary across the latitudes in question (see Table 4.1), they are of particular interest as possible causative factors in population differentiation.

Significant linear relationships were found in both males and females measured under four of the five laboratory environments (25° , 29° , 33° and 37°C) when DT was regressed on the mean annual temperature (TMEAN) corresponding to each locality sampled. Populations originating from warmer climates had slower rates of development than those from cooler climates. In females a significant linear relationship was found when EPEAK was regressed on TMEAN at 25° , 29° , and 33°C , such that populations from warmer northern climates produced more eggs than populations from cooler southern climates. Also significant at 25°C in males, and at 25° and 33°C in females, were the linear regressions for growth rate (GR) on TMEAN. Populations originating from warmer climates had slower growth rates than populations from cooler climates. The regression of adult body weight (BWT) on TMEAN, like the regression of BWT on LAT, was non-significant at all five laboratory temperatures in both sexes.

These significant regression equations suggest that temperature may be an important selective factor acting on developmental rate and early fecundity of beetles in natural populations of *T. castaneum*. This is not unexpected since *T. castaneum* is a poikilothermic species and temperature is expected, through its direct effects on biochemical processes, to

profoundly influence the expression of traits closely associated with fitness.

Unlike the regression on TMEAN, a significant linear relationship was found in both sexes at most laboratory temperatures when adult body weight (BWT) was regressed on mean annual (9 am) relative humidity (RhMEAN). The only non-significant regression was in females at 21°C. Populations originating from the more humid climates (see Table 4.1) had higher body weights than those from less humid environments. RhMEAN also explains a significant proportion of the observed genetic variation in growth rate (GR) in both sexes when measured under all five laboratory temperatures, such that populations originating from the more humid climates had faster growth rates than those from less humid climates. In contrast to the regressions on LAT and TMEAN, the regressions of developmental time (DT) in both sexes, and early fecundity (EPEAK) in females on RhMEAN, were non-significant at all laboratory temperatures. This is consistent with the low and non-significant correlation between RhMEAN and LAT ($r = 0.13$), and RhMEAN and TMEAN ($r = -0.33$) for the localities sampled. These results suggest that humidity may be an important selective factor acting, either directly or indirectly, on body weight and growth rate of beetles in natural populations of *T. castaneum*.

Since *Tribolium* do not imbibe water but can produce it by hydrolysis of carbohydrates, and since the beetles are able to reduce perspiration loss by building galleries in the culture medium (Sokoloff 1974), the physiological consequences of relative humidity as an important selection pressure are not clear. However, the influence of relative humidity on the body temperature of an insect through its effects on evaporation as well as its influence on the respiration rate of stored grain might be important.

In natural populations of *T. castaneum* occupying grain habitats, many ecological forces, rather than single environmental factors may be involved in the process of natural selection shaping life-histories. Multiple regression analysis can be used to identify, among a set of putative causal variables, those which affect the dependent variable significantly and appreciably, as well as estimating the relative magnitudes of their contributions (Sokal and Rohlf 1981).

The multiple regressions of DT simultaneously on TMEAN and RhMEAN for males (Table 4.6) and females (Table 4.7) within each temperature were unable to explain significantly more variation than when DT was regressed just on TMEAN. Similarly, the multiple regressions of both BWT and GR simultaneously on TMEAN and RhMEAN were unable to explain significantly more variation than the appropriate simple linear regressions just

on RhMEAN. These results suggest that temperature, independently of relative humidity, is an important selective factor affecting developmental rate in natural *T. castaneum* populations. However, for growth rate and body weight it is humidity and not temperature which is important.

The multiple regression of EPEAK in females on TMEAN and RhMEAN does explain significantly more variation in this trait, at 25°C, 29°C, 33°C and 37°C, than either of the two separate simple linear regressions. At these laboratory temperatures, the statistically significant standardized partial regression coefficients for EPEAK are those associated with TMEAN and RhMEAN. In contrast, the coefficients from the simple linear regressions of EPEAK on RhMEAN were non-significant at these same temperatures. This suggests that both temperature and humidity are important selective factors influencing early fecundity in natural populations of *T. castaneum*.

The multiple correlation coefficient increases with the number of independent variables included in the equation. For example, the multiple R^2 is larger when the traits are simultaneously regressed on LAT, TMEAN and RhMEAN, as compared with the multiple regression on the two climatic variables, TMEAN and RhMEAN. However, the critical R^2 at a given probability level of significance also increases (Steel and Torrie 1981). Therefore, the inclusion of two independent variables, LAT and TMEAN, which are highly correlated, reduces the level and number of significant multiple regression equations found. Further, the standardized partial regression coefficients corresponding to LAT and TMEAN are generally non-significant. In contrast, the coefficients from the simple linear regressions on LAT and TMEAN, for DT (both sexes), and EPEAK (females) were generally significant at the different laboratory temperatures. The inclusion of LAT in the multiple regression equations along with TMEAN and RhMEAN did explain significantly more variation in DT in males at 25°C and 33°C, and in females at 25°C, than the multiple regressions on TMEAN and RhMEAN. The significance of individual location and environmental variables in the full regression equation must only be used as a guide to their possible importance, given that each is determined with all other independent variables held constant (Mulvey et al. 1979; Taylor and Mitton 1974).

Clines related to a geographic gradient can be attributed either to adaptation to different environments or to random processes (Capy, David, Allemand, Carton, Febvay and Kermarec 1986). Schaffer and Johnson (1974) suggest that adjustment for geographic location is necessary to eliminate as far as possible associations due to random drift and

migrational gene flow. However, in the latitudinal cline under study adjustment for location removes a major fraction of the selective effects of temperature, since TMEAN is highly negatively correlated ($r = -0.86$) with geographical location (LAT). Therefore, selective effects of temperature are confounded with those due to non-selective location dependent factors. Potentially, the selective influences of RhMEAN on BWT and GR in both sexes, and EPEAK in females can be distinguished from gene flow, since patterns in RhMEAN are not linearly related to geographic location. The significant standardized partial regression coefficients corresponding to RhMEAN, while holding LAT and TMEAN constant, suggest that humidity is an important selective factor influencing body weight, growth rate and early fecundity in natural populations of *T. castaneum*. That is, natural selection seems to be at least partially responsible for the observed spatial patterns of genetic variation in these traits.

The natural populations assayed in the Clinal experiment were derived from wild populations which had presumably adapted to, among other things, different thermal regimes. Not only does climate differ among localities, but beetles occupying a given habitat are subjected to fluctuations in temperature because of seasonal and diurnal changes. Therefore, the distribution of *T. castaneum* depends on its ability to adapt, either physiologically or genetically, to these different conditions. Since poikilothermic organisms are particularly affected by external temperatures, and since the sampled populations are known to be genetically differentiated with respect to early life-history traits (see Tables 4.2 and 4.3), then genotype-environment interactions might be expected when population samples are reared under several laboratory temperatures.

Since genotype-environment interaction is equivalent to genetic variation in phenotypic plasticity (Via and Lande 1985, 1987), a character must be phenotypically flexible before any genotype-environment interaction can occur. The profiles of phenotypes produced by these 34 natural populations of *T. castaneum* are shown in Figures 4.2 to 4.8 for DT, BWT and GR in males and females, and EPEAK in females. Clearly, developmental time (DT), adult body weight (BWT) and growth rate (GR) in both sexes, and early fecundity (EPEAK) in females, are phenotypically flexible at these different temperatures. The highly significant ($P < 0.001$) main effect of temperature in the fixed model analyses of variance which were used to test for the presence of genotype-environment interaction, confirmed this.

Genotype-environment interaction can be measured when genetically different groups of an outbreeding species are raised under different environmental conditions (Bulmer 1980).

In this experiment the populations are genetically heterogeneous themselves, but they are differentiated in mean genotypic value, and it is how these mean values behave in the different environments which is important.

Significant F-ratios from the fixed model analysis of variance (Tables 4.8 and 4.9) indicate the presence of genotype-environment interaction across each pairing of laboratory temperatures. Clearly, the interactions were significant for some temperature combinations in all traits in both sexes. Significant interaction effects from the fixed model ANOVAs for developmental rate (DT) measured in both sexes were found for all temperature combinations, with one exception, that between 33° and 37°C in females. These significant interactions are not unexpected since the regression analyses implicated climatic temperature (TMEAN) as an important selective factor acting on developmental rate in natural populations of *T. castaneum* — that is, the geographic populations appear to have evolved different combinations of genes which influence developmental rate, thus suiting them to different thermal regimes.

Fewer significant interactions across the temperature combinations were found for BWT and GR. This is expected since both these traits, generally, were not linearly related to climatic temperature (TMEAN) in the regression analyses. Therefore, the populations from different thermal regimes were not expected to show temperature specific adaptations in these traits. The significant genotype-environment interactions in early fecundity (EPEAK), with the exception of that between 29° and 37°C, involved 21°C. Generally, for all the early life-history traits the interactions involving 21°C as one of the temperatures were significant. This suggests that phenotypes at temperatures which are close to the biological limit of the species, as compared with more conducive environments, are influenced either by some different alleles or differently by the same alleles. It would be of interest in future studies with this species to include more temperatures closer to the upper biological threshold, that is around 40°C at the same relative humidity (after Howe 1956).

A better appreciation of the biological importance of genotype-environment interaction is given by the genetic correlation between character states expressed in different environments, since a significant interaction effect from the analysis of variance reveals only that the across environment correlation is less than unity (Via and Lande 1985, 1987). The concordance of the genetic correlation estimates from the standard family mean (Via 1984b), Robertson's (1959b) and Yamada's (1962) methods, with those from Spearman's rank correlation (see Tables 4.8 and 4.9) suggest that the observed genotype-environment

interactions are due to a change in population ranking and not simply due to heterogeneity of genetic variances across environments. Since transformations on the data prior to the analyses of variance failed to remove the significant interactions, these interactions might represent a real biological phenomenon. Further, the consequences of a change in ranking of genotypes measured in different environments is more important from the evolutionary perspective than are interactions arising from scaling effects.

For the early life-history traits measured on males and females, the genetic correlations across temperatures show greater departures from unity when the combinations include 21°C. This, like the ANOVAs, suggests that genotype-environment interactions might be more important when the performance of individuals is severely perturbed under stressful conditions. Alternatively, it might also suggest that the underlying genotype has little effect in determining the phenotype under such harsh conditions. For DT, BWT and GR in both sexes, correlations between the different temperature pairings involving 25°, 29°, 33° and 37°C, are generally high. When the interaction component was significant in the ANOVAs, the departures from unity for the corresponding correlations were more obvious.

The relatively lower genetic correlations for developmental time in both sexes, as compared with those estimated for growth rate and body weight, like the ANOVAs, suggest genotype-temperature interactions are more important in this trait. Faster developing populations in one laboratory temperature were not necessarily faster developing at other temperatures. In other words, the phenotypic expression of developmental rate in each environment is influenced either by some different alleles or differently by the same alleles. This is further evidence that the natural populations were locally adapted to the specific thermal regimes from which they were sampled.

Robertson (1959b) suggested that a correlation around 0.8 or less would be of biological importance. The cross-temperature correlations between combinations of 25°, 29°, 33°, and 37°C in BWT and GR in both sexes suggest that largely the same alleles or sets of alleles influence the expression of these traits in each environment. However, the cross-temperature correlations for EPEAK in females, which show greater departures from unity, suggest that the expression of early fecundity is influenced either by some different alleles or differently by the same alleles at different laboratory temperatures.

Yamada's (1962) method for estimating the genetic correlation between character states was included only for comparison with the other methods since it produces biased estimates

when the data are unbalanced and the genetic and residual variances in the separate environments are not equal (Fernando et al. 1984). The estimates from this method were in general agreement with estimates from the other methods, at least for analyses among the four higher temperatures.

The results from the analysis of genotype-environment interaction across more than two temperatures at a time are presented in Tables 4.10 and 4.11. From the ANOVAs the population-temperature interaction effect was significant for DT, BWT and GR in both sexes, and for EPEAK in females. Generally, the level of significance was higher for the interaction effect when all temperatures were considered (Table 4.10). Further, when only the four higher temperatures were considered (Table 4.11), the correlations were closer to unity for each trait in males and females, suggesting that interactions between 21°C and the other temperatures contribute substantially to the interaction component.

The presence of significant genotype-environment interaction across these temperatures which are representative of those experienced by *T. castaneum* in the natural habitat, suggests that these different populations are adapted to specific thermal regimes. Although performance and therefore selection response in some environments can be accurately predicted from performance in other environments, such a relationship is not general. The differential expression of developmental time, body weight, growth rate and early fecundity in these populations across the different laboratory temperatures suggests that fluctuating selection pressures in heterogeneous environments may be involved in the maintenance of the genetic variation in life-history traits which is commonly observed in natural populations of *T. castaneum* and other species. Since the regression analyses (Tables 4.4 to 4.7) implicated humidity (RhMEAN) as an important selective factor affecting body weight and growth rate in natural *T. castaneum* populations, it would be desirable in future studies to measure the performance of different populations across several environments differing in humidity, rather than temperature. Such a study may find more biologically important interactions in these traits.

The ability of the life-history to respond to natural selection depends upon the relationships among important fitness traits (Stearns 1976). The intra-locality correlations between DT and BWT in both sexes, and DT, BWT and GR with EPEAK in females are presented in Tables 4.12 to 4.16. Generally, the significant intra-locality correlation coefficients between developmental time (DT) and body weight (BWT) in males (Table 4.12) and females (Table 4.13) were positive at the different temperatures. The slower developing beetles at

these localities had higher body weights. These significant correlations may reflect common epigenetic control for these two traits due to pleiotropy or linkage (Thorpe 1976). However, due to the sometimes non-normal distribution of developmental time in *Tribolium*, correlations between DT and other traits must be interpreted with caution (see King and Dawson 1972).

In females, the intra-locality correlations between DT and EPEAK (Table 4.14) are generally non-significant at all temperatures. Since sample sizes are less than or equal to 30, a coefficient larger than 0.35 is needed for the coefficient to be significantly different from zero (Steel and Torrie 1981). Generally, the significant intra-locality correlation coefficients between BWT and EPEAK in females (Table 4.15) at each temperature were positive. The heavier beetles from these populations produced more eggs during the 48 hour sample than lighter individuals. Further, the intra-locality correlation coefficients between GR and EPEAK in females (Table 4.16), when significant, were positive at all laboratory temperatures. Within these populations, beetles with faster growth rates produced more eggs. These significant correlations suggest that early fecundity shares common epigenetic control with female body weight and growth rate. However, it must be remembered these estimates are only phenotypic correlations which may not necessarily reflect the underlying genotypic relationships.

In Table 4.17, the correlation between mean character states for each locality measures the concordance of their patterns of geographic variation. Generally, the inter-locality correlation coefficients between DT and BWT were non-significant in both sexes. The exception was in males at 21°C. There were significant inter-locality correlations between DT and EPEAK in females at 21°, 25° and 33°C. These results suggest that developmental time and early fecundity may share common epigenetic control, or else, have responded similarly to geographic variation in selection pressures. At 21°C populations which were faster developing produced more eggs. This correlation might be simply an artifact of the time at which peak fecundity was assayed. Since the egg collections for all populations at this temperature were taken at day 134, faster developing populations may have reached peak fecundity, whereas slower developing ones may not have. The inter-locality correlation between BWT and EPEAK in females was significant and positive at 25°, 29°, 33°, and 37°C. The same correlation between GR and EPEAK in females was significant and positive at 21°, 29° and 37°C. This suggests early fecundity may be under common epigenetic control with body weight and growth rate, or is responding similarly to geographic variation in

selection pressures. A similarity in response to selection pressures could be due to the characters responding to the same selection pressures, or else, responding to different selection pressures which display similar patterns of geographic variation (Thorpe 1976).

In the Clinal experiment both males and females from each population were assayed for developmental rate, adult body weight, and growth rate under the five laboratory temperatures. In Table 4.18 the main effect of SEX from the ANOVAs was significant for BWT and GR at all five laboratory temperatures. Females had significantly higher adult body weights and faster growth rates than males at each temperature. However, for developmental rate (DT) the sexes were only significantly different at 21° and 25°C. At these temperatures females were faster developing than males.

Significant population-sex interactions were not found for DT, BWT or GR at any of the five laboratory temperatures. This suggests, at least for these early life-history traits, that the relative performance of the different genotypes was consistent across the two sexes. Comparison of the phenotypic profiles for males with those from females at each laboratory temperature (Figures 4.2 with 4.5, 4.3 with 4.6, and 4.4 with 4.7) are useful in appreciating the lack of significant genotype-sex interaction.

Chapter 5

General Discussion and Conclusions

The empirical work reported in this thesis has addressed specific areas concerning life-history evolution in natural populations. In the Nested experiment (Chapter 3), the methods of quantitative genetics were used to give a statistical description of the genetic sources of variation, covariation and genotype-environment interaction for several life-history traits measured on females derived from two geographically distinct natural populations of *T. castaneum*. These results may be used to make inferences regarding the potential of populations to respond to natural selection, as well as the past selective regimes experienced by the populations. However, it must be recognised that the parameters (heritabilities and genetic correlations) used to describe this variation and covariation are only statistical descriptions and not ones based on direct analysis of gene action (Barker and Thomas 1987).

Evolutionary change in response to natural selection requires that phenotypic variation be heritable, as well as that fitness varies according to the phenotype. The results of the Nested experiment show that there is abundant additive genetic variation for life-history traits in natural populations of *T. castaneum*. Paternal half-sib heritability estimates significantly different from zero were found for both reproductive and non-reproductive traits in both the Mangoplah and Coalstoun Lakes populations at two laboratory temperatures. In agreement with Fisher's (1930, 1958) Fundamental Theorem of Natural Selection, the reproductive traits generally displayed lower levels of heritable variation than the non-reproductive traits, in both populations at both laboratory temperatures. Furthermore, although age-specific components of reproduction showed significant and sometimes high

heritabilities, the estimates for lifetime reproduction were low and generally not significantly different from zero. Thus, although components of fitness may have significant heritability values, fitness itself need not be heritable. Clearly caution must be exercised when making inferences about total fitness from individual fitness components.

Because natural selection operates on the whole phenotype rather than on characters in isolation, the additive genetic covariances among life-history characters can substantially influence the rate and direction of evolution. In the Nested experiment, both positive and negative genetic correlations between life-history traits were found, some of which were significantly different from zero. Negative genetic correlations are of major importance in establishing an empirical basis for the concepts of "trade-off" in general, and "reproductive cost" in particular.

The negative genetic correlations between early reproductive traits and adult lifespan in both populations suggests that a cost associated with high early reproduction is manifested through a reduction in future survival. However, consistently positive genetic correlations between early and late reproductive traits in the two populations at both laboratory temperatures implies that a cost due to high early reproduction is not manifested through a reduction in later fecundity. That is, beetles which have a high rate of oviposition early in their life also oviposited at a relatively faster rate later in life.

Negative genetic correlations between life-history traits not only address the problem of reproductive cost, but also the role of "antagonistic pleiotropy" in the maintenance of quantitative genetic variation. The finding of negative genetic correlations between life-history traits, associated with abundant heritable variation in these traits, provides empirical evidence to support the role, at least in part, of antagonistic pleiotropy in the maintenance of the additive genetic variation which is commonly observed in natural populations of many species.

The often neglected component in many quantitative genetic analyses of phenotypic variation is the component due to the interaction between the genotype and the environment (V_{GE}). Although the heritability and genetic correlation estimates for the two natural populations of *T. castaneum* were, in general, compatible across the two laboratory temperatures (33° and 37°C), they were sufficiently different to suggest that the expression of the genetic architecture underlying the life-history of natural populations of this species changes under different environments. Further, even though genotype-environment interaction was not a general phenomenon in the Nested experiment, significant sire-temperature

and or dam-temperature interaction effects were found for developmental period, body weight, growth rate and lifetime reproduction. This, and the observation that the genetic correlations between character states expressed in different environments were not all unity, indicates that some temperature specific responses had occurred.

The Clinal experiment (Chapter 4) also gave empirical evidence for genotype-environment interaction when samples of progeny from different geographic populations were raised under different laboratory temperatures. The presence of significant genotype-environment interaction across these temperatures, which are representative of those that the beetles experience in the natural habitat, suggests that the different populations were adapted to specific thermal regimes.

The implications of these interactions are that, although performance and therefore selection response in some environments can be accurately predicted from performance in other environments, such a relationship is not general. Thus, for organisms occupying heterogeneous environments, only studies which address the possibility of genotype-environment interaction will produce realistic estimates of the quantitative genetic parameters required for the development of life-history evolutionary theory. Not only does this body of empirical evidence reinforce the consensus that estimates of quantitative genetic parameters are specific to the environments under which they are determined, it also provides evidence in support of the hypothesis that genotype-environment interaction and fluctuating selection pressures in heterogeneous environments play some role in the maintenance of quantitative genetic variation.

A limitation of the Nested experiment in documenting life-history variation, covariation and genotype-environment interaction in the two natural populations of *T. castaneum* was that only half the available genotypes (i.e. females) were assayed for the different life-history characters. However, this is not considered a serious deficiency, as there were no significant genotype-sex interactions in the Clinal experiment for developmental period, adult body weight or growth rate at any of the five laboratory temperatures studied — the relative performance of the different populations was independent of sex. However, there is no guarantee that traits other than these early life-history traits, such as reproductive investment and longevity, will not show differential performance across the sexes. Although information on the male life-history was not included in the Nested experiment so that the male effect across genotypes could be standardized (using the black mutant) and the number of females assayed could be increased, future studies including both sexes would be

desirable.

An underlying assumption pervading much of life-history evolutionary theory is that life-history differences among geographically separate populations within a species reflect differences among their environments in ecologically important selective pressures. The Nested experiment documented genetically based differences in life-history traits between two natural populations of *T. castaneum* sampled from geographically distinct locations. Under uniform laboratory conditions, female beetles from the temperate Mangoplah population had significantly faster rates of development and lower adult body weights than beetles from the sub-tropical Coalstoun Lakes population. Contrasting trends in the heritability and genetic correlation estimates from these two natural populations, although associated with large standard errors, provide further evidence that the genetic architecture underlying the life-history of these populations is different. Although this evidence suggests that genetically based life-history differences are observable at the population level, not all life-history traits are necessarily differentiated. The lack of significant population differentiation for growth rate, at either laboratory temperature, suggested that the relationship between developmental period and adult body weight may be physiologically constrained within the species. No significant differences between the populations were found for longevity and lifetime reproduction at either laboratory temperature. This lack of differentiation in major fitness components could mean they are highly canalized in this species, or it may simply reflect their high coefficients of variation.

In the Clinal experiment significant differentiation among natural populations of *T. castaneum* originating from 34 geographically separate localities in Eastern Australia was found for developmental period, adult body weight and growth rate in both sexes, and peak fecundity in females, when measured under five laboratory temperatures. Again, these differences must be genetically based since the beetles, which were two generations removed from the wild, were reared under uniform laboratory conditions. This extensive documentation of life-history variation among populations of *T. castaneum* showed that intraspecific comparisons are valuable and necessary for establishing the importance of life-history adaptation.

One of the most persuasive pieces of evidence that natural selection is acting on the genetic structure of natural populations is the occurrence of latitudinal clines. To demonstrate a relationship between natural selection, the environment and the genotype, the natural populations used in the Clinal experiment had been sampled at approximately regular

distances along a latitudinal gradient covering more than 15 latitudinal degrees. Significant latitudinal clines were found for developmental rate in males and females at four of the five laboratory temperatures studied, with populations originating from higher latitudes faster developing than those from lower latitudes. Further evidence for latitudinal clines was found at three laboratory temperatures for early fecundity in females, where populations from higher latitudes produced fewer eggs than those from lower latitudes. In contrast, significant latitudinal clines were not found for adult body weight or growth rate at any of the five laboratory temperatures in either sex.

Since life-history traits are synonymous with fitness components, and assuming geographic variation is ordered by natural selection, strong associations are expected between life-history traits and the measures of environment that influence adaptation. The empirical evidence from the regression analyses in the Clinal experiment implicated temperature, independently of humidity, as an important selective factor affecting developmental rate in natural populations of *T. castaneum*. However, for body weight and growth rate, relative humidity and not temperature was the important climatic variable associated with genetic differentiation. The multiple regression analyses found both temperature and relative humidity to be important selective factors influencing early fecundity in these natural populations of *T. castaneum*.

Similar adaptive interpretations can be made for the genetic differences found in the Nested experiment for female developmental period and adult body weight, since samples of these two populations when tested in the Clinal experiment were generally compatible with observed clinal patterns of geographic variation. Thus, the faster developmental rate in the Mangoplah population seems to be an adaptation to a cooler climate, whereas the lower body weight in the same population seems to be an adaptation to a drier climate, both relative to the slower developing and heavier beetles from the warmer and more humid Coalstoun Lakes climate.

Temperature and humidity, although important to poikilotherms, are not the only environmental factors capable of affecting populations of *T. castaneum* in the natural habitat. Undoubtedly population density, interactions with other species, the type of food supply, the stability of the habitat, and fluctuations in climatic variables, to mention but a few, are also involved. Therefore detailed monitoring of the natural habitat in future studies, in conjunction with multivariate techniques, should help to identify the selection pressures responsible for life-history adaptation in this species.

In this study, like many others, it is difficult to interpret the observed spatial patterns of genetic variation unambiguously in terms of natural selection, since several other stochastic processes can also produce and maintain clinal variation. Additional and more convincing evidence to support the hypothesis that natural selection is responsible for geographic variation in the life-history would entail the finding of complementary latitudinal clines in other continents (after Knibb 1982; Knibb et al. 1981; Oakeshott et al. 1981, 1982), and or the finding of more geographical non-linearities in genetic patterns which are correlated with corresponding non-linearities in environmental patterns (after Schaffer and Johnson 1974).

When comparing existing populations it is assumed that the conditions under which these populations are living represent the conditions under which they evolved. Even though attempts were made to sample only *T. castaneum* populations which had infested their respective localities for many generations, the extent to which this assumption is valid for a synanthropic species like *Tribolium* is currently unknown, and requires further investigation.

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