

Sexual selection and temporal phenotypic variation in a damselfly population

D. B. STEELE¹, A. M. SIEPIELSKI & M. A. McPEEK

Department of Biological Sciences, Dartmouth College, Hanover, NH, USA

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Odonata;
sexual selection;
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Abstract

Temporal variation in selection can be generated by temporal variation in either the fitness surface or phenotypic distributions around a static fitness surface, or both concurrently. Here, we use within- and between-generation sampling of fitness surfaces and phenotypic distributions over 2 years to investigate the causes of temporal variation in the form of sexual selection on body size in the damselfly *Enallagma aspersum*. Within a year, when the average female body size differed substantially from the average male body size, male body size experienced directional selection. In contrast, when male and female size distributions overlapped, male body size experienced stabilizing selection when variances in body size were large, but no appreciable selection when the variances in body size were small. The causes of temporal variation in the form of selection can only be inferred by accounting for changes in both the fitness surface and changes in the distribution of phenotypes.

Introduction

Most organisms reside in temporally variable environments. As a result, the form and strength of selection that organisms experience should vary through time as the changing ecology of a system alters the relationship between their phenotype and fitness (Levins, 1868; Grant & Grant, 2002; Siepielski *et al.*, 2009; Bell, 2010). For example, temporal variation in ecological factors such as predator regimes (Reimchen & Nosil, 2002), pollinator assemblages (Schemske & Horvitz, 1989), density of mate colour morphs (Gosden & Svensson, 2008), density of conspecifics (Calsbeek *et al.*, 2009; Svanbäck & Persson, 2009; Punzalan *et al.*, 2010), resource abundance (Siepielski & Benkman, 2007) and sex ratio (Madsen & Shine, 1993; Punzalan *et al.*, 2010) have all been implicated as underlying causes of temporal variation in natural and sexual selection.

The changing form and strength of selection experienced by a population through time is typically implicitly

interpreted as a change in the shape or position of the fitness surface overlying the phenotypic distribution (Siepielski *et al.*, 2009; Bell, 2010). At different times, the fitness surface may shift from directional selection favouring higher or lower values of a trait, to stabilizing selection favouring intermediate values (Fig. 1a). Other forms of selection such as disruptive selection or more complex fitness surfaces are also possible. For example, seedling plants may experience selection for early germination dates in years with warm springs when the last frost happens early, but may experience selection for later germination dates in years when the last frost occurs late in the spring (Kalisz, 1986). Such variability may occur either within or between generations, and the net effect will be a function of combining these various episodes of selection into the overall form and strength experienced by the population (e.g. Arnold & Wade, 1984; Wade & Kalisz, 1989; Hunt *et al.*, 2009; McGlothlin *et al.*, 2010; Shaw *et al.*, 2008).

The form and strength of selection on a trait in a population may also vary through time not because of a changing relationship between fitness and the phenotype, but rather because of a change in the phenotypic distribution of the population. Organisms may frequently produce different phenotypes in response to different ecological environments in which they develop, and this

Correspondence: Mark A. McPeck, Department of Biological Sciences, Dartmouth College, Hanover, NH 03755, USA.

Tel.: +1 603 646 2389; fax: +1 603 646 1541;

e-mail: mark.mcpeek@dartmouth.edu

¹Present address: River Valley Community College, Claremont, NH 03743, USA.

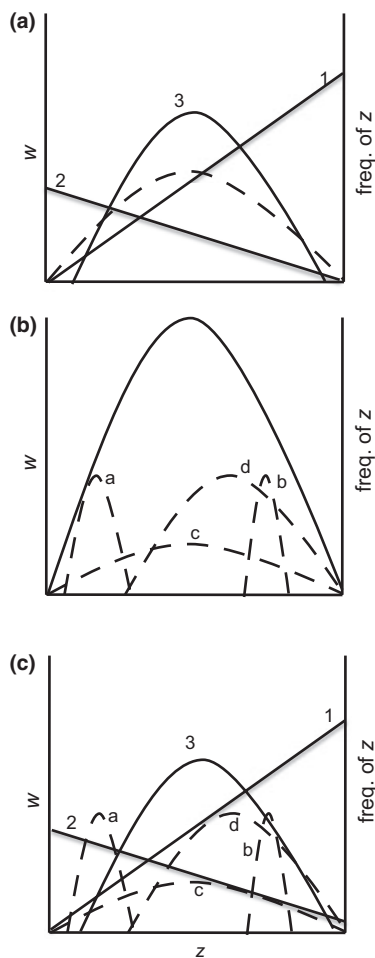


Fig. 1 Conceptual model depicting three scenarios of temporal variation in selection in relation to fitness surfaces (solid lines) and phenotypic distributions (dashed lines). In each panel, the solid lines are fitness surfaces specifying the relationship between individual fitness (w) and an individual's phenotype (z). The dashed lines identify frequency distributions of phenotypes in the population. In panel a, the fitness surface varies temporally, but the phenotypic distribution does not change. In panel b, the fitness surface is static but the phenotypic distribution varies in position and width through time. In panel c, both fitness surfaces and phenotypic distributions vary in position with time.

phenotypic plasticity will necessarily change the shape and position of the population's phenotypic distribution. This plasticity may be adaptive [i.e. organisms adjust their phenotypes in ways that increase their fitness (Via, 1993; Via *et al.*, 1995; Pigliucci, 2001; Ghalambor *et al.*, 2007; Charmantier *et al.*, 2008)] or nonadaptive (e.g. individuals may simply be larger in years when resources are more plentiful because they eat more), but in either case the phenotypic distribution will vary with changing ecological conditions. For example, plants germinating early may have a different size distribution than plants

germinating later (Kalisz, 1986), insects emerging as adults earlier in the season are generally larger than those emerging later in the season (Vannote & Sweeney, 1980; Anholt, 1991; Rowe & Ludwig, 1991; De Block & Stoks, 2005; Lowe *et al.*, 2009), and birds typically lay larger clutches earlier in a given breeding season (Rowe *et al.*, 1994). Similarly, stochastic factors, migration, developmental changes, and natural selection itself will cause phenotypic distributions to vary both within and between generations (Wade & Kalisz, 1990).

To illustrate, imagine a population that experiences a static fitness surface favouring an intermediate phenotype (stabilizing selection: Fig. 1b). As the position of the phenotypic distribution changes, at any given time the population may experience directional selection for larger values of the phenotype (phenotypic distribution a in Fig. 1b), directional selection for smaller values of the phenotype (distributions b and d) or stabilizing selection for intermediate values (distributions c and d). Each of these episodes of selection contributes to moving the population to the optimal phenotype, but one might conclude that the fundamental form of selection operating on this population is varying wildly if each episode is considered in isolation and the change in the phenotypic distribution is not noted (e.g. Wade & Kalisz, 1990). Consequently, brief snapshots of selection in nature owed to this sampling of phenotypic distributions may result in misleading representations of the true underlying form of selection.

In addition, the variance of the phenotypic distribution can have a strong influence on the ability to detect significant selection in a population. With a broad phenotypic distribution (e.g. phenotypic distribution c in Fig. 1b), ample statistical power will be available to estimate the shape of the fitness surface above the phenotypic distribution. However, if the phenotypic distribution has little variance (e.g. distribution b in Fig. 1b), even a strong fitness relationship may not be detected because the small range in phenotypes will generate only a very small difference in expected fitness across that phenotypic range relative to the variance around the fitness surface (e.g. Bulmer, 1980; Draper & Smith, 1981; Arnold & Wade, 1984; Schluter, 1988; Wade & Kalisz, 1990; Sinervo *et al.*, 1992).

Obviously, temporal variation in measures of selection is likely to be driven by changes in both the relationship between fitness and the phenotype and the position and shape of the phenotypic distribution (Fig. 1c). Here, we use within- and between-generation sampling to investigate the causes of temporal variation in the form and strength of sexual selection on body size in the damselfly *Enallagma aspersum* (Hagen). Temporal variation in sexual selection arising from variation in mating success is common in damselflies (e.g. Anholt, 1991; Gosden & Svensson, 2008), where males compete for access to females and females choose among males. Selection on body size is one of the main phenotypic traits under

selection from both male–male competition and female choice in damselflies (Fincke, 1982; Banks & Thompson, 1985; Stoks, 2000; Sokolovska *et al.*, 2000; Thompson & Fincke, 2002). Moreover, the distributions of male and female body sizes vary over the course of a breeding season (i.e. within a generation; Anholt, 1991; De Block & Stoks, 2005; Lowe *et al.*, 2009) providing an opportunity to investigate how temporal variation in body size distributions may generate temporal variation in sexual selection (Fig. 1).

Because female mate choice in damselflies is partly determined by the fit between male (cerci) and female (mesostigmal plates) reproductive structures (e.g. Paulson, 1974; Robertson & Paterson, 1982; McPeck *et al.*, 2008, 2009), which scale with body size (McPeck *et al.*, 2008, 2011), the distribution of female sizes at any given time largely shapes the fitness surface experienced by males. We, therefore, consider how temporal variation in the phenotypic distributions of both male and female body size may affect the temporal dynamics of sexual selection on male body size. Specifically, we test the hypothesis that the form and strength of selection on male body size via sexual selection through mating success is influenced by the variation in these phenotypic distributions through time. Our results illustrate how temporal variation in selection is driven by both temporal variation in phenotypic distributions and the form of the fitness surface – indirectly inferred via the distribution of female body sizes.

Materials and methods

Study system

Enallagma aspersum (Hagen) are found throughout the eastern half of the continental United States and adjacent areas of Canada in ponds and lakes lacking fish. Eggs are laid in mid-summer, hatch, and individuals spend approximately 11 months as aquatic larvae. Individuals emerge the following early summer (mid- to late June) as aerial adults. During the first few days of their adulthood, males and females forage away from ponds to mature (Anholt, 1992). Males then return to the pond and spend all their time actively searching for females (Bick & Hornuff, 1966). *Enallagma* males are not territorial, but rather simply mill about the pond's edge in search of females. In contrast, females spend almost all their time foraging away from the pond feeding for egg production and maturation, and they only return to ponds to mate and oviposit (Fincke, 1982; Anholt, 1992). As the vast majority of damselflies at a pond are males, and females visit ponds only when ready to mate and oviposit, the operational sex ratio at a pond is always highly male-skewed (Fincke, 1982, 1986; Stoks, 2001). When a female returns to the pond, she is quickly swarmed by multiple males (Fincke, 1982, 1986). Thus, males engage in intense scramble competition for females. Males

struggle for control of the female by clasping her thorax with four terminal appendages at the end of his abdomen. Even after one male has established a hold of a female, other males may try to dislodge him from his hold (M. A. McPeck, pers. obs.). The female uses the tactile cues from the contact of the male cerci (the two dorsal terminal appendages) with her mesostigmal plates (which form the anteriodorsal surface of the mesothorax) to discriminate heterospecific from conspecific males (Paulson, 1974; Robertson & Paterson, 1982; Tennessen, 1982).

A male's body size – particularly relative to female body size – may influence his success at gaining matings in a number of ways. Although males engage in scramble competition for mates, males do not directly fight with one another; instead, the scramble is for the proper hold on the female's thorax. We have witnessed as many as four males simultaneously trying to secure the hold on a female (M. A. McPeck, pers. obs.). A male that is small relative to the female he is attempting to grasp may not be able to secure a strong grip on the female. Likewise, because the male's claspers contact the female's thorax on a pair of plates that are of a characteristic shape (Westfall & May, 2006; McPeck *et al.*, 2008, 2009), a male that is too large may also have difficulty in securing a sufficient grip on the female because of an improper fit between these parts. In addition, from the female's perspective, males that are more extreme in size (both large and small) may not be preferred because of a less than desirable fit between his claspers and her thoracic plates, which may lead her to reject more extreme males. Moreover, because a female must bend her abdomen up to engage the male's secondary genitalia, males cannot force females to copulate. A female rejects a male with whom she is in tandem by moving about roughly until the male releases her (Fincke, 1984). In this study, we cannot distinguish between these two potential causes of selection; both probably contribute to our assessment of male mating success, because only those males possessing traits that allow them access to mates through male–male competition will be subjected to female mate choice. Based on these considerations, we predicted that male body size would experience mainly stabilizing selection, because (i) male and female body sizes typically overlap broadly and (ii) males that best matched the distribution of female sizes in the population should be best able to secure a strong grip on females and should be preferred by females once gripped.

Cross-sectional sampling of selection

Selection via male mating success was quantified for a population of *E. aspersum* at Sylvester's Pond, a small (0.18 ha) pond located in Norwich, VT, USA (43°44'N, 72°18'W). We used hand-held nets to collect damselflies that were either in tandem or found singly between 29 June–23 August 2004 and between 20 June–2 September

2005. Because *E. aspersum* is univoltine, these two summers represent consecutive generations of a single population. Single males and tandems were collected between 10.00 and 19.00 h, the time when damselflies are generally most active, on days that were partially or fully sunny and ≥ 18 °C. These dates capture almost the entire breeding season for each generation and thus span the period of time that sexual selection based on male mating success may occur. Because we collected as many paired *E. aspersum* damselflies as we could find and as many single *E. aspersum* damselflies as time allowed, this study provides an accurate assessment of daily mating activity. This technique of quantifying mating success is often used to quantify sexual selection on damselflies (e.g. Cordero, 1995; Svensson *et al.*, 2006; Gosden & Svensson, 2008). However, this study does not measure lifetime mating success, because males captured singly may have mated previously or later, unobserved, and males captured mating may have done so previously or later, unobserved, either more or less than average.

After collecting, damselflies were temporarily placed in a transparent plastic bag and photographed. After photographing, individuals were released after being marked with a small dot on the wing using a permanent marker to avoid measuring them again. We then measured individuals from their photographs using the computer program Image-Pro Plus 5.1 (Media Cybernetics, Bethesda, MD, USA). Seven linear measures were taken for each individual: head width, tibia length of the second leg, thorax length, forewing length, abdomen length (along all ten segments, accounting for any bends), abdomen width at the junction between the fourth and fifth segments, and abdomen width at the junction between the eighth and ninth segments. All measurements were made to the nearest 0.1 mm.

We considered two temporal scales of selection, weekly and yearly. The weekly analysis allows us to investigate how the relationship between mating success and male phenotype varied over short time periods within a generation (Wade & Shuster, 2004). Too few samples were obtained on a daily basis for meaningful inference and statistical analyses, so we combined them into weekly estimates. We then combined data across an entire summer to develop an overall estimate of selection on body size because of mating success for one generation.

We performed a principal components analysis (PCA) on the correlation matrix of all of the traits for each sex to create a composite variable for each sex. All traits were positively correlated (Table S1) and loaded positively on the first PC (PC1) for each sex, which accounted for most of the variation (Table 1), and loaded similarly between males and females (correlation coefficient between males and females for eigenvectors of each trait $r = 0.95$, $P < 0.0001$). PC analyses conducted separately for the 2 years showed nearly identical patterns (results not shown). Thus, we considered PC1 for each sex as an

Table 1 Eigenvectors from a principal components analysis of male and female damselfly traits.

Trait	PC1 Eigenvector	
	Males	Females
Abdomen length	0.465	0.478
Wing length	0.474	0.494
Thorax length	0.405	0.380
Head width	0.439	0.437
Tibia length	0.269	0.273
Abdomen width on 8th and 9th segment	0.243	0.282
Abdomen width on 4th and 5th segment	0.265	0.192
Percentage variation explained	49.13	45.42

overall measure of body size, as is frequently carried out for damselflies (Svensson *et al.*, 2006; Gosden & Svensson, 2008) and focused on this composite trait representing 'body size' for our analyses.

To estimate the form and strength of selection on male body size (PC1), we used simple linear regression analyses to estimate selection coefficients (Lande & Arnold, 1983). We estimated both linear (β) and quadratic (γ) components. The strength of selection is defined by the magnitude of each selection coefficient, whereas the sign of the linear selection coefficient defines the direction of selection and the sign of the quadratic coefficient defines whether stabilizing (negative) or disruptive (positive) selection were evident. For completeness, we also present full multivariate analyses performed on each trait (Appendix 1). We also visually inspected relationships using cubic splines (Schluter, 1988) to verify the accuracy of quadratic relationships (Shaw & Geyer, 2010). For the purposes of defining the fitness component, mating success, we considered males captured in tandem to be 'mated' and thus assigned them a fitness of '1', whereas males captured without females were assigned a fitness of '0'. For each time set (week or year), fitness (defined here as mating success) was first converted to relative fitness by dividing individual fitness by the population mean fitness at that time set, and PC1 was standardized to a mean of zero and standard deviation of one. Although we used simple linear regression to estimate the selection coefficients, tests of statistical significance were made using logistic regression because the response variable is binary (e.g. Janzen & Stern, 1998).

Assessing the role of male and female phenotypic distributions in sexual selection

To test our hypothesis that the form and strength of selection that males experience through sexual selection is determined by variation in male and female phenotypic distributions through time we conducted a series of additional analyses. First, to quantify how body size changed through time, we used graphical analyses and

conducted linear regressions of the relationship between both average weekly male and female body size (PC1) and week for each year.

Second, for each year we constructed logistic regression models of the relationship between individual male body size and mating success (as defined earlier) that included weekly terms for the mean (as a variable representing average body size at a given time set) and standard deviation (as a variable representing variation in body size at a given time set) of both male and female body size (PC1; mean male body size was not included in this model as individual male body size is the focal term). This model allowed us to assess how the relationship between male body size and fitness varied as a function of the average and standard deviation in body size of both males and females. We assessed the importance of these factors in explaining selection on males by including all possible combinations of them and their interaction terms in the logistic regression model for each year. We used Akaike's Information Criterion (AIC) to compare the fit of the top 10 (based on AIC rankings) different models with different combinations of the aforementioned terms.

Third, we used simple correlational analyses to examine how variation in the strength and direction of linear selection captured by the linear regression coefficients

varied with average female body size across weeks. To do this, we examined the relationship between the selection coefficients estimated from the weekly linear regression models and mean weekly female body sizes using simple correlation analyses.

Finally, if our hypothesis is correct that the match between male and female body size is important in determining male mating success, then as the absolute difference in body size between males and females increases, males should be further from the optima body size for mating successfully. To test this prediction, we parameterized a simple quantitative genetics model. Phillips & Arnold (1989) extended earlier models developed by Lande (1979) to derive an equation that could be used to estimate how far a population trait mean was from its phenotypic optima [equation 7 in Estes & Arnold (2007)]. Under the assumption that a quadratic function approximates the individual fitness surface (Phillips & Arnold, 1989), the absolute value of the ratio of directional selection gradients to their respective quadratic gradients ($|\beta/\gamma|$, where β are the linear selection gradients and γ the quadratic selection gradients), gives an estimate of how far a population trait mean is to its optimum in phenotypic standard deviations. We used the values from our weekly regression analyses of selection (Table 2) to estimate each of these latter terms. Simple

Table 2 Results from regression analyses examining sexual selection on damselfly male body size (PC1) based on mating success for each individual week and the combined data across all weeks (overall) during 2004 and 2005. The linear (β) and quadratic (γ) selection coefficients, and associated standard errors (SE), are from linear regression models between relative fitness and PC1, with tests of significance from logistic regression models. Week refers to the calendar week. *N* refers to the number of individuals sampled at each time set. Bold *P* values are statistically significant ($P < 0.05$).

Year	Week	<i>N</i>	β (SE)	<i>P</i> value	γ (SE)	<i>P</i> value
2004	26	139	0.141 (0.172)	0.387	-0.594 (0.172)	0.094
	27	180	0.128 (0.128)	0.327	-0.366 (0.130)	0.178
	28	74	0.369 (0.241)	0.131	0.312 (0.241)	0.739
	29	283	0.027 (0.098)	0.770	-0.132 (0.098)	0.499
	30	345	-0.086 (0.080)	0.187	-0.542 (0.080)	0.001
	31	401	-0.068 (0.076)	0.205	-0.372 (0.076)	0.011
	32	212	0.274 (0.100)	0.006	-0.180 (0.10)	0.187
	33	185	0.291 (0.149)	0.008	-0.724 (0.149)	0.014
	34	26	0.423 (0.622)	0.536	-0.192 (0.622)	0.609
	Overall	1845	0.047 (0.038)	0.490	-0.360 (0.038)	< 0.0001
	2005	24	14	0.027 (1.669)	0.352	1.848 (1.669)
25		73	-0.039 (0.471)	0.932	0.360 (0.471)	0.967
26		64	0.108 (0.337)	0.740	-0.330 (0.337)	0.619
27		165	-0.044 (0.200)	0.825	0.052 (0.200)	0.899
28		250	0.051 (0.111)	0.652	0.226 (0.111)	0.340
29		223	0.013 (0.099)	0.908	-0.164 (0.099)	0.416
30		328	0.006 (0.083)	0.975	-0.282 (0.083)	0.094
31		201	-0.208 (0.120)	0.096	0.506 (0.120)	0.042
32		85	-0.012 (0.184)	0.937	0.278 (0.184)	0.457
33		75	-0.716 (0.252)	0.067	0.572 (0.252)	0.696
34		144	-0.027 (0.150)	0.852	-0.066 (0.150)	0.819
35		56	-0.084 (0.281)	0.762	-0.012 (0.281)	0.969
Overall		1678	-0.045 (0.04)	0.315	0.062 (0.042)	0.676

correlation analysis was then used to determine whether there was a positive correlation between the absolute difference in weekly mean body size between males and females and the estimated distance male body sizes are from the optima for mating successfully during that week.

Results

In 2004, we collected 512 tandem pairs of males and females and 1333 single males; in 2005, we collected 496 tandem pairs and 1182 single males. Significant differences existed in mean male body size (i.e. PC1, hereafter we refer to PC1 as 'body size') among weeks in both 2004 (ANOVA $F_{8,1839} = 3.47$, $P = 0.0006$) and 2005 (ANOVA $F_{11,1666} = 24.80$, $P < 0.0001$), with male body size declining over the course of the breeding season in both years (2004: $F_{1,1846} = 6.28$, $P = 0.01$; 2005: $F_{1,1676} = 116.91$, $P < 0.0001$, Fig. 2). Overall (across the entire breeding season) male were smaller in 2004 than in 2005 ($F_{1,3524} = 50.66$, $P < 0.0001$). In addition, across weeks, male body size was significantly more variable in 2004 (mean SD of male PC1: 1.97 ± 0.37 SD) than in 2005

(mean SD of male PC1: 1.28 ± 0.21 SD; ANOVA $F_{1,19} = 28.09$, $P < 0.0001$).

Patterns of female body size were similar to those of males in 2005 but not in 2004. Significant differences existed in mean female body size among weeks in 2005 (ANOVA $F_{11,482} = 8.16$, $P < 0.0001$, Fig. 2b), but not in 2004 (ANOVA $F_{8,506} = 1.64$, $P = 0.110$, Fig. 2a). Mean female body size did not show a steady decline over the course of the breeding season in 2004 ($F_{1,513} = 2.70$, $P = 0.101$, Fig. 2a) as it did in 2005 ($F_{1,492} = 27.58$, $P < 0.0001$, Fig. 2b). Rather, in 2004 female body size exhibited a more variable pattern. Overall (across the entire breeding season) female body sizes were significantly smaller in 2004 than in 2005 ($F_{1,1007} = 3.75$, $P = 0.05$). In addition, across weeks female body size was on average significantly more variable in 2004 (mean SD of female PC1 = 1.87 ± 0.34 SD) than in 2005 (mean SD of female PC1 1.28 ± 0.28 SD; ANOVA $F_{1,19} = 19.36$, $P = 0.0003$).

When data were combined across the entire breeding season, the form of selection on male body size differed between years (Fig. 3). In 2004, male body size experienced stabilizing selection (Fig. 3a), whereas in 2005 male body size experienced no significant selection (Fig. 3b; Table 2).

During 2004, weekly estimates of selection varied from directional, to stabilizing, to more complex fitness surfaces (Fig. 4, Table 2). Consistent with our hypothesis, variation in the form of selection was associated with differences in the relative size of males to females through the breeding season. For example, during weeks when average female body size was most different from average male body size (Fig. 2), selection during these time points was most consistently directional, with mated males being more similar in size to the female distribution than unmated males (Fig. 4, Table 2). In contrast, when males were of comparable size to females (Fig. 2), selection was more consistently stabilizing (Fig. 4, Table 2). The logistic regression model, which included weekly terms for male and female body size distributions, also showed that selection on male body size was best explained by a model including male PC1 and its quadratic term, as well as the interaction between male PC1 and female PC1 (Table S2 and Table 3). That is, the best model was one in which the relationship between male mating success and body size depended on female body size. Indeed, we also found strong correlations between female PC1 and the strength of selection on male PC1 (Fig. 5a).

Overall, the pattern in 2004 suggests that males who were successful in obtaining mates were those of comparable body size as females, in a year where female body size differed considerably from one point in time to the next (Fig. 2). Not surprisingly, we found that in 2004 as male body size differed in absolute magnitude from female body size, male body size was estimated to be increasingly further from the optimal body size for mating success (Fig. 5b).

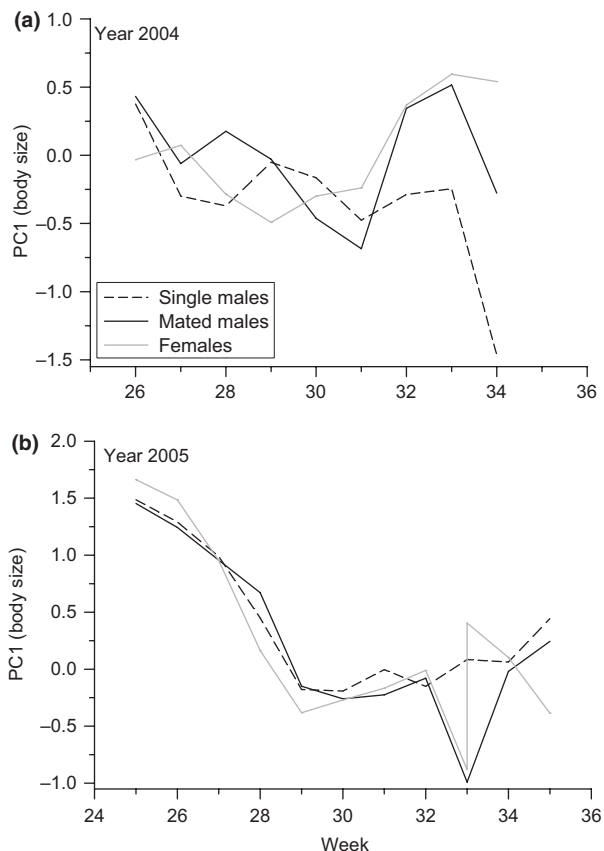


Fig. 2 Temporal variation in average male and female *Enallagma aspersum* body sizes (PC1) at Sylvester's Pond in Norwich, VT over the course of two breeding seasons.

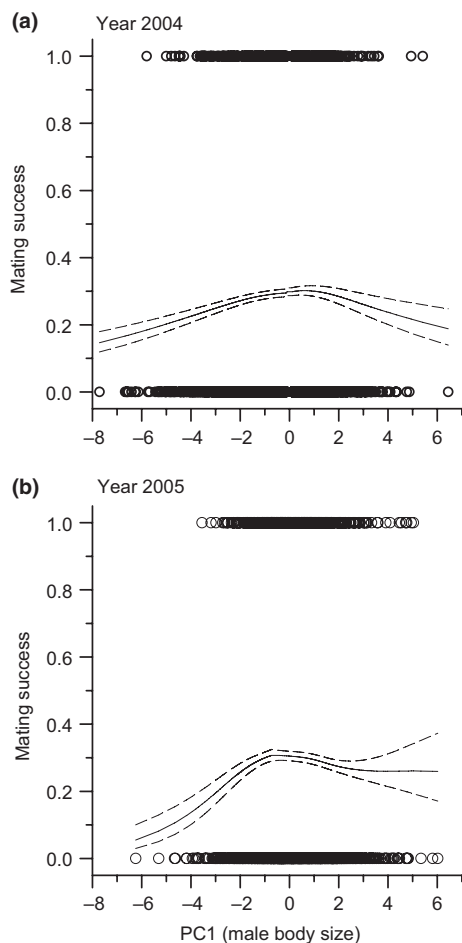


Fig. 3 The form of phenotypic sexual selection on male damselfly body size (PC1) based on mating success for 2 years. Males that were captured in tandem with a female were assigned fitness values of 1, whereas single males were assigned a fitness value of 0. In each panel, the solid line is the fitness surfaces derived from cubic spline analysis, and the dashed lines are ± 1 standard error.

During 2005, weekly estimates of selection revealed only a single episode of statistically significant selection (disruptive selection during week 31; Table 2, Fig. S1). Cubic spline analyses were largely consistent with results from the regression models, but did reveal variable fitness surfaces similar to 2004 (Fig. S1). Because we did not find consistent evidence for selection (despite comparable sample sizes as in 2004; e.g. Table 2) we do not present the analysis of male optimal body size relative to female body size as we did for 2005.

Discussion

Consistent with our predictions, the pattern of selection on male body size that resulted from male mating success was variable both from week to week within a genera-

tion and between generations, and this variability depended in part on changes in the distributions of both male and female body sizes. The match between male and female body size appears to be a critical feature for male mating success, presumably through both male scramble competition for holds on females and female choice. Thus, the distribution of female body sizes in the population defines the function for male mating success based on male phenotype, which is a critical component of male fitness (Lande, 1981; Sved, 1981a,b). The relationship between male mating success and male body size must then change as the distribution of female body size changes through time (e.g. as in Fig. 1a). Presumably, this function has a maximum at a male body size that matches the bulk of the female body size distribution, and declines away from this size in both directions (e.g. Lande, 1981; Fig. 5b). In addition, the distribution of male body size also changed from week to week (as in Fig. 1b), and in 2004 changes in the distributions of male and female body size did not track one another. As a result, whether directional or stabilizing selection was evident on males depended on the position of the male distribution relative to the female distribution. Finally, whether we detected significant selection in the population likely depended on the variances in body size in the population; little selection was evident in 2005 when male and female body sizes were much less variable than in 2004.

Thus, our results suggest that the patterns of short-term sexual selection via female preference on male damselfly body size are a consequence of fluctuations in male and female body size distributions. Variation in body size, and declines in body size in particular, over the course of the breeding season are common for damselflies (Vannote & Sweeney, 1980; Anholt, 1991; Corbet, 1999; Lowe *et al.*, 2009; but see Rantala *et al.*, 2001) and many other insects (Rowe & Ludwig, 1991; Atkinson, 1994; Jann *et al.*, 2000). Damselfly males exhibited a decline in body size in 2004 and 2005, as did females in 2005 but not in 2004. Rather, in 2004 damselfly females and successfully mating males exhibited a more variable pattern of change in body size through time. Why body size was more variable during 2004 relative to 2005 is unknown.

Regardless of the mechanism, the more variable pattern of variation in female body size in 2004 appears critical in driving the temporal variation in selection within the breeding season, relative to 2005 in which evidence for such selection was limited. Presumably in 2005, because female size declined more or less monotonically throughout the breeding season, and male body size so closely followed female body size, the opportunity for selection, in terms of variation in male body size relative to that of females, was greatly reduced. Comparative support for the importance of female body size in determining the strength and form of sexual selection on male body size comes from studies of the Eurasian

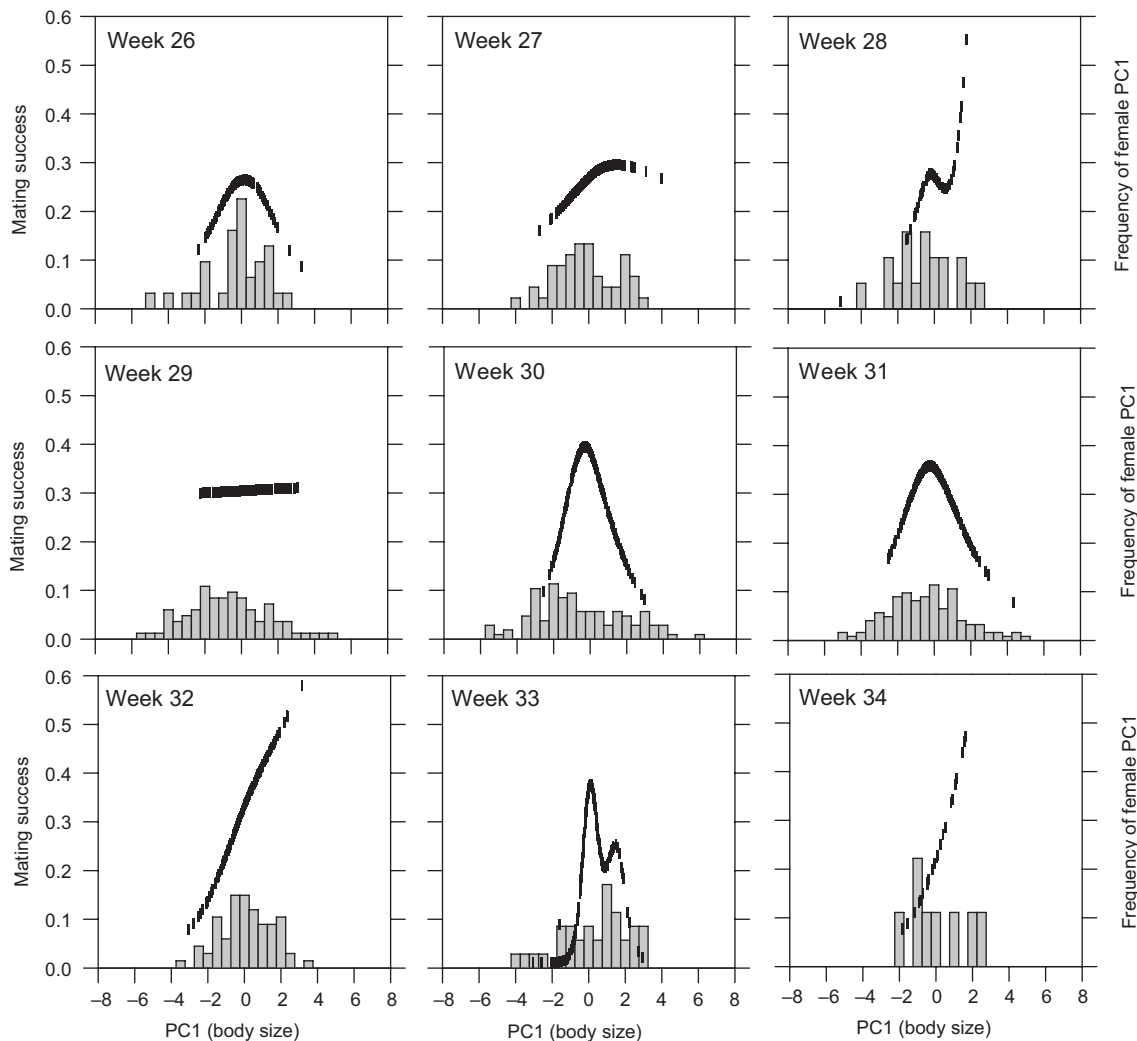


Fig. 4 The form of sexual selection on damselfly male body size (PC1) in relation to female body size distributions (PC1) during each week of the breeding season in 2004. The grey bars show the frequency distribution of female body sizes during that week, and the black dashed line is a cubic spline based on the relationship between male body size and mating success calculated for that week.

Table 3 Logistic regression model examining the effects of damselfly male body size (male PC1) and female body size (female PC1) on male mating success in 2004. Full model: Wald ($\chi^2 = 26.478$, d.f. = 3, $P < 0.0001$), $n = 1845$ individuals.

Model terms	d.f.	Estimate	SE	Wald χ^2	P
Intercept	1	-0.988	0.054	339.719	< 0.0001
Male PC1	1	0.105	0.063	2.794	0.0946
Male PC1 ²	1	-0.310	0.071	19.193	< 0.0001
Male PC1*Female PC1	1	0.518	0.181	8.193	0.0042

damselfly *Ischnura elegans* (*Ischnura* is the sister genus to *Enallagma*; Gosden & Svensson, 2008). In *I. elegans*, sexual selection on male body size was influenced by

female body size; however, why this pattern is apparent was not clear (Gosden & Svensson, 2008).

Sexual selection driven via female preferences is common (Andersson, 1994). In some cases, such preferences may have direct benefits. For example, Chaine & Lyon (2008) showed that female preferences for male ornaments in Lark buntings (*Calamospiza melanocorys*) varied considerably in strength, and to a lesser degree in direction, among years. This shift in female preference paralleled shifts in male traits that predicted female reproductive success in a given year. In the case of damselflies and many organisms where males provide no resources to either females or offspring, the ultimate reason females might exercise such preferences are less clear. A variety of models have been proposed to explain the evolution of female preferences with no direct

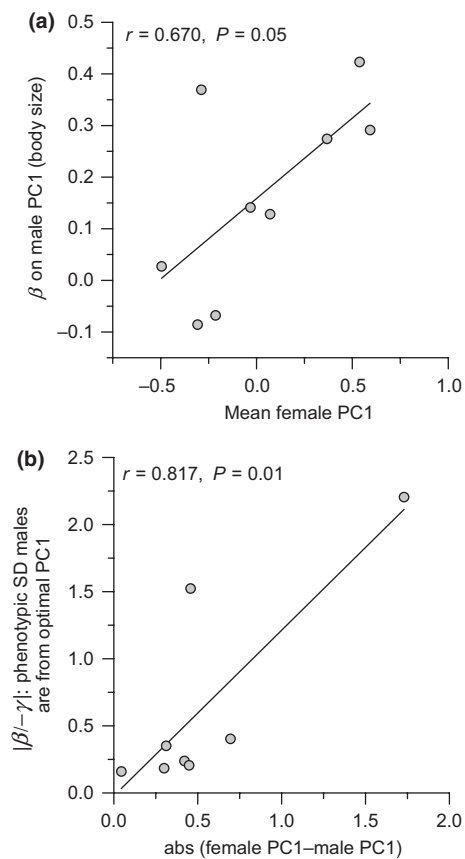


Fig. 5 The importance of female and male body size in determining sexual selection on males. In (a) the relationship between the strength and direction of linear sexual selection on male body size and female body size across weeks indicates that as females become larger this results in stronger selection for larger males; the ordinate is the linear selection coefficient from the linear regression of mating success on male body size for each week (Table 2). In (b) we show the relationship between the magnitude of the differences in male and female body sizes for a given week and the predicted distance (in phenotypic standard deviations) males are from the optimal male body size for successfully mating. The positive correlation indicates that the match between male and female body size is important in determining male mating success.

benefits – the so-called indirect benefit models (Mead & Arnold, 2004; Kokko *et al.*, 2006; Kotiaho & Puurtinen, 2007). In the case here, we suspect such preferences may evolve simply so that females avoid heterospecific matings (e.g. McPeck & Gavrillets, 2006), and so intraspecific sexual selection is an indirect consequence species recognition. The evolution of such preferences may further have had a key role during speciation in *Enallagma* damselflies (McPeck *et al.*, 2009).

The temporal variation in selection we observed throughout 2004 is essentially a form of frequency-dependent selection, as variation in the frequency of

female (and male) body sizes determines the form of selection males experience (e.g. Fig. 4). Frequency-dependent selection operates on continuous traits when the form of selection is context dependent and influenced by the average phenotype (Kopp & Hermisson, 2006; Gosden & Svensson, 2008). These results also suggest that the evolutionary dynamics of male–female coevolution (e.g. McPeck *et al.*, 2009) are at least partially driven by variation in female body size. Such dynamics have been described by models of social effects, where the phenotype of one individual affects the fitness of a conspecific (Moore *et al.*, 1997; Wolf *et al.*, 1998, 1999; Bleakley *et al.*, 2010; McGlothlin *et al.*, 2010; Wolf & Moore, 2010).

We must emphasize though that we have only focused on one component of fitness affected by sexual selection. Other forms of sexual selection (e.g. Hunt *et al.*, 2009), viability selection or selection through other fitness components (Andersson, 1994; Kokko *et al.*, 2002; Siepielski *et al.*, 2011) on body size may also be important in this system, as may selection acting during the larval stage (McPeck, 1997; Fincke & Hadrys, 2001; Strobbe *et al.*, 2009). While we have no data on viability selection from this study, the effects of selection through viability prior to the occurrence of sexual selection may be quite important for understanding the dynamics of sexual selection, as such selection can shape the phenotypic distributions when sexual selection is operating (e.g. Arnold & Wade, 1984; Wade & Shuster, 2004; Klug *et al.*, 2010). In some damselflies, viability selection can be quite strong (Anholt, 1991; Svensson *et al.*, 2006). *Enallagma* male damselflies only live about 4 days as adults and such a short period of time to find a mate may result in intense viability selection. However, in studies that quantified temporal variation in both natural and sexual selection (Anholt, 1991; Svensson *et al.*, 2006), sexual selection through mating success was consistently much stronger than viability selection. This latter pattern is consistent with comparative studies of the strength of selection in relation to fitness components (Endler, 1986; Hoekstra *et al.*, 2001; Kingsolver *et al.*, 2001; Siepielski *et al.*, 2011). If viability selection acts in the same direction on body size (or a trait correlated with body size) as sexual selection, such combined selection could potentially accentuate the magnitude of adaptive evolution. In contrast, if viability selection acts in the opposing direction, this would act to maintain variation, or even cause apparent stasis. Although researchers often focus on one fitness component, evolutionary responses are as a result of the combined effect of selection through multiple fitness components (Arnold & Wade, 1984; Wade & Kalisz, 1989; Preziosi & Fairbairn, 2000; Shaw *et al.*, 2008; Hunt *et al.*, 2009; McGlothlin, 2010; Siepielski *et al.*, 2011).

Studies have increasingly sought to identify the causes of selection, namely the ecological causes of the relationship between the fitness of individuals and their phenotypes (Wade & Kalisz, 1990). However, most of these

studies have concentrated on identifying correlations of the strength or direction of selection with environmental factors [i.e. $\text{Cov}(\beta, E)$ in the framework presented in Wade & Kalisz (1990)]. Such analyses are crucial, but for such analyses to identify the ecological causes of selection, they must assume temporal variation in the shape of the fitness surface and little else (e.g. Whitlock, 1997; Siepielski *et al.*, 2009; Punzalan *et al.*, 2010). If variation in the form and strength of selection is caused primarily by a change in the phenotypic distribution, such analyses will not identify the ecological causes of selection. Identifying the causes of selection requires both careful statistical analyses of selection in the wild that associate the form and strength of selection to specific ecological agents and functional experimental manipulations that directly associate changes in the phenotype with changes in survival, growth or fecundity because of that ecological agent (e.g. Wade & Kalisz, 1990; McPeck *et al.*, 1996; McPeck, 1997; Reznick & Ghalambor, 2005; Losos *et al.*, 2006; Strobbe *et al.*, 2009; Calsbeek & Cox, 2010). Given that the ultimate goal should be to understand the causes of the relationship between fitness and phenotype, differences in measures of selection caused by fluctuations in the phenotypic distribution versus changes in the fitness surface must be partitioned.

The results of this study show that simply characterizing selection as directional, stabilizing or disruptive or stating that selection varies through time (and presumably through space as well) is inadequate to understand the multifarious causes for these simple characterizations. Changes in the distribution of available phenotypes can have as much to do with changes in the form and strength of selection as changes in the shape of the fitness surface (Wade & Kalisz, 1990). Quantifying the operation of selection in the wild necessarily requires the statistical evaluation of whether the phenotype covaries with some component of fitness in some way. However, we must remember that our ultimate goal is to understand the true shape of that relationship and its ecological and social causes.

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Supporting information

Additional Supporting Information may be found in the online version of this article:

Figure S1 Weekly estimates of the form of sexual selection on male damselfly body size (PC1) through variation in mating success for each week of the breeding season in 2004 and 2005.

Table S1 Correlation matrix (Pearson's correlation coefficients) of various damselfly traits.

Table S2 Comparison of AIC scores from several logistic regression models including various explanatory terms for quantifying selection on damselfly male body size (PC1) based on mating success during 2004.

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Appendix 1

Results of multivariate regression analysis on damselfly mating success in relation to several body traits for each week during 2004 and 2005. Shown are the linear (Beta) and non-linear (Gamma: quadratic coefficients along the diagonal, correlational coefficients along the off diagonal). Tests of statistical significance are from logistic regression models, bold = $P < 0.05$.

		Year 2004							
		Beta	Gamma THL	AL	AW4-5	AW8-9	WL	HW	TL
Week 26 (N = 139)									
THL		-0.156	0.109						
AL		0.406	-0.293	-0.294					
AW4-5		-0.146	-0.491	-0.545	-0.129				
AW8-9		-0.593	0.355	0.232	0.223	0.076			
WL		0.072	-0.369	0.437	0.123	0.007	-0.259		
HW		0.254	0.090	0.040	0.722	-0.730	0.065	0.021	
TL		-0.586	0.302	-0.121	0.329	0.039	-0.250	0.242	0.248
Week 27 (N = 180)									
THL		-0.123	-0.085						
AL		-0.245	0.159	0.875					
AW4-5		0.216	-0.203	-0.172	-0.204				
AW8-9		0.282	-0.058	-0.326	0.289	-0.072			
WL		0.129	-0.172	-1.230	0.389	0.314	0.194		
HW		0.149	-0.005	-0.492	0.172	0.452	0.129	0.042	
TL		0.120	0.469	-0.350	0.052	-0.456	-0.009	0.280	-0.193
Week 28 (N = 74)									
THL		1.366	0.602						
AL		0.190	-2.103	0.519					
AW4-5		0.172	1.590	-0.159	0.278				
AW8-9		-0.300	0.658	0.979	-0.599	0.298			
WL		0.300	1.280	0.310	-0.297	-0.500	0.010		
HW		-0.676	1.020	-1.180	0.065	-0.367	-0.057	-0.025	
TL		-0.444	-1.067	0.989	-0.685	-0.050	-0.852	0.338	-0.292
Week 29 (N = 283)									
THL		0.137	0.134						
AL		-0.192	-0.110	0.485					
AW4-5		0.010	-0.097	0.099	0.015				
AW8-9		-0.129	-0.195	0.068	-0.080	-0.088			
WL		0.006	-0.045	-1.107	-0.033	0.277	0.459		
HW		0.347	0.097	0.436	0.035	-0.113	-0.467	-0.075	
TL		-0.246	0.118	-0.062	-0.035	0.120	0.053	0.134	-0.060
Week 30 (N = 346)									
THL		-0.089	-0.170						
AL		0.053	-0.067	-0.077					
AW4-5		0.094	0.211	-0.122	-0.004				
AW8-9		0.021	-0.209	-0.330	0.151	-0.077			
WL		0.079	0.366	0.372	-0.152	0.294	-0.557		
HW		-0.181	-0.022	-0.043	0.076	0.045	0.166	-0.098	
TL		0.005	-0.023	-0.101	-0.155	0.032	0.012	0.196	-0.071
Week 31 (N = 401)									
THL		0.091	-0.219						
AL		0.306	-0.278	0.021					
AW4-5		-0.135	0.043	0.235	-0.009				
AW8-9		-0.239	-0.314	0.035	0.075	-0.061			
WL		-0.085	0.333	0.080	-0.309	0.159	-0.230		
HW		-0.056	0.331	0.006	0.064	0.052	0.075	-0.098	
TL		-0.157	-0.086	0.006	-0.014	0.101	-0.010	-0.022	0.075

Appendix 1 (Continued)

		Year 2004							
		Beta	Gamma THL	AL	AW4-5	AW8-9	WL	HW	TL
Week 32 (N = 212)									
	THL	0.064	-0.228						
	AL	0.114	0.266	-0.062					
	AW4-5	-0.020	0.131	-0.160	0.059				
	AW8-9	-0.297	0.194	-0.100	-0.189	0.159			
	WL	0.059	-0.076	-0.178	0.093	-0.176	0.181		
	HW	0.322	0.219	0.225	0.019	-0.110	-0.184	-0.123	
	TL	-0.194	0.486	0.044	-0.167	0.428	-0.096	0.279	0.005
Week 33 (N = 185)									
	THL	0.419	-0.071						
	AL	0.337	0.600	-0.315					
	AW4-5	-0.389	-0.521	0.064	-0.243				
	AW8-9	-0.327	-0.577	-0.025	0.047	0.025			
	WL	-0.098	0.246	0.367	-0.079	-0.094	-0.247		
	HW	0.230	-0.215	0.153	0.203	0.481	-0.658	-0.004	
	TL	-0.006	0.170	-0.581	0.277	0.132	0.128	0.346	-0.020
Week 34 (N = 26)		insufficient data to complete this full analysis							
	THL								
	AL								
	AW4-5								
	AW8-9								
	WL								
	HW								
	TL								
		Year 2005							
Week 24 (N = 14)		insufficient data							
	THL								
	AL								
	AW4-5								
	AW8-9								
	WL								
	HW								
	TL								
Week 25 (N = 73)									
	THL	-0.397	-0.498						
	AL	-0.121	1.309	-0.890					
	AW4-5	-0.165	0.144	-0.947	0.241				
	AW8-9	-0.480	0.173	0.207	-0.347	-0.049			
	WL	0.499	-1.038	0.456	-0.331	0.113	-0.440		
	HW	-0.141	0.172	0.757	0.907	0.181	0.461	-0.279	
	TL	-0.261	-0.445	0.132	-0.395	0.287	-0.066	-0.057	0.153
Week 26 (N = 64)									
	THL	-0.793	-0.192						
	AL	0.267	0.629	0.081					
	AW4-5	-0.005	1.090	0.260	-0.087				
	AW8-9	0.280	0.160	0.140	-0.271	0.086			
	WL	0.260	0.031	-0.961	-0.318	-0.480	0.349		
	HW	-0.397	-0.498	0.133	0.455	0.080	0.529	-0.024	
	TL	-0.192	0.460	-0.121	0.457	-0.333	0.037	0.222	-0.319
Week 27 (N = 165)									
	THL	-0.225	-0.010						
	AL	-0.097	-0.045	-0.222					
	AW4-5	0.095	0.288	-0.194	0.091				
	AW8-9	-0.219	0.061	-0.178	0.033	-0.038			

Appendix 1 (Continued)

Year 2005								
	Beta	Gamma THL	AL	AW4-5	AW8-9	WL	HW	TL
WL	0.008	-0.402	0.884	0.005	0.206	-0.219		
HW	0.103	-0.050	0.067	-0.244	0.036	-0.084	-0.115	
TL	-0.009	-0.042	0.146	0.118	-0.021	-0.271	0.149	0.214
Week 28 (N = 250)								
THL	-0.042	-0.029						
AL	0.056	0.094	-0.221					
AW4-5	0.045	0.012	0.335	-0.098				
AW8-9	0.098	0.249	0.109	-0.156	-0.026			
WL	0.078	-0.261	0.312	-0.160	-0.171	0.121		
HW	-0.133	-0.071	-0.003	0.034	0.102	-0.177	0.138	
TL	0.158	0.352	-0.052	-0.126	-0.022	0.163	-0.292	0.098
Week 29 (N = 223)								
THL	-0.105	-0.085						
AL	0.203	0.287	-0.141					
AW4-5	0.266	-0.091	0.332	0.041				
AW8-9	-0.192	-0.006	0.304	0.087	-0.062			
WL	0.094	-0.552	0.455	0.026	-0.042	-0.092		
HW	-0.095	0.181	-0.224	-0.293	-0.008	0.247	-0.222	
TL	0.072	-0.152	0.378	-0.094	0.078	-0.551	0.260	0.026
Week 30 (N = 328)								
THL	-0.103	-0.077						
AL	0.071	0.270	-0.424					
AW4-5	0.025	-0.003	-0.389	0.054				
AW8-9	-0.342	-0.103	0.289	0.075	0.011			
WL	0.306	-0.182	0.519	0.251	-0.071	-0.320		
HW	0.027	0.259	-0.270	0.076	-0.027	0.179	-0.113	
TL	-0.079	-0.306	0.067	0.090	-0.004	0.088	-0.002	0.056
Week 31 (N = 201)								
THL	-0.342	0.128						
AL	0.333	-0.236	0.108					
AW4-5	-0.212	0.094	0.219	0.056				
AW8-9	-0.178	-0.269	0.039	0.020	0.064			
WL	0.162	-0.048	0.099	0.195	-0.287	-0.029		
HW	-0.071	-0.081	0.485	-0.040	0.359	0.153	-0.289	
TL	-0.177	0.066	-0.152	0.009	0.176	-0.013	0.029	-0.041
Week 32 (N = 85)								
THL	0.516	0.071						
AL	-0.303	0.528	-0.538					
AW4-5	0.115	-0.253	0.367	-0.216				
AW8-9	-0.111	0.019	-0.499	-0.127	0.144			
WL	-0.113	0.177	-0.481	0.121	-0.175	-0.140		
HW	0.044	0.120	1.211	0.139	0.291	0.037	-0.529	
TL	-0.429	-0.703	-0.087	0.221	-0.110	0.728	0.457	0.176
Week 33 (N = 162)								
THL	0.029	0.353						
AL	0.406	1.630	-0.283					
AW4-5	0.317	-0.157	-0.054	0.118				
AW8-9	-0.582	0.225	0.167	-0.426	0.103			
WL	-0.583	-2.091	-0.511	-0.320	-0.079	0.392		
HW	0.039	0.243	-0.542	0.491	-0.359	1.340	-0.031	
TL	-0.356	0.182	-0.143	0.520	0.206	-0.038	-0.722	-0.027
Week 34 (N = 144)								
THL	-0.302	0.135						
AL	0.339	-0.191	-0.913					
AW4-5	0.193	-0.346	0.427	0.238				
AW8-9	-0.682	-0.062	0.295	0.099	0.211			

Appendix 1 (*Continued*)

Year 2005								
	Beta	Gamma THL	AL	AW4-5	AW8-9	WL	HW	TL
WL	0.662	-0.214	1.619	-0.298	-0.352	-0.516		
HW	-0.227	-0.120	-0.026	0.098	-0.102	0.589	-0.380	
TL	-0.469	0.163	-0.053	0.184	0.150	-0.292	0.222	-0.095
Week 35 (<i>N</i> = 56)								
THL	-0.186	0.460						
AL	-0.454	1.288	-0.665					
AW4-5	0.138	-0.647	-1.109	-0.163				
AW8-9	-0.294	-0.721	1.759	-0.488	0.156			
WL	0.465	-2.089	-0.878	1.476	-0.298	2.139		
HW	-0.272	0.347	2.749	0.367	-1.323	-2.272	-0.498	
TL	-0.144	-0.705	-0.306	0.041	0.534	-0.492	1.521	-0.353

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