

## UNPREDICTABLE OFFSPRING SURVIVORSHIP IN THE DAMSELFLY, *MEGALOPREPUS COERULATUS*, SHAPES PARENTAL BEHAVIOR, CONSTRAINS SEXUAL SELECTION, AND CHALLENGES TRADITIONAL FITNESS ESTIMATES

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**Abstract.**—Evolutionary biologists typically assume that the number of eggs fertilized or developing embryos produced is correlated with an individual's fitness. Using microsatellite markers, we document for the first time estimates of realized fitness quantified as the number of offspring surviving to adulthood in an insect under field conditions. In a territorial damselfly whose males defend tree hole oviposition sites, patterns of offspring survivorship could not be anticipated by adults. Fewer than half of the parents contributing eggs to a larval habitat realized any reproductive success from their investment. The best fitness correlate was the span over which eggs in a clutch hatched. Among parents, female fecundity and male fertilization success were poor predictors of realized fitness. Although body size was correlated with female clutch size and male mating success, larger parents did not realize greater fitness than smaller ones. The uncoupling of traditional fitness surrogates from realized fitness provides strong empirical evidence that selection at the larval stage constrains selection on mated adults.

**Key words.**—Fitness, hatching asynchrony, larval survivorship, Odonata, selection.

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Many reproductive traits are thought to be shaped by sexual selection, resulting from variation among individuals in mating or fertilization success (Thornhill and Alcock 1983; Waage 1984; Clutton-Brock 1988; Andersson 1994). Evolutionary explanations for such traits depend on estimates of fitness, the precision of which determines the validity of selection models. For example, a male's fitness is typically thought to depend primarily upon the number of mates he obtains (sexual selection), fecundity of his mates whose eggs he fertilizes, and his life span (i.e., two components of natural selection) (e.g., Arnold and Wade 1984; Fincke 1988). Often, body size is viewed as the target of strong natural and/or sexual selection because it is commonly correlated with female clutch size or the number of mates or fertilizations that a male obtains (e.g., Howard 1988; Partridge 1988; Fincke 1992a; Andersson 1994; Choe 1994; Alcock and Houston 1996; Olsson and Shine 1996).

Nevertheless, such conclusions about the relative strength of selective episodes and their effect on the evolution of specific traits remain premature for most species. This is because fitness of adults in natural conditions, particularly for animals lacking parental care, has been measured only indirectly, in terms of mating or fertilization success, or the number of eggs laid (e.g., Fincke 1986; Conner 1989; Moore 1990; McLain 1991; Barrowclough and Rockwell 1993; Hadrys and Siva-Jothy 1994). Whether these traditional fitness surrogates are proportional to the number of surviving offspring a parent produces is typically unknown, due to the difficulty of following the fate of an individual's offspring after its eggs have hatched.

The Neotropical damselfly, *Megaloprepus coerulatus* (Odonata: Pseudostigmatidae) offers a rare opportunity to follow under field conditions the fate of a parent's offspring from the egg stage to emergence as adult insects. Females mate and oviposit exclusively at water-filled tree holes, which

are limiting reproductive resources for several sympatric odonate species (Fincke 1992b). Male *M. coerulatus*, the larger sex, defend large holes in light gaps that are usually created when a tree falls and depressions in its trunk fill with rainwater. Sexual selection favors large males, which are more successful than smaller ones in defending tree holes and consequently, in obtaining mates. A male requires a female to mate with him before permitting her to lay eggs in the hole he defends. The longer a male defends a site, the more fertilizations he obtains (Fincke 1992a). As is typical of odonates (Waage 1984, 1986; Fincke 1984a; Hadrys et al. 1993), the last male *M. coerulatus* to mate with a female before she oviposits fertilizes all the eggs in her clutch (H. Hadrys, T. Gerken, and O. Fincke, unpubl. data).

During the eight to nine month breeding season at our study site in Panama, a large defended tree hole may be colonized by the offspring of more than a dozen territorial males and twice as many females, with a single female laying up to several hundred eggs in a hole. However, larval cannibalism reduces the density to about one final instar per 1–2 liter of water. Before dying up, even large tree holes rarely produce more than 15 emerging adult *M. coerulatus* annually (Fincke 1992a, 1994, 1998). Females also lay in small, undefended holes in forest understory, but holes smaller than one liter rarely produce more than a single adult (Fincke 1992a, 1998) and account for less than 10% of the yearly *Megaloprepus* adult recruitment. *Megaloprepus coerulatus* larvae do not survive in dry tree holes. Adults aestivate during late dry season and females begin ovipositing again about 1–2 months after the first tree hole filling rains of wet season (Fincke 1984b, 1992b).

Here, we developed microsatellite markers to answer three major questions: (1) Within a tree hole, is there a predictable pattern of offspring survivorship to which parents can cue? (2) Do most parents realize at least some fitness from the

larval habitat they use? (3) Among mated individuals, which traits best predict parental fitness?

#### MATERIALS AND METHODS

The work was conducted in 1994–1997 on Barro Colorado Island, Panama (hereafter, BCI), where the population dynamics of *Megaloprepus coerulatus* and the interactions of this species with other tree hole predators have been studied extensively (Fincke 1992a,b, 1994, 1998, 1999). The island's lowland moist forest experiences a dry season from December to April (for detailed site description, see Leigh 1999). Typically, tree holes dry up completely by late March and refill by late May each year.

##### *Natural Territory Tenure Duration and Tree Hole Use by Marked Adults*

For each of three years, we monitored 5–18 defended sites in the mature forest of the island's central plateau, noting the presence of marked adults. Male territories at tree-fall gaps were checked multiple times per day and multiple times per week over the course of the wet season. We marked adults by writing a number on the wing with an indelible marker. With forceps, we removed a single middle tibia for later DNA analysis. Adults occasionally lose tibia naturally; our procedure did not affect a male's mating ability nor his territory tenure. Forewing length was measured as a correlate of body size. In sexually mature individuals, hind-wing length is significantly correlated with abdomen length ( $r = 0.98$ ,  $P = 0.001$ ,  $n = 12$  males;  $r = 0.89$ ,  $P = 0.02$ ,  $n = 6$  females) and wet weight ( $r = 0.96$ ,  $P = 0.0001$ ,  $n = 12$  males;  $r = 0.86$ ,  $P = 0.03$ ,  $n = 6$  females). Relative age was scored on a scale of 1–3. Young individuals (age 1) had a fresh appearance and iridescent wings. Old individuals (age 3) had dull wings with signs of wear, pruniose (whitish) abdomens, and often had algae on the thorax or wings. Individuals between these two extremes were scored as age 2. Unless otherwise noted, data refer to sexually mature individuals.

A territorial male was one that was known to defend at least one site for three or more consecutive days. Males may leave a territory voluntarily or because they are displaced after an agonistic encounter, usually with a larger or similar-sized male (Fincke 1992a). When no such encounters were noted before a male left a site, he was credited with leaving voluntarily if no other males were known to defend the site within two days from the last time he was seen on the territory.

##### *Determining Patterns of Larval Survivorship*

In 1994 and 1995, we measured the fitness of 48 unique mated pairs by following the fate of all of their offspring in one of six identical, large larval habitats with abundant nutrient input from which other major predators were excluded (i.e., the best case scenario for offspring survivorship). The pairs represented a subset of 36 territorial males and their 48 mates from the above field study. After mating with a marked territorial male, a female was caught and a tibia was removed for later analysis. She was then placed in a small, screened oviposition cage supplied with moistened filter paper. Most

females began egg laying within 10 min. They were left undisturbed in the containers until later that same afternoon or the next morning, when they were released. The eggs are large (circa 1.5 mm in length) and easy to count accurately. Within a day of being laid, eggs were counted and a clutch was assigned to an artificial hole. Starting in September 1994 a total of six such clutches, laid at roughly two-week intervals (i.e., the median time it took for a male to encounter a female at a territory), were added to each of three artificial tree holes. These holes simulated the case of new larval habitats created by tree falls in mid-wet season. To minimize possible ambiguity in parentage determination of the surviving offspring, clutches from different females that were sired by the same territorial male were distributed among the holes.

Under natural conditions *M. coerulatus* insert eggs into bark just above the water line. In the experimental holes, the filter paper containing the clutch was placed on a piece of bark with the end of the paper touching the water so eggs remained moist. One such clutch was attacked by mold before any eggs could have hatched and consequently was excluded from analysis. To quantify the number of newly hatched larvae ("neonates") actually entering the holes, in 1995 we modified the above procedure to include a measure of hatching success. Then, each clutch was kept separately, submerged in water in a 400 ml plastic jar. The jars were held in an outdoor insectary, sheltered from rain and direct sun, where they experienced ambient temperature and photoperiod. The minimum time for egg hatch is 14 days. After two weeks, each clutch was checked daily for neonates, which were deposited into their assigned hole. In 1995, starting in mid-July, each of three artificial holes received all neonates from each of 10 clutches laid at roughly two-week intervals over most of the wet season. These holes simulated natural larval habitats that fill with water in the beginning of wet season; the last egg inputs were in late December. Egg input was at the same approximate rate, but over a longer time span than in 1994, with each hole receiving about twice the total eggs as in the previous year (Table 1). As the dry season progressed, holes were topped off with water periodically to prevent any mortality due to hole drying.

The artificial larval habitats were made of nine-liter plastic tubs containing two liters of loosely packed fallen leaves, all collected from the same area, and a large piece of bark that provided a perch site for ovipositing prey species (primarily mosquitos). These artificial holes were larger by volume than 90% of the natural tree holes on BCI (Fincke 1992b). Artificial holes such as these are colonized by the same array of prey species as the natural tree holes (Fincke et al. 1997). The tubs were positioned in one of two shaded sites at the edge of forest clearings and covered with chicken wire enclosures to permit the passage of prey species while preventing oviposition by predatory odonates or frogs. Predatory larvae of *Toxorhynchites theobaldi* mosquitoes could not be excluded but were removed when detected during a census. Final instar *Toxorhynchites* are able to kill small odonate larvae (i.e., <7 mm, Fincke 1999). Control tubs lacking *M. coerulatus* larvae were used to estimate prey abundance. The abundance of mosquito larvae prey was kept consistent with bimonthly additions of 0.5 g yeast after day 170 (necessary because the enclosure prevented the natural input of detritus).

TABLE 1. Mean (and range) of egg input, larval characteristics, hole productivity, and adult success in the larval habitats ( $n = 3$  each year). In 1994, egg input was spaced over a 12-week span, whereas in 1995, egg input was spaced over a 20-week span. \*  $P < 0.05$ ,  $t$ -tests.

	1994	1995
Total clutches/hole	5.6 ± 0.3 (5–6)	10 ± 0 (10)*
Total eggs/hole	304 ± 42 (250–386)	776 ± 98 (651–969)*
Windows/hole	2.0 (2)	3.7 ± 0.3 (3–4)*
Final instars/hole	6.0 ± 0.6 (5–7)	8.0 ± 1.5 (6–11)
Maximum estimated time to emergence (days)	143.8 ± 8.6 (85–215)	161.7 ± 7.8 (109–236)
Final instar size (mm)	29.06 ± 0.5 (27–34)	29.1 ± 0.4 (26.5–33.0)
Proportion of females successful	0.41 ± 0.05 (0.33–0.50)	0.47 ± 0.06 (0.4–0.6)
Offspring/successful female	2.7 ± 0.4 (2.0–3.5)	1.7 ± 0.1 (1.50–1.75)*

At bimonthly intervals, the contents of the holes were censused and all *M. coeruleus* larvae 6 mm or more in size were measured from the head to the end of the final abdominal segment (excluding the leaflike caudal lamellae used in respiration). When their wing pads became swollen, indicative that feeding had ceased and emergence was imminent, final instar larvae were collected. They were permitted to emerge in an insectary, after which a leg was collected. Adults were marked and released. Maximum developmental time was the time span between the day the clutch was laid and the day the surviving offspring emerged. After the last final instar was removed, a hole was checked weekly for two to three weeks to insure that no other larvae were still present. Throughout, means are reported with ± SE. A Pearson correlation is indicated by  $r$ ; a Spearman rank correlation by  $r_s$ . When  $P$ -values fall between 0.05 and 0.3, the power ( $1 - \beta$ ) of a statistical test is also reported.

#### Identification of Parents and Their Surviving Offspring

Of the individuals monitored during the field study of 1994–1995, a total of 200 individuals were genetically characterized by PCR typing. These included the individuals of the above-mentioned 48 mated pairs, all 42 of their surviving offspring, and eight “test” families (parents and single larvae) of known pedigree. The latter were used to demonstrate that paternity could be correctly assigned using the four microsatellite loci. Also typed were 50 unrelated individuals, which served as an exclusion control for the paternity assignment and were used to estimate genotypic and allelic diversity (H. Hadryis, W. Schroth, B. Streit, and O. Fincke, unpubl. ms.).

Total genomic DNA was isolated according to standard procedures (Hadryis et al. 1992). Microsatellite loci were detected and isolated using the RAMS method (Randomly Amplified Microsatellites; Ender et al. 1996; Siva-Jothy and Hadryis 1998). A total of 45 different RAPD profiles from three unrelated individuals (average of 10–15 RAPD fragments/profile) were blotted onto nylon membrane (Boehringer, Roche Diagnostics, Mannheim, Germany) and checked for hybridization signals with the digoxigenin-labelled oligonucleotides (GA)<sub>10</sub>, (GT)<sub>10</sub>, and (AAT)<sub>9</sub> (see Ender et al. for details). Positive DNA fragments (i.e. RAPD fragments that gave a hybridization signal for any one of the labeled oligonucleotide sequences) were gel purified, cloned and sequenced, each for three unrelated individuals. This way it was possible to isolate not only the sequences but also to detect allelic polymorphisms of the microsatellite sequences.

For use in PCR typing, four microsatellite loci were chosen that had revealed a high allelic and genotypic diversity. Primers were designed from conserved flanking regions designed to amplify between 150 and 250bp of PCR products (For primer sequences and complete microsatellite sequences see: <http://www.rz.unifrankfurt.de/~hadryis/microsat.html>). The observed heterozygosity values for the four loci were: MeAB3/11 = 0.75; MeM12/15 = 0.89; MeAB3/16 = 0.93 and MeAB5/19 = 0.72 (H. Hadryis, W. Schroth, B. Streit, and O. Fincke, unpubl. ms.).

The genetic characterization of all 200 individuals revealed a total of 42 different alleles, the distribution of which permitted paternity and maternity assignment for all but two offspring. Parentage of the latter was resolved using date of oviposition and estimated developmental rate.

#### Determination of Adult Fitness

The fitness that a female gained from laying a clutch in a given hole was simply the number of her offspring that emerged as adults. Our experiment was designed to detect any predictable patterns of offspring survivorship rather than to measure variation in male fitness resulting from differences among males in territory tenure at a given hole. Thus, here we use the data on offspring survivorship to compare the fitness of two male tactics: (1) males that stay at a site only long enough to get a single mating, and (2) males that stay 60 days, the maximum observed tenure duration in the field study. The fitness of a male staying only long enough to obtain a single mating would depend only on his ability to fertilize his mate's clutch. Thus, the fitness of tactic 1 was calculated as the mean number of surviving offspring from each of the 47 clutches in the experimental holes. The fitness of a male staying the maximum tenure duration would vary, depending on when the male began defending the hole. For convenience, we calculated the fitness of hypothetical males beginning their tenure at 10-day intervals from each other (about the average time a male spent at a site). For example, a male playing tactic 2 that arrives on day 1 would sire all offspring from the clutches laid between days 1–60. Thereafter, fitness was calculated for hypothetical males arriving at 10-day intervals and staying a total of 60 days (i.e., the second male stays from day 20–80, the third male from day 30–90, etc.). The last male would be the one whose 60-day tenure includes the final clutch. Reiterating this calculation for each of the six holes resulted in 51 hypothetical males, whose mean fitness was compared with the above 47 males playing tactic 1. Estimated male lifetime fitness, based on

the field data on tenure duration, male life span, female encounter rate, and larval growth and survivorship is presented elsewhere (O. Fincke, O. Eikemeier, and H. Hadrys, unpubl. ms.).

#### *Hatching Asynchrony over a Reproductive Season*

Hatching span, independent of clutch size, was found to be the best predictor of fitness that females realized from our experimental holes. We monitored egg hatching in a larger sample of 111 clutches, each laid by a different female during the wet seasons of 1995–1997, to confirm that the span over which eggs hatched was not correlated with clutch size and to determine possible seasonal effects on hatching patterns. In each year, study day 1 was standardized to May 1, about two weeks after the first tree hole-filling rains of wet season, and before most *M. coerulatus* start to oviposit (Fincke 1992b). A female was collected at a defended site before she began laying eggs in a hole. After her clutch was collected in a monolayer of filter paper, it was kept submerged in a separate jar under ambient conditions as described above. Two weeks after it was laid, and up to 60 days thereafter, the clutch was checked daily and any neonates were removed. Thereafter, it was checked at least once every five days, until all the eggs had hatched or until 150 days after the first hatch, whichever came first. After 150 days, any clutch that still contained unhatched eggs was checked at haphazard intervals; any larvae found were assigned a hatch date midway between the day of the previous check and the day of detection.

## RESULTS

### *Patterns of Offspring Survivorship*

The average size of the clutches used in the larval survivorship experiment was  $68.9 \pm 7.1$  eggs (range 8–214). Density of final instars in the experimental holes (Table 1) were within the ranges noted for similar-sized natural tree holes at territories frequented by ovipositing females throughout the wet season (Fincke 1992a, 1998). On 80% of the censuses, the density of mosquito prey available (as measured in controls) ranged from moderate to high (i.e., 50–150 mosquitoes/census). For 28% of the surviving larvae, even the maximum estimated time from egg to emergence as an adult was less than 130 days, as fast as the minimum rate known (Fincke 1992a). The only evidence of colonization by other odonates were three small *Mecistogaster* larvae removed from a control hole after the piece of bark was mistakenly left in contact with the screening, and a *Triacanthagyna dentata* dragonfly larva found in hole 5 at the end of the experiment.

Among the six larval habitats, periods favorable to offspring survivorship varied considerably, despite the standardized timing of egg input (Fig. 1). The only consistent pattern of *M. coerulatus* survivorship was that the first clutch laid, regardless of its size, always produced at least one surviving offspring (range, 1–5 offspring). Subsequently, survivorship was less predictable. Females that produced the next surviving offspring laid a clutch as few as 15 days and as many as 78 days after the first female.

The first larva entering a hole enjoyed a preemptive ad-

vantage. Larger individuals ate and killed smaller conspecifics, evidenced by an occasional larval body part found during a census (see also Fincke 1994, 1996). Cannibalism reduced larval density within a hole to less than seven larvae ( $\geq 6$  mm) on any given census. Multiple, small larvae were found only shortly before final instars emerged, or when the largest larva(e) present was 15 mm or smaller. The *M. coerulatus* that survived to emergence were thus a subset of those hatching during a “window of opportunity,” either when no large larvae were present, or shortly before larger larvae emerged (Fig. 1). The presence of a favorable window depended on larval growth rates coupled with the timing of egg hatch in clutches laid previously and subsequently to a female’s own. In 1994, when clutches were deposited over a 12-week span, holes experienced fewer such windows than in 1995, when egg input was over a 20-week span (Table 1). Using data from only the first six clutches in each hole (i.e., controlling for between-year differences in the time span of egg input), the number of final instars produced was not correlated with the number of eggs a hole received ( $r_s = -0.40$ ,  $P = 0.42$ ,  $n = 6$  holes). Mean productivity of the holes, measured as the number of adults produced per day over which holes were occupied, was nearly identical between years, ( $0.030 \pm 0.00$  vs.  $0.027 \pm 0.00$ , 1994 and 1995 respectively,  $t = 0.47$ ,  $P = 0.66$ ).

### *Female Fitness and Phenotypic Predictors of Fitness*

On average, fewer than half of the pairs that contributed eggs to a hole produced any surviving offspring (Table 1). Survivorship of eggs in a clutch varied from 0 to 0.25 ( $\bar{x} = 0.02 \pm 0.06$ ,  $n = 47$  clutches, excluding the one attacked by mold). Of offspring known to hatch, survivorship varied from 0 to 0.33 ( $\bar{x} = 0.03 \pm 0.01$ ,  $n = 30$  females). Successful and unsuccessful females did not differ significantly in the hatching success of their clutch ( $t = 0.42$ ,  $n = 47$ ,  $P = 0.67$ ), time to first hatch, clutch size, or the number of neonates produced (Fig. 2a–c).

Even though larger females produced larger egg clutches (Fig. 3), the number of surviving offspring was not a function of a female’s body size ( $r = 0.03$ ,  $n = 47$ ,  $P = 0.86$ ) or that of her mate ( $r = -0.03$ ,  $n = 41$ ,  $P = 0.86$ ). Indeed, reproductive success was not correlated significantly with the number of eggs a female laid ( $r = 0.20$ ,  $n = 47$ ,  $P = 0.17$ ,  $1 - \beta = 0.39$ ), or with the number of eggs that actually hatched (Fig. 4a). Even amongst females that produced at least one surviving offspring, increasing clutch size was not correlated with the number of surviving offspring ( $r_s = 0.04$ ,  $n = 21$ ,  $P = 0.86$ ). Rather, the best predictor of female reproductive success was the span between hatching of the first and last egg in a clutch (range = 4–84 days; Fig. 4b). The hatch span of successful clutches was about 1.5 times longer than unsuccessful ones (Fig. 2d). Hatching span was not a function of clutch size ( $r = 0.24$ ,  $n = 30$ ,  $P = 0.20$ ,  $1 - \beta = 0.37$ ) in this experiment, nor in a larger sample described below. However, the time required for the first egg in a clutch to hatch was negatively correlated with clutch size ( $r = -0.36$ ,  $n = 30$ ,  $P = 0.05$ ).

The first clutch to be laid in a hole, even one as small as eight eggs, always produced some surviving offspring due

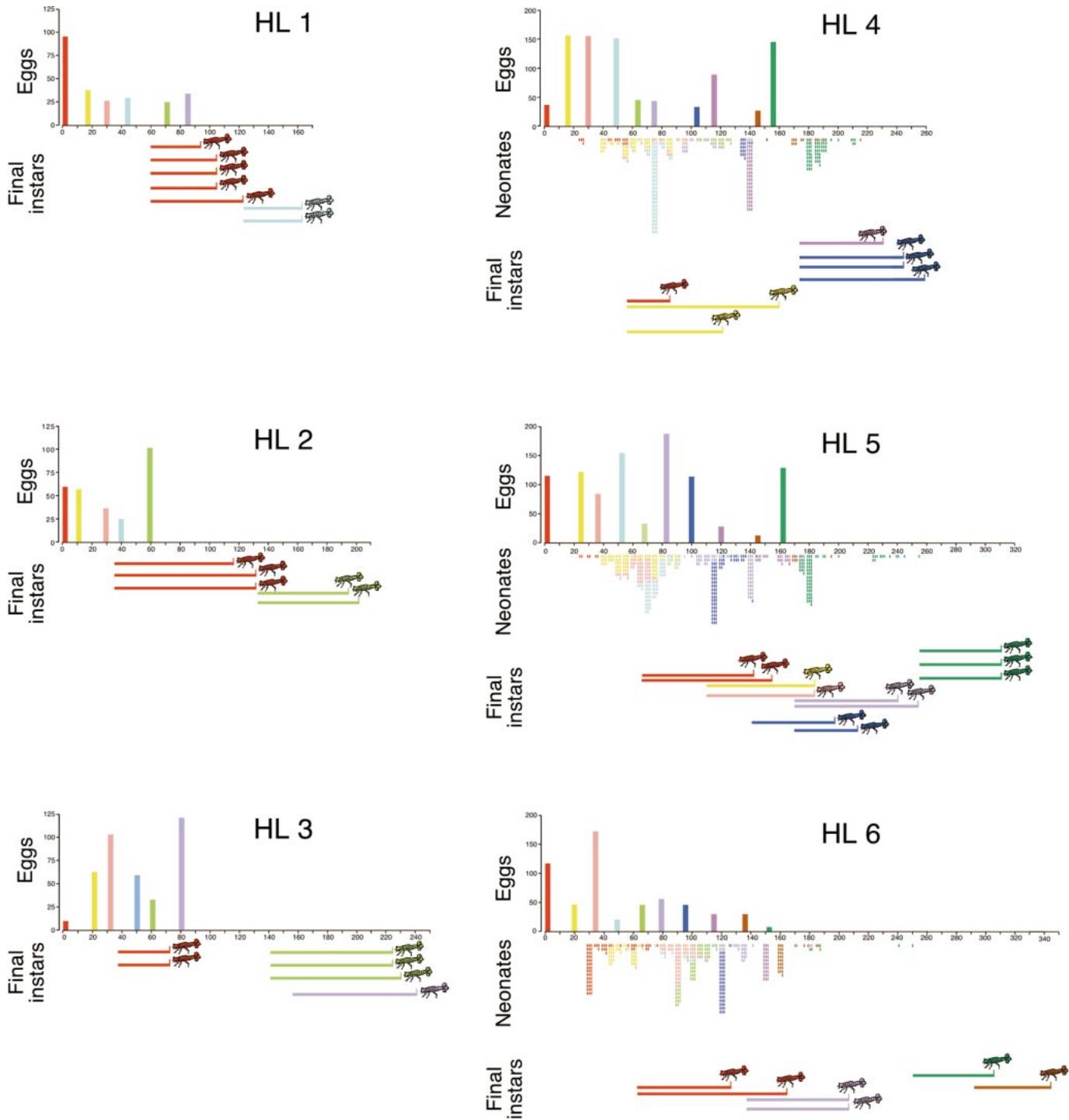


FIG. 1. Color-coded parentage of eggs (bars), hatchlings (dots, determined in 1995 only), and surviving final instars, in 9-liter larval habitats. Lines indicate the span between detection of successful offspring as 7–15 mm larvae and the day of their removal as final instars, shortly before emergence. Holes 1–3, 1994 data; holes 4–6, 1995 data.

to the preemptive advantage of earliest-hatching larvae. Small initial clutches were not responsible for the generally poor relationship between clutch size and the number of surviving offspring a mother produced. After eliminating first clutches from the analysis, the correlation between clutch size and surviving offspring remained insignificant ( $r = 0.20$ ,

$n = 41$ ,  $P = 0.21$ ,  $1 - \beta = 0.36$ ), whereas variance in hatching span accounted for an even greater percentage of the fitness variance ( $r = 0.44$ ,  $n = 27$ ,  $P = 0.02$ ). Furthermore, hatching span still explained a significant portion of the fitness variance after controlling for clutch size (partial  $r = 0.41$ ,  $n = 27$ ,  $P = 0.04$ ), whereas clutch size remained

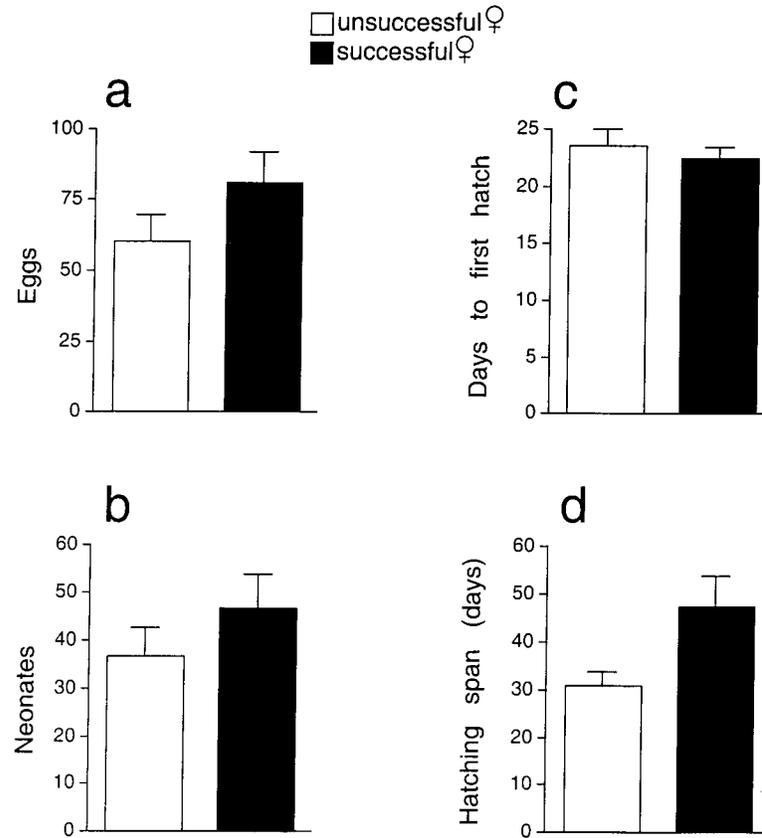


FIG. 2. Comparison of females that produced at least one surviving offspring from a clutch, with those producing none (a) clutch size,  $t = -1.45$ ,  $n = 47$ ,  $P = 0.15$ ,  $1 - \beta = 0.41$ ; (b) number of neonates,  $t = -1.0$ ,  $n = 30$ ,  $P = 0.30$ ,  $1 - \beta = 0.25$ ; (c) time to first hatch,  $t = 0.63$ ,  $n = 47$ ,  $P = 0.53$ ; and (d) hatching span,  $t = -2.16$ ,  $n = 30$ ,  $P = 0.04$ .

insignificantly correlated with surviving offspring after controlling for hatching span (partial  $r = 0.11$ ,  $n = 27$ ,  $P = 0.59$ ).

#### Seasonal Effects on Clutch Size, Hatching Patterns, and Body Size

One female caught on day 1 of the study in 1995 laid 514 eggs (18 days to first hatch; hatching span = 41 days), considerably larger than the second largest clutch of 344 eggs. We conservatively excluded this female from the following analysis; including her does not change any conclusion.

In the larger sample of 111 clutches collected throughout the wet season, hatching was highly asynchronous. The average clutch size was  $109.6 \pm 6.5$  eggs (range = 9–344). Eggs in a clutch hatched over a span of as little as four days, or as many as 184 days ( $\bar{x} = 59.3 \pm 3.6$  days). Hatching span was not correlated with clutch size in this larger sample ( $r = 0.08$ ,  $P = 0.38$ ). Limiting the analysis of hatching span to the clutches with a documented hatching success of  $\geq 0.70$  ( $\bar{x} = 0.81 \pm 0.01$ ) did not change this result (Fig. 5). As shown in Table 2, the most variable portion of the hatching sequence was the span over which the final quartile of the eggs in a clutch hatched. As was true for the smaller sample in our experiment above, the time required for the first egg in a clutch to hatch was negatively correlated with clutch size (Fig. 6). In clutches of 50 or more eggs, the mean time

to first egg to hatch was  $20.6 \pm$  day (range 14–30 days), about four days earlier than the minimum hatch time of smaller clutches ( $\bar{x} = 24.8 \pm 1.6$  days, range 18–32 days,  $t = 3.1$ ,  $P = 0.003$ ). Clutch size ( $r = -0.12$ ,  $n = 111$ ,  $P = 0.19$ ,  $1 - \beta = 0.35$ ), hatching span ( $r = -0.14$ ,  $n = 57$ ,  $P = 0.29$ ,  $1 - \beta = 0.28$ ), and the time to first hatch ( $r = -0.14$ ,  $n =$

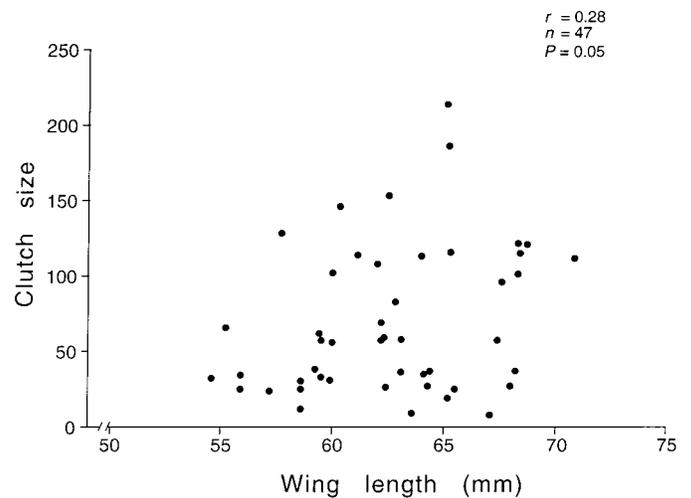


FIG. 3. Clutch size as a function of wing length of females used in the experiment.

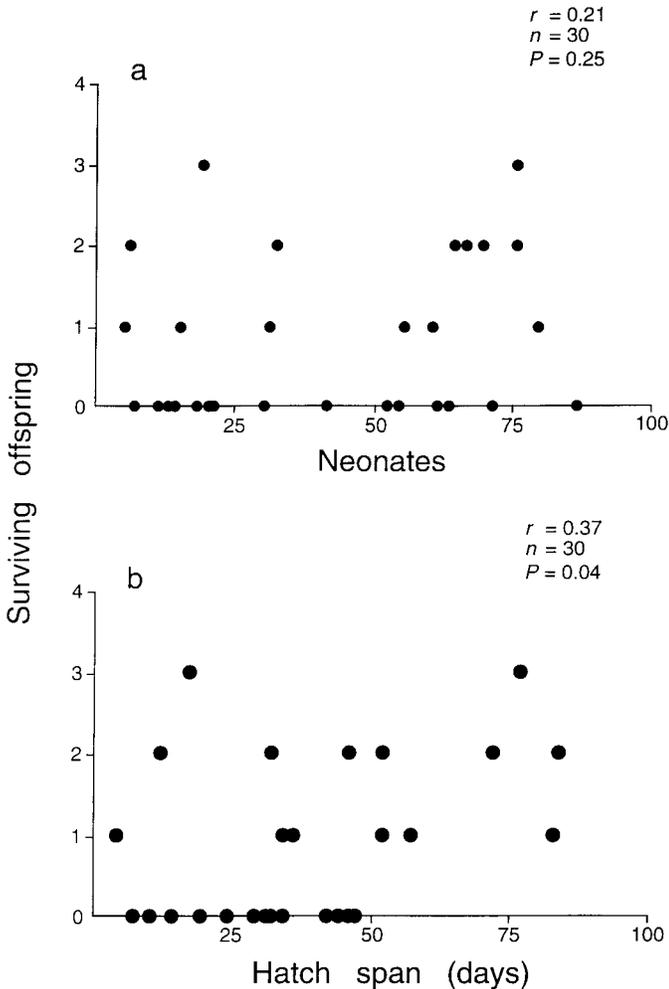


FIG. 4. Reproductive success of females as a function of (a) the number of larvae known to hatch and (b) the span between the time the first and last eggs in a clutch hatched.

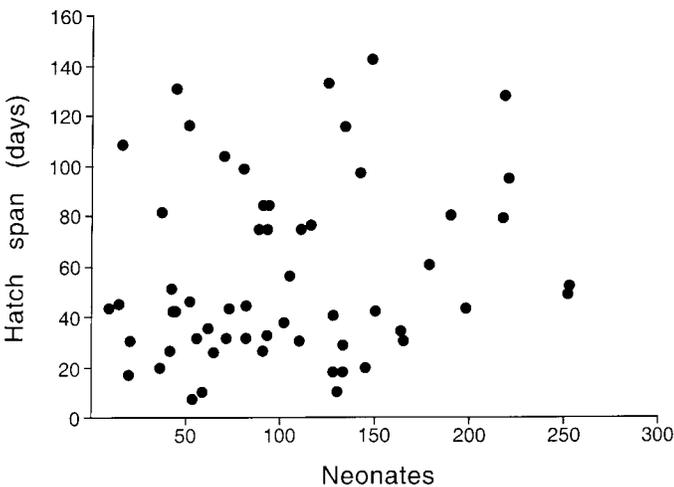


FIG. 5. Hatching span as a function of the neonates known to hatch from clutches laid over the wet seasons of 1995–1997. Controlling for laying date, partial  $r = 0.15$ ,  $n = 57$  clutches with  $\geq 70\%$  hatching success,  $P = 0.28$ ,  $1 - \beta = 0.30$ .

TABLE 2. Variation in hatching asynchrony (in days) of 57 clutches having  $\geq 0.70$  hatching success, each laid by a different female. The span of a quartile could be zero if  $\geq 25\%$  of the eggs in a clutch hatched on a single day.

	$\bar{x} \pm SE$	Range
Time to first hatch	$20.7 \pm 0.46$	14–33
Span of 1 <sup>st</sup> quartile	$5.4 \pm 0.09$	1–27
Span of 2 <sup>nd</sup> quartile	$4.1 \pm 0.05$	0–15
Span of 3 <sup>rd</sup> quartile	$7.1 \pm 1.22$	0–54
Span of 4 <sup>th</sup> quartile	$37.7 \pm 3.3$	1–128

57,  $P = 0.29$ ,  $1 - \beta = 0.28$ ), all tended to decrease with the day of oviposition, though not significantly.

A negative correlation between wing length of individuals marked at age 1 and the day of marking ( $r = -0.25$ ,  $n = 79$  females,  $P = 0.02$ ;  $r = -0.35$ ,  $n = 256$  males,  $P = 0.001$ ) indicated that body size decreased as the wet season progressed. Controlling for this seasonal effect, the age class of the mother had no detectable effect on her clutch size (partial  $r_s = -0.04$ ,  $n = 49$ ,  $P = 0.78$ ), hatching span ( $r_s = -0.003$ ,  $n = 49$ ,  $P = 0.98$ ) nor time to first hatch ( $r_s = -0.05$ ,  $n = 49$ ,  $P = 0.74$ ). Controlling for the day of laying, clutch size was no longer correlated significantly with female size (partial  $r = 0.07$ ,  $n = 98$ ,  $P = 0.51$ ).

Controlling for day of marking, female body size was not correlated with relative life span (partial  $r = 0.08$ ,  $n = 234$ ,  $P = 0.20$ ), but only 15 females were seen more than once. For this subset, the span over which a female was seen ( $\bar{x} = 21.1 \pm 7.0$  days, range = 2–88 days) was correlated with body size (partial  $r_s = 0.58$ ,  $P = 0.03$ ). Seven of these 15 females were resighted at defended tree holes, on average  $11.7 \pm 4.3$  days (range 3–35 days) after the first sightings. No female was seen to lay more than once in the same tree hole.

*Male Fitness and Phenotypic Predictors of Fitness*

The mean span over which marked, five-legged males were seen in this study was  $12.8 \pm 1.3$  days (range = 1–155 days,

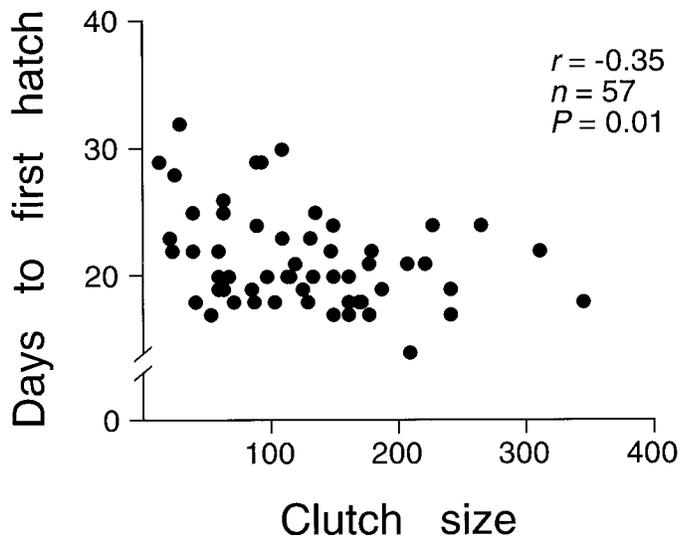


FIG. 6. Days to first egg hatch, as a function of clutch size.

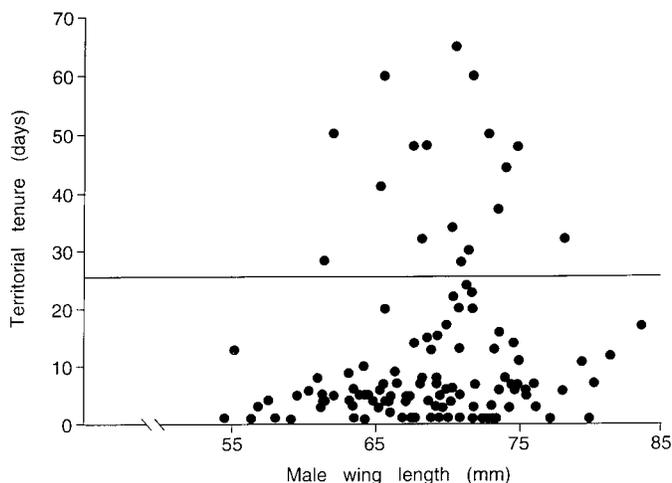


FIG. 7. Length of residency at a site as a function of male size (47 territorial sites, 1994–1996 wet seasons). Controlling for day of marking, partial  $r = 0.15$ ,  $n = 116$  males,  $P = 0.10$ . Horizontal bar indicates males holding territories for  $\leq 25$  days, about the time required to encounter a female. For this group, partial  $r = 0.2$ ,  $n = 99$ ,  $P < 0.05$ , see text).

$n = 365$ ). This was not significantly different from the mean span of  $14.6 \pm 1.8$  days (range 1–165 days,  $n = 236$ ,  $t = -0.84$ ,  $P = 0.39$ ) over which males were observed in a 1983–1984 study when no legs were removed (see Fincke 1992a). The longest span over which a marked *M. coerulatus* was seen was 193 days. This male emerged in the insectary in 1996 and was resighted as an old individual in 1997 (i.e., he was not included in the above sample). Controlling for the seasonal decline in body size, wing length was correlated with the number of matings a male obtained (partial  $r = 0.13$ ,  $n = 359$ ,  $P = 0.01$ ). In contrast, the span over which a mature male was seen was not a function of male wing length (partial  $r = 0.06$ ,  $n = 359$ ,  $P = 0.26$ ; partial  $r = -0.01$ ,  $n = 178$  males seen more than once,  $P = 0.92$ ).

A male defending one of our experimental holes for the maximum time observed in the field (60 days) would have, on average, a realized fitness of only  $2.6 \pm 0.19$  surviving offspring (range = 0–7), regardless of the number of matings ( $r = 0.13$ ,  $n = 51$ ,  $P = 0.35$ ) or fertilizations obtained ( $r = 0.10$ ,  $n = 51$ ,  $P = 0.46$ ). At best, he would hit three windows of opportunity for larval survivorship; at worst, none. In contrast, a male staying at a site only long enough to obtain a single mating would produce, on average,  $0.89 \pm 0.18$  offspring (range 0–5). However, he would have a ninefold fitness payoff per day of defense ( $\bar{x} = 0.35 \pm 0.14$  offspring per day versus  $0.04 \pm 0.00$  for males staying 60 days,  $t = 2.25$ ,  $P = 0.03$ ). In other words, a male is not assured fitness simply by maximizing the number of matings or fertilizations. Rather, the number of favorable windows to which he contributes offspring is the best predictor of his success, explaining 74% of variation in realized fitness among mated males in this example ( $r = 0.87$ ,  $n = 98$ ,  $P = 0.001$ ).

Contrary to expectations if males were maximizing lifetime fertilization success, the largest territorial males did not defend holes for the longest time (Fig. 7). However, tenure duration was correlated positively with body size for terri-

torial males with the relatively short residency time of 25 days or less (Fig. 7). Mean residency of a territorial male at a site was  $11.4 \pm 14.1$  days. Because the average time to encounter a female was  $22.9 \pm 3.1$  days (median = 14 days, range 1–69 days), these results suggest that the largest, most competitive males remained on a territory only long enough to obtain one to two matings. Indeed, controlling for the day a male was first seen, body size was correlated with the number of different tree hole sites a male frequented and left voluntarily (partial  $r = 0.27$ ,  $n = 82$  males seen at more than one site,  $P = 0.01$ ).

## DISCUSSION

### *Adult Fitness in Megalopterus coerulatus*

Because the experimental holes were designed as a best case scenario for larval survivorship, our results likely overestimate survivorship of *M. coerulatus* in natural holes for several reasons. First, we limited egg input to one clutch every two weeks. The number of surviving larvae was effectively limited by the size of a tree hole and the time span over which it received eggs, rather than by the total number of eggs it received. At newly created larval habitats in a fallen tree, adult activity can be five times higher than average, and consequently, some holes receive multiple clutches per week, even though the total number of emerging adults remains low (Fincke 1992a). Secondly, we curtailed egg input at the end of wet season and kept holes filled, preventing mortality that would result from hole drying (see Fincke 1994). Finally, whereas other major intraguild predators were excluded from all but one of our experimental holes, about half of the natural tree holes on BCI that are defended by *M. coerulatus* are also occupied by *Triacanthagyna* or *Gynacantha* dragonflies. These predators reduce the total number of *M. coerulatus* that a hole can support, and in extreme cases, can eliminate all *M. coerulatus* offspring (Fincke 1992a, 1999).

Even under the favorable conditions for offspring survivorship in our experiment, variation in reproductive success among parents was extreme, with typically less than half of the parents realizing any fitness from their reproductive investment. Contrary to a common prediction of behavioral ecologists, the fitness that a female realized from using a particular larval habitat was not proportional to the number of eggs she laid there. Larger sample sizes would have, in hindsight, provided more power for our statistical tests, but at considerable cost in terms of time and man power, given the low encounter rate with ovipositing females in this system. However, even if the low correlation between clutch size and fitness were found to be significant with a larger sample size, clutch size would still explain much less of the variance than does hatching span. Larger than average clutches did not improve a female's realized fitness because hatching span was not correlated with clutch size, even in our larger sample where the power to detect a small but significant trend was more robust. But more importantly, the windows of opportunity revealed by the microsatellite data offer the explanation for the lack of strong correlation between clutch size and fitness. These unpredictable windows also explain why the number of matings a male obtains is a poor indicator of the fitness he realizes from a defended hole. Not

only are many of the females that use a given hole unsuccessful in producing a single surviving offspring, but increasing the number of mates that contribute embryos to a hole decreases the fitness gain per successful mate (see Table 1). Females hedge their bets by producing highly asynchronous clutches, which effectively makes multiple matings at a given hole more redundant than they might be otherwise.

The maximum observed hatching span within a given clutch in this study was 184 days, greater than that known for any odonate laying nondiapauses eggs (see Miller 1992; Corbet 1999). Although under natural conditions they develop in bark above the water line, eggs in our study were in a monolayer, submerged under water, eliminating the possibility of a moisture or oxygen gradient (the latter is a known hatching cue in an odonate, Miller 1992). A sudden drop in ambient temperature, which occurs during a heavy rain, is a proximate cue for hatching in *M. coerulatus*; neonates suffer relatively low mortality before reaching the water when they crawl over wet bark as opposed to dry bark (A. van't Hof and O. Fincke, unpubl. data). However, eggs within a clutch develop at different rates, suggesting that females have some ultimate control over the timing of egg hatch. Little is known about inherent control of the rate of embryogenesis, particularly in odonates (see Corbet 1999), but female age can play a role (reviewed by Mousseau and Dingle 1991; Sternberg 1995). However, in our study a female's relative age had no detectable effect on hatching span; other possible factors, such as egg size and laying order, are under investigation.

Aside from greater insurance against mortality between egg laying and the time neonates enter a hole, what might females gain by laying a large clutch? In another study, (O. Fincke, unpubl. ms.), a clutch of 20 eggs developing in a large hole with abundant prey produced, on average, three surviving offspring, about four fewer than a clutch of 75 eggs. However, the latter produced no more offspring than a clutch of 100 eggs. Moreover, a clutch of 20 eggs produced larger offspring than clutches of 75 or 100. In our experiment, even the largest clutches were ineffective at swamping cannibalistic larvae already present in the holes; large clutches are also ineffective in swamping preexisting dragonfly larvae as well (O. Fincke, unpubl. ms.).

The first egg to hatch did so more quickly in clutches with more than 50 eggs, although this apparent facilitation could be a larval response to increased competition, rather than a phenomenon under female control. This effect did not translate into a detectable advantage in our experiment, but might be advantageous when multiple females compete for an unoccupied hole. For example, if multiple clutches had been deposited simultaneously into our experimental holes, larger clutches would be expected to have a preemptive advantage over smaller ones, at least for the initial egg input. Once a hole has been colonized by neonates however, a four-day lead on hatching from any subsequent clutch would be unlikely to improve the odds of hitting the next unpredictable window. Alternatively, a female might lay excess eggs if it is more difficult for her to find a tree hole than it is to amass the energy needed to produce eggs. The female that laid an unusually large clutch did so early in wet season, after weeks during which tree holes would have been dry. She may have "dumped" her entire load of mature eggs simply because it

had been a long time since she encountered a water-filled tree hole. For example, the best predictor of clutch size in *Coenagrion puella*, a British damselfly constrained from laying on rainy or overcast days, is the time since the last clutch was laid (Banks and Thompson 1987).

Although studies on a variety of insects (often under lab conditions) have demonstrated a positive correlation between female body size and fecundity (e.g., Boggs 1986; Wiklund and Karlsson 1988; Gwynne 1988; Honek 1993), for *M. coerulatus*, that relationship appears to be a statistical artifact. Body size declined as the season progressed, coupled with a tendency for clutch size to decrease independently over the wet season. Rather, for the few females that were resighted, larger females were seen over a longer time span, although no such relationship was detected in males, which were resighted more often. However, after controlling for the seasonal decline in body size, larger males were still more likely to mate. This result corroborates earlier data demonstrating that the large size advantage in mating occurs because large relative size best predicts the winners of territorial fights (Fincke 1992a).

*Megalopterus coerulatus* has a maximum adult life span that is longer than that for any odonate species studied to date (reviewed by Corbet 1999). Adults roam widely over the island (Fincke 1984b), and must use more than a single tree hole in order for the yearly replacement of the population, which, on BCI, appears to have been stable over the past 15 years (Fincke 1998). Although our study was not designed to measure fitness of individuals over their life span, given the dynamics of larval survivorship, our results suggest that among parents, lifetime fitness is unlikely to be correlated with the total number of embryos produced. Rather, the number of tree holes (or windows) over which both males and females distribute their embryos should be a better surrogate of lifetime fitness than the traditional ones such as female-clutch size or male-territory tenure duration or total fertilizations. Indeed, females appear to rarely, if ever, lay multiple clutches in the same tree hole. Although staying at a territory as long as possible maximizes a male's fertilization success at a given territory (Fincke 1992a), that strategy is unlikely an optimal one for the most competitive males. Upon leaving one site, the largest males have the best chance of securing another territory, not because they are better at finding them, but because they can most easily oust any male defending another site. A simulation model incorporating field estimates for larval growth rates, male and female encounter rates, and travel times between sites, demonstrated that fitness was maximum for males that stayed at a site only long enough to obtain one to two matings (O. Fincke, O. Eikemeier, and H. Hadryis, unpubl. ms.). This is consistent with our current finding that the largest males changed territorial sites after a relatively short time.

Our results have broad implications for studies of reproductive strategies, particularly in animals lacking parental care. First, understanding the pattern of offspring survivorship clarifies how larval ecology shapes adult reproductive strategies. For *M. coerulatus*, unpredictable larval survivorship favors bet-hedging strategies by adult females and males in ways that could not be predicted by focusing solely on the dynamics of adult reproductive behavior. Females bet

hedge by producing clutches with extreme hatch asynchrony, thereby increasing the chances that at least one offspring hatches during a window of opportunity. The timing of these windows cannot be anticipated by ovipositing females or territorial males, which explains why neither males nor females discriminate against tree holes that are already occupied by con- or heterospecific odonate larvae (Fincke 1992a). Our results also explain the otherwise puzzling observations that very large males often abandon tree holes even though they are not challenged by competitors, and why the newest larval habitats are those where male competition is greatest.

Secondly, uncertain patterns of offspring survivorship constrains natural selection on female fecundity and sexual selection on males. Females and males that maximize the number of larval habitats to which they contributed offspring would have a selective advantage over those that maximize their input at a given site. Because neither clutch size nor fertilization success was a good predictor of parental fitness, selection on mated individuals was constrained. If fitness is not proportional to male fertilization success or female fecundity, then using these traditional fitness surrogates to estimate the opportunity for selection or to calculate selection differentials for adult traits, as is done often (e.g. Arnold and Wade 1984; Brown 1988), can be misleading. For example, had we used territory tenure (or mating success) as a fitness surrogate, we would have incorrectly concluded that sexual selection on male size was stabilizing (Fig. 7). In *M. coeruleatus*, both sexual and natural selection favors large males. In addition to a mating advantage, large males are best able to maximize their chances of producing surviving offspring by distributing offspring among the greatest number of larval habitats. Jia and Greenfield (1997) provide a contrasting case in which a trait important for mating success is not necessarily the trait that makes a successful parent. Under poor larval conditions, the offspring of male wax moths that were not preferred mates experienced greater growth and survivorship than the offspring of preferred males.

Finally, quantifying fitness as the number of surviving offspring is critical to understanding population processes. The effective population size ( $N_e$ ), an important determinant of population stability and health (Soule and Wilcox 1980), would be significantly overestimated for *M. coeruleatus* if calculated by simply noting the number of reproductive adults. Although most sexually mature females and 30% of adult males are expected to produce embryos (Fincke 1992a), our current results suggest that fewer than half of all parents actually contribute genes to the next generation. Mortality by intraguild predators (Fincke 1992b, 1999) would further reduce our estimate of  $N_e$ . We are currently measuring the effects of this low offspring survivorship on the genetic structure of *Megaloprepus coeruleatus*, whose habitat is restricted to the increasingly fragmented forests of the Neotropics.

The uncoupling of clutch size or fertilization success from realized fitness at a site is likely to be common whenever ecological conditions that cannot be anticipated by adults result in windows that disproportionately favor offspring survivorship. Whereas larval cannibalism is the mechanism that makes offspring survivorship unpredictable in tropical tree holes, in a bromeliad-breeding frog, snake predators that consume entire egg clutches produce a similar effect. Although

larger frogs produced larger egg clutches, Haugen (2001) found no correlation between the size of a female and the number of offspring surviving to metamorphosis. Even for noncontainer breeders, the number of embryos entering a habitat is usually far in excess of its carrying capacity, and larval survivorship is typically low (e.g., Berryman 1988, Ohgushi 1991; Willis and Hendrick 1992; Tinkle and Dunham 1993; Duffy 1994; Dempster and McLean 1998; Dixon et al. 1999). Ecological factors such as deterioration of larval habitats or fluctuations in the density of food, predators, cannibals, or parasites can result in unpredictable windows of offspring survivorship (e.g., Smith 1987; Newman 1989; So and Dugeon 1989; Morin et al. 1990; Messina 1991; Anholt 1994; Dixon et al. 1999). Our findings call for caution in the design of future studies aimed at obtaining evolutionary meaningful estimates of fitness, particularly for species with complex life histories.

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