Male development tracks rapidly shifting sexual versus natural selection pressures

Michael M. Kasumovic* and Maydianne C.B. Andrade

Theory predicts that interplay between sexual and natural selection shapes phenotypic distributions over evolutionary time [1–3]. We show that this also significantly affects individual development. Developmental plasticity, whereby individuals vary their ontogeny in response to variation in the selection to be encountered upon maturity [4–6], has previously been demonstrated in response to single selective pressures, such as predation and sperm competition [7,8]. We show that the relative magnitude of opposing natural and sexual selection can trigger developmental shifts and rapidly change the distribution of phenotypic traits critical to reproductive success.

Males of the sexually cannibalistic redback spider (*Latrodectus hasselti*) show a tactical, condition-dependent shift between conflicting developmental strategies favoured by scramble competition or surviving mate search. Male condition, developmental rate and body size changed with the relative importance of these selective pressures, which naturally fluctuate throughout a breeding season [9–11]. This has important implications for studies comparing fitness values of fixed traits without regard for plasticity.

We exposed penultimate-instar redback spider males to non-contact, pheromonal cues [12,13] simulating dense (females present) or sparse (females absent) populations. This treatment was combined with high, intermediate or low diet levels, respectively. When females are sparse, natural selection for provisioning to survive mate searching, during which 80% of males perish [14], will be more intense than sexual selection for scramble competition for virgin females (90% median paternity for the first male to mate) [15]. As multiple males commonly settle on females' webs [16], male density will also affect competitive success. We, therefore, examined male growth, development time, and body condition as a function of diet, female treatment and male density. We also assessed male phenotypes as a function of female proximity in the field (Supplemental Data).

Our laboratory and field results collectively show that redback males adjust their development in response to pheromonal cues of female and male density. When females are absent, males trade-off rapid development for increased body size and condition (Table 1; Figure 1) as larger males in better condition are more likely to survive mate searching and direct competition when females are sparse. In contrast, males trade-off size and body condition for rapid development when females are present (Table 1; Figure 1), which would ensure that they can reach virgin females first [15]. Similarly, in the field, as female proximity increases, male size (Two-way ANCOVA, F = 8.96, p = 0.004) and body condition (Two-way ANCOVA, F = 5.14, p = 0.028) decrease. Sexual selection for scramble competition has been proposed to contribute to sexual size dimorphism as a side-effect of rapid development of males [17]. These results show that the degree of dimorphism could change within seasons as selection fluctuates.

Although increased female density resulted in smaller males of poorer condition that developed rapidly, increased male density led to the development of smaller males in better condition (Table 1). This independent effect of neighbouring males suggests a trade-off between size and body condition. Thus, the relative importance of these traits to male fitness apparently changes as a function of both female and male density.

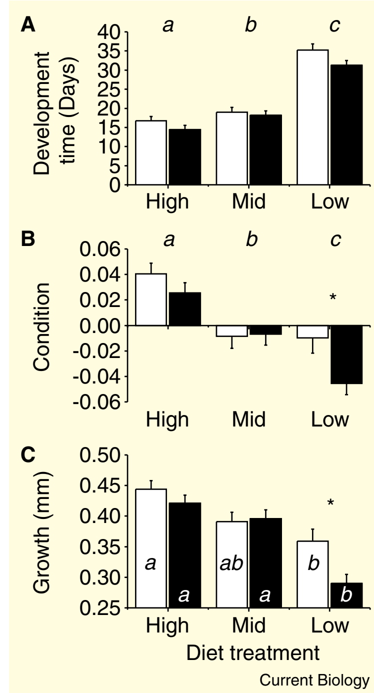

Figure 1. Developmental plasticity under varying selection.

Development time (A), body condition (B) and growth (C) of males reared in the absence (white bars) or presence (black bars) of virgin females across high, mid and low diet treatments (X-axis). Error bars represent one standard error. Asterisks and letters within bars represent significance in Tukey-Kramer HSD post-hoc tests. In (A and B), data for post-hoc tests were pooled across female presence treatments. Post-hoc tests in (C) were completed separately for the different female treatments due to a significant interaction between female presence and diet when controlled for male density. In (B and C), asterisks represent significant differences between female presence treatments within the low-diet.

Although conflicting selection usually results in non-optimal phenotypes with moderate fitness [18,19], in redback spiders, conflicting pressures acting on phenotypic plasticity yield phenotypes optimized for specific competitive challenges [6]. This is critical because redback males are under strong selection to succeed in their single mating opportunity [16,20]. Similar plasticity may be important in cases where males have few mating opportunities that occur over small spatial or temporal scales, where juveniles can detect cues reliably predicting adult challenges and/or where allocation of limited resources

Table 1. Female presence and diet affect growth, body condition and development time of males.

MANOVA				
	Pillai's Trace	F	d.f.	*p*
Female	0.086	6.01	3, 198	**0.0006**
Diet	0.584	27.27	6, 398	**<0.0001**
Female x Diet	0.059	1.83	6, 398	0.09
Males	0.084	5.73	3, 198	**0.0009**
Female x Males	0.009	0.48	3, 198	0.70
Diet x Males	0.016	0.97	6, 398	0.44
Female x Diet x Males	0.073	2.32	6, 398	**0.032**

Univariate Analyses			
	Source	F	*p*
Development time	Female	4.80	**0.03**
	Diet	80.70	**< 0.0001**
	Female x Diet	0.25	0.78
	Males	0.34	0.56
	Female x Males	0.01	0.90
	Diet x Males	0.058	0.95
	Female x Diet x Males	0.08	0.92
Body condition	Female	4.62	**0.033**
	Diet	23.15	**< 0.0001**
	Female x Diet	1.84	0.16
	Males	15.22	**0.0001**
	Female x Males	1.25	0.26
	Diet x Males	2.68	0.07
	Female x Diet x Males	2.67	0.07
Experimental growth	Female	5.23	**0.023**
	Diet	23.73	**< 0.0001**
	Female x Diet	2.58	0.078
	Males	4.41	**0.037**
	Female x Males	0.06	0.81
	Diet x Males	0.07	0.94
	Female x Diet x Males	3.21	**0.042**

Values in bold are significant (table-wise $p < 0.05$).

yields disproportionate increases in selected fitness components. Such conditions may occur in other mate-searching species with variable population density and relatively short male lifespan [17].

We demonstrate that short-term shifts in conflicting sexual and natural selection can be a major source of variation in male phenotypic traits important to sexual competitiveness [1,17]. Although decreases in resource availability can decrease male size and body condition (Table 1; Figure 1) [8], small size may also arise because the net fitness benefit of decreased development time outweighs the potential costs of small size in the local environment. Thus the maintenance of classes of individuals thought to be competitively inferior [1] could be explained by plasticity and fine-scale environmental heterogeneity, rather than variation in condition [7]. This highlights the critical need to expand definitions of male quality beyond fixed adult traits to include an individual's ability to respond to changes in varying selection pressures [9]. Most importantly, for studies of sexual selection on male phenotypes, assessments of fitness effects measured without consideration of local conditions and development could seriously overstate the importance of fixed, heritable traits to lifetime reproductive success.

Acknowledgments
We thank M.D. Biaggio, J.M. Brandt, R. Brooks, D.O. Elias, D.T. Gwynne, J.C. Johnson, A.P. Moczek, M. Polak, L. Rowe and two anonymous reviewers for comments on this paper. This project was funded by an NSERC PGS B to M.M.K. and grants from NSERC, CFI and OIT to M.C.B.A.

Supplemental data
Supplemental data are available at http://www.current-biology.com/cgi/content/full/16/7/R242/DC1/

References

1. Andersson, M. (1994). Sexual Selection (Princeton: Princeton University Press).
2. Darwin, C. (1871). The Descent of Man, and Selection In Relation to Sex (London: Murray).
3. Fisher, R.A. (1930). The Genetical Theory of Natural Selection (Oxford: Clarendon Press).
4. Roff, D.A. (1992). The Evolution of Life Histories: Theory and Analysis (New York: Chapman & Hall).
5. Stearns, S.C. (1992). The Evolution of Life Histories (Oxford: Oxford University Press).
6. West-Eberhard, M.J. (2003). Developmental Plasticity and Evolution (New York: Oxford University Press).
7. Benard, M.F. (2005). Predator-induced phenotypic plasticity in organisms with complex life histories. Annu. Rev. Ecol. Syst. *35*, 651–673.
8. Gage, M.J.G. (1995). Continuous variation in reproductive strategy as an adaptive response to population density in the moth *Plodia interpunctella*. Proc. R. Soc. Lond. B *261*, 25–30.
9. Meyers, L.A., and Bull, J.J. (2002). Fighting change with change: adaptive variation in an uncertain world. Trends Ecol. Evol. *17*, 551–557.
10. Jann, P., Blanckenhorn, W.U., and Ward, P.I. (2000). Temporal and microspatial variation in the intensities of natural and sexual selection in the yellow dung fly *Scathophaga stercoraria*. J. Evol. Biol. *13*, 927–938.
11. Kassen, R. (2002). The experimental evolution of specialists, generalists, and the maintenance of diversity. J. Evol. Biol. *15*, 173–190.
12. Andrade, M.C.B., and Kasumovic, M.M. (2005). Terminal investment strategies and male mate choice: Extreme tests of Bateman. Int. Comp. Biol. *45*, 838–847.
13. Kasumovic, M.M., and Andrade, M.C.B. (2004). Discrimination of airborne pheromones by mate-searching male western black widow spiders (*Latrodectus hesperus*): species- and population-specific responses. Can. J. Zool. *82*, 1027–1034.
14. Andrade, M.C.B. (2003). Risky mate search and male self-sacrifice in redback spiders. Behav. Ecol. *14*, 531–538.
15. Snow, L.S.E., and Andrade, M.C.B. (2005). Multiple sperm storage organs facilitate female control of paternity. Proc. R. Soc. Lond. B *272*, 1139–1144.
16. Andrade, M.C.B. (1996). Sexual selection for male sacrifice in the Australian redback spider. Science *271*, 70–72.
17. Thornhill, R., and Alcock, J. (1983). The evolution of insect mating systems (Cambridge, Massachusetts: Harvard University Press).
18. Candolin, U. (2004). Opposing selection on a sexually dimorphic trait through female choice and male competition in a water boatman. Evolution *58*, 1861–1864.
19. Bonduriansky, R., and Rowe, L. (2003). Interactions among mechanisms of sexual selection on male body size and head shape in a sexually dimorphic fly. Evolution *57*, 2046–2053.
20. Forster, L.M. (1992). The stereotyped behaviour of sexual cannibalsim in *Latrodectus hasselti* Thorell (Aranea: Theridiidae), the Australian redback spider. Austral. J. Zool. *40*, 1–11.

Integrative Behaviour and Neuroscience Group, University of Toronto at Scarborough, Toronto, Ontario, M1C 1A4, Canada.
*E-mail: m.kasumovic@utoronto.ca