

Original Article

Excess offspring as a maternal strategy:
constraints in the shared nursery of a giant
damsselfly

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Maternal reproductive strategies should optimize the quality and quantity of surviving offspring. In *Megaloprepus caerulatus*, a damsselfly that exhibits male-biased size dimorphism, larval siblicide, and a disproportionate fitness advantage from large sons, mothers lay many more eggs in water-filled tree holes than can survive to emergence. Using field experiments, I tested the siblicide advantage of excess offspring (i.e., faster development and/or larger survivors) in small and large holes and 2 alternative functions of excess offspring (predator satiation and insurance against nonpredator mortality). In small pots, the sole siblicidal survivors emerged larger than noncannibals but no sooner. However, doubling or even quadrupling a modest clutch of 25 failed to produce larger offspring. In large tubs, the size advantage that survivors gained from siblicide was constrained by a trade-off between offspring size and number. A clutch of 20 produced half as many but larger offspring than one of 100. When multiple females contributed eggs to a large nursery, size of survivors was independent of the mother's clutch size. Finally, large clutches failed to satiate dragonfly predators, and although 25 neonates were better than 2 as insurance against nonpredator mortality, a clutch of 50 provided no additional benefit. In natural and experimental holes, survivorship was female biased, suggesting that sons suffered greater mortality than daughters. Because mothers seemed unable to adaptively bias offspring sex ratio, excess offspring may compensate for the lower survivorship of sons, particularly in large nurseries where males garner a disproportionate size advantage relative to females. *Key words:* cannibalism, clutch size, *Megaloprepus*, parent-offspring conflict, sex allocation, sexual size dimorphism. [*Behav Ecol*]

Female reproductive strategies are expected to optimize the number and quality of offspring that survive to reproductive age (Courtney 1984; Nur 1984; Smith et al. 1989; Godfry et al. 1991; Wilson 1994). In response to variation in resource availability and/or competitors, many females that lay eggs on discrete resource patches (e.g., dung pats, carcasses, plants, or insect hosts) can adaptively manipulate clutch size (e.g., Mayhew 1998; Michaud and Grant 2004; Creighton 2005) and, in some cases, even the sex of offspring (e.g., Godfry 1987; Herre 1987). Maternal culling of offspring allows mothers to optimize the trade-off between offspring number and offspring size, whereas control over offspring sex permits optimal allocation when a mother reaps disproportional fitness from sons and daughters depending on offspring quality (Charnov et al. 1981; Charnov and Downhower 1995).

When only a single pair of parents controls the nursery, overproduction of offspring may be an adaptive way to hedge one's bets against environmental uncertainty, producing an excess of surviving young in good times and fewer in bad times (Mock and Forbes 1995). When multiple females share the nursery, a female may forfeit some fitness in order to maintain her priority over resources. For example, a female burying beetle may crop the total eggs on a carcass if she detects another female in the area, thereby reducing the brood of a competitor at some cost to her own fitness (Eggert and Müller 2000).

When offspring, rather than parents, are the vehicles of culling, cannibalism has usually been considered as an adaptive strategy for the individual cannibal (reviewed by Elgar and Crespi 1992) because it reduces a mother's reproductive output (Anholt 1994; Lounibos et al. 1996; De Block and Stoks 2004). Nevertheless, a numerical loss to parents may be outweighed by fitness gains accrued if surviving offspring grow to a larger size (Breden and Wade 1985, 1987) or develop faster (Wissinger et al. 2004) than would be possible otherwise. However, overproduction of cannibalistic siblings as a maternal strategy becomes difficult to explain when 2 or more mothers share a discrete nursery. Then, mothers are vulnerable to reproductive parasitism because unrelated young can eat one's own offspring (Summers and Amos 1997). Not surprisingly, there is little empirical work on within- and between-cohort cannibalism as a maternal allocation mechanism in species that exploit a limiting resource shared by multiple females.

Here, I examine the potential function of offspring overproduction by *Megaloprepus caerulatus*, a territorial damsselfly in which brood culling occurs via larval cannibalism (Fincke 1994). Sexual size dimorphism of adult *Megaloprepus* is male biased, and male, but not female, size is correlated positively with the volume of the tree hole nursery in which offspring develop (Fincke 1992b). Because body size is more variable in males than in females and is a strong predictor of male mating success, mothers gain a disproportionate fitness benefit from large sons relative to large daughters (Fincke 1992b; Fincke and Hadrys 2001). For simplicity, *M. caerulatus*, a monospecific genus, is hereafter referred to by genus name only.

Female *Megaloprepus* mate only at defended territories and lay their eggs in multiple water-filled tree holes that vary in

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size from 0.1 to over 50 l. Nutrient input into these detritus-based food webs is limiting (reviewed by Kitching 2000). The number of eggs a female lays is positively correlated with tree hole volume (Fincke 1992b). The proximal mechanism for this phenomenon appears to be behavioral and related to the size of the tree hole opening. After a period of egg laying, a female flies up from a hole and then back down. If the hole perimeter is small, she is unlikely to reland on the rim and departs. If the hole perimeter is large, she has a higher probability of relanding on the edge of the same hole and continues egg laying (Fincke OM, personal observation). Because of its multiple repeated copula cycles (Fincke 1984a) whose stages are identical to those of species with last male sperm precedence (e.g., Fincke 1984b; Córdoba-Aguilar et al. 2003), eggs laid immediately after copula with a resident male are likely full siblings. Females often lay more than 10 times as many eggs as the number of adults that emerge from a nursery (e.g., 1–30 from small and large holes, respectively) over a wet season (Fincke 1992b, 1998). Even with ad libitum prey, *Megaloprepus* larvae cannibalize conspecifics until their density stabilizes at one larva per 1–2 l of water (Fincke 1994, 1999). Hence, the number of eggs laid by a female or fertilized by a male is not correlated with the number of offspring that survive to emerge as adults (Fincke and Hadrys 2001). Instead, the span of time over which eggs in a given clutch hatch (ranging from 14 to 185 days) is the best predictor of the number of surviving offspring. An increase in clutch size above a minimum of 50 eggs does not increase hatching span, raising the question of what, if anything, *Megaloprepus* females gain by laying many more eggs into a hole than can survive to emergence.

Hypotheses to be tested

Siblicide advantage

One obvious potential benefit a *Megaloprepus* mother might gain by laying excess eggs is producing surviving offspring that emerge sooner or at a larger size than would be possible in the absence of sibling cannibalism (hereafter, “siblicide”). In “small holes” of a liter or less, the first larva to hatch is able to patrol the entire space, enabling it to cannibalize all later-hatching larvae (Fincke 1996, 1999). “Large holes,” greater than a liter in volume, can produce multiple adults because they are usually too big for a single larva to control and the per capita prey is higher than in small holes. In either type of nursery, a positive relationship between maternal clutch size and offspring size and/or development rate would support the “siblicide advantage” hypothesis of offspring over production.

In a tropical forest, small holes should typically be harder for a female to find and thus more likely to contain offspring from a single female than large holes. The latter often form in a fallen tree where they are defended by a territorial male, attract multiple females, and support several larval cohorts. Any advantage of providing excess offspring as additional food should be the most constrained for a mother laying in these large shared nurseries (but less constrained for her territorial polygamous mate) because her offspring could provide food for larger unrelated cannibals. Indeed, in 9-l holes, reproductive parasitism prevented more than 60% of the mothers from producing even a single surviving offspring (Fincke and Hadrys 2001).

Given the male-biased size dimorphism of adult *Megaloprepus*, I expected that experiments testing the siblicide advantage might yield sex-specific effects not only on offspring body size but also on larval survivorship. If males have lower survivorship than females, I expected female-biased sex ratios of adults emerging from both small and large holes. In contrast, if mothers could adaptively manipulate the sex ratio

of eggs, I expected to find male-biased sex ratio of adults emerging from large natural tree holes but not from small ones (i.e., the former produce disproportionately large sons relative to daughters).

Predator satiation

In addition to the siblicide advantage, I tested 2 alternative, nonmutually exclusive possible functions of offspring overproduction. Excess offspring might function to swamp preexisting intraguild predators, such as the larvae of the dragonflies *Gynacantha membranalis* or *Triacanthagyna dentata*. Together, these top predators occupy about 20% of all tree holes and about 40% of the large holes defended by male *Megaloprepus* at my Panamanian study site (Fincke 1992a, 1992c). In contrast with cannibalistic *Toxorhynchites* mosquitoes whose females can detect egg clutches of conspecifics that float on the water surface (Sherratt and Church 1994), female *Megaloprepus* appear unable to detect predatory dragonfly larvae, which often lurk at the bottom of tree holes. In any case, ovipositing females do not discriminate against tree holes that are occupied by conspecifics or other intraguild predators (Fincke 1992b, 1998). The predator satiation hypothesis would be supported by finding, above some threshold required for satiation, a positive relationship between clutch size of *Megaloprepus* and the number of offspring surviving to emerge from large holes with preexisting dragonfly predators.

Insurance policy

Finally, excess eggs may function as an insurance policy against hatching failure, failure of newly hatched larvae (hereafter “neonates”) to reach the water, or other nonpredator mortality, such as during molting. Eggs are laid into the bark just above the water line away from aquatic predators. Because hatching failure is typically low in odonates (Corbet 1999), I tested the insurance hypothesis only as it refers to posthatching nonpredatory mortality. Support for the insurance hypothesis would be a positive relationship between clutch size and the probability of producing a single surviving offspring from a small hole occupied only by siblings from a given clutch.

MATERIALS AND METHODS

General treatment of egg clutches, larvae, and emerging adults

The study was conducted on Barro Colorado Island (BCI) in Soberania National Park, Panama (see Fincke 1992b, 1992c, 1994, 1998 for life history and ecology of the study species). Fieldwork was conducted in the wet seasons in 1996, 1997, and 1998. For each year, the first study day was standardized as 15 April in early wet season. Typically, dry season begins in December, with tree holes drying up by mid-February. Mated females were found at defended tree holes and held over night in small cages with moist filter paper into which a female laid eggs. Egg clutches were held individually in water-filled jars until neonates hatched and were added to artificial holes used in the experiments. These were either small, 0.6-l plastic pots, or large 9-l tubs with standardized leaf detritus that were set up in the field 18–25 days before the first hatch to permit colonization of microinvertebrate prey for the neonates. To reduce the variance among replicates in hatching span and hatching failure, “synthetic clutches” consisting of neonates were used. With “clutch day 1” as the day of the first egg hatch, neonates were added to a treatment on the following schedule: A quarter of the treatment total neonates were added between clutch days 1–3, another 25% were added between days 4–6, another 25% between days 7–13, and the

final quartile added between days 14–44. This schedule mimicked the average pattern of natural egg hatch (Fincke and Hadrys 2001) while eliminating most of the natural variance around the mean. Within a treatment, eggs for a given replicate were from a single clutch; whenever possible, eggs from a single clutch supplied all treatments within a replicate set. Otherwise, 2 clutches that were laid within a day of each other were used.

To exclude predators but not mosquito prey, artificial holes were covered with wire cages (illustrated in Yanoviak and Fincke 2005). Because additional detritus was also prevented from entering, yeast was added as a nutrient source. Once every 2 weeks, the contents of the holes were emptied into pans and mosquito and *Megaloprepus* larvae were counted. Any of the latter over 5 mm were measured from the head to the end of the abdomen, excluding the leaf-like caudal lamellae (used in oxygen absorption). Pots were kept topped off with water during dry season. Final instars with swollen wing pads were transferred to an outdoor insectary where they emerged after a mean of 9.7 ± 0.58 days ($n = 125$). Maximum development time was scored as the span between the entry date of the first neonate and the emergence of an adult. Wing and abdomen lengths of emerging adults, which correlate positively with body mass at emergence (see Anholt et al. 1991), were measured using electronic calipers. Throughout, means are reported \pm standard error; unless noted, binomial and Student's *t* tests are 2-tailed. Bonferroni post-hoc tests insured an alpha of 0.05 across results of an experiment.

Siblicide advantage

To determine the possible maternal fitness payoffs that excess offspring provided by contributing to sibling growth, I compared the size and development time of adults emerging from small pots provided with a clutch of 25, 50, or 100 neonates (i.e., siblicide treatments) and from pots in which cannibalism was restricted (i.e., 2 neonates). In the latter, the additional neonate reduced the need for a replacement replicate if neither survived to the first census. Each pot contained 8 medium-sized fallen leaves from the same tree at a given site and a standardized piece of bark as oviposition substrate for mosquitoes. "Mosquito controls," used to measure the density of available mosquito prey, lacked *Megaloprepus*. A replicate set consisted of 5 pots: the restricted-cannibal control, 3 siblicide treatments, and a mosquito control. Each pot was attached with hooks within a small wire cage tied at breast height to a small tree (one pot per tree) and received 0.05 g of yeast at bimonthly intervals. Replicate sets were placed at 9 different sites in forest understory, each separated from another by at least 0.1 km. After a census, the contents were returned to the pot with the exception of *Megaloprepus* final instars, and any predatory *Toxyrhinches theobaldi* mosquito larvae, *Dendrobates auratus* tadpoles, or (rarely) odonates other than *Megaloprepus*. If no *Megaloprepus* were found in a treatment pot, it was scored as "failed," and a replacement pot was started.

In 1996, the density of mosquito larvae in the mosquito controls was greater than is typical in small natural tree holes. To determine if siblicide had a greater effect on offspring size or development time when alternative prey levels were lower and more realistic, I repeated the experiment in 1997 wet season with the following modifications. Pots were left uncovered to collect falling detritus; no yeast was added. Once a month, 2 newly fallen leaves were added to each pot. Because there were no differences between 50- and 100-neonate treatments in 1996, the latter was eliminated in the 1997 trials. A replicate set of 4 pots was secured to a single large

tree; a total of 10 replicate sets were attached to trees within a 50-m radius.

Data were analyzed using multivariate analysis of covariance (MANCOVA) (SAS 9.1) with wing and abdomen length and development time as dependent variables and sex, year, and treatment as main effects. The study day that the first egg within a clutch hatched was entered as a covariate to control for a possible seasonal decline in body size (e.g., Fincke and Hadrys 2001) or possible effect on development time. Excluded from analyses of small pot treatments were 2 offspring that survived after the first emerged and 8 females and 5 males that took an exceptionally long time to develop ($\bar{x} = 381.1 \pm 27.39$ days), exceeding the duration over which natural tree holes contained water (~ 290 days) before drying up seasonally. Including these data inflated mean development time but otherwise did not change any conclusions. In a few cases, due to complications at emergence, wings or abdomens were damaged and could not be measured.

To test for a siblicide advantage in large unshared holes, I compared the size and development time of survivors from 2 levels of siblicide (20 and 100 neonates) in the 9-l tubs of the controls from the predator swamp experiment below. The siblicide advantage hypothesis for large holes would be supported if survivors of 100-neonate clutches were larger and/or developed faster than those from 20-neonate clutches. To determine the effect of interfamily interactions on any siblicide advantage in large holes, results from the 9-l unshared nurseries were compared with those from shared nurseries in an earlier experiment designed to determine the parentage of survivors (Fincke and Hadrys 2001). In that study, neonates from clutches of 6 females laid at 2-week intervals were added as they hatched to a 9-l tub ($N = 6$ tubs). Otherwise, the protocols and nutrient input were identical to controls of the predator swamp experiment below. Here, I report only unpublished data from that earlier study (i.e., on the relationship between a mother's clutch size and the size of surviving offspring in shared nurseries). Finally, to test hypotheses regarding sex ratio, I analyzed the sex ratio of offspring emerging from the above experiments. Those data were compared with unpublished data on the sex of larvae emerging from natural tree holes varying in volume from 0.2 to 32 l during the 1983–1984 wet season (see Fincke 1992b for details).

Predator satiation

To test whether large clutches of *Megaloprepus* were more likely than smaller ones to satiate intraguild predators and thus more likely to produce one or more offspring, I compared the number and size of *Megaloprepus* that emerged from large water-filled tubs with and without larvae of the dragonfly, *Tr. dentata*. Each 9-l tub contained 3 liters of freshly fallen leaves from the same tree and 2 standardized pieces of bark. The screened tubs were placed on metal tables in shade. One gram of yeast was added to each tub at the beginning of the experiment and bimonthly thereafter, which insured that mosquito larvae prey were available in densities similar to those of large natural tree holes (see Fincke et al. 1997). Predator treatments contained 5 dragonflies varying in size from 5 to 24 mm (largest: $\bar{x} = 14.2 \pm 1.4$ mm; smallest: $\bar{x} = 8.8 \pm 0.4$ mm) to which were added synthetic clutches of either 20 or 100 *Megaloprepus* neonates. In the latter treatment, some replicates had as few as 75 eggs because of the difficulty of finding gravid females. Controls lacked *Tr. dentata* predators.

Insurance policy

I tested the insurance policy hypothesis (i.e., for nonpredatory mortality) by comparing the frequency with which clutches of

2, 25, 50, or 100 neonates failed to produced a surviving offspring in the small pots of the above siblicide advantage experiment. Because final instars that emerged as adults varied from 22.8 to 31 mm, the 15 final instar larvae ≥ 22.8 mm that disappeared between checks ($\bar{x} = 25.5 \pm 0.43$ mm) were assumed to have emerged in the field.

RESULTS

Do excess siblings increase size or development rate of survivors in small holes?

None of the siblicide-restricted control pots contained more than a single larvae after the first census. In the siblicide treatments, within the first 3 weeks, as many as 20 larvae were found in a single small pot. After 60 days, more than 2 individuals rarely coexisted, although a few pots harbored 2 individuals for as long as 3 months. Typically, the size hierarchy of larvae within a given pot remained stable across censuses, and then the largest larva detected initially was assumed to be the one that emerged. However, in 4 cases, the largest larva (sometimes missing a leg or caudal lamellae) was displaced by an individual 2–5 mm smaller. The mean size of the largest larva found coexisting with other larvae was 14.3 ± 0.76 mm; the mean difference between the 2 largest coexisting larvae was 8.7 ± 0.72 mm. All but 2 pots harbored only a single *Megaloprepus* survivor. In these 2 exceptions, the second surviving larva was detected (at ≤ 5 mm) shortly before the first one emerged.

As shown in Figure 1, for both sexes, adult body size of the survivors was inversely correlated with development time, controlling for hatch date (wing length: partial $r = -0.41$, $N = 45$ males, $P = 0.006$; $r = -0.44$, $N = 51$ females, $P = 0.0013$ and abdomen length: partial $r = -0.30$, $N = 45$ males, $P = 0.05$; $r = -0.56$, $N = 51$ females, $P < 0.0001$). In 1996, there was no difference in the effect of 50- and 100-neonate clutches on body size or developmental time (Bonferroni contrasts, $P > 0.05$), so these treatments were pooled to gain power in the model. Interactions among independent variables were not significant ($P \geq 0.21$ for all) and were eliminated from the MANCOVA model. Effects of sex, year, and treatment were all significant. Males were larger than females (wing: $F_{1,105} = 23.2$, $P < 0.0001$ and abdomen: $F_{1,105} = 47.5$, $P < 0.001$) but developed as fast as females ($F_{1,105} = 1.0$, $P = 0.22$). In 1996, individuals emerged at a larger size (wing: $F_{1,105} = 11.1$, $P = 0.001$ and abdomen: $F_{1,105} = 34.0$, $P = 0.0001$) and developed faster ($F_{1,105} = 8.2$, $P < 0.005$) than in 1997 (Figures 2 and 3).

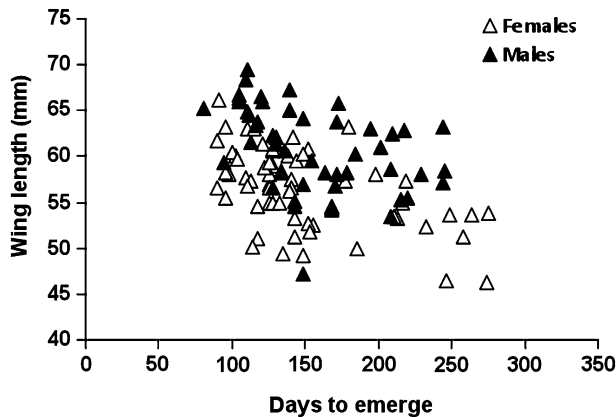


Figure 1
Wing length as a function of development time of offspring emerging from the siblicide advantage experiments.

Differences between years were attributed to the higher nutrient level in 1996. Although the mean number of mosquitoes in control pots did not differ among sites in either year (1996: $F_{10,65} = 1.1$, $P = 0.41$ and 1997: $F_{17,19} = 5.32$, $P = 0.17$), in 1996, when pots received yeast, the mean number of mosquitoes in the mosquito controls was significantly higher ($\bar{x} = 16.5 \pm 2.3$) than in 1997 ($\bar{x} = 6.3 \pm 0.1$, $t = 4.05$, $P = 0.001$), when leaf detritus was the only nutrient source. In 1996, wing length of males ($r = 0.42$, $N = 28$, $P = 0.03$) but not females ($r = 0.23$, $N = 24$, $P = 0.29$) was correlated positively with mean number of mosquitoes present per census. In 1997, wing length of both sexes increased with the mean number of mosquitoes present ($r = 0.74$, $N = 26$ females, $P = 0.001$; $r = 0.45$, $N = 17$ males, $P = 0.08$).

There was a significant treatment effect on body size of survivors (wing: $F_{3,105} = 2.7$, $P = 0.05$ and abdomen: $F_{3,105} = 3.4$, $P = 0.02$), although survivors from clutches of 50 and 100 were no larger than those from clutches of 25 (all Bonferroni contrasts, $P > 0.05$). Survivors of pooled siblicide treatments

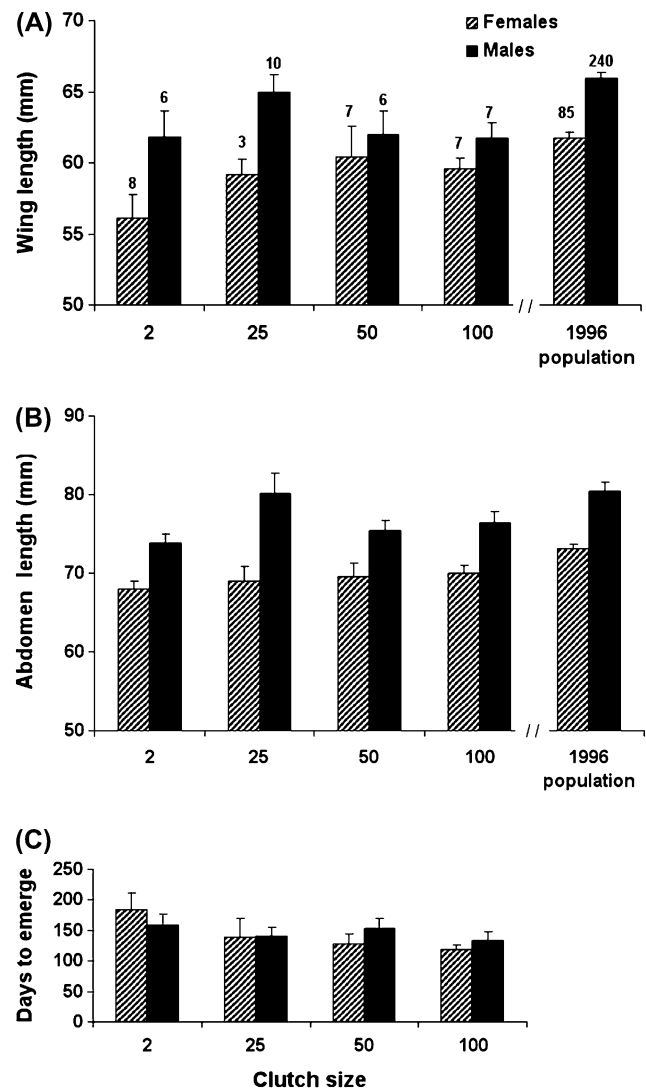


Figure 2
Results from the siblicide advantage experiment in 1996. (a) Mean \pm standard error (SE) wing length of sole survivors. Sample sizes are above error bars. Size of natural population at far right. (b) Mean \pm SE abdomen length of survivors. (c) Mean \pm SE development time of survivors.

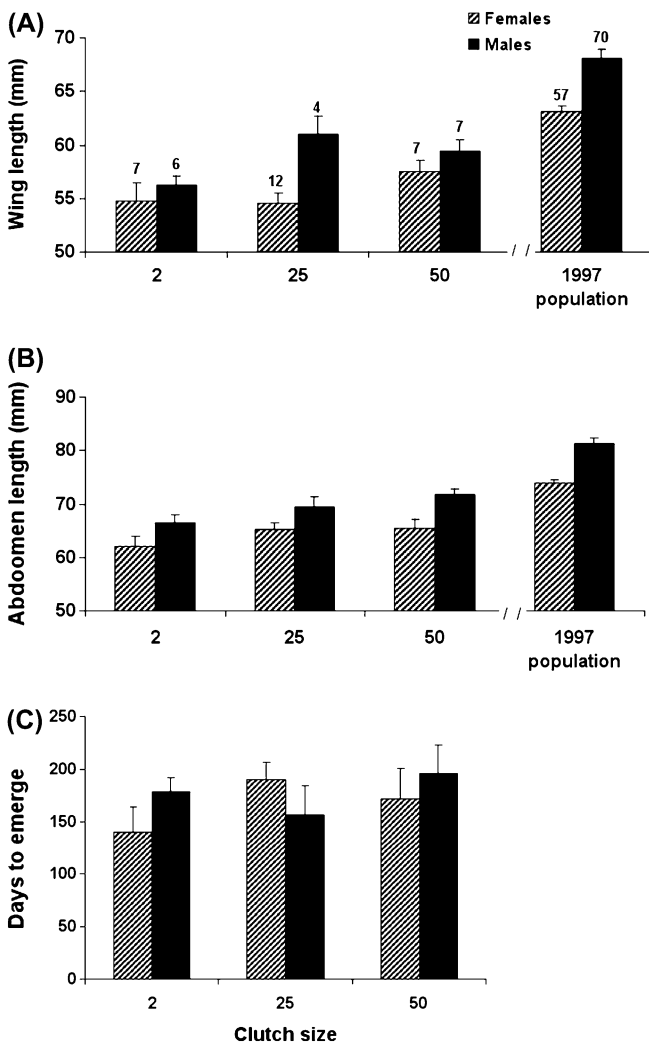


Figure 3
Results from the siblicide advantage experiment in 1997. (a) Mean \pm SE wing length of sole survivors. Sample sizes are above error bars. Size of natural population at far right. (b) Mean \pm SE abdomen length of survivors. (c) Mean \pm SE development time of survivors.

were larger than siblings unable to cannibalize (females: $t = 3.03$, $P < 0.01$ and males: $t = 2.76$, $P < 0.01$). Nevertheless, in both years, survivors emerged at sizes smaller than the mean of the natural population (Figure 2, females: $t = 3.03$, $P < 0.01$ and males: $t = 2.76$, $P < 0.01$; Figure 3, females: $t = 7.10$, $P < 0.01$ and males: $t = 7.93$, $P < 0.0001$). The exceptions were males from the 25-neonate clutches in 1996, which were as large as males in the wild population (wing: $t = 0.62$, $P = 0.54$ and abdomen: $t = 0.13$, $P = 0.89$). In contrast with their positive effect on body size, siblicide treatments did not decrease development time of survivors ($F_{3,105} = 1.02$, $P = 0.39$) relative to controls unable to cannibalize siblings.

Survivorship in this experiment was female biased (51 males:73 females, $P = 0.06$, binomial test). Of the total 166 final instars collected from large and small natural tree holes, 25 adults emerged from holes of 1 l or less in volume of which 15 were male and 10 were females ($P = 0.42$, binomial test). Of the 141 adults emerging from holes greater than a liter, 60 were males and 81 were females ($P = 0.09$). Grouping the holes into size classes of 3 l or less (29 males:29 females,

Table 1
Results of the predator swamp experiment using 9-l tubs

Clutch size	N	# successful	# of survivors when successful
With predators			
20	7	2	1.0 \pm 0 ^a
100	10	4	2.0 \pm 0.29 ^a
Without predators			
20	10	10	3.3 \pm 0.4 ^b
100	9	9	6.9 \pm 0.7 ^c

Successful clutches were those that produced at least one surviving offspring. Letters designate means that are significantly different ($P < 0.05$).

$P = 1.0$) and over 3 l (46 males:62 females, $P = 0.28$) did not change the conclusion that mothers did not adaptively bias the sex ratio of their eggs. Moreover, pooling survivors of the siblicide experiment with those from natural tree holes only strengthened the conclusion that sons had lower survivorship than daughters (126 males:164 females, $P = 0.03$).

Do excess siblings increase size or development rate of survivors in large holes?

The single-foundress nonpredated 9-l tubs with 100 neonates produced about twice the number of adults as did those with only 20 neonates (Table 1, $t = -4.60$, $P = 0.0003$). Interactions were not significant ($P > 0.20$ for all) and were eliminated from the analysis below. As seen in Figure 4, offspring from 20-neonate clutches were larger than those from 100-neonate clutches (wing: $F_{1,75} = 8.25$, $P = 0.005$ and abdomen: $F_{1,75} = 4.51$, $P = 0.04$), but development time did not differ between treatments ($F_{1,75} = 1.89$, $P = 0.17$). Males were larger than females (wing: $F_{1,75} = 37.8$, $P < 0.001$ and abdomen: $F_{1,75} = 45.96$, $P < 0.001$) and took longer to develop ($F_{1,75} = 4.6$, $P = 0.03$). Males from the 20-neonate clutches were larger than those in the natural population (wing: 1-tailed $t = 2.3$, $P < 0.05$ and abdomen: $t = 2.84$, $P < 0.05$). Females had longer abdomens (1-tailed $t = 2.52$, $P < 0.05$) than the wild population but not longer wings (1-tailed $t = 0.96$, $P > 0.2$). The largest male from the 9-l tubs achieved a wing size 1.15% of the largest male from the 0.6-l pots in the siblicide experiment. In contrast, the maximum gain for females emerging from large tubs was only 1.07% of the largest females from small pots.

When multiple females shared a large nursery, of the offspring that survived to emergence, those from clutches of 50 or more neonates were no larger than those from smaller clutches ($t = -0.31$, $P = 0.76$, $N = 15$ males; $t = -0.33$, $P = 0.75$, $N = 15$ females). Figure 5 shows the combined data on neonate input from the 9-l unshared nurseries in the current study and the shared 9-l nurseries from Fincke and Hadrys (2001). Although there was a positive correlation between the total number of neonates a tub received and the number of emerging larvae, the maximum number of adults produced was only 11.

Do excess siblings satiate intraguild predators?

Within a month, the larval dragonflies in the predator treatments cannibalized each other until their numbers were reduced from 5 per 9-l tub to a mean of 2.4 ± 0.17 per tub. On average, these *T. dentata* remained in the tubs for a total of 138.7 ± 41.5 days (range = 74–193 days), reaching a size of

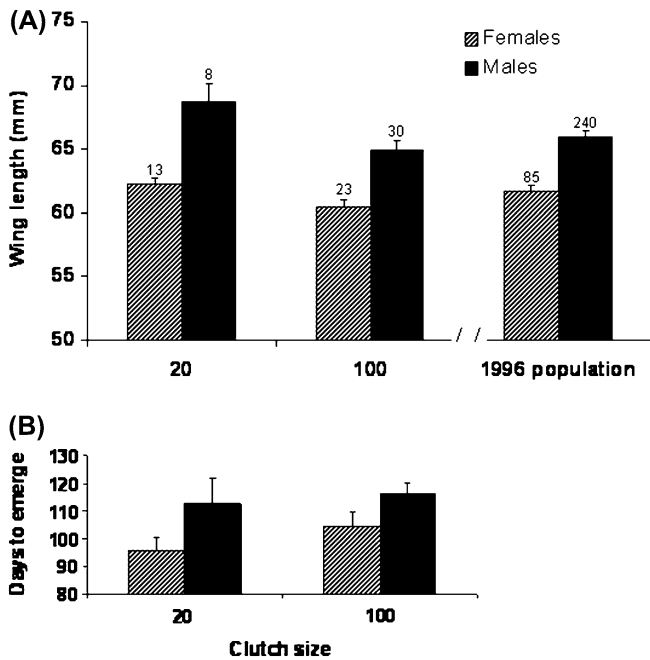


Figure 4
Surviving offspring from 9-l predator-free control replicates of the predator swamp experiment. (a) Mean \pm SE wing length; sample sizes are above error bars; natural population is shown for comparison. (b) Mean \pm SE development time of survivors.

36.4 ± 0.25 mm ($N = 10$) before emerging. Whereas all the 20- and 100-neonate controls produced multiple *Megaloprepus* adults, only 35% of the predator treatments produced one or more larvae (Table 1). In the presence of *Tr. dentata*, clutches of 100 were no more likely to produce at least one survivor than those of 20 ($\chi^2 = 0.01$, degrees of freedom [df] = 1, $P = 0.90$). Of the predator treatments that produced at least one surviving offspring, the 100-neonate clutches produced no more adults than did the 20-neonate clutches (Wilcoxon 2-sample test, $P = 0.20$).

The nonpredator controls produced more survivors than the 6 replicates with dragonfly predators that produced at least one *Megaloprepus* ($t = 7.15$, $P < 0.001$). In 4 of the latter 6 replicates, the successful *Megaloprepus* were detected as small larvae shortly before the emergence of dragonfly predators.

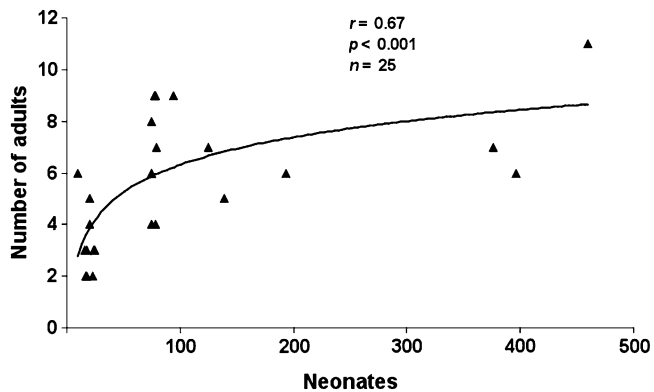


Figure 5
Number of adults emerging from 9-l tubs as a function of total neonate input. r value refers to correlation using the log of neonate numbers.

One *Megaloprepus* coexisted with a single dragonfly. In only 1 of the 6 replicates did the surviving *Megaloprepus* larva coexist with multiple (i.e., 4) large dragonfly larvae.

Do excess siblings function as an insurance policy?

As shown in Table 2, clutches of 2 neonates failed to produce an adult more often than those with 25 or more neonates ($\chi^2 = 4.9$, $df = 1$, $P = 0.03$). However, the failure rate of 25-neonate clutches was no greater than that of 50- or 100-neonate clutches ($\chi^2 = 2.78$, $df = 2$, $P = 0.25$). Of the 36 clutches that failed to produce an offspring, more than half failed when the sole remaining larva was less than 10 mm in size; clutches of 25 or greater offered insurance against this nonpredator mortality ($\chi^2 = 5.1$, $df = 2$, $P = 0.02$). In only one case of the latter, the disappearance of young larvae (< 4 mm) could be attributed to predation, namely by two 5-mm *D. auratus* tadpoles found during the census. In a few failed clutches with medium-sized larvae and even some successful ones, the largest remaining individual found was missing caudal lamellae, evidence of interference by siblings.

Unexpectedly, 22% of the failures occurred when the sole surviving larvae were between 20 and 22 mm in size. In all but 2 of these, the larva disappeared completely between censuses. The exceptions were a 17.8-mm sole occupant that disappeared on the next census, leaving some of its legs, and a large larva found in 2 pieces along with a small unidentified brown frog in the cup. The same species of frog (but never its tadpoles) was present at 6 other pots, one of which was also missing its larva. A ctenid spider was present at 3 pots missing larvae.

DISCUSSION

My results indicated that excess siblings functioned to produce larger surviving offspring, but this maternal advantage of sibling cannibalism was found only for the small-hole treatments. Although tree holes of a liter or less comprise about 60% or more of the available nurseries on BCI, they produce only a minority of the *Megaloprepus* recruits in each generation (Fincke 1992b, 2006). In both years, adults (especially males) from the sibicide treatments were larger than those unable to cannibalize siblings. In all cases, the sole surviving larva was among the first larvae entering a pot, one of which eventually eliminated all others. Under natural conditions in which more than one female laid eggs in small holes, this priority effect would result in an effectively unshared nursery, monopolized by offspring of the first mother to find the hole.

Table 2
Number of successful and unsuccessful clutches from small pots in the sibicide advantage experiment

	Clutch size (# of neonates)			
	2	25	50	100
N	56	49	53	33
Produced one offspring	40	41	43	31
Produced no offspring	16	8	10	2
Size at disappearance:				
<10 mm	10	5	5	0
$\geq 10 < 20$ mm	2	3	3	0
> 20 mm	4	0	2	2

The largest size before which the larva was found missing is given for the 36 failed clutches.

Two possible mechanisms might explain the above siblicide advantage to increase the size of emerging offspring: 1) siblings function as packets of stored food or 2) siblings function as multiple mouths of variable sizes that enable the surviving larva to increase its feeding efficiency before cannibalizing its last sibling. The first mechanism, known as the “icebox” hypothesis (Mock and Parker 1997, also referred to as the “lifeboat mechanism,” van den Bosch et al. 1988), predicts that siblings should only be eaten when other food is scarce. The second mechanism, which I call the “multiple mouths” hypothesis, derives from the dynamics of larval siblicide. Among a single cohort of *Megaloprepus* that hatch on the same day, a size hierarchy is established within a few days of hatching. Neonates feed on cladoceran and other prey too small to be eaten by larger siblings. With abundant prey, *Megaloprepus* exhibit size-specific foraging, preferentially taking the largest available prey (Fincke et al. 1997). Thus, the largest larva in a pot might have refrained from eating smaller siblings, thereby exploiting a greater range of prey size than would be possible than if it consumed siblings as small prey. My results offered tentative indirect support for the multiple mouths hypothesis. The sole survivors coexisted with siblings that were larger than the typical mosquito prey (i.e., 3–5 mm), often refraining from eating the last of their siblings until the survivors reached about 50–70% of their final instar size, after the fastest period of growth (see Fincke 1992c; Fincke et al. 1997). To directly test whether a survivor increased its feeding efficiency by farming smaller siblings, I would have had to control for the absolute amount of food present in siblicide treatments and controls. Unfortunately, this could not be done in my field experiments but could be tested under laboratory conditions that would afford greater control over available prey.

Conflict between parents and offspring (Godfry and Parker 1992) appeared to be lowest in the small nurseries, where siblicide maximized the size of the sole surviving offspring, in the best interest of both the survivor and its parents. Only rarely did a smaller sibling gain priority over a larger one, an event that would conflict with the parental interest of producing an offspring in the fastest time possible. However, conflict between the cannibalized offspring and the parent seems to explain why the advantage of siblicide was relatively modest. Doubling or even quadrupling a clutch of 25 resulted in no additional size gain for the survivor, likely due to interference competition among offspring, evidenced by finding large larvae lacking caudal lamellae. Moreover, survivors were generally smaller than the average male or female in the wild population. Hence males from small holes were unlikely as competitive as males in the population at large. The exceptions were males in 1996, when nutrient input to the pots was abnormally high, a result that emphasizes the importance of knowing natural alternative prey densities when evaluating the effects of cannibalism. For example, Church and Sherratt (1996) concluded that cannibalism increased larval survivorship of *Toxorhynchites*, a predatory mosquito. However, the levels of alternative prey at which their results were significant were so low that none of the cannibals survived to emergence, raising doubts about the maternal fitness advantage of cannibalism in that system under natural conditions.

Results from large holes revealed additional constraints on the use of excess offspring to increase the quality of surviving offspring. Contrary to the siblicide advantage hypothesis, in the 9-l nurseries with a single foundress, survivors of both sexes from 100-neonate clutches were smaller than those from 20-neonate clutches. Surprisingly, sibling competition resulted in a trade-off between offspring size and number; the 20-neonate clutch produced on average one final instar per 2.7 l (Table 1) and never more than 4, albeit very large off-

spring. The mean density of final instars in the 100-neonate treatment was one per 1.3 l similar to that of large natural holes (Fincke 1998). Interestingly, surviving individuals in 100-neonate treatments were unable to reduce their density further, which would have increased a survivor's body size (Figure 4) and a male's fitness. Because the size of offspring emerging from the 100-egg clutches did not differ from the average adult size in the wild population and mothers faced sharply diminishing returns on increases in clutch size above about 10 eggs per liter (Figure 5), the equilibrium density of the 100-neonate treatment may be close to that at which the number and size of offspring is optimal for maternal fitness. If true, then parental interests would appear to trump those of individual offspring. Finally, as expected, in large 9-l nurseries shared by multiple foundresses, mothers were unable to affect the size of surviving offspring by increasing their clutch size.

Contrary to results from other odonates (e.g., Claus-Walker et al. 1997) and invertebrates (e.g., Wissinger et al. 2004; Roy et al. 2007), sibling cannibalism did not reduce development time of the survivors (here, conservatively estimated as the maximum possible time). Nevertheless, the trend was in the expected direction; body size of both sexes was inversely related to development time (Figure 1), and cannibals were larger than siblings unable to cannibalize. I suspect that development time was unnaturally prolonged during the unusually dry el Niño year of 1997, when many larvae in replacement replicates were initiated in late wet season, and consequently developed during the prolonged dry season, when levels of mosquito prey were typically low.

The female-biased sex ratio of survivors in the small pots and from both large and small natural tree holes suggested that male larvae suffered greater mortality than female larvae. In the more benign conditions of the predator swamp controls, sex ratios were 50:50, and then, males took longer to emerge than females. Emergence from large natural tree holes was female biased, the opposite of that expected if mothers preferentially laid male eggs in large holes (which produce large sons favored by sexual selection). Hence, I concluded that females *Megaloprepus* were unable to adaptively bias offspring sex. However, molecular markers that identify the sex of eggs are required to rigorously test the assumption of an unbiased primary sex ratio of eggs laid by females. As is the case in natural tree holes (Fincke 1992b), males gained a disproportionately greater size advantage relative to females when they developed in large tubs as opposed to the small pots (compare Figures 3a and 4a). Because males do not reject small females as mates, but small males are inferior in defending territories and hence, rarely mate (Fincke 1992b), *Megaloprepus* parents gain less fitness from small sons than from small daughters. Hence, the inability of a mother to preferentially allocate male offspring to large nurseries is an additional constraint on an adaptive maternal sex allocation strategy.

Excess offspring did not satiate intraguild dragonfly predators (for a contrasting example, see Klingenberg and Spence 1996). In only 1 of the 6 predator replicates did a surviving *Megaloprepus* coexist with multiple predators as might be expected if excess siblings functioned to satiate preexisting predators. Moreover, a 5-fold increase over a clutch of 20 did not increase the survivorship odds, and even when the 100-neonate treatment produced surviving *Megaloprepus*, only one more offspring survived (Table 1), a meager return on a female's investment. The appearance and disappearance of *Megaloprepus* larvae greater than 5 mm suggested that it was the timing of the larva's entry or its small size rather than predator satiation that enabled coexistence with the dragonfly larvae similar to the case when the preexisting predators were conspecifics (Fincke and Hadrys 2001). In my predator swamp experiment, the time span over which *Megaloprepus* entered

the hole (here, standardized to 44 days) sometimes enabled one or more late-arriving larvae to coexist with or avoid a predator if they hit a window of opportunity by entering shortly before the predatory dragonfly larvae emerged. In the presence of larger conspecifics, smaller *Megaloprepus* larvae “freeze” and consequently grow more slowly (Fincke 1999; see also Ferris and Rudolf 2007; Johansson and Crowley 2008), which may have resulted in late-arriving survivors remaining small until the dragonfly larvae emerged. Furthermore, the pattern of natural egg hatch is not evenly distributed across the range of hatching days as might be expected if large clutches evolved to satiate dragonflies or other intraguild predators. Presumably in response to the strong benefit of priority, 75% of the eggs within a given clutch typically hatch within 2 weeks of the first egg that hatches (Fincke and Hadrys 2001). Finally, a female *Megaloprepus* has about a 75% chance of encountering preexisting conspecific larvae in a large tree hole compared with only about a 50% chance of laying into a large hole with dragonfly larvae, even though the latter, if present, persist longer (Fincke 1992c).

The number of eggs needed to compensate for nonpredator mortality, such as complications during molting, was greater than 2 but no more than 25 neonates. Clutches of 50 were no better insurance against early mortality (i.e., that occurred before siblicide reduced a clutch to a sole survivor of 14 mm, on average), even though a clutch of 100 reduced the risk of early mortality to zero. In all but one case, early mortality was attributed to nonpredator effects on survivorship. The 20% mortality rate of late instar larvae (Table 2) was higher than that found among sole occupants of natural tree holes (see Fincke 1999) whose rough and sometimes convoluted interior likely provide larvae more protection from predators outside of the nursery. Low oxygen levels in the small pots may have resulted in larvae resting close to the water surface, increasing their risk of being grabbed by ctenid spiders (see Fincke 1992b) or other terrestrial predators. Although several frogs are known to develop in tree holes on BCI (Fincke 1998), I have never seen the unidentified frog in the current study around natural tree holes on BCI.

In conclusion, my results suggested that the optimal clutch size for maximizing the number of surviving offspring should be that which results in the successful hatching of no more than 25 neonates in small holes and more than 20 but not much more than 100 in large 9-l holes or roughly 10 eggs per liter. The latter is consistent with the previous finding that a clutch of at least 50 eggs maximizes hatching asynchrony, the best predictor of a mother's fitness (Fincke and Hadrys 2001). However, to produce some optimal number of male offspring above the size threshold at which they are competitive in territorial encounters, a female *Megaloprepus* may have to lay twice the number of eggs she would if she could adaptively control offspring sex ratio. This may explain why females often lay more than 50–100 eggs in large tree holes. Alternatively, large holes may simply be effectively rare, such that large clutches reflect the time it takes a female to find such a resource, as predicted by optimality theory (see Parker and Courtney 1984).

A more certain conclusion from the current study is that, for *Megaloprepus*, the value of siblicide as an adaptive maternal strategy is considerably constrained by both its larval ecology and its adult behavior. In small holes, the maternal investment of viable excess eggs that hatch into food for successful siblings is analogous to trophic eggs provided by other insect mothers in low food environments (e.g., Kudo and Nakahira 2004; Perry and Roitberg 2005). However, because the form of food a *Megaloprepus* mother provides is itself cannibalistic, her investment is more constrained by larval competition. Interestingly, among poison frogs, Brown et al. (2010) found that production of trophic eggs was favored in a species that uses

small nutrient-poor pools in bromeliads, whereas a congener that uses larger pools lacks this form of maternal care, presumably because larger nurseries provide sufficient nutrients to prevent offspring starvation. In contrast, the advantage of excess maternal investment by *Megaloprepus* mothers in large holes is constrained by reproductive parasitism resulting from multiple mothers laying eggs into the same nursery.

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