Allometry and Proximate Mechanisms of Sexual Selection in *Photinus* Fireflies, and Some Other Beetles[1]

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Synopsis.   Ever since Darwin identified it as the force responsible for the evolution of exaggerated male characters, sexual selection has been the focus of research aimed at understanding the most bizarre and intriguing morphologies and behaviors in Nature. Two congeneric species in the firefly genus *Photinus*, *P. pyralis* and *P. macdermotti*, afford a unique opportunity to examine the interaction between sexual and countervailing natural selection that act to shape the evolution of mating behavior and body size in closely related species with very different courtship strategies. *Photinus pyralis* males emit very bright flashes during their extended patrolling flights and form 'love knots' of competing suitors, while *P. macdermotti* males, whose courtships seldom exceed two competing males, produce weaker flashes during a shorter patrolling period.

Possibly as a consequence of their scramble competition and long flights, not only is there an extremely wide range of body sizes in *P. pyralis* males, but they also exhibit wing allometric slopes greater than one, and lantern allometries less than one. In contrast, *P. macdermotti* males do not have allometric slopes significantly different from one. Small males, when tested in an artificial scramble situation move faster than large males, an advantage in the intense competition that ensues once a female is located. Females answer several males in alternation and fail to respond to all male flashes, with the evident consequence that love knots frequently develop around such fickle females. Allometric relationships in two non-luminescent beetle species with non-visual courtship protocols are compared. Visual, sexually selected characters showed positive allometric slopes, while non-visual characters showed isometry or negative slopes. Data presented here support the existence of distinct patterns in modality-specific sexual selection.

Introduction

Charles Darwin (1859, 1871) first observed that many of the most elaborate and exaggerated traits of animals, such as peacock trains and rhinoceros beetle horns, had nothing to do with ecological adaptation, but instead, served to enhance success in competition for mates. He regarded these traits as evolving under sexual, rather than natural selection, because such bizarre traits appeared to be effective in gaining mates but costly in terms of survival. Although there is ultimately no evolutionary difference between the two types of selection in terms of net fitness (Otte, 1979; Endler, 1986), the process of sexual selection—reproductive variance due to differential mating success—is an important and distinguishable subset of natural selection. Unlike natural selection, *sensu lato*, sexual selection is constant, since every reproducing individual of every generation must come under its influence, and thus it likely may be a major catalyst for rapid, and profound, evolutionary change (West-Eberhard, 1983). Using the approaches of quantitative genetics, Arnold (1983) was the first to explore in detail the mechanisms of sexual selection that shape relationships between morphology, performance, and their consequences for individual fitness in the context of mate competition. First employed by Huxley (1932), allometry—the differential analysis of size relation-

ships between different body parts—is an older, but still powerful quantitative approach, used to examine how selection impacts the relationship between morphology and performance. For example, linear measurements of many sexually selected morphological characters used as weapons, or as visual advertisements, exhibit positive allometries when scaled against other body parts. The relation between a non-sexually selected, 'house-keeping' trait, y, and the exaggerated sexual trait, x, is expressed by the equation:

$$\log y = \log \alpha + \beta \log x$$

where α is a constant, and β, the slope of the regression of y on x. If β, the slope of the trait linear regression exceeds one, trait y is disproportionately increasing in size relative to the neutral trait, x, and is said to indicate positive allometry. If $\beta = 1$, isometry exists while a $\beta < 1$ indicates negative allometry.

The spectacular bioluminescent displays of fireflies evolved as an efficient means of nocturnal mate localization, and as such, they posses many relatively stereotyped features that serve to indicate gender and species-specific identity. Essential for reproductive success, firefly flash behavior is a visual, code-like communication system and therefore an obvious candidate for sexual selection. Lloyd (1979) first proposed that firefly flash behavior might well be a competitive display, and thus subject to sexual selection by female choice. Despite extensive work over fifty years on flash mimicry, species recognition, and flash synchrony, very little is known about how sexual selection has shaped flash behavior in particular and the non-lumi-

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nescent aspects of firefly courtship and morphometrics in general.

Fireflies of the genus *Photinus* (Coleoptera: Lampyridae) are attractive subjects for the investigation of sexual selection. For example, the photic signaling system of *P. pyralis* is typical of most firefly courtships: roving males broadcast species-specific flashes, or flash patterns, to locate sedentary females, who, if conspecific, emit species-specific, time-delayed flashes in response. Flash exchanges continue until the male achieves propinquity with the female, and is able to mate with the female.

What is most striking about *P. pyralis* courtships is their intense competitiveness. Aggregations of males regularly attain astonishingly high densities. Males in the vicinity of an incipient courtship will congregate, approach, and court the same female. Once on foot, rival males scurry toward the female and often physically jostle for access to her, forming ''love-knots'' of suitors (Maurer, 1968). Thus, two distinct selective events can be discerned in male competition for mates in this species: (1) photic competition in searching, and (2) direct male-male scramble competition once a female has been located (Vencl and Carlson, 1998).

There are several interesting features of *P. pyralis* morphology that appear to bear on how courtships succeed in the field. Vencl and Carlson (1998) showed that males have an extremely wide range of body sizes and lantern areas. Furthermore, overall male size was found to be an important predictor of the outcomes in both the search, and in scramble selective events in *P. pyralis* courtships. Although both elytral length and lantern area were important in overall competitive success, the effect of size depended on the intensity of male competition. Larger than average males tended to win in single-male courtships, while smaller males tended to win in courtships with several males. Small males, when tested for performance in a simulated scramble situation, move faster than large males, an obvious advantage in the intense competition that ensues once a female is located (Vencl and Carlson, 1998). Although suspected to operate in many organisms where competition for mates is intense, and males possess exaggerated sexual traits, including butterflies and horned beetles (Eberhard, 1979; Connor, 1988; Deinert *et al.*, 1994; Andersson, 1994), allometric effects on competitive ability and mating success have, thus far, not been demonstrated in fireflies.

In this paper, I examine the relationship between the mating behavior of *Photinus pyralis* (L.), the most widespread, abundant NA firefly species, and male morphology used in mate acquisition. I present data that compares male allometric patterns in *P. pyralis* with those of *P. macdermotti*, a sympatric species with a contrasting courtship protocol. I then show how male morphometric patterns relate to the outcomes of courtships observed in the field, and in simulated competitions. Additional examples of male allometric patterns are presented from other beetles with non-luminescent, non-visual courtship protocols. *Lucidota*

punctata lacks photic courtship and scramble competition, relying instead on olfactory means of mate localization. The leaf beetle *Cerotoma salvini* also lacks luminescent capability but has intensely competitive courtships that rely upon a remarkable male antennal clamp structure. In the limit, if we desire to better understand the mechanisms of sexual selection that shape morphology and its relation to fitness, more studies are needed that quantitatively compare variation in phenotypic traits, traits proven by observation to be important in mate competition, with indices of whole-organism performance, and with mating success in the field.

METHODS AND MATERIALS

Study site and courtships

Since behavioral data are absolutely necessary for understanding the significance of patterns in morphology, I measured the outcomes of courtships in the field to determine the influence of size differences among male on their mating success. The study site in Crystal Brook Park, Suffolk Co., on Long Island, New York, consisted of a 2.5 hectare field of tall grass surrounded by low vegetation and mixed hardwood tress. I collected and measured the participants, both winners and losers, in 65 *P. pyralis* courtships in the field (see Vencl and Carlson, 1998).

Morphometrics

Random samples of flying males of *P. pyralis* (n = 31), *P. macdermotti* (n = 30), and *Lucidota punctata* (n = 33), a sympatric, non-luminescent firefly, were collected in the second week of July, using an aerial net. Males were measured alive, and then preserved in alcohol-filled vials. All measurements of male structures, except elytral length, were made with an ocular micrometer in a dissecting microscope. Clear reference points were used after positioning structures with their longitudinal axis perpendicular to the axis of the ocular scale. Pronotal width, measured as the widest margin-to-margin, straight-line distance, is considered to be a fair indicator of overall body size in many insects (Emlen, 1994; Eberhard *et al.*, 1998). Pronotal width is used herein as the index of body size in all regression analyses for the study's species (Fig. 1a). Elytron length (EL) was measured with calipers from the apex to humeral edge of the left elytron to the nearest 0.05 mm.

Lantern length was measured as the straight-line distance from the anterior edge of the medial notch of the fifth abdominal sternite to the posterior edge of the 7th. Lantern width was taken as the maximal width of the 6th (Fig. 1b). Lantern area (LA) was calculated as the length-width product to the nearest 0.2 mm^2. The width and length of *Lucidota punctata's* 7th sternite was measured because it has two dysfunctional larviform discs instead of an adult lantern. Linear measures of LA were calculated by taking their square roots and transforming these to base 10 logs and likewise, for *L. punctata's* 7th sternite area. The typical swelling that

occurs when specimens are stored in alcohol was avoided. Additionally, to minimize error due to movement during measuring, beetles were chilled to immobility at 10°C for 20 minutes prior to the measurement process. Individuals could thus be manipulated easily, and measurement variation minimized. The abdomen was gently suppressed to the substrate using soft forceps. The inter-sternal membrane, a pale tissue that connects the abdominal segments that contrasts strongly with the yellowish white of the lantern itself, was never exposed during the measurement process. Thus, the abdomen was never pulled to an extreme degree, but merely aligned and straightened. All specimens were handled and oriented in same fashion so as to reduce between-measurement variation. The F-test between pronotal width and lantern area was not significant, which strongly supported the idea that there was no untoward measurement error incurred due to abdominal stretching during the lantern measurement process ($F = 1.0$; n = 65; $P = 0.5$; critical value, $\propto$, for $F_{60,60} = 1.53$; therefore, P not significant).

In addition to fireflies, males of the leaf beetle, *Cerotoma salvini* (Chrysomelidae: Galerucinae) were collected (n = 44) in Gamboa, Colón Province, Panamá, on 15 June 1996. *Cerotoma salvini* possesses a remarkable anatomical feature—antennal clamps—which are used in courtship (Vencl, personal observation). An antennal clamp is formed by the 3rd and 4th segments, which close upon, and embrace the female's 4th antennal segment during their *en face* courtships (Vencl, personal observation). The male also possesses a frontal plate, or flat ridge, which protrudes down and forward below the frons and between the eyes. Frontal plates were measured at their widest straight-line point (Fig. 1c). Antennal characters were measure from fixed landmarks with an ocular micrometer inside a stereoscope as per the linear dimensions in Figure 2d.

I measured the longest, straight-line distance between rigid, sclerotized parts of the base and the apex of the aedeagus in all four of the study's species. Landmarks, with well-defined, sharp edges, and with clear and repeatable reference points, were selected in each species to determine the aedeagal measurements. The aedeagi of all species were oriented consistently on the right side in order to align them with the linear ocular scale in the dissecting stereoscope.

Regression analysis and the coefficient of variation

Morphometric data from random samples of field-collected males of each species were base 10 log transformed and analyzed using SYSTAT 5.1 and Model II, reduced major axis regression, hereafter RMA. Regressions of base 10 log-transformed data were used to quantify relationships since the slopes obtained are unaffected by the units of measurement in different structures if they are of the same order of magnitude (Smith, 1980). Since both of the characters used in the present study were measured with error, I selected Model II regression, instead of Model I, the traditional

linear approach. In Model II regression, both the x and y variables are measurement variables. Moreover, unlike Model I regression, Model II makes no assumption of a causal relationship between the trait variables (see Sokal and Rohlf, 1995; Tsutakawa and Hewett, 1977; Clark, 1980; Fairbairn, 1997). Reduced major axis regression, wherein the sum of the areas of triangles formed by each datum is minimized, was chosen since there were no differences in the sign of the slopes obtained by either major axis or RMA regressions. The major axis slope was always greater than the RMA. With data measured at the same scale and logarithmic transformed, RMA regression will estimate β accurately and permit the testing of the null hypothesis of β = 1 using 95% confidence intervals (Sokal and Rohlf, 1995).

A second, potentially independent source of information about relationships between different body parts is the coefficient of variation, CV, which is calculated as the percentage of the standard deviation/mean. The CV indicates the relative amount of variation in the size of a body part, independent of the magnitude of the mean. A high variance, shown by a high CV value, is thought to be an important indicator of sexual selection when compared to measures of overall body size (Pomiankowski and Møller, 1995; but see Eberhard *et al.*, 1998).

Behavioral observations of Cerotoma salvini

The leaf beetle *C. salvini*, was observed in the field in Gamboa, Panamá, in June of 1996. Males and females gathered on their leguminous food plant, *Stylosanthes sp.*, in the late mornings and began to court. A male would confront a female in an *en face* orientation and attempt to grasp the female's antennae with its antennal clamps (Fig. 1d). If successful for some seconds, the male would release her and try to mount from the rear. The function of the male's frontal plate structure is not certain. Like a typical beetle horn, the plate may function as a ram to dislodge rivals by battering and shoving them. Head butting was observed frequently. Males were seen to defend leaves with females by head butting intruding males. It appeared that females engaged in biting the plate, although this was not possible to confirm. Scanning micrographs show two dark pore-like pits beneath the plate, and specimens we covered with an insoluble wax-like substance that might be a secretion issuing from them.

RESULTS

In the two congeneric photinid fireflies examined here, the reduced major axis (RMA) regression analyses of the putatively sexually selected traits, elytron length (EL) and lantern area (LA), against an indicator of body size, pronotal width, revealed contrasting morphometric patterns (Fig. 2). *Photinus pyralis* had a RMA slope significantly greater than one, while the sympatric congener *P. macdermotti*, had an isometric slope not differing significantly from one for EL (Fig. 2; Table 1). In contrast, the RMA regression of lantern
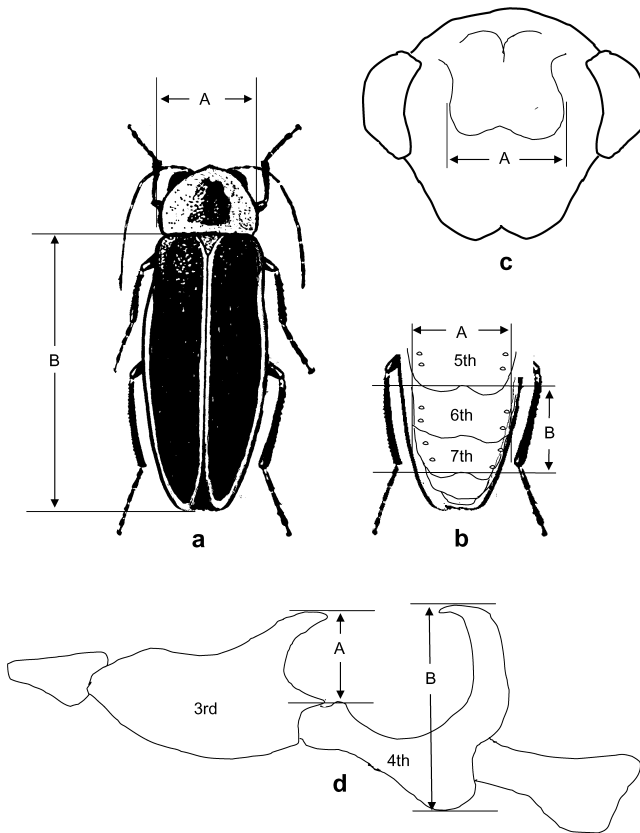
FIG. 1. Male character dimensions measured in mm. a) pronotal width (A) measured at the widest point near the base, and left elytron length (B), measured from humerus to apex in fireflies; b) ventral view of firefly lantern showing measured width (A), and length (B) dimensions of the 6th and 7th sternites. The length and width of the 7th sternite in *Lucidota punctata* was measured since it lacks an adult lantern; c) frontal plate width dimension (A), measured in *Cerotoma salvini*, and; d) measurements taken of the 3rd antennal segment's aperture width (A), and of the thumb width (B), of the 4th antennal segment in *C. salvini*.
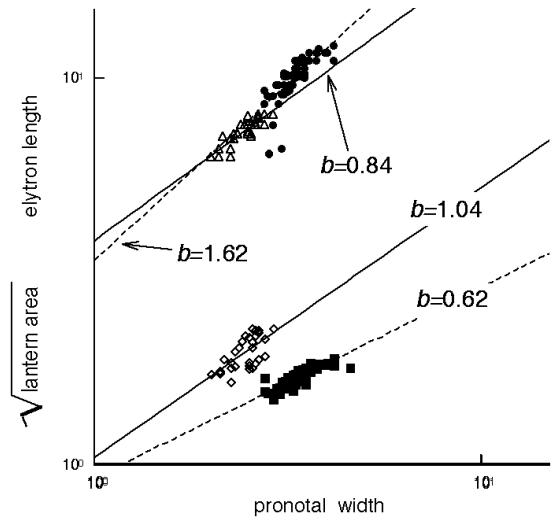

FIG. 2. Log x log scatter plots and RMA regression slopes of elytral lengths (top), and the square root of lantern areas (bottom), for *Photinus pyralis* (filled symbols, dashed lines), and for *P. macdermotti* (open symbols, solid lines), against a general indicator of body size, the pronotal widths of the respective species.

20%, similar to other traits used as weapons or as visual advertisements (Pomiankowksi and Møller, 1995).

DISCUSSION

The very evident morphological variation in male *P. pyralis* fireflies led me to question whether or not size was predictive of mating success, especially where courtship is elaborate and mate competition intense (Vencl and Carlson, 1998). Because detectable between-male variation is a prerequisite for female choice (West-Eberhard, 1983), I was particularly interested to know if male trait size, particularly wing length and lantern area, exhibited positive allometry like many other sexually selected display characters and weapons.

Results of a previous study showed that competition for mates is intense in *P. pyralis* (Vencl and Carlson, 1998). This is because *P. pyralis* females appear to be choosy. More than half of the courtships observed (n = 65) involved more than one male (mean = 3.6 males/courtship). As competition increased, so did the cost of success: courtships not only took longer, but the time spent "mate-guarding" also increased. The high courtship failure rate (~25%), even after dialoging, also suggests females are choosy. Three indices of flash behavior further support this view. Males without rivals produced as many dialogs as did successful males in multi-male competitions. Second, the dialog-failure rate (*e.g.,* number of flashes failing to elicit female replies) was as high for solo males (34%) as it was for successful males with rivals (39%). Third, females were often seen to address their responses alternately to different males. Females thus appear to require some minimum amount of flash information before accepting a particular male. The ultimate consequence of these female behaviors is that "love

area (LA) on pronotal width for *P. pyralis* was significantly negative, while that of *P. macdermotti* was again isometric (Fig. 2; Table 1).

As with *P. macdermotti*, *Lucidota punctata* had isometric allometric values for all structures measured, while the leaf beetle, *Cerotoma salvini* showed a negative allometry for EL (Table 1). All fireflies showed isometry for aedeagus length, while that for the leaf beetle had a negative RMA regression slope (Table 1). The antennal clamp of structure formed from the 3rd and 4th antennal segments of the leaf beetle, *C. salvini*, had isometric slopes. In contrast, the frontal plate structure had a strongly positive allometric slope (Table 1).

The coefficient of variation, CV, one possible indicator of sexual selection, was calculated for all of the structures measured in the four beetle species (Table 1). The CVs for all structures, with the exception of *C. salvini's* frontal plate, were low, not exceeding 11%. The frontal plate had a high CV, in the range of

TABLE 1. *Comparison of male morphometric relationships among three species of sympatric fireflies with luminescent, and non-luminescent courtships, and a non-luminescent leaf beetle with a tactile courtship.*

Species	N	Male trait	Mean[a]	sd[b]	CV[c]	95% L_1[d]	β RMA[e]	95% L_2[d]	$h_o = \beta = 1$[f]
Photinus pyralis	31	pronotum	3.26	0.24	7.4				
		elytron length	9.85	1.09	11.1	1.19	1.62	2.05	(+)[g]
		√ lantern area[h]	2.69	0.24	9.13	0.50	0.62	0.74	(−)
		aedeagus length	1.32	0.10	7.45	0.65	1.02	1.385	(=)
P. macdermotti	31	pronotum	2.45	0.22	9.17				
		elytron length	7.21	0.55	7.69	0.68	0.84	1.00	(=)
		√ lantern area[h]	1.96	0.19	9.80	0.74	1.04	1.35	(=)
		aedeagus length	1.85	0.10	5.86	0.61	0.99	1.37	(=)
Lucidota punctata	33	pronotum	3.30	0.15	4.62				
		elytron length	8.37	0.46	5.52	0.46	0.83	1.20	(=)
		√7th segment[i]	1.07	0.09	8.00	0.92	1.40	1.90	(=)
		aedeagus length	1.98	0.08	4.34	0.63	1.00	1.37	(=)
Cerotoma salvini	44	pronotum	1.68	0.17	10.4				
		elytron length	3.65	0.27	7.62	0.51	0.70	0.88	(−)
		ant clamp 3rd seg	0.20	0.02	14.2	0.87	1.20	1.53	(=)
		ant clamp 4th seg	0.30	0.03	10.2	1.29	0.98	0.68	(=)
		frontal plate	0.63	0.10	16.0	1.01	1.41	1.81	(+)
		aedeagus length	1.77	0.13	7.67	0.52	0.72	0.91	(−)

[a] mean in mm; [b] sd is the standard deviation; [c] CV is the coefficient of phenotypic variance, calculated as sd/mean × 100; [d] 95% intervals, L_1 and L_2, is RMA β ± critical value of t × standard error of the mean; [e] the slope, β, of the reduced major axis regression line; [f] null hypothesis is that 95% confidence intervals of RMA embrace isometric slope of 1; [g] (+) = RMA slope significantly > 1; [h] square root of lantern area; [i] square root of 7th non-luminescent abdominal segment.

knots" frequently develop around such fickle females and provide a potentially strong selective setting for competition to shape not only flash behavior itself, but perhaps morphological traits that affect the outcome of courtships.

Among *P. pyralis* males, not only is there an extremely wide range in body sizes, there are size-dependent consequences for the outcome of courtships (Vencl and Carlson, 1998). The comparison of allometric values—the reduced major axis regressions of log transformed traits against body size—for elytral length (EL) and lantern area (LA) in the two congeneric and a non-luminescent sympatric firefly revealed striking differences.

Elytron length

Photinus pyralis, with its more intensely competitive scramble courtships and long patrolling flights, exhibits positive wing allometry, while the sympatric co-gener, *P. macdermotti*, with its less competitive courtship, has wing length isometry. Previous findings indicate that when competition for a female exceeds three males, smaller males tend to win in the ensuing scramble after males have landed and try to reach the female on the ground (Vencl and Carlson, 1998). Landing commits a male to a sub-optimal situation for the most effective use of line-of-sight, flashed signals within the complex three-dimensional configuration of vegetation and vagaries of lantern orientation. Results of a simulated scramble competition, where smaller males had greater mobility, support the field observations (Vencl and Carlson, 1998). Longer wing length may relate to greater aerodynamic performance that

would be advantageous during long patrolling flights to find rare, receptive conspecific females in *P. pyralis*.

If overall larger size and lower ground agility is disadvantages in scramble courtships, EL allometry should be isometric or negative. A trade-off might exist that favors maximal locomotor ability on the ground. That there appears to be directional selection favoring larger, rather than smaller males is not surprising since the nearly half of the observed courtships involve fewer than two males (Vencl and Carlson, 1998).

Lantern area

The primary function of the lantern organ is to broadcast signals that locate receptive females. Males with relatively larger lanterns should be favored by selection in situations where searching alone is the only event prior to mating. Since light intensity decreases as the square of distance, and, assuming that lantern size is proportional to potential maximum output, a larger lantern would be an obvious advantage because of its increased effective range (Otte, 1974; Vencl and Carlson, 1998). The RMA slope for lantern area (LA) differed significantly among the three firefly species. *Photinus pyralis* had a negative allometry for LA. This was surprising since it was predicted that sexual selection by female choice would favor greater broadcast range during all phases of the courtship protocol. Intensity, which halves over twice the distance, has never been examined precisely. However, Vencl and Carlson (1998) demonstrated both a flash precedence effect and a flash intensity effect under laboratory conditions wherein *P. pyralis* females responded

more often to flashes arriving slightly sooner than the average response. But this effect was cancelled if the intensity of the later arriving flash was increased.

It could well be that the lantern organ, one of the most elegant structures in Nature, may be very costly to make relatively larger, due to its complexity. A cost-for-size trade-off may constrain lantern size in species with patrolling courtship and also a scramble competition. In *P. pyralis*, the negative allometry may indicate the countervailing selection of the scramble; wherein smaller males gain a speed advantage over larger males once courtship commences on the ground. Further, if the effective courtship arena for a female is no larger than a meter in circumference, as it is in *P. pyralis*, a larger lantern, with its greater output, is less of an advantage, even in protocols with long distance patrolling flights that rely solely on distanced, visual communication (Vencl and Carlson, 1998).

Aedeagus, clamp, and frontal plate morphometrics

The aedeagal RMA regressions for each species exhibited isometry, or in the case of *C. salvini*, very weak negative allometry. Aedeagal RMA slopes were lower than those of other body parts examined and lower than expected for display characters thought to be under sexual selection. However, these low values agree with those found in an earlier study of a wide variety of insects and spiders (Eberhard *et al.*, 1998). In contrast to visual displays, female confirmation has been suggested to play a greater role in determining the overall size of male genitalia wherein tactile stimuli and proper alignment may favor intermediate sizes in the absence of strict size-positive assortative mating. These findings do not support earlier ideas about male-female conflicts of interest in courtship and the evolution of larger male traits (Lloyd, 1979). Moreover, other, non-sexual selection hypotheses could explain the allometric values observed here. For instance, isometries are expected if proper alignment between male and female during copulation serves as an isolating mechanism. Although predicted by it, the isometric values seen here do not necessarily support a "lock-and-key," species isolation explanation. The exact significance of these data must await a precise understanding of the female counterpart to the aedeagus, the spermatheca and its duct, and whether or not they are rigid, exclusionary structures.

The evolution of male morphometrics under sexual selection

Allometry in trait size is evident only in the courtship protocols with separate search and scramble selective episodes. Size effects are not confounded when the two courtship episodes are considered together. If elytral length and lantern area are correlated, it is conceivable that selection acts directly on one trait and indirectly on the other. However, behavioral observations suggest that EL and LA are alternately targets of selection. If males with relatively long elytra and large lanterns are favored only in the searching phase, while males with relatively shorter elytra and smaller lanterns are favored in scrambling part of the courtship, then the respective RMA slopes should have opposing signs indicative of such disruptive selective pressures. In fact, significant disruptive selection was detected acting on these traits in *P. pyralis*. The RMA for both EL and LA were both significantly different from one, and, opposite in sign. Furthermore, there should be no selection favoring small elytra in a species lacking scramble competition and its RMA for LA should be low due to normalizing selection. To test this hypothesis, I compared a common, sympatric congener lacking scramble competition, *P. macdermotti*, with *P. pyralis*. My hypothesis would be rejected if no significant differences in the slopes of LA or EL existed between the two species. Not only was the non-scrambling species significantly smaller in both traits, the RMA regressions were not significantly different from one.

The evolution of male morphology under sexual selection appears to follow very different trajectories depending on whether the structures are involved in contact/tactile versus visual modes of courtship. In this study, male traits under tactile/contact sexual selection tended to have similar coefficients of phenotypic variation compared to other, housekeeping body parts of the same species. Sexual selection is expected to be stabilizing, and to ultimately exhaust phenotypic variation in sexual traits (Kirkpatrick and Ryan, 1991). However, in Pomiankowski and Møller's (1995) survey, CVs above 20% were common for sexually selected characters while those of non-sexually selected characters averaged near 8%. These authors argue that sexual selection favors modifiers that reduce the degree of developmental control on quantitative traits with result that they might be expected to have higher, rather than lower CVs. The degree of phenotypic variation is critically important since differences between males must be discernable by females if sexual selection by female choice can operate to produce exaggerated male ornaments or displays (West-Eberhard, 1983).

With the notable exception of *P. pyralis* morphology, clamps, wings, aedeagi, and lanterns of the other beetles lacked significant departures from isometry. The isometric RMA slopes observed in these data for species without scramble competitions support the idea that sexual selection on the short time scale measure by this type of sampling may be normalizing for most traits not directly involved in visual displays. For example, Eberhard *et al.* (1998) observed negative linear regression slopes for aedeagal morphology when they examined what they believed to be species engaging in contact/tactile courtship under the influence of cryptic female choice. Here too, isometric or negative allometry was also observed in the non-visual, close-range contact/fit antennal clamp mating system of *Cerotoma*. Allometric values predicted to be greater than one would indicate male-female conflict if the outcomes of courtships were decided by mere force (Al-

exander *et al.*, 1977; Lloyd, 1979). In contrast many other structures not involved in courtship per se show allometric values at or just below one (Harvey and Pagel, 1991). As pointed out by Eberhard *et al.* (1998), the intricacies of male-female genitalic coupling via mechanical fit may impose selective constraints limiting the enlargement of male morphologies. Selection imposed by alignment with female structures may even force the corresponding male morphology to lower allometric values when compared to other sexually selected, long-distance visual characters, if tactile surface area is maximized.

Additional support for the existence of different modality-dependant types of sexually selected allometries is provided by the leaf beetle antennal clamp structure. The same pattern seen in aedeagal isometry occurs in the clamp, a non-intromittive, non-visual, contact coupling mechanism involving precise alignment between male and female structures.

In contrast to clamps and aedeagi, *C. salvini's* frontal plate showed strongly positive allometry and a high CV. Although the exact function of the plate remains unknown, these measurements constitute evidence that sexual selection has shaped plate morphology, perhaps via combinatorial selective influences like those operating on crab claws, or deer antlers (Andersson, 1994).

Photic interactions in *P. pyralis* fireflies implicate the firefly lantern as a sexually selected implement for inter-male competition. This last point is important because I believe that flash communication in this species serves not only to bring conspecifics together; it also—and primarily—functions in the arena of male competitive display before discriminating females. When compared to related species, a functional shift occurred in *P. pyralis*: male morphology may well have evolved first in the context of mate localization and recognition, and later, in the context of competition and within the limits of the sensory preferences of selective females. The morphometric patterns and female biases described here and in other studies are in accord with the idea that inter-male competition and female choice are important proximate forces that have led to the evolution of both high, and low male allometric relationships and to competitive flash behavior in the unique intense courtship protocol of *P. pyralis*.

Given sufficient morphological variation, directional selection acting on multiple traits like body size, lantern size and wing length, must lead to an increase in fitness in the context of mate competition. However, constraints and trade-offs, like those observed in the two-phased courtship of *P. pyralis* fireflies in present study, may limit the allometric, linear effects of sexual selection on trait evolution. Constraints and trade-offs were anticipated by other workers concerned with multi-trait, selective interactions (Arnold, 1983; Deinert *et al.*, 1994; Ghalambor *et al.*, 2003). In the limit, if we want to better understand the mechanisms of sexual selection that shape the relationships between performance, fitness, and the evolution of exaggerated display traits, more studies are needed that measure whole-organism performance in the field.

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