

LIFETIME REPRODUCTIVE SUCCESS, SELECTION, AND THE
OPPORTUNITY FOR SELECTION IN THE WHITE-TAILED SKIMMER
PLATHEMIS LYDIA (ODONATA: LIBELLULIDAE)

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Abstract.—We present estimates of lifetime reproductive success in *Plathemis lydia*, a territorial dragonfly. We partition the opportunity for selection into multiplicative episodes using the techniques of Arnold and Wade (1984a, 1984b) and measure selection on several morphological and behavioral characters. For both sexes, variance in survivorship was the largest contribution to variance in lifetime reproductive success. Covariance effects are also strong for both sexes, suggesting considerable non-independence of episodes. Opportunity for selection calculated on a daily basis did not approximate analogous values determined from lifetime reproductive success.

Phenotypic characters for which we investigated selection included body mass, hind wing length, first date of reproduction, and (for males) an index of territorial aggressiveness. We failed to find any significant direct targets of selection in either males or females. However, the combined effects of direct and indirect selection on early reproduction were significant for males, acting primarily through increased survivorship and increased time per day spent at the pond. Similarly, females present earlier in the season had shorter interclutch intervals. Partitioning of selection acting on male hind wing length and on aggressiveness reveals relationships between selective episodes, possibly indicative of phenotypic trade-offs between natural and sexual selection through male-male competition for females.

Division of selection into episodes is a useful technique for identifying the source of selection. However, ordering effects can bias results, except when episodes occur in strictly chronological sequence. We present a method for circumventing this difficulty.

Received July 22, 1985. Revised December 16, 1985. Accepted September 23, 1986

Despite general agreement that lifetime reproductive success is the best measure of fitness that can be collected (see Cavalli-Sforza and Bodmer, 1961; Grafen, 1982; Clutton-Brock, 1983; Partridge and Halliday, 1984), measures of this critical parameter have been obtained to date in only a handful of species (see, for example, Clutton-Brock, 1987). Instead, analyses of selection are typically performed on longitudinal data from one or more breeding seasons, or on cross-sectional data gathered on a single selection event. Such data can provide important insights into the workings of selection, but may nonetheless be misleading. In particular, phenotypic trade-offs between survivorship and other components of fitness may eliminate or even reverse trends found during a fraction of the lifespan of an organism (Bell, 1980), espe-

cially if variance in mating success is determined in part by age- or size-correlated characters (Arnold and Wade, 1984a). Detecting such trade-offs is critical for determining the relative strengths of natural and sexual selection.

Here we present data on lifetime reproductive success in the white-tailed skimmer *Plathemis lydia* (Odonata: Libellulidae). Adults of this species do not overwinter, and survivorship of adults of both sexes is 83–89% per day (Koenig and Albano, 1985); thus, a reasonable number of individuals can be followed throughout their lifetimes. We examine the opportunity for selection ($I = \sigma^2/\bar{x}^2$, the variance in individual fitness divided by the mean fitness squared) and selection itself on several characters. I values are calculated following Arnold and Wade's (1984a, 1984b) method of partitioning selection occurring in an arbitrary number of "episodes." In order to measure selection on correlated characters we use the

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partial correlational techniques of Lande and Arnold (1983). These techniques provide a powerful program for analyzing and interpreting selection.

Biology of Plathemis lydia

Plathemis lydia is a medium-sized dragonfly common throughout much of North America. Sexual dimorphism in size is slight (see below). However, the sexes are dichromatic; males have bluish-white abdomens and wings with a dark median band, while females have dark brown abdomens and wings with median and terminal dark spots (see Jacobs, 1955). Males display their abdomens in territorial chases (Jacobs, 1955; Campanella and Wolf, 1974) but not in courtship. Thus, differing selective pressures on the sexes have apparently influenced body and wing coloration to a greater extent than size.

Plathemis breeds in ponds; males defend ephemeral territories ≈ 10 m in length around the perimeter of the ponds. At medium-to-high population densities, individual males spend only a few hours a day in territorial behavior (Koenig and Albano, 1985). Consequently, territories are defended by a series of males during a day, although the same male may return to a territory (usually but not always the same one) on successive days (Koenig and Albano, 1985).

Females visit ponds solely to mate and lay eggs. Female arrival is relatively synchronous, peaking in the early afternoon (Campanella and Wolf, 1974; Koenig and Albano, 1985). Copulation lasts only a few seconds; then the male disengages and hovers above the female while she flies over the water looking for an oviposition site ("non-contact" guarding; Parker, 1970; Alcock, 1982; Sherman, 1983; Waage, 1983; McMillan, 1984). The male continues to guard the female during oviposition (usually somewhere in the male's territory); then the female immediately leaves and the male resumes territorial behavior. Eggs develop unattended.

This mating system can be considered to be one of resource defense polygyny (Emlen and Oring, 1977; Thornhill and Alcock, 1983), with males monopolizing females indirectly by defending spatially clumped ovi-

position sites (Koenig and Albano, 1985). Further details concerning the natural history of *Plathemis lydia* can be found in Jacobs (1955), McMillan (1984), and Koenig and Albano (1985).

MATERIALS AND METHODS

The study was conducted at Blompond, a small (380 m²) man-made stock pond located adjacent to Hastings Natural History Reservation, Monterey Co., California. The perimeter of the pond was marked at 3-m intervals. Beginning on 10 June 1984, we caught as many individuals as possible. The wings of captured individuals were secured with a hairpin, then we weighed individuals to the nearest 0.01 gm, measured hind wing length, and marked wings and abdomens with dots of enamel paint for individual recognition.

We marked 180 males and 84 females at Blompond during the study. Of these, 78 males (43%) and 38 females (45%) were not subsequently seen at Blompond. This level of disappearance following marking is comparable to that reported earlier (Koenig and Albano, 1985), and is probably the consequence of emigration following the trauma of capture and handling. Virtually all individuals were marked as breeding adults. Breeding activity at Blompond begins in the second week of May; thus, we conducted our study during the latter half of the breeding season.

Between 19 June and 5 August (no *Plathemis* remained at Blompond after this date), we and two field assistants were present from 0700 (before any dragonflies arrived at the pond) until all individuals had left for the day (usually by 1830). Every 20 minutes we recorded all males present as well as (if territorial) their territorial boundaries. In addition, we continuously scanned the pond for females. Whenever a copulation or oviposition was observed we recorded its location, length, and the identity of participants.

McVey (1984) found that *Plathemis* in New York oviposited at a mean rate of 22.8 eggs per second. However, we do not have comparable data from our population, and thus we report reproductive success in units of "seconds of oviposition." For males, reproductive success was estimated from the

seconds of oviposition of females, but only if the male was the female's last mate (see below).

The three nearest breeding sites to Blompond are approximately 0.6, 1.2 and 1.7 km away. The two nearest of these sites were surveyed for marked individuals one or two times per day for 15 to 20 min each per visit. This allowed us to detect many males emigrating to and remaining at either of these ponds. However, because of the briefness of female visits, we were unlikely to see marked females ovipositing at these sites.

To examine the opportunity for selection, we compiled two sets of data. The first consisted of daily reproductive success. For each individual seen at least once on a day following marking, the number and length of ovipositions were compiled for every day alive following marking. We then analyzed these "daily" data by: 1) including individuals only on days they were observed at the pond, and 2) including individuals on all days, whether they came to the pond or not, as long as they were seen on a later day and thus known to have been alive. Reproductive success for individuals on days they were not observed at the pond was set to zero. For males, this assumption is based on the direct observation that males rarely wandered temporarily to other ponds. With few exceptions, females also appeared not to switch ponds (see Fig. 1 and below).

Females ovipositing at the pond did so at intervals of 2.21 ± 1.47 days ($\bar{x} \pm SD$; $N = 87$ intervals from 31 individuals). Intervals ranged from 1 to 5 days with a strong mode at 2 days, except for one interval each of 7 and 12 days (Fig. 1). These two longest intervals were eliminated, as it is likely that these females oviposited elsewhere during these periods. In total, we used data on 912 male and 291 female dragonfly-days taken from 113 individual males and 50 individual females. Males were present on the pond for 672 (73.7%) dragonfly-days and females for 132 (45.4%); oviposition actually occurred on 126 of these).

The second data set consisted of total reproductive success. For males, we included individuals meeting the following criteria: 1) they were observed at least once on a day following marking; 2) they were marked at Blompond on or subsequent to 19 June,

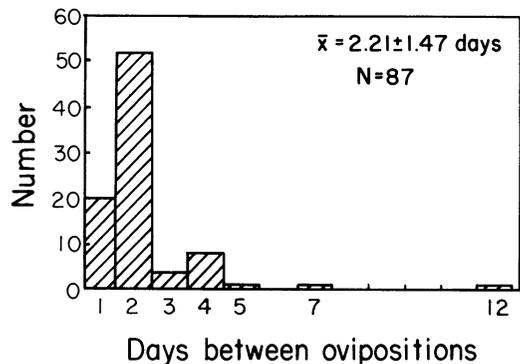


FIG. 1. Distribution of the number of days between observed ovipositions for marked females at Blompond ($\bar{x} \pm SD$).

when we began continuous watches; 3) their wings were fresh when captured; and 4) they were not observed at another pond. As exceptions to (4), we included 10 males last seen at another pond on one or two occasions after having been present at Blompond for at least several days. Such individuals appeared to be following a pattern of post-reproductive wandering (Koenig and Albano, unpubl.) and are unlikely to have reproduced after emigrating from Blompond.

A total of 46 males met the above criteria (45% of the 102 males marked at Blompond and observed at least once on a day subsequent to capture). Because virtually all males at Blompond were marked during the study, we are confident of having captured these 46 individuals soon after they reached reproductive maturity. These data thus estimate lifetime reproductive success. Unfortunately, because a high proportion of matings (85.3% of 1,242) involved unmarked females, we were unable to obtain lifetime data for this sex. However, 42 females were observed after marking for which we had data on all subsequent matings and ovipositions. In order to avoid bias arising from data from individuals seen only once (Fincke, 1986), we used only data collected after the date females were marked. These data correspond to an unknown fraction of lifetime reproductive success. (If, however, there is an even adult sex ratio, as was found in *Plathemis lydia* by Campanella and Wolf [1974], this fraction can be roughly estimated by the ratio of the mean

total number of eggs laid by females divided by the mean lifetime number of eggs fertilized by males; this ratio [from the mean lifetime seconds of oviposition in Table 1] is 0.41.) Assuming that the fraction of lifetime reproductive success sampled is unbiased, trends derived from these data will be unaffected. Thus, the "total" reproductive success we obtained for females, although not as reliable, provides data which can at least be tentatively compared with our more complete data from males.

We arranged and analyzed these measures as multiplicative "episodes" of selection (Arnold and Wade, 1984*a*, 1984*b*). For males, the episodes considered included: 1) days alive after marking, 2) proportion of days alive in which the individual was observed at the pond, 3) number of hours per day spent at the pond, 4) matings obtained per hour present at the pond, 5) proportion of matings in which the female oviposited for at least one second, and 6) mean duration of ovipositions obtained by mates. These episodes measure survivorship (1), reproductive effort (2 and 3), mating efficiency (4), mate-guarding ability (5), and a combination of guarding ability and female fertility (6). For females, episodes were: 1) days alive after marking, 2) proportion of days alive in which the individual was observed to have oviposited at the pond, and 3) duration of oviposition obtained per day on days the individual was observed. The first of these episodes again measures survivorship. Because females produce only one clutch every several days (see above), the second episode estimates the clutch interval, while the third estimates primarily clutch size and, to a lesser extent, the ability to avoid or circumvent interference during oviposition. For both males and females, the episodes we considered do not occur strictly sequentially, and thus the precise ordering of episodes is unavoidably arbitrary (see below).

We tested for selection on four characters. The first was the date individuals were marked. For males, this measure represents seasonal effects and tests whether individuals emerging early in the season were at an advantage compared to those emerging later. For females, this measure does not directly indicate emergence date, as we were

unable to mark females the first time they came to the pond. Nonetheless, although provisional, this measure still reflects seasonal trends in fecundity, and thus assesses selection on adults acting to alter the seasonal timing of reproduction.

We also measured selection on body mass and hind wing length. In order to eliminate measuring the mass of eggs carried by females coming to oviposit, we only included body mass for females weighed after oviposition. We do not, however, have data on fluctuations in body mass over the lifespan in individuals. Both characters were log transformed prior to analysis.

We also measured the relative time spent in flight by territorial males as an index of territorial aggressiveness. We determined this character as follows. Focal watches (Altmann, 1974) were conducted on arbitrarily chosen territorial males. Watches lasted 1 hr or until the male left the pond. During the watch, the location and activity of the focal male and the number of conspecific males within 1 m of the focal individual were recorded at 12-sec intervals. For each watch, we determined the proportion of time the focal male spent in flight, and the proportion of time one or more conspecifics were present within 1 m of the focal male. Both measures were arcsin transformed for analysis.

Since the activity of territorial males increases with the density of intruding conspecifics (Koenig and Albano, 1985), we performed a regression of the time spent in flight on the proportion of time that no conspecifics were present within 1 m of the focal male. As expected, the proportion of time spent flying by territorial males increases with the density of intruding conspecifics ($F = 34.9$, $d.f. = 1, 46$, $R^2 = 0.43$, $P < 0.001$).

We then calculated the standardized residuals of the time spent in flight from the above regression for each focal watch. Next we averaged these residuals for all focal watches conducted on the 13 males for which we eventually acquired lifetime data. This yielded an index of territorial aggressiveness for these males, controlling for differences resulting from population density. In all, we performed 35 focal watches (1–7 per male, $\bar{x} = 3$) lasting a total of 26 hours for these 13 individuals.

Following Arnold and Wade (1984a), the selection differential (Falconer, 1981) at episode k , s_k , was calculated as the shift in the mean resulting from the action of selection during the current episode, starting from the mean at the beginning of the episode. In contrast, s_k' values were calculated as the shift in the original mean occurring through the action of each episode of selection independent of any other episodes. Thus, s_k' values provide a measure of the relative importance of selection at each episode independent of the ordering of the episodes (see below).

Selection intensity (Falconer, 1981) at episode k , i_k , was calculated by dividing the selection differential s_k by the standard deviation of the original character (Arnold and Wade, 1984a). Similarly, i_k' values are calculated by dividing s_k' by the standard deviation of the original character. In addition, we calculated a third measure of the selection intensity, i_k^* . This value is the shift in the mean due to selection at an episode in units of the standard deviation of the character at the start of the action of that episode, rather than the original standard deviation. Of these three measures of selection intensity, only s_k values are additive (Arnold and Wade, 1984a).

Selection gradients (β_k) are the regression coefficient of standardized fitness on the character at episode k ; this is mathematically equivalent to the selection differential (s_k) divided by the variance in the character (Arnold and Wade, 1984a). As with selection intensities, we calculated three β values. For the first (β_k), we divided by the original variance in the character at each episode. For β_k^* , we divided by the changed variance at the start of each episode rather than the original variance. Finally, for β_k' values, we independently regressed each episode of fitness on the original distribution of the character. Although only β_k values are additive, the other two selection gradients provide a less biased measure of selection at each episode. β_k^* values take into account the degree to which the character variance is changed at each episode, and thus correspond to true selection gradients (Kalisz, 1986). However, both β_k and β_k^* values are potentially sensitive to ordering effects of the episodes, and thus may be mis-

leading when episodes do not occur strictly sequentially. In contrast, β_k' values are defined so as to be independent of any ordering effects, and thus provide an unbiased measure of selection occurring due to the independent effects of a given episode. Furthermore, β_k' values can be directly tested for statistical significance by examination of the regression coefficient. Neither β_k nor β_k^* values can be readily derived from a regression analysis, and thus cannot be directly tested for significance.

Several limitations of our data and analyses should be noted. First, we assumed that all eggs were fertilized by the male mating with a female immediately prior to oviposition. This is consistent with data on sperm competition in odonates, which indicate that the last male to copulate fertilizes the vast majority (an average of 99.5% in *Erythemis simplicicollis*) of the eggs she lays (McVey and Smittle, 1984; see also Waage, 1979, 1983; Fincke, 1984). However, because of the extremely short copulations in *Plathemis lydia* (≈ 3 sec [McMillan, 1983] compared with 12–18 sec in *Erythemis* [McVey, 1981]), it is unlikely that sperm precedence is complete. A second problem involves females that did not mate immediately prior to oviposition; such cases involved 13.9% of ovipositions. Sperm precedence by the last male to mate drops considerably on subsequent days (McVey and Smittle, 1984). Combined with the low proportion of marked females in our study, this means that paternity of eggs laid by lone females could not be determined. Third, a small proportion of reproduction involved unmarked or unknown males; 2.2% of the 1,132 ovipositions in which the female mated shortly beforehand, and 1.6% of the 16.5 hr of oviposition seen after an observed mating were not attributable to a known male.

We also did not correct for the temperature dependence of oviposition rate (McVey, 1984; Fincke, 1985). However, because of the thermoregulatory abilities of dragonflies (May, 1976; Heinrich and Casey, 1978), it is likely that abdomen temperatures vary much less than the ambient temperature. To the extent that this is true, oviposition rates will be relatively uniform, and consequently the length of oviposition

TABLE 1. Intersexual comparison of the opportunity for selection (σ^2/\bar{x}^2) in *Plathemis lydia*.

	Mean	σ^2	<i>N</i>	<i>I</i>	I_s/I_o
Days alive					
Males	8.87	62.6	46	0.80	} 1.17
Females	6.04	25.0	50	0.68	
Seconds of oviposition					
Lifetime or total					
Males	727	1.58×10^6	46	2.99	} 2.37
Females	299	1.13×10^5	42	1.26	
Daily (all days)					
Males	64	1.52×10^4	912	3.65	} 1.95
Females	47	4.17×10^3	291	1.87	
Daily (only days when present at pond)					
Males	88	1.86×10^4	672	2.43	} 10.13
Females	104	3.28×10^3	132	0.24	

bouts will provide a good index of number of eggs fertilized or laid. Because the number of males and females at the pond varies continuously, we have also not corrected our *I* values for the operational sex ratio (Emlen and Oring, 1977). However, the operational sex ratio is almost always biased towards males (at any one time, there are usually no females at all at the pond), and thus the effective intensity of selection may be considerably greater on males than our results indicate (Wade and Arnold, 1980). Also, because of small sample sizes, we have not attempted to analyze for stabilizing or disruptive selection. Finally, we cannot be certain that some of the characters we use, such as the index of aggressiveness and body mass, do not change ontogenetically.

Our results must thus be considered provisional until these shortcomings can be dealt with satisfactorily.

RESULTS

Opportunity for Selection

Table 1 summarizes the opportunity for selection (*I*) for survivorship and reproductive success. In all cases *I* values are higher for males than females, although those for longevity are similar. When all days are included, *I* values are higher for daily reproductive success than for lifetime or total reproductive success. The opposite is true, however, when only days in which individuals were actually present are included. The I_s/I_o ratio for reproductive success is lower

on a daily basis than on a lifetime basis when all days are included, but much higher on a daily compared with lifetime basis when only days in which individuals appeared at the pond are included. The distributions of lifetime (for males) and total (for females) reproductive success are presented in Figure 2; data for daily reproductive success are presented in Figure 3.

Partitioning of the opportunity for selection on lifetime reproductive success in males is presented in Table 2. Listed are the opportunity for selection associated with individual episodes (w_i), the running subtotals for the total opportunity for selection (w_1, w_2, \dots, w_n), the opportunity for selection associated with correlations between fitness components (the "cointensity" terms), and the total opportunity for selection (*W*). Also listed are the percentages of the total opportunity for selection represented by each episode and subtotal.

By far the largest single contribution to *I* (27% of the total) is provided by variance in days alive (survivorship). Matings per hour present at the pond (mating efficiency) is second with 11% of the total. Hours present per day on the pond contributes another 6%, while each of the other three episodes accounts for only 2% or less of the total opportunity for selection. The various cointensity terms, measuring in part covariances among variables (Arnold and Wade, 1984a), are generally positive and often substantial, contributing a total of 52% to the total opportunity for selection.

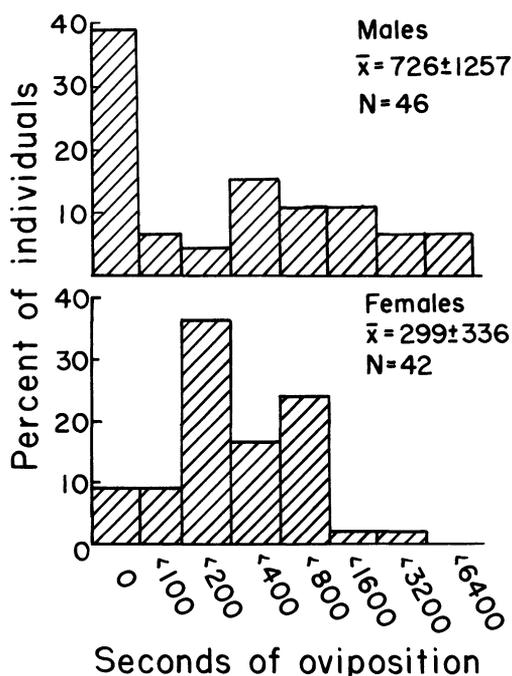


FIG. 2. Frequency distribution of lifetime reproductive success (males) and total reproductive success (females) for *Plathemis lydia*, based on seconds of oviposition ($\bar{x} \pm SD$).

The analogous partitioning of the total opportunity for selection on females is presented in Table 3. Survivorship contributes nearly half (48%) to the total I value. Clutches per day alive (the interclutch interval) contributes 14% to I , while clutch size contributes only 10%. Covariance effects are again strong, contributing a total of 28% to the total I .

Selection on Correlated Characters

The two morphologic characters measured (hind wing length and body mass) are both indicative of body size. Mean \pm SD (N) hind wing length was 31.57 ± 0.87 mm (276) for males and 32.61 ± 0.95 mm (94) for females; mean body mass was 0.462 ± 0.035 g (271) for males and 0.470 ± 0.044 g (22) for females. Females have significantly longer hind wings than males (ANOVA, $F = 95.2$, $d.f. = 1,368$, $P < 0.001$), but there is no sexual dimorphism in body mass ($F = 0.9$, $d.f. = 1,291$, ns). Coefficients of variation for both characters are all relatively small, between 2.0 and 2.9%.

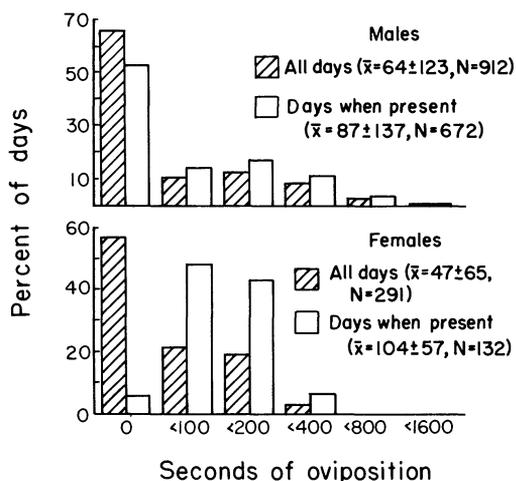


FIG. 3. Frequency distribution of daily reproductive success for male and female *Plathemis lydia*. The most successful male obtained a total of 890 sec (14.8 min) of oviposition in one day; the most successful female oviposited for 379 sec (6.3 min). Data ($\bar{x} \pm SD$) are given for all days and for only those days when individuals were observed at the pond.

Correlations between the four characters used in the analyses and between the characters and the fitness components we measured are given for lifetime or total reproductive success in Table 4. There is a strong seasonal effect on lifetime reproductive success in males (due to effects on survivorship and time spent per day on the pond), and a weaker, but nonsignificant ($P < 0.10$), seasonal effect on total reproductive success in females; for both sexes, earlier individuals have a reproductive advantage. There was no significant correlation between aggressiveness (time spent in flight) by males and lifetime success; however, there was a significant positive correlation between aggressiveness and the matings per hour males achieved while at the pond. There were also several significant correlations between characters; for both sexes, body mass declined seasonally (see Banks and Thompson [1985] for a similar result in the damselfly *Coenagrion puella*), and heavier individuals had longer wings.

The relative magnitude of direct selection on a trait, controlling for correlated effects on other measured traits, is indicated by the standardized partial regression coefficient (β) resulting from a multiple regression of

TABLE 2. Partitioning of the opportunity for selection on lifetime reproductive success in male *Plathemis lydia* ($N = 46$ individuals). Lines separate running subtotals.

Source of variation in relative fitness	Contribution to total opportunity for selection		
	Symbol	Value	Percentage
Days alive (w_1)	I_1	0.81	27%
Proportion of days present at pond (w_2)	I_2	0.07	2%
Cointensities (12)	*	0.00	0%
Days present at pond ($w_1 w_2$)	I_{12}	0.84	28%
Hours per days on pond (w_3)	I_3	0.17	6%
Cointensities (123)	*	0.50	17%
Hours present ($w_1 w_2 w_3$)	I_{123}	1.51	50%
Matings per hour present (w_4)	I_4	0.33	11%
Cointensities (1234)	*	0.53	18%
Matings ($w_1 w_2 w_3 w_4$)	I_{1234}	2.37	79%
Ovipositions per mating (w_5)	I_5	0.07	2%
Cointensities (12345)	*	0.28	9%
Ovipositions ($w_1 w_2 w_3 w_4 w_5$)	I_{12345}	2.73	91%
Eggs fertilized/oviposition (w_6)	I_6	0.02	1%
Cointensities (123456)	*	0.24	8%
Eggs fertilized (total selection, W)	I	2.99	100%

* Cointensities include covariance terms between the current episode and all prior episodes; e.g., "Cointensities (12)" = $COI(1,2) + COI(12|2) + COI(12,2|1) - COI(12,2)$. For formulae, see Arnold and Wade (1984a).

fitness on the characters involved (Lande and Arnold, 1983). The results of such analyses using the three non-behavioral characters are presented in Table 5. For males, the only significant effect is that between survivorship and hind wing length; individuals with wings one standard deviation shorter than the mean experienced relative survivorship 47% longer than average. All three characters have comparable direct influences on lifetime fitness; none are significant. For females, there are again no significant direct effects of the three characters on either survivorship or total reproductive success.

Episodes of Selection

We calculated selection parameters for characters showing potentially significant effects on some episode of fitness as indicated by the analyses in Tables 4 and 5. The characters included were first date on the pond for both sexes, male hind wing length, and the index of territorial aggressiveness (time spent in flight). The results are presented in Table 6. First we list the mean and variance of the character following the combined action of all prior episodes; then the selection differentials, selection intensities, and the selection gradients.

For females, those present earlier in the season had higher fitness, and this effect acted through all three episodes (Table 6). The total effect of selection was to figuratively shift the mean date of marking 0.31 standard deviation units earlier in the season. Based on the β' values, the only significant effect is due to decreased interclutch interval early in the season.

For males, selection again consistently favors seasonally early individuals, except for a small tendency for later males to obtain more eggs per mating. In sum, selection fig-

TABLE 3. Partitioning of opportunity for selection on total reproductive success in female *Plathemis lydia* ($N = 42$ individuals).

Source of variation in relative fitness	Contribution to total opportunity for selection		
	Sym- bol	Value	Percentage
Days alive (w_1)	I_1	0.60	48%
Clutches per day alive (w_2)	I_2	0.18	14%
Cointensities (12)	*	-0.03	-2%
Clutches ($w_1 w_2$)	I_{12}	0.75	60%
Seconds of oviposition per clutch (w_3)	I_3	0.13	10%
Cointensities (123)	*	0.38	30%
Seconds of oviposition (total selection, W)	I	1.26	100%

* See footnote to Table 2.

TABLE 4. Correlations with episodes of lifetime reproductive success (males) and total reproductive success (females). Both body mass and hind wing length are log transformed. For explanation of the index of aggressiveness (percent time in flight) see text. Sample sizes are given in parentheses. Two-tailed test; * $P < 0.05$; ** $P < 0.01$.

Variable	Date marked	Body mass	Hind wing length	Index of aggressiveness
Males				
Body mass	-0.34* (41)	—	—	-0.14 (11)
Hind wing length	0.07 (41)	0.36* (40)	—	-0.10 (12)
Survivorship	-0.43** (46)	0.11 (41)	-0.27 (41)	0.18 (13)
Hours present per day alive	-0.44** (45)	0.20 (40)	-0.09 (40)	-0.41 (13)
Matings per hour on pond	-0.24 (46)	0.14 (41)	0.11 (41)	0.59* (13)
Seconds of oviposition per mating	0.17 (31)	-0.02 (28)	0.20 (28)	0.10 (13)
Total seconds of oviposition	-0.38** (46)	0.16 (41)	-0.04 (41)	0.23 (13)
Females				
Body mass	-0.56* (15)	—	—	—
Hind wing length	0.18 (40)	0.57* (15)	—	—
Survivorship	-0.15 (42)	-0.01 (15)	-0.04 (40)	—
Interclutch interval	-0.31* (42)	0.45 (15)	0.04 (40)	—
Clutch size	-0.20 (38)	0.12 (13)	-0.32 (36)	—
Total seconds of oviposition	-0.28 (42)	0.11 (15)	-0.10 (40)	—

uratively shifts the date of marking for males 0.64 standard deviations earlier in the season. The majority of this effect results from significantly increased survivorship and increased time per day males spend on the pond early in the season.

There is little overall selection on male hind wing length. However, this probably results from a trade-off between survivorship and the other episodes of selection, particularly mating efficiency; individuals with longer wings obtain more matings per hour at the pond but do not live as long as short-winged individuals. This trend is also suggested by the correlations in Table 4, although they are not significant.

For the 13 males for which we had both behavioral and lifetime data there was little overall selection on time spent in flight (the index of territorial aggressiveness), due in

part to a trade-off between episodes. In particular, more aggressive territory holders obtained significantly greater mating efficiency, but this effect was largely cancelled by the shorter number of hours per day such individuals spent at the pond.

DISCUSSION

Opportunity for Selection

The dominant contribution to the opportunity for selection for male *Plathemis lydia* is through differential survivorship (Table 2). The second most important contribution is from mating efficiency, followed by hours present per day at the pond. Additional components, except for the covariance terms, are negligible. Unfortunately, the covariance terms are not readily interpretable (Arnold and Wade, 1984a); however, they reflect at least in part, correlations

TABLE 5. Selection gradients (standardized partial $\beta \pm$ SE) for date marked and body mass with survivorship and reproductive success. $N = 40$ males and 15 females.

Episode	Date marked	Body mass	Hind wing length	Multiple R^2
Males				
Survivorship	-0.31 \pm 0.16	0.22 \pm 0.15	-0.47 \pm 0.15**	0.28
Lifetime eggs fertilized	-0.29 \pm 0.19	0.16 \pm 0.17	-0.21 \pm 0.17	0.15
Females				
Survivorship	0.06 \pm 0.36	0.07 \pm 0.40	-0.09 \pm 0.37	0.01
Total eggs laid	-0.07 \pm 0.36	0.10 \pm 0.40	-0.06 \pm 0.37	0.02

** $P < 0.01$.

TABLE 6. Analysis of directional selection on seasonal timing, body size, and aggressiveness (measured as total time in flight, see text) in *Plathemis lydia* based on lifetime reproductive success (males) and total reproductive success (females). Means $\pm \sigma^2$ are calculated at the start of each episode, except for the values given for "total selection," which are the final values. For date on pond, mean values are days since 1 June; those for total time in flight are residuals from the predicted regression value (see text). For discussion of the selection gradients, see text.

Character Selection episode	$\bar{x} \pm \sigma^2$	Selection differentials		Selection intensities			Selection gradients		
		s_k	s_k'	i_k	i_k^*	i_k'	β	β^*	β'
Females: date on pond (days, $N = 42$)									
Survivorship	27.3 \pm 156.4	-1.29	-1.29	-0.10	-0.10	-0.10	-0.008	-0.008	-0.008
Clutch interval	26.0 \pm 139.2	-1.60	-2.26	-0.13	-0.14	-0.18	-0.010	-0.011	-0.015*
Clutch size	24.4 \pm 122.5	-1.02	-1.04	-0.08	-0.09	-0.08	-0.007	-0.008	-0.009
Total selection	23.4 \pm 118.8	-3.91	—	-0.31	—	—	-0.025	—	—
Males: date on pond (days, $N = 46$)									
Survivorship	33.8 \pm 127.5	-4.23	-4.23	-0.37	-0.37	-0.37	-0.033	-0.033	-0.033**
Hours present per day	29.6 \pm 79.7	-2.15	-3.38	-0.19	-0.24	-0.30	-0.017	-0.027	-0.027**
Matings per hour present	27.4 \pm 59.9	-0.83	-2.64	-0.07	-0.12	-0.23	-0.007	-0.014	-0.021
Seconds of oviposition per mating	26.6 \pm 47.6	0.05	1.23	0.00	0.01	0.11	<0.001	<0.001	0.011
Total selection	26.6 \pm 56.5	-7.17	—	-0.64	—	—	-0.056**	—	—
Males: hind wing length ($N = 38$)									
Survivorship	3.461 \pm 5.38 $\times 10^{-4}$	-0.0054	-0.0054	-0.23	-0.23	-0.23	-9.85	-9.85	-9.85
Hours present per day	3.456 \pm 7.44 $\times 10^{-4}$	0.0008	-0.0013	0.03	0.03	-0.06	1.44	1.08	-2.37
Matings per hour present	3.457 \pm 6.44 $\times 10^{-4}$	0.0025	0.0027	0.11	0.10	0.12	4.51	3.88	4.94
Seconds of oviposition per mating	3.459 \pm 8.41 $\times 10^{-4}$	0.0005	0.0029	0.02	0.02	0.13	0.90	0.59	5.27
Total selection	3.460 \pm 7.31 $\times 10^{-4}$	-0.0016	—	-0.07	—	—	-2.89	—	—
Males: time spent in flight ($N = 13$)									
Survivorship	-0.93 \pm 162.2	0.689	0.689	0.05	0.05	0.05	0.004	0.004	0.004
Hours present per day	-0.24 \pm 157.7	-1.762	-1.891	-0.14	-0.14	-0.15	-0.011	-0.011	-0.013
Matings per hour present	-2.01 \pm 181.4	4.177	3.733	0.33	0.31	0.29	0.026	0.023	0.025*
Seconds of oviposition per mating	2.17 \pm 186.6	-0.893	0.529	-0.07	-0.07	0.04	-0.005	-0.005	0.004
Total selection	1.28 \pm 216.1	2.210	—	0.17	—	—	-0.014	—	—

Statistical tests were performed on the β value for total selection only and on all β' values; * $P < 0.05$, ** $P < 0.001$.

between selective episodes. Thus, in Table 2, the large positive COI(123) and COI(1234) terms suggest that males obtaining more matings per hour also tend to be at the pond longer per day and to live longer as well. In general, there is no indication of trade-offs between performance at different selective episodes for males.

For females, differential survivorship again dominates, contributing 48% to the total opportunity for selection (Table 3). Of secondary importance is variance in the interclutch interval, followed by variance in clutch size.

Similar to our findings here, studies on other odonates have also indicated that survivorship contributes substantially to variance in lifetime reproductive success. Fincke (1982) reported relative variance in male survivorship of the damselfly *Enallagma hageni* to be 78% of the variance in lifetime mating success; for the same species, Fincke (1986) found that I values for male survivorship contributed 39% to the total lifetime fertilizations achieved by males, whereas for females, I values were 2.4 times as great for survivorship than for the estimated total number of eggs laid. Banks and Thompson (1985) draw a similar conclusion; in their study of the damselfly *Coenagrion puella*, differences in lifespan accounted for 70% of the variance in male mating success. Finally, McVey (1987), studying the dragonfly *Erythemis simplicicollis*, found that variance in survivorship accounted for 57% of the relative variance in estimated male lifetime reproductive success and 68% of the relative variance in estimated female lifetime reproductive success. Taken together, these studies suggest that, for many species of odonates, variance in longevity provides an important, if not the dominant, contribution to the total opportunity for selection among both sexes, whether males are territorial (as in the dragonflies *Plathemis* and *Erythemis*) or not (as in the damselflies *Enallagma* and *Coenagrion*).

One consequence of this pattern is that variance in lifetime mating success will be largely due to variance in survivorship, and thus mating success will not represent the opportunity for sexual selection (McCauley, 1983; Koenig and Albano, 1986; see below). Another consequence is that characters in-

fluencing survivorship will have considerable opportunity to exert strong positive effects on lifetime fitness regardless of their influence on other episodes of selection. For example, a reduction in reproductive effort which serves to increase survivorship nevertheless may increase fitness. Conversely, characters influencing short-term reproductive success may have little overall effect on fitness.

For males, our analysis differs from similar analyses presented earlier (e.g., Arnold and Wade, 1984b) in that we divided fitness into a relatively large number of episodes. This procedure has the potential advantage of identifying very specific episodes of importance out of the wide spectrum of selective episodes experienced during the lifetime of an individual. A potential disadvantage, however, is the production of relatively large "cointensity" terms which are not readily interpretable, although they represent, at least in part, covariance between episodes (Arnold and Wade, 1984a). Thus, it may be desirable in some circumstances to minimize the number of episodes used.

Short-term versus Lifetime Reproductive Success

Our data confirm some of the difficulties of extrapolating lifetime data from short-term information. I values calculated from daily reproductive success data are considerably different from those calculated using the lifetime/total data (Table 1). Using only days when individuals came to the pond, the opportunity for selection is 81% of the lifetime value for males and only 19% of the total value for females. I values calculated by including days when individuals known to be alive did not come to Blompond overestimated the lifetime/total values. Estimates of the relative opportunity for selection on males compared with females are similarly misleading: using only days when individuals were present, the I_s/I_q ratio is 4 times greater than the lifetime/total estimate of I_s/I_q . The I_s/I_q ratio derived from using all days is, however, close to the lifetime/total estimate ($I = 1.95$ vs. 2.37 , Table 1). Data using all days comes closer to approximating lifetime data, as it assumes knowledge of survivorship of marked

individuals even when they are not present at the pond. However, both measures of I using daily data suffer the additional difficulty of non-independence among different days of data taken from the same individuals.

Similar comparisons of daily and lifetime data for the territorial dragonfly *Erythemis simplicicollis* are given by McVey (1987). For males, McVey's estimates of relative variance in male daily reproductive success exceed I values for lifetime reproductive success (daily values ranged from 2.13 to 6.22 depending on the particular data set used, lifetime values ranged from 1.29 to 1.90). In contrast, relative variance in female daily reproductive success was considerably lower than estimated lifetime values (daily values were 0.44 and 0.83 [excluding days when females were not seen and including such days, respectively], the lifetime estimate was 1.35). Fincke (1986) similarly shows that daily data are not necessarily a good indication of the relative opportunity for selection present on a lifetime scale for *Enallagma hageni*.

Neither McVey's nor our data are as reliable for females as they are for males. Nevertheless, it clearly seems inadvisable to infer lifetime patterns of opportunity for selection, either within or between sexes, from short-term data (see also Clutton-Brock, 1983; Banks and Thompson, 1985). In both our study and McVey's (1987), estimates of the opportunity for selection based on daily success better approximated lifetime estimates when all days were included, whether or not individuals actually came to the pond.

Intersexual Comparisons

Our estimate of relative variance in lifetime/total reproductive success of male *Plathemis lydia* is 2.4 times greater than that for females (Table 1). I values for lifetime reproductive success of other polygynous species have usually, though not always, followed a similar pattern. Banks and Thompson (1985), studying mating success in the damselfly *Coenagrion puella*, report an I_s/I_o ratio of 2.1, while estimates of the I_s/I_o for the damselfly *Enallagma hageni* range between 2.9, based on lifetime mating success (Fincke, 1982), and 1.7, based on life-

time reproductive success (Fincke, 1987). Among vertebrates, Clutton-Brock (1983) reports an I_s/I_o ratio of 3.4 for the polygynous red deer *Cervus elaphus*. However, an exception to this trend is reported by McVey (1987) for *Erythemis simplicicollis*, in which the I_s/I_o ratio was 0.94. Unfortunately, there are data from few monogamous species for comparison; the data from kittiwakes *Rissa tridactyla*, studied by Coulson and Thomas (1985), yield an I_s/I_o ratio of 1.2, whereas Fitzpatrick and Woolfenden (1987) indicate that the I_s/I_o ratio for the Florida scrub jay *Aphelocoma coerulescens*, is very close to one. Thus, although the opportunity for selection may often be greater for males than females in polygynous species and greater in polygynous compared with monogamous species (see Clutton-Brock, 1983), McVey's results indicate that this may not hold generally.

Patterns of Selection

For female *Plathemis*, selection favored individuals reproducing earlier in the season; overall, the mean date females were first on the pond figuratively decreased 3.91 days or 0.31 standard deviations (Table 6). Based on the β' values, however, the only episode during which selection was significant was the interclutch interval, which increased later in the season. No significant direct selection was detected on any of the three characters measured for females (Table 5).

Of the four characters measured for males, only date of first reproduction is significantly correlated with lifetime fitness (Table 4). A univariate analysis indicates that selection on this character is significant at two life history stages; males living earlier had higher survivorship and were present at the pond more hours per day than those living later, again as indicated by the β' values (Table 6).

The selection for seasonally earlier reproduction is interesting in view of the seasonal decline in body mass for both sexes (Table 4). These correlations suggest that the decline in body mass may be the indirect result of selection to speed up development as the season progresses so as to mitigate the lower success of later individuals. This could be accomplished by a reduction in the variable

number of instars through which the larvae develop (Benke and Benke, 1975). As we found no selection for larger body size, this trend would not be countered by selection for body mass per se. However, an alternative hypothesis that mass declines late in the season due to lower food availability (Harvey and Corbet, 1985) cannot be rejected.

None of the three non-behavioral characters has a significant direct effect on lifetime fitness when controlling for the other two characters (Table 5). Although the low variance in the two morphological characters undoubtedly is partly responsible, this lack of significance is also due to trade-offs between selective effects at different life-history stages. For example, males with shorter hind wings survive longer but have lower mating efficiency; the result is almost no overall selection on hind wing length (Table 6). A similar trade-off is suggested for male territorial flight; males that fly a greater amount of time experience greater mating efficiency, but are on the pond a shorter period each day than less aggressive individuals (Table 6). Possibly males that fly more contact more females while at the pond or are more successful at competing for mates. The decreased duration of time more active males spend at the pond follows from the apparent energetic constraints of maintaining a territory in *Plathemis* (Koenig and Albano, 1985).

Measuring Episodic Selection

Here we have used three different selection gradients to measure the strength of selection occurring at particular episodes (Table 6). The first two of these (β_k and β_k^* values) are discussed in Arnold and Wade (1984a). β_k values have the advantage of being additive, but are not true selection gradients, as they are calculated using the original variance rather than the adjusted variance existing at the start of each episode. β_k^* values are calculated using adjusted variances, and thus yield a more realistic approximation of selection occurring at a specific episode (Kalisz, 1986). However, both these selection gradients are sensitive to the ordering of individual episodes (Albano and Koenig, unpubl.). Thus, the confidence that can be placed in them depends

on the extent to which episodes occur in an unambiguous chronological sequence. For example, the three episodes of hatchability, followed by juvenile survivorship, followed by adult reproductive success, follow each other in chronological order with no temporal overlap. This is not the case for the episodes we use here. Although we arranged episodes in a logical sequence, all occur simultaneously during the lifetime of individuals, and other orderings are possible. In order to circumvent this difficulty, we calculated selection gradients for individual episodes independent of the action of any other episodes (β_k' values).

Mating Success and Sexual Selection

Several recent authors have equated variance in mating success with the opportunity for sexual selection (Wade and Arnold, 1980; Fincke, 1982; Price, 1984; Arnold, 1983; Arnold and Wade, 1984b). Our results indicate some of the shortcomings of this operational definition, especially when applied to lifetime data (see also Banks and Thompson, 1985; Sutherland, 1985; Koenig and Albano, 1986). From Table 2, for example, the proportion of the total opportunity for selection on male lifetime reproductive success due to variance in mating success (I_{1234}) is very high (79%). However, to then conclude that the opportunity for sexual selection is large obscures the fact that the largest single contribution to the total I value is the variance in survivorship—an episode of selection which cannot be easily interpreted as sexual selection.

This problem arises because mating success is the collapsed result of several selective episodes (see Arnold and Wade, 1984a), only some of which may represent Darwinian sexual selection (Koenig and Albano, 1986). In *Plathemis*, for example, variance in mating efficiency (w_4) could result in part from female choice or male-male competition, and thus may represent sexual selection. Similarly, variance in hours present per day on the pond (w_3) may in part be due to variance among males in territory-holding ability due to male-male competition; to this extent it may be appropriate to view this episode as one of sexual selection. However, at least some of the variance in hours per day males spend at the pond, as well as

the proportion of days males come to the pond (w_2), is probably due to energetic constraints imposed by variance in male foraging ability; hence, much or all of these two episodes may be more appropriately viewed as episodes of natural selection, as is, of course, variance in survivorship (w_1). Thus, the actual proportion of the opportunity for selection in lifetime reproductive success for male *Plathemis* due to sexual selection is probably somewhere between 11% (I_4) and 17% ($I_3 + I_4$) rather than the 79% estimated from the total variance in mating success (I_{1234}).

For *Plathemis*, selection acting through both mating efficiency and time devoted to reproduction may be strong, and in some cases may reflect sexual selection. For example, selection acting to increase time in flight of territorial males through increased mating efficiency seems particularly likely to reflect male-male competition, and thus sexual selection. As shown in Table 6 and discussed above, such selection was countered by the tendency for less aggressive males to spend a longer period of time per day on the pond, a result possibly due to a combination of natural and sexual selection. Similarly, selection acting on male hind wing length through increased mating efficiency may also be a consequence of direct male-male competition for mates (hence sexual selection), and was countered by lower survival (hence natural selection).

Thus, trade-offs between natural and sexual selection via male-male competition are suggested by our data. Whether any of the selective effects we document acting through increased mating efficiency result from female choice, however, is unresolved with the present analyses. Indeed, mate choice independent of resources (e.g., oviposition sites) has yet to be documented in any odonate.

ACKNOWLEDGMENTS

We thank our field assistants, A. Peters and M. Peterson, for helping with the project. R. Noyce kindly gave us permission to work at Blompond. O. Fincke, S. Kalisz, and M. McVey kindly provided us with preprints of papers; M. Wade helped us calculate the opportunity for selection; and S. Arnold helped us understand sexual selec-

tion. We also thank J. Dickinson, O. Fincke, M. McVey, K. Sullivan, J. Waage, E. Waltz, L. Wolf, P. Williams, and the reviewers for their extensive comments and help on the manuscript. This paper is dedicated to Frank Pitelka in honor of his 70th birthday.

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