

## Is selection ready when opportunity knocks?

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### ABSTRACT

The opportunity for selection,  $I$ , defined as the variance in relative fitness, has been called an estimate of the 'total amount of selection'. However, while a non-zero  $I$  is a necessary condition for selection, it is not a sufficient one. We investigated the relationship between  $I$  and the magnitude of standardized linear and non-linear selection gradients for body size in the water-strider *Aquarius remigis*, measured over three episodes of selection. Male  $I$  exceeded female  $I$  for daily reproductive success, but the difference was not statistically significant and had little impact on net adult  $I$ . Linear selection gradients were only weakly correlated with  $I$ , while non-linear gradients were uncorrelated with  $I$ . Partitioning  $I$  among the three episodes of selection revealed that variance in net adult fitness was largely generated by variance in pre-reproductive survival. The patterns of selection across the adult life stage suggested by analysis of the opportunity for selection differed qualitatively and quantitatively from those revealed by selection gradient analysis. In particular, the former identified pre-reproductive survival as the key component of net adult fitness, even though there is little selection on total length in this life stage. We conclude that  $I$  is a useful adjunct to selection gradient analyses, but is perhaps most useful in the analysis of life-history evolution where the traits themselves are direct estimates of fitness.

*Keywords:* *Aquarius remigis*, fitness, Gerridae, opportunity for selection, partitioning, selection gradient.

### INTRODUCTION

Crow (1958) suggested that the best measure of the 'total amount of selection' is the variance in fitness divided by the square of the mean fitness, a statistic that he named the 'index of total selection', and designated  $I$ . Some authors have referred to  $I$  as the 'intensity of selection' but 'opportunity for selection' is preferable because it is nearer the intuitive meaning of  $I$ , and because it avoids confusion with the standardized selection differential  $i$ , also called the 'intensity of selection' (Arnold and Wade, 1984).

The opportunity for selection can be calculated as the variance in relative fitness, which emphasizes its relationship to selection: the change in mean relative fitness within a generation is equal to  $I$ , and the square root of  $I$  is the maximum number of standard deviations that any trait can be moved by directional selection (Arnold and Wade, 1984;

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Walsh and Lynch, 2000). Thus, opportunity for selection is a necessary but not a sufficient condition for natural selection, which requires an association between a trait and relative fitness (Sutherland, 1987; Wade, 1987; Wilkinson *et al.*, 1987; McVey, 1988).

There is room for confusion when  $I$  is said to estimate the 'amount of selection', independent of any character (Walsh and Lynch, 2000). Futuyma (1998, p. 349) provides the following definition of natural selection: 'any consistent difference in fitness [i.e. survival and reproduction] among phenotypically different biological entities'. If fitness itself is considered a phenotype, then this definition becomes tautological. Therefore, fitness must be defined in terms of phenotypes other than fitness. Walsh and Lynch (2000) note that  $I$  is independent of any particular character, which emphasizes that it is an estimate of the opportunity for selection, not of actual selection on any character.

Wilkinson *et al.* (1987, p. 238) drew attention to two studies in which some estimates of  $I$  had either no correlation or a negative correlation with the estimated selection gradients on certain traits. However, the opportunity for selection is still sometimes presented as an estimate of the strength of selection. Nishida (1989) included  $I$  with selection gradients and differentials among 'selection parameters', Vasi *et al.* (1994, p. 441) discussed 'opportunity for selection acting directly on each fitness component', Møller *et al.* (1998, p. 606) used an indicator of variance in male reproductive success as a measure of 'the intensity of sexual selection', and Walsh and Lynch (2000) state that partitioning  $I$  'allows the relative strength of selection to be compared across episodes'. These statements suggest an expected correlation between  $I$  and selection acting on specific phenotypes.

In this paper, we explore the relationship between opportunity for selection and the strength of actual selection on body size in the waterstrider *Aquarius remigis*. First,  $I$  is compared between the sexes separately for each of three components of fitness, because differences between the sexes in selection on body size have been detected in this species (Ferguson and Fairbairn, 2000; Preziosi and Fairbairn, 2000). Second, the correlations between  $I$  and the standardized selection coefficients  $\beta$  and  $\gamma$  are estimated, to determine whether  $I$  provides information on the strength of observed selection. Third,  $I$  for net adult fitness is partitioned among three components to relate selection in each episode to total selection through the adult lifespan.

### Study animal

The waterstrider *Aquarius remigis* is a large semi-aquatic true bug found on the surfaces of streams and small rivers throughout most of temperate and subtropical North America (Preziosi and Fairbairn, 1992). In southern Quebec, females lay eggs from late April to early July on rocks under water. Young climb to the surface and develop through five nymphal instars to the adult, but the adults do not become reproductively active until the following spring. Mortality over the winter is 70–90% (Fairbairn, 1985a; Blanckenhorn, 1994; Ferguson and Fairbairn, 2000). Both sexes mate repeatedly with different partners through the reproductive lifespan (Krupa and Sih, 1993; Preziosi and Fairbairn, 1996), which lasts about 4 weeks (Preziosi and Fairbairn, 1997; Ferguson and Fairbairn, 2000).

### METHODS

Our mark-recapture study followed two populations of *A. remigis* through two generations (1993–94 and 1994–95). These populations are located on South Creek and West Creek,

respectively, at the McGill University Research Station on Mont St-Hilaire, Quebec, Canada, about 35 km south-east of Montreal. The study area on South Creek included an upper recapture-only area (30 m long), a central mark-recapture area (100 m) and a lower recapture-only area (100 m). On West Creek, these areas are 50, 200 and 100 m long, respectively. On both streams, the study areas are bounded by barriers to dispersal such as waterfalls. Since *A. remigis* on these streams rarely move more than 100 m from where first captured (Fairbairn, 1985b), any individuals marked in the central mark-recapture areas are unlikely to move out of the study areas. Nevertheless, each month we searched 100–200 m beyond the study areas for marked individuals. Fewer than 1% of the marked individuals were ever observed outside of the study area, and thus death and dispersal are unlikely to be confounded in this study.

From spring until fall, the study areas were carefully searched weekly for *A. remigis*, and the number on each marked adult was recorded. All unmarked adults found in the mark-recapture areas were captured using hand nets, sexed, photographed in a ventral aspect and marked with a unique number on the dorsal surface using enamel paint (see Preziosi and Fairbairn, 1996, 1997). For each individual, total length was measured from the photographic negatives using a computerized digitizing system with MTV software (Updegraff, 1990). We estimated the following components of fitness: pre-reproductive survival (0 = did not survive to the reproductive season, 1 = did survive to the reproductive season), reproductive lifespan (in days), mating frequency for males and daily fecundity for females. Mating frequency was estimated as the proportion of observation days that the individual was found mating. Observation days included all mark-recapture days plus one (1994) or two (1995) additional searches of the creeks each week (during the reproductive season). To assess daily fecundity, we confined solitary females in plastic containers in the creeks and counted the eggs laid over 48 h. (For a detailed description of these methods, see Ferguson and Fairbairn, 2000.)

Net adult fitness was estimated as pre-reproductive survival  $\times$  reproductive lifespan  $\times$  daily reproductive success (mating frequency for males, daily fecundity for females). Female fecundity varied through the reproductive season in the second generation, making meaningful estimates of lifetime fecundity impossible; therefore, net adult fitness was not estimated for females in the second generation. Relative fitness was estimated within each population, generation and sex as absolute fitness divided by the mean absolute fitness. Standardized linear and non-linear selection gradients were estimated by regressing each relative fitness on standardized total length and standardized total length squared according to Lande and Arnold (1983). Statistical significance was determined by randomization (Manly, 1992) and was not corrected for experiment-wise error. The levels of significance were used only to indicate our degree of confidence in the estimates, rather than to test specific hypotheses about selection. (For a complete analysis of selection in these samples, see Ferguson and Fairbairn, 2000.)

The opportunity for selection,  $I$ , was estimated as the variance in relative fitness for each sex in each population and generation. The total opportunity for selection (through net adult fitness) was partitioned among pre-reproductive survival, daily reproductive success and reproductive lifespan according to the methods of Arnold and Wade (1984) for each sex, population and generation. We report both the relative and absolute contribution of each episodic  $I$ , and the contribution of covariance between components of fitness, to the total opportunity for selection. The contribution of covariance may be due to non-independence of selection (between episodes) or zero fitnesses at an early episode (Arnold

and Wade, 1984). The latter was expected to be a factor in this study, because pre-reproductive survival includes zero fitness for many individuals. Partitioning was repeated with the second two components of fitness combined (reproductive lifespan  $\times$  daily reproductive success) to isolate the contribution of covariance between pre-reproductive survival and overall reproductive success. The statistical analyses were performed using RT 1.02 (Manly, 1992), Microsoft Excel 97 (Microsoft Corp., 1997) spreadsheet functions and SPSS 8.0 (SPSS Inc., 1997).

### RESULTS

Mean opportunity for selection did not differ significantly between the sexes for pre-reproductive survival or reproductive lifespan, but males experienced slightly higher  $I$  for daily reproductive success, which approached statistical significance (Table 1). Although  $I$  for net adult fitness was higher for males than females, this difference was not significant.

When all 24 samples were used (2 populations  $\times$  2 generations  $\times$  2 sexes  $\times$  3 episodes of selection; Tables 2 and 3), the correlation between the absolute value of the linear selection gradients and the opportunities for selection was positive and just significant ( $r_s = 0.34$ ,  $n = 24$ , one-tailed  $P = 0.050$ ). However, this relationship was weak (Pearson  $r^2 = 0.095$ ) and the largest, statistically significant selection gradients, pre-reproductive survival on South Creek in 1994–95, were not associated with the highest opportunities for selection (Table 3). The non-linear gradients were not significantly correlated with  $I$  ( $r_s = 0.07$ ,  $n = 24$ , one-tailed  $P = 0.37$ ).

Partitioning  $I$  revealed that the episode that contributed the most to  $I$  for net adult fitness in both sexes was pre-reproductive survival (Table 4, Fig. 1). In 9 of 12 samples (6 for reproductive lifespan and 6 for daily reproductive success), less than 10% of net adult  $I$  was caused by variance in components of fitness in the reproductive season; this contribution was never greater than 29%. In contrast, variance in pre-reproductive survival always contributed at least 36% of net adult  $I$ . However, the greatest single contributor to  $I$  was covariance between components of fitness (Table 4, Fig. 1). When reproductive lifespan and daily reproductive success were combined into one estimate of overall reproductive success, partitioning the opportunity for selection yielded similar contributions for covariance (43–55%), indicating that it was covariance between pre-reproductive survival

**Table 1.** Between-sex comparison of opportunity for selection in *Aquarius remigis* at Mont St-Hilaire

	Opportunity for selection		Wilcoxon test	
	Males	Females	$n^a$	$P$
Pre-reproductive survival	5.61	4.22	4	0.62 <sup>b</sup>
Reproductive lifespan	0.81	0.82	4	0.97 <sup>b</sup>
Daily reproductive success	1.51	0.92	4	0.061 <sup>c</sup>
Net adult fitness	13.37	11.34	2	0.49 <sup>c</sup>

*Note:* The Wilcoxon paired sample tests were conducted on square-transformed data ( $x^2$ ) to correct for skew; probabilities ( $P$ ) were generated by the Monte Carlo procedure.

<sup>a</sup> Number of samples (=populations  $\times$  generations); <sup>b</sup> two-tailed test; <sup>c</sup> one-tailed test.

**Table 2.** Univariate linear ( $\beta$ ) and non-linear ( $\gamma$ ) selection gradients for total length, sample size ( $n$ ) and opportunity for selection ( $I$ ) in male *Aquarius remigis* at Mont St-Hilaire

		South Creek		West Creek	
		1993-94	1994-95	1993-94	1994-95
Pre-reproductive survival	$\beta$	-0.16	-0.38*	0.04	-0.42
	$\gamma$	0.14	0.13	-0.12	0.06
	$n$	466	427	151	121
	$I$	7.34	4.22	2.53	8.38
Reproductive lifespan	$\beta$	-0.07	0.02	0.09	-0.41
	$\gamma$	0.19	-0.17	-0.13	0.29
	$n$	56	82	43	13
	$I$	1.25	0.71	0.59	0.70
Daily reproductive success	$\beta$	-0.14	-0.06	0.22	0.07
	$\gamma$	0.05	-0.17*	-0.02	0.18
	$n$	152	246	89	101
	$I$	1.50	0.63	1.96	1.95

\* Statistically significant:  $P < 0.05$ .**Table 3.** Univariate linear ( $\beta$ ) and non-linear ( $\gamma$ ) selection gradients for total length, sample size ( $n$ ) and opportunity for selection ( $I$ ) in female *Aquarius remigis* at Mont St-Hilaire

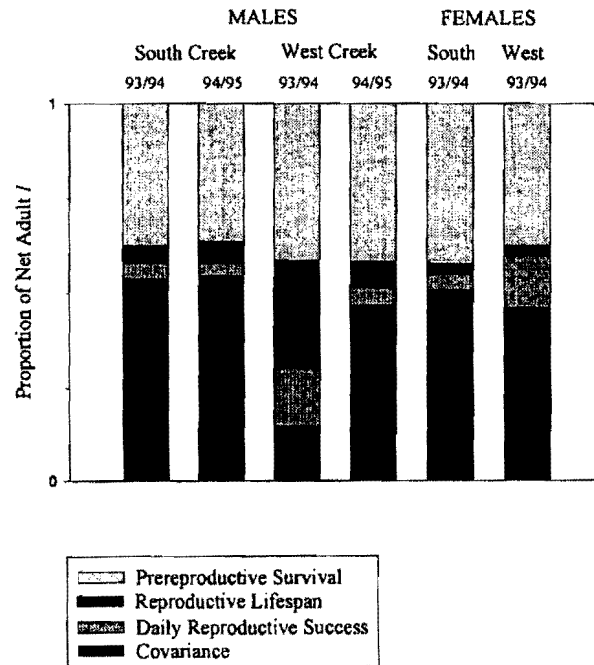
		South Creek		West Creek	
		1993-94	1994-95	1993-94	1994-95
Pre-reproductive survival	$\beta$	0.01	-0.30*	0.10	0.28
	$\gamma$	-0.05	-0.21	0.16	0.23
	$n$	476	484	209	146
	$I$	6.45	4.45	2.68	3.32
Reproductive lifespan	$\beta$	0.07	0.04	-0.03	0.12
	$\gamma$	-0.03	-0.06	-0.10	0.09
	$n$	64	89	57	34
	$I$	1.03	0.56	0.79	0.91
Daily reproductive success	$\beta$	0.01	0.12	0.08	-0.10
	$\gamma$	0.12	0.18	-0.13	-0.14
	$n$	35	60	36	48
	$I$	0.86	0.45	0.81	1.54

\* Statistically significant:  $P < 0.05$ .

and overall reproductive success (rather than between reproductive lifespan and daily reproductive success) that was responsible for the large contribution of covariance to the total opportunity for selection.

**Table 4.** Opportunity for selection in *Aquarius remigis* at Mont St-Hilaire, partitioned according to Arnold and Wade (1984)

	Males				Females	
	South Creek		West Creek		South	West
	1993-94	1994-95	1993-94	1994-95	1993-94	1993-94
Pre-reproductive survival	7.21	4.01	2.57	6.32	6.46	2.47
Reproductive lifespan	1.01	0.70	1.87	1.11	0.42	0.21
Daily reproductive success	0.70	0.39	1.00	0.67	0.46	0.90
Covariance	10.56	6.11	0.92	7.19	7.80	3.10
Net adult fitness	19.48	11.21	6.34	15.28	15.33	6.69

**Fig. 1.** Partitioning the opportunity for selection,  $I$ , for *Aquarius remigis* at Mont St-Hilaire, Canada. The proportion of net adult  $I$  is presented for each episode of selection in each sample.

## DISCUSSION

The estimated  $I$  for daily reproductive success tended to be higher for males than for females, although this pattern was not statistically significant. Despite this, no significant selection on total length was detected on males in this episode. This does not rule out selection on other male traits. In fact, certain components of male body size were found to

be under directional sexual selection in the same South Creek samples (Ferguson and Fairbairn, 2000). The key point is that the presence of opportunity for selection does not indicate selection on any particular trait. We did find a weak correlation between the opportunity for and the strength of directional selection but, with  $r^2$  less than 10%,  $I$  provides little information about the magnitude of the selection gradient. Furthermore, the samples in which statistically significant selection was detected did not have higher opportunity for selection than those in which no significant selection was detected, and there was no evidence of a correlation between non-linear selection gradients and  $I$ . Thus,  $I$  was a poor estimate of the strength of selection in this study.

The opportunity for selection,  $I$ , has been reported in a number of studies (Table 5); and some of these studies also provide estimates of the strength of selection, such as the selection differential,  $s$  or  $C$  (e.g. Anholt, 1991), or the selection gradient,  $\beta$  or  $\gamma$  (e.g. Howard, 1988), but none that we are aware of has estimated the relationship between  $I$  and the strength of selection. The values for  $I$  in this study fall into the range of previously published values (Table 5), suggesting that the lack of a strong relationship between the opportunity for selection and the strength of selection is not due to  $I$  being exceptionally high or low. The standardized linear selection gradient,  $\beta$ , is expected to be correlated with  $I$  only because  $I$  sets the upper limit for  $\beta$ , so it should not be surprising that the correlation is weak. The relationship with the non-linear gradient,  $\gamma$ , is expected to be even weaker, as Arnold (1986) showed that non-linear (e.g. stabilizing) selection is not informatively limited by the opportunity for selection unless  $I$  is less than 0.5. The failure of the opportunity for selection to adequately predict the strength of selection is consistent with Sutherland's (1987) theoretical conclusion, that 'it is not useful to measure variance in reproductive success as this is neither evidence for sexual selection nor a good measure of its intensity'.

Partitioning net adult opportunity for selection among the episodes of selection on these waterstriders revealed that variance in net adult fitness was largely generated by variance in pre-reproductive survival (the covariance component is due to zero fitnesses in pre-reproductive survival; see Arnold and Wade, 1984). This may explain why previously reported significant selection through pre-reproductive survival favouring smaller males resulted in smaller males enjoying a significant advantage in net adult fitness (Ferguson and Fairbairn, 2000). This pattern is not unique to waterstriders; Howard (1988) found that survival contributed more to opportunity for selection than fecundity in two species

**Table 5.** The ranges of estimated opportunity for selection,  $I$ , in selected studies

	Opportunity for selection		Taxon
	Minimum	Maximum	
Anholt (1991)	0.8	114.8	Damselflies
Cabana and Kramer (1991)	0.01	1.49	Birds
Houck <i>et al.</i> (1985)	0.01	0.074	Salamanders
Howard (1988)	0	3.18	Frogs
LeBoeuf and Reiter (1988)	7.08	27.00	Elephant seals
McVey (1988)	0.440	6.22	Dragonflies
Pruett-Jones and Pruett-Jones (1990)	2.27	3.94	Birds
Present study	0.45	19.48	Waterstriders

of frogs. It could also explain why selection in the reproductive season may be swamped by random variance in pre-reproductive fitness, as described by Preziosi and Fairbairn (2000).

Thus, as we expected,  $I$  is not a good predictor of the strength of selection on total length (as estimated by linear and non-linear selection gradients). However,  $I$  is useful precisely because it is independent of any particular phenotype (Walsh and Lynch, 2000). In a sense,  $I$  may be characterized as a measure of the relative impact of the various life-history components on lifetime fitness. For example, we have identified pre-reproductive survival as a key life-history component in *A. remigis*. Individual fitness through the adult stage is most strongly determined by ability to survive from eclosion to first reproduction, and hence we would expect selection to act most strongly in this phase of the adult life cycle. Because pre-reproductive survival is not strongly correlated with total length, our selection gradient analyses did not reveal the importance of pre-reproductive survival in determining net adult fitness (Ferguson and Fairbairn, 2000; Preziosi and Fairbairn, 2000). Our comparisons of the two methods of analysing selection suggest that, although  $I$  is a useful adjunct to selection gradient analysis in studies of the adaptive significance of trait values, its most important contribution may lie in studies of the evolution and adaptive significance of life histories.

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