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DARWINIAN FITNESS IN *Drosophila*. IV. ARE FITNESS COMPONENTS NEUTRAL OR ADAPTIVE?

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ABSTRACT

Data for individual females of *Drosophila prosaltans* concerning 16 fitness components were analysed to verify the neutral and the adaptive hypothesis of fitness components to Darwinian fitness. Significant correlations between fitness components and Darwinian fitness and the principal components analysis results showed a differential importance of the components studied.

INTRODUCTION

The adaptation of organisms is the outcome of the evolutionary process. The environment continuously exerts a selective pressure on organisms, shaping the population's adaptability. Different types survive and reproduce at different rates due to morphological, physiological and ethological traits adjusted to their environment.

The theory of natural selection describes the process of adaptive evolution in terms of variation among individuals in their capacity to contribute with progeny to future generations. Fitness is an individual trait on which natural selection acts.

It is reasonable to assume that all the biological processes are important in the determination of the reproductive success. However, the relative importance of each to net fitness is not clear, not even whether one or a few components have major importance (Mueller and Ayala, 1981).

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We know of only two papers which deal with the relative importance of fitness components to Darwinian fitness. The first was Wills' attempt (1981) to classify fitness components of domestic fowl, cattle and swine in a descending order of importance for total fitness; however, as the author himself stated, based on his personal feelings. The second was Carareto and Mourão's (1991b) estimation of Darwinian fitness, establishing a hierarchical order of importance for 23 fitness components for three strains of *Drosophila prosaltans.*

For Reeve *et al.* (1990), any aspect of the phenotypes that is determined by *interaction of many components must*, at best, be poorly correlated with any one component and even important components of fitness are effectively neutral in equilibrium populations. Their proposition was based on a "purely intellectual exercise": *considering 10 columns with 20 random digits each and another column* with the sums of the digits of each row, the correlation between the latter column with any single column is weak. The correlation tends to zero as the number of columns increases.

In analogy with the above deductions, Reeve *et al.* (*op. cit.*) claimed that any aspect of the phenotype that is not correlated with fitness is by definition neutral, and so, under an extended view of neutrality, even important components of fitness are effectively neutral in equilibrium populations. The exceptions to this "general rules" are discussed by Wallace (in press) calling attention that under some circumstances, a correlation between total fitness and one of its components may be detected in a highly selected populations, but under most circumstances this correlation all but vanishes.

According to Wallace (in press), "neutrality requires that there be numerous components of fitness, that they possess intermediate optimal values, and that they be negatively correlated with one another", but "population of organisms in which individuals are identified by name, for which measurements of numerous components of fitness are available for each individual, and whose standings relative to other individuals (i.e., measures of total fitness) have been established by pair-wise competitions are unknown. In this paper, these are approximately satisfied: measures of 16 fitness components of 86 individual flies of *D. prosaltans*, used by Carareto and Mourão (1991a,b), were analysed concerning the hypothesis of adaptivity and neutrality of fitness components to total fitness.

MATERIALS AND METHODS

Eighty-six females of three strains of *D. prosaltans* were studied. Due to innumerous generations in laboratory cultures, under nearly constant selective pressures, their populations can be assumed to be in equilibrium. The fitness components analysed are: duration of the pre-copula (**DPC**), absolute duration of the copula (**ADC**), relative duration of the copula (**RDC**), longevity (**L**), absolute duration of the oviposition period

(**AOP**), relative duration of the oviposition period (**ROP**), total number of eggs (**TNE**), daily number of eggs (**DNE**), number of viable eggs (**NVE**), number of pupa (**NP**), number of imagines (**NI**), egg-pupa viability (**EPV**), pupa-imago viability (**PIV**), egg-imago viability (**EIV**), duration of the pupation period (**DPP**) and duration of the imaginal emergence period (**DIEP**). A description of the strains and fitness components is found in Carareto and Mourão (1991a,b).

A matrix with 16 columns and 86 rows contains the values of 16 fitness components for 86 females, computed as percentages of the weighted average of the means for the three strains, as described in detail in Carareto and Mourão (1991b). The percentages, presented as decimals in the Appendices, were analysed in two ways: (1) the correlation method proposed by Reeve *et al.* (1990), both for the multiplicative adaptation index (**W"**) described in Carareto and Mourão (1991b) and the additive-neutrality method (**SUM**) descrived in Reeve *et al.* (*op. cit.*); and (2) the principal components analysis (**PCA**) described in Anderson (1984), for both the multiplicative and additive estimations of Darwinian fitness, using a matrix of correlation coefficients.

RESULTS AND DISCUSSION

Table I shows the correlation coefficients of each fitness component with that of the product **W"** or the **SUM** of each row. It also shows the factor loadings of the **PCA**, performed both for the **W"** and **SUM** columns.

Of the 16 correlations, eight and 12 were significant, respectively with **W"** and **SUM**. According to the Reeve *et al.* (1990) neutrality hypothesis, the 12 significant values of **r** obtained with the **SUM** were unexpected. However, the four strongest in both cases were those with **NI, NP, NVE** and **TNE**. Taking the values of **r** as a measure of the relative importance of fitness components to total fitness (product or sum), three forms of analysis point out these components as most important: the two presented here, in perfect concordance with that of Carareto and Mourão (1991b) which also indicated **NI, NP, NVE** and **TNE** to be among the most important components.

The **PCA** detects those components with major contributions to sample variability, through the searching of linear combinations of 17 fitness components, the 16 described in Materials and Methods, plus the **SUM** or **W"**, which have the highest variances.

The **PCA** run on the correlation matrix of 16 components and the **SUM** showed that from among 17 factors for variability four principal components explained 73.4% of the total inertia, and that the first alone retained 30.9%. This principal component can be viewed as a "factor of composition of almost all fitness components" (see the signs of the factor loadings in Table I). It gives the highest factor loadings to **SUM, NI, NP, NVE** and **TNE**.

Table I - Correlation coefficients and principal components (PCA) values of 16 fitness components for 86 females of *D. prosaltans* with the W" (product) and the SUM.

Fitness components	W"		SUM		PCA	
	r	t(84)	r	t(84)	W"	SUM
DPC	0.002	0.02	0.055	0.50	0.095	0.071
ADC	-0.022	0.20	-0.141	1.30	0.105	0.098
RDC	0.017	0.16	0.080	0.74	0.034	0.019
L	0.071	0.65	0.296	2.84**	-0.099	-0.104
AOP	0.088	0.81	0.325	3.15**	-0.113	-0.117
ROP	0.109	1.00	0.282	2.69**	-0.110	-0.110
TNE	0.334	3.25**	0.745	10.24**	-0.319	-0.305
DNE	0.043	0.39	0.306	2.94**	-0.120	-0.117
NVE	0.356	3.49**	0.805	12.44**	-0.353	-0.336
NP	0.505	5.36**	0.887	17.60**	-0.409	-0.381
NI	0.505	5.36**	0.891	17.99**	-0.413	-0.385
EPV	0.246	2.33*	0.500	5.29**	-0.250	-0.231
PIV	0.041	0.38	0.197	1.84	-0.116	-0.108
EIV	0.241	2.28*	0.505	5.36**	-0.256	-0.237
DPP	0.234	2.20*	0.632	7.47**	-0.288	-0.276
DIEP	0.238	2.24*	0.652	7.88**	-0.301	-0.288

t for significance of **r**; *: $P < 0.05$; **: $P < 0.01$.

In the **PCA** carried out with the correlation matrix of the 16 components alone, and plus **W"**, the factor loadings were almost identical for the first four principal components, which explained 76.7% of the total inertia in the first case and 73.4% in the latter.

The factor loadings to the **SUM** and **W"** were respectively -0.393 and -0.223, which leads to the conclusion that from the point of view of these factors, **SUM** and **W"** are so valued as the four components **NI, NP, NVE** and **TNE.**

Positive or negative **r** and **PCA** values represent the effect of fitness components to total fitness. Therefore, disconsidering the signs, the values of Table I were used to plot the scatter diagrams in Figure 1, which showed a remarkable agreement among the methods employed.

A remarkable agreement was also shown when the factor loadings of the first four principal components, obtained with the three forms of **PCA**, were plotted in scatter diagrams, each against the others (Figures 2 and 3).

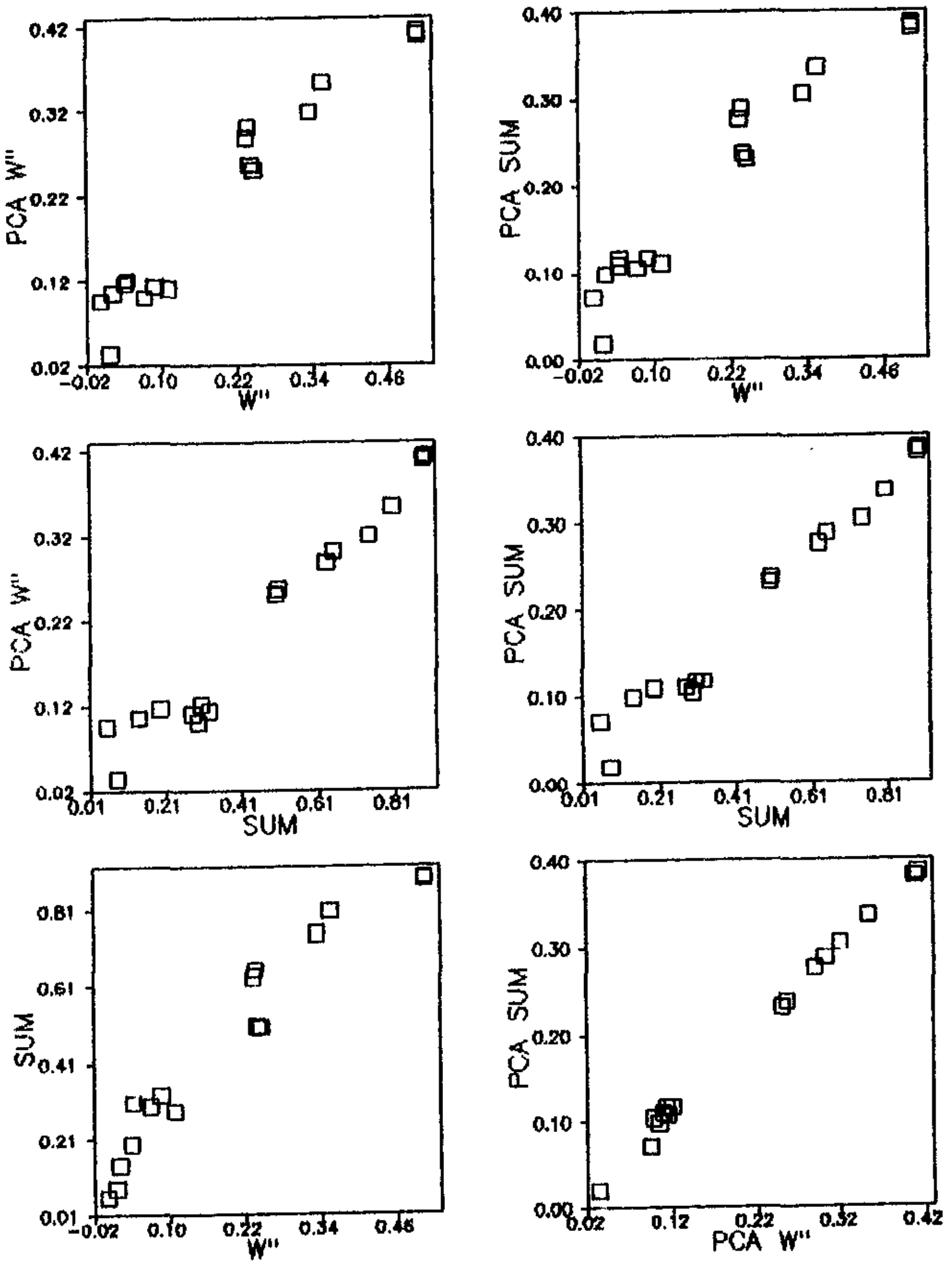

Figure 1 - Scatter diagrams of r and PCA values of W" and SUM.

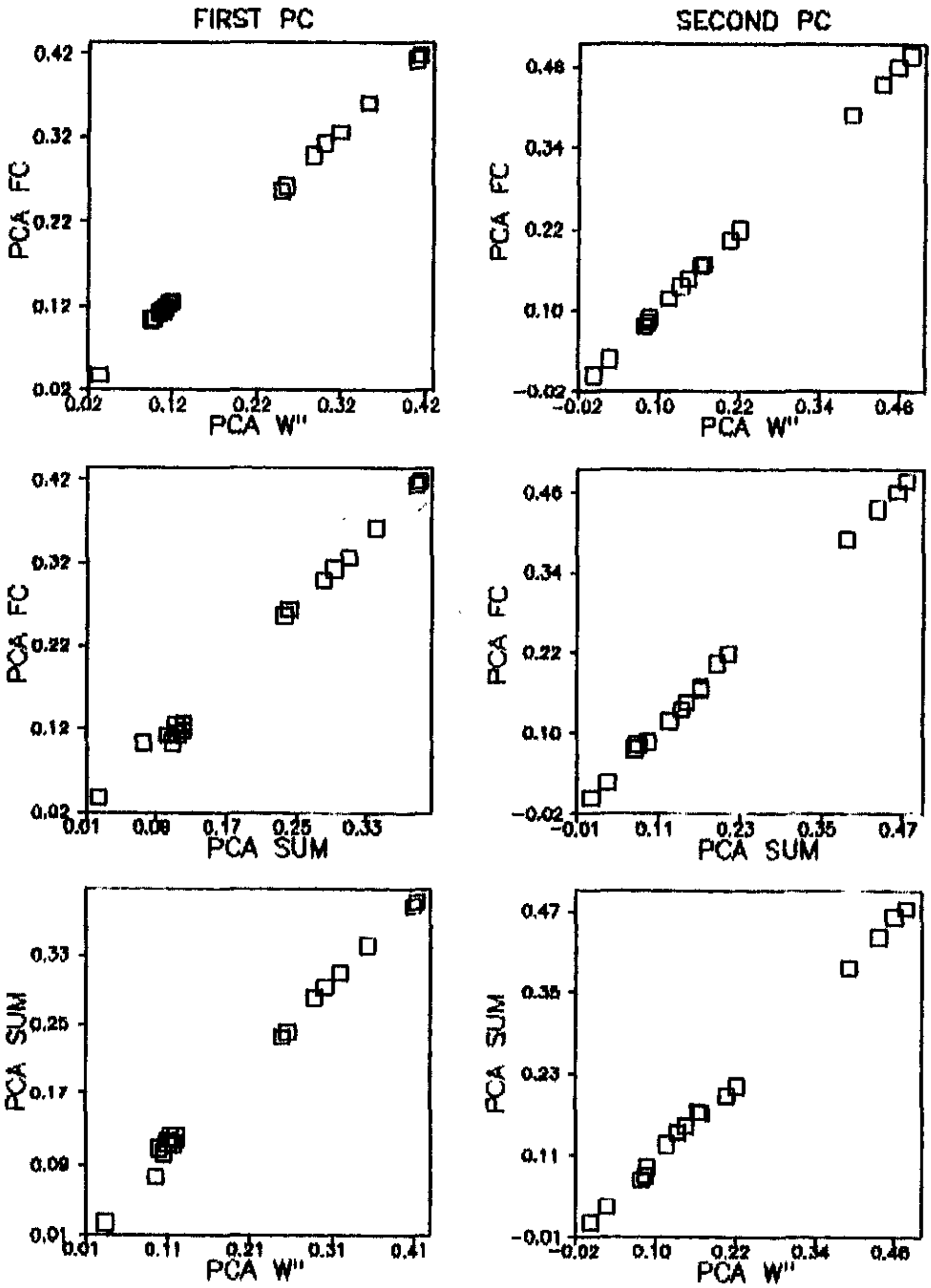

Figure 2 - Scatter diagrams of factor loadings of the first and second principal components for 16 fitness components in three PCA (with the 16 fitness components alone - PCA FC, with the product - PCA W'' and the sum - PCA SUM).

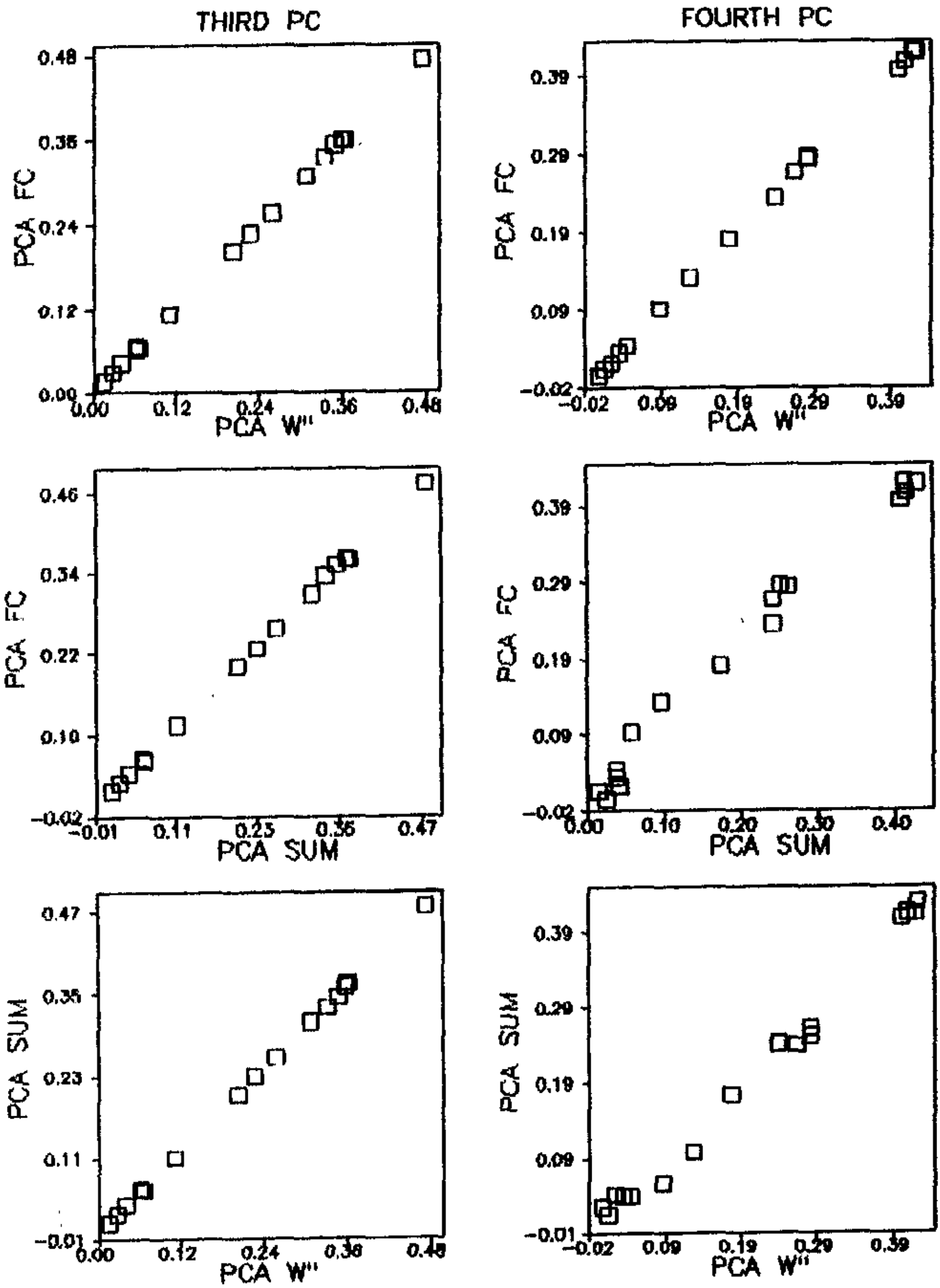

Figure 3 - Scatter diagrams of factor loadings of the third and fourth principal components for 16 fitness components in three PCA (with the 16 fitness components alone – PCA FC, with the product – PCA W" and the sum – PCA SUM).

Carareto and Mourão (1991b) argued that the most important components for total fitness should be those most variable among the strains, which in different expression combinations could represent different adaptive strategies. Eleven components were so considered in the three strains of *D. prosaltans* studied, among which **NI, NP, NVE** and **TNE** were included. Of the 11 variable components, **DPC, DNE, DPP** and **DIEP** were also used in this paper. The last three were correlated with the **SUM** and the last two with the product **W"**.

The present results show the adequacy of correlation analysis, as well as that of **PCA**, for detecting the most important fitness components for total fitness (product or sum). Although several fitness components behaved as neutral, others clearly showed an adaptive nature.

ACKNOWLEDGMENT

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RESUMO

Dados relativos a 16 componentes do valor adaptativo de fêmeas de *D. prosaltans* foram analisados para verificar as hipóteses da neutralidade e da adaptatividade de componentes do valor adaptativo para o valor adaptativo total. Correlações significativas de alguns componentes com o valor adaptativo total e os resultados da análise de componentes principais mostraram uma importância diferencial dos componentes estudados.

APPENDIX

APPENDIX 1. BR flies decimal values of the 16 fitness components.

	DPC	ADC	RDC	L	AOP	ROP	THE	DNE	NVE	NP	NI	EPV	PIV	EIV	DPP	DIEP
1	1.007	0.990	0.960	0.380	0.302	0.875	1.486	4.454	1.539	2.438	2.107	1.628	0.874	1.415	0.598	0.618
2	0.632	0.619	0.960	0.620	0.549	0.972	0.853	1.454	0.898	1.334	1.311	1.528	0.999	1.508	1.087	1.124
3	2.475	1.524	1.205	0.694	0.742	1.167	0.756	0.909	0.656	0.253	0.000	0.400	0.000	0.000	0.924	0.000
4	1.134	1.166	0.937	0.750	0.659	0.956	1.169	1.591	1.197	1.495	1.465	1.280	1.000	1.266	0.978	1.011
5	1.007	1.414	0.759	0.806	0.769	1.037	1.692	2.000	1.553	0.736	0.822	0.482	1.135	0.540	0.870	0.899
6	1.295	0.900	1.138	0.843	0.962	1.248	1.678	1.591	1.738	2.415	2.390	1.428	1.000	1.415	1.739	1.798
7	0.716	0.990	0.759	0.843	0.824	1.070	1.265	1.409	1.126	1.449	1.568	1.329	1.101	1.434	1.033	1.067
8	0.566	1.100	0.603	0.861	0.907	1.151	0.839	0.818	0.670	0.969	0.951	1.478	1.000	1.471	0.598	0.618
9	1.433	1.100	1.094	0.861	0.907	1.151	1.376	1.364	1.325	1.150	1.208	0.897	1.067	0.931	0.890	0.899
10	0.907	1.100	0.848	0.917	1.016	1.216	1.596	1.409	1.325	1.656	1.645	1.279	1.011	1.285	1.087	1.124
11	1.942	1.319	1.161	0.991	0.769	0.843	1.197	1.409	1.211	1.380	1.285	1.163	0.942	1.100	1.522	1.573
12	1.701	1.100	1.183	0.991	0.989	1.086	2.132	1.954	2.095	2.507	2.390	1.229	0.965	1.173	0.870	0.899
13	1.510	1.238	1.049	1.028	0.907	0.956	1.458	1.454	1.510	2.438	2.540	1.661	1.056	1.732	1.793	1.854
14	1.510	1.100	1.166	1.065	1.319	1.345	0.990	0.682	0.983	1.242	1.388	1.296	1.135	1.452	0.870	0.899
15	1.295	1.166	1.004	1.194	1.428	1.313	2.104	1.318	2.180	3.358	3.341	1.578	1.011	1.583	1.630	1.685
16	2.717	1.166	1.406	1.306	0.852	0.713	1.376	1.454	1.382	1.886	1.979	1.395	1.067	1.471	0.924	0.955
17	0.735	0.900	0.826	1.417	1.786	1.378	1.403	0.727	1.454	1.978	1.773	1.395	0.908	1.266	1.576	1.629
18	0.680	1.238	0.647	1.435	1.346	1.021	2.160	1.454	2.223	2.645	2.801	1.229	1.078	1.304	1.359	1.404
19	0.680	1.042	0.714	1.454	0.989	0.746	1.540	1.000	1.596	2.070	2.262	1.329	1.122	1.452	1.739	1.798

APPENDIX 2. CR flies decimal values of the 16 fitness components.

	DPC	ADC	RDC	L	AOP	ROP	THE	DNE	NVE	NP	NI	EPV	PIV	EIV	DPP	DIEP
1	3.021	1.166	1.451	0.231	0.110	0.519	0.138	1.136	0.142	0.230	0.257	1.661	1.135	1.862	0.163	0.168
2	0.604	1.319	0.558	0.398	0.247	0.681	1.774	6.500	1.838	1.587	1.465	0.880	0.942	0.819	0.489	0.506
3	5.435	1.238	1.706	0.472	0.467	1.086	1.362	2.636	1.411	1.058	1.002	0.764	0.965	0.726	0.924	0.955
4	1.510	1.650	0.893	0.676	0.659	1.070	1.087	1.500	1.126	0.575	0.540	0.532	0.953	0.484	1.087	1.011
5	0.579	1.524	0.491	0.676	0.742	1.199	2.380	2.909	2.465	2.231	2.416	0.930	1.101	1.006	0.924	0.955
6	0.566	1.414	0.513	0.750	0.742	1.086	1.348	1.636	1.396	1.196	1.105	0.880	0.942	0.819	0.924	0.955
7	1.815	1.166	1.183	0.898	0.797	0.972	0.633	0.727	0.456	0.368	0.411	0.830	1.135	0.931	0.489	0.506
8	1.236	1.100	1.004	0.917	0.797	0.956	0.894	1.000	0.926	0.299	0.283	0.332	0.965	0.316	1.033	1.067
9	0.544	1.166	0.558	0.917	0.604	0.713	1.430	2.136	1.311	0.736	0.694	0.581	0.953	0.540	0.598	0.618
10	2.092	1.166	1.272	0.954	0.742	0.843	0.812	1.000	0.356	0.046	0.051	0.133	1.135	0.149	0.054	0.056
11	1.510	0.582	1.451	0.991	0.687	0.762	1.568	2.091	1.624	1.863	1.902	1.179	1.033	1.210	1.141	1.180
12	0.800	4.950	0.223	1.046	0.577	0.600	0.729	1.136	0.242	0.184	0.154	0.781	0.851	0.652	0.217	0.225
13	0.697	1.100	1.094	1.065	1.319	1.361	0.908	0.636	0.527	0.345	0.360	0.664	1.056	0.521	0.217	0.225
14	1.088	1.042	0.960	1.083	0.494	0.502	1.486	2.727	1.425	0.667	0.437	0.482	0.670	0.316	0.598	0.449
15	2.717	1.042	1.473	1.102	0.549	0.551	0.179	0.273	0.100	0.046	0.026	0.465	0.568	0.261	0.326	0.056
16	1.360	1.414	0.915	1.102	0.769	0.762	1.032	1.227	0.869	0.138	0.129	0.166	0.942	0.149	0.598	0.618
17	0.477	1.166	0.513	1.232	1.236	1.102	1.994	1.454	2.066	2.944	2.981	1.462	1.033	1.490	1.141	1.180
18	3.891	1.238	1.562	1.250	0.769	0.681	0.289	0.364	0.299	0.299	0.257	1.030	0.874	0.893	0.870	0.899
19	1.701	1.042	1.205	1.306	1.703	1.426	1.169	0.636	1.211	1.196	1.182	1.013	1.001	1.006	0.924	0.955
20	1.433	1.238	1.027	1.361	1.758	1.410	0.866	0.454	0.770	0.483	0.437	0.648	0.919	0.577	0.380	0.281
21	0.716	1.042	0.736	1.398	1.236	0.972	1.678	1.227	1.738	0.989	0.951	0.581	0.976	0.559	1.141	1.180
22	1.701	1.798	0.915	1.435	1.868	1.426	0.715	0.364	0.627	0.414	0.437	0.681	1.067	0.726	0.380	0.393
23	1.701	1.524	1.004	1.454	1.896	1.426	1.871	0.909	1.183	0.069	0.077	0.066	1.135	0.074	0.109	0.112
24	1.295	1.166	1.004	1.454	1.538	1.151	0.605	0.364	0.527	0.069	0.051	0.133	0.760	0.093	0.489	0.506
25	1.088	1.100	0.937	1.472	1.897	1.410	1.018	0.500	0.598	0.506	0.540	0.864	1.078	0.931	0.978	0.337
26	1.510	0.990	1.183	1.472	1.154	0.859	1.197	0.954	0.271	0.253	0.257	0.963	1.033	0.987	0.163	0.168
27	0.755	1.238	0.692	1.472	0.689	0.502	2.283	3.000	1.966	1.058	1.054	0.548	1.011	0.559	0.706	0.730
28	0.680	1.238	0.647	1.491	0.742	0.551	1.609	1.954	1.667	1.840	1.670	1.130	0.919	1.043	1.141	1.180
29	0.579	0.942	0.692	1.509	1.813	1.313	1.430	0.727	1.482	1.219	1.131	0.847	0.942	0.782	1.033	0.899
30	2.475	0.990	1.428	1.620	1.978	1.329	1.403	0.636	1.282	0.920	0.925	0.731	1.022	0.745	0.543	0.562

APPENDIX 3. TR flies decimal values of the 16 fitness components.

	DPC	ADC	RDC	L	AOP	ROP	THE	DNE	NVE	NP	NI	EPV	PIV	EIV	DPP	DIEP
1	1.510	1.042	1.138	0.472	0.385	0.891	0.220	0.500	0.228	0.138	0.154	0.631	1.135	0.708	0.217	0.225
2	1.088	0.990	0.982	0.491	0.412	0.924	0.564	1.227	0.584	0.897	0.874	1.578	0.988	1.546	0.815	0.843
3	0.486	0.638	0.804	0.509	0.275	0.583	0.633	2.091	0.656	0.690	0.745	1.080	1.101	1.173	0.489	0.506
4	1.701	0.792	1.362	0.546	0.522	1.037	0.866	1.500	0.898	1.357	1.388	1.561	1.042	1.601	1.033	1.067
5	1.007	0.792	1.071	0.546	0.549	1.102	0.591	1.000	0.613	0.736	0.797	1.229	1.101	1.341	1.087	1.124
6	0.938	0.860	0.982	0.583	0.412	0.778	0.344	0.773	0.285	0.253	0.257	0.914	1.033	0.931	0.598	0.618
7	0.735	0.792	0.893	0.602	0.549	1.005	0.371	0.636	0.385	0.391	0.360	1.046	0.931	0.968	1.033	1.067
8	0.716	0.990	0.759	0.602	0.604	1.102	0.756	1.136	0.727	0.621	0.617	0.880	1.011	0.875	1.196	1.236
9	1.600	0.792	1.339	0.657	0.687	1.134	0.949	1.273	0.983	1.403	1.465	1.462	1.056	1.546	1.250	1.292
10	1.046	0.990	0.982	0.676	0.714	1.151	0.536	0.682	0.484	0.690	0.771	1.462	1.135	1.639	0.652	0.674
11	0.579	2.475	0.312	0.694	0.742	1.167	0.605	0.727	0.598	0.736	0.617	1.262	0.851	1.061	0.435	0.449
12	2.717	0.495	1.786	0.806	0.907	1.232	1.004	1.000	0.855	0.963	1.028	1.163	1.078	1.248	0.924	0.955
13	1.815	0.707	1.451	0.843	0.934	1.216	0.248	0.227	0.214	0.161	0.154	0.781	0.976	0.745	0.815	0.843
14	1.295	1.524	0.848	0.843	0.934	1.216	0.646	0.636	0.670	0.828	0.565	1.280	0.692	0.875	1.630	1.685
15	1.182	1.524	0.804	0.880	0.934	1.167	0.275	0.273	0.242	0.299	0.283	1.262	0.965	1.210	0.870	0.899
16	0.523	1.042	0.603	0.935	0.604	0.713	0.633	0.954	0.527	0.368	0.386	0.714	1.067	0.745	0.598	0.618
17	1.942	0.762	1.451	0.935	1.099	1.280	0.812	0.682	0.798	1.150	1.259	1.478	1.112	1.639	1.522	1.573
18	1.815	0.942	1.295	0.935	1.071	1.248	0.688	0.591	0.128	0.138	0.154	1.113	1.135	1.248	0.435	0.449
19	1.600	0.707	1.384	0.935	0.907	1.053	0.633	0.636	0.613	0.345	0.360	0.581	1.057	0.596	0.489	0.506
20	0.544	0.792	0.736	0.935	0.687	0.810	0.866	1.136	0.898	0.644	0.720	0.731	1.135	0.819	1.359	1.404
21	0.461	0.707	0.714	1.028	1.236	1.313	0.605	0.454	0.413	0.391	0.437	0.980	1.135	1.100	1.250	1.292
22	2.092	0.508	1.674	1.046	1.044	1.086	0.977	0.864	0.912	0.529	0.514	0.600	0.988	0.577	1.576	1.629
23	1.942	0.360	1.786	1.046	1.346	1.410	1.293	0.864	1.340	0.437	0.437	0.332	1.022	0.335	2.663	2.753
24	1.134	0.792	1.138	1.102	1.154	1.151	1.073	0.818	0.955	1.127	1.182	1.213	1.067	1.285	1.630	1.685
25	0.972	3.300	0.403	1.157	1.428	1.345	0.812	0.500	0.841	0.506	0.565	0.615	1.135	0.689	1.522	1.573
26	2.268	0.900	1.451	1.213	1.484	1.329	1.802	1.091	1.510	1.426	1.542	0.963	1.101	1.061	1.956	2.022
27	1.942	0.792	1.428	1.232	1.484	1.313	0.935	0.545	0.869	0.690	0.745	0.814	1.101	0.894	1.902	1.966
28	0.566	2.825	0.290	1.306	1.236	1.037	0.481	0.364	0.470	0.690	0.668	1.512	0.988	1.471	0.652	0.674
29	0.533	0.619	0.870	1.509	1.950	1.410	1.389	0.636	1.439	1.771	1.902	1.262	1.090	1.359	2.663	2.753
30	2.092	0.762	1.496	1.676	2.198	1.427	1.018	0.409	0.955	1.150	1.131	1.246	1.000	1.229	1.413	1.461
31	1.942	0.619	1.562	1.750	2.308	1.442	0.853	0.318	0.613	0.897	0.822	1.512	0.931	1.378	0.489	0.506
32	1.046	0.860	1.049	1.806	2.390	1.442	1.265	0.500	1.183	1.472	1.439	1.279	1.000	1.266	1.413	1.461
33	0.697	0.860	0.826	1.843	2.418	1.426	1.169	0.454	1.183	0.966	0.900	0.847	0.942	0.782	2.554	2.640
34	2.092	0.762	1.496	1.880	2.500	1.459	1.210	0.454	1.154	1.380	1.491	1.229	1.101	1.341	1.359	1.404
35	1.007	1.650	0.692	1.898	2.528	1.459	1.252	0.454	1.211	1.219	1.285	1.030	1.067	1.100	1.848	1.629
36	0.850	1.042	0.826	1.954	2.582	1.442	0.963	0.318	0.812	1.127	1.131	1.428	1.022	1.434	1.359	1.404
37	0.800	2.475	0.424	1.954	2.610	1.459	0.344	0.136	0.228	0.207	0.231	0.930	1.135	1.043	0.326	0.337

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