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Life History Comparison of Two Green Lacewing Species *Chrysoperla johnsoni* and *Chrysoperla carnea* (Neuroptera: Chrysopidae)

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ABSTRACT We investigated the life histories of two green lacewing species, *Chrysoperla johnsoni* Henry, Wells, and Pupedis from western North America, and *Chrysoperla carnea* (Stephens) (Neuroptera: Chrysopidae) from western Europe in the laboratory. There were both similarities and differences in their life history characteristics. *C. johnsoni* exhibited a significantly longer developmental time for egg, first instar, and pupal stage than *C. carnea. C. carnea* exhibited a significantly shorter egg to adult developmental time than *C. johnsoni*. Except for the pupal stage, the survival of all other life history stages was not species-specific. All *C. carnea* pupae were able to develop into adults, whereas only 92% of adult eclosion was observed from *C. johnsoni* pupae. There was no difference in egg to adult survival between the two species. Adult longevity was not species- or gender-specific. Sex ratio of emerged adults was ≈50% in both species. *C. johnsoni* had a longer preoviposition period than *C. carnea*, while the oviposition period was similar for both species. *C. carnea* had higher lifetime fecundity and fertility than *C. johnsoni*, as measured by total number of eggs laid and production of fertile eggs, respectively. Egg viability did not differ between the two species. Intrinsic rates of increase (r_m) for *C. carnea* and *C. johnsoni* were 0.161 and 0.132, respectively. All lacewings used in this experiment were laboratory reared under environmental conditions similar to field as possible. This is the first available information on the life history parameters of *C. johnsoni*.

KEY WORDS green lacewing, biological control, life history, biology, intrinsic rate of population increase

Green lacewings (Neuroptera: Chrysopidae) are important predators of arthropod pests (Ridgway and Kinzer 1974, Ridgway and Murphy 1984). They are found in many horticultural and agricultural cropping systems, including vegetables, fruits, nuts, fiber and forage crops, ornamentals, green house crops, and forests (Ridgway and Kinzer 1974, Ridgway and Murphy 1984). Green lacewings are important both in the context of indigenous natural enemies as well as augmentative release programs (Nordlund et al. 2001, Pappas et al. 2011). Natural populations of chrysopids can be augmented by inoculative or inundative releases (Ridgway and Jones 1969, Nordlund et al. 2001). Worldwide they rank as some of the most commonly used and commercially widely available natural enemies (Tauber et al. 2000). The major predatory impact of green lacewings occurs during their predatory, polyphagous larval stage, as most adult chrysopids are free living and feed on honeydew and pollen (New 1975, Principi and Canard 1984, Stelzl and Devetak 1999, Pappas et al. 2011). Lacewing larvae have effective prey-searching strategies and are voracious predators of insect and mite eggs and a wide spectrum of soft-bodied insects including aphids, caterpillars, cicadellids, psyllids, coccids, thrips, mealybugs, and other arthropods including mites (Ridgway and Murphy 1984, Hagley and Miles 1987, Borror et al. 1992, Senior and McEwen 2001).

It is important to have life history information about natural enemies to successfully use them in biological control and integrated pest management (IPM) programs. In this study, we compared the life histories of two green lacewing species from different continents. The European species, *Chrysoperla carnea* (Stephens), is considered to be an important green lacewing species and has frequently been used as a model insect for understanding beneficial arthropods (Henry et al. 2001). It has been mass-reared and released in croplands all over the world, including North America (Henry et al. 2001). *Chrysoperla johnsoni* Henry, Wells and Pupedis is a North American green lacewing species that is very similar in appearance to *C. carnea* (Henry et al. 1993, Wells and Henry 1994, Henry and Wells 2007). It is one of the common green lacewing species found in the western United States, including Washington, Oregon, Idaho, California, and Arizona (Henry 1993; Henry et al. 1993, 2013).

Currently, there is no information on the life history of *C. johnsoni*, although the life history of *C. carnea* s. lat. has been widely studied throughout the world. If *C. johnsoni* has suitable life history characteristics to be

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an efficient generalist predator as *C. carnea*, there is a potential for it to be an effective natural enemy in conservation biological control. Hence, information on the development, reproduction, and survival of *C. johnsoni* is important if we are to understand its effectiveness as a generalist predator either as naturally occurring populations or augmented releases in western U.S. agricultural systems. The current study measures the life history of *C. carnea* and *C. johnsoni* in the laboratory.

Materials and Methods

C. *johnsoni* and *C. carnea* Colony Rearing. Colonies of *C. carnea* and *C. johnsoni* were maintained at 23°C, 50–60% relative humidity (RH), and a photoperiod of 16:8 (L:D) h in the laboratory (www.youtube.com/watch?v = 4ahDEimhDCk). The *C. carnea* colony was initiated with commercially purchased larvae (BioBest, Leamington, ON, Canada), and the *C. johnsoni* colony was initiated using field-collected larvae from pear orchards in Hood River, OR (summer 2010 and 2011). The species identity of both species was confirmed by song analysis (Henry et al. 2013). Adults of each species were reared in an open-top glass aquarium (26 by 30 by 50 cm) (Aqua Culture [size 10], Wal-Mart, Bentonville, AR) with a wire mesh lid (http://www.glasscages.com). To facilitate egg laying, the opening at the top of the aquarium was covered with a piece of cheesecloth (56 by 92 cm) (#90, 17.3 by 14.2 threads per cm, http://www.onlinefabricstore.net) and secured with the wire mesh screen top. Artificial diet consisting of chicken eggs (whole egg plus one egg yolk), honey (30 g), fructose (20 g), wheat germ (50 g), dry brewer's yeast (30 g), condensed milk (15 ml), and water (drinking, de-ionized, or distilled) (45 ml) (Vogt et al. 2000) was prepared in the laboratory and used to feed the adults. A thin layer of the adult diet was applied to the nonabsorbent side of a piece (12 by 24 cm) of Benchkote surface protector paper (Fisherbrand, Fisher, Pittsburgh, PA) and attached to the interior wall of the adult cage using masking tape (Cinta Adhesiva [Premium], Ace Brand Hardware Corp., Oak Brook, IL). Water was provided by a15-cm medium cotton wick (Ref. No. 201208, Richmond Dental, Charlotte, NC) inserted through the lid of a clear plastic vial (5 cm in diameter, 196 ml) filled with water. Adults were provided with food, water, and cheesecloth cover three times a week.

Immature green lacewings are cannibalistic (Duelli 1981, Rojht et al 2009); thus, each larva was reared individually in a covered 28-ml translucent plastic portion cup (Georgia Pacific Dixie, Atlanta, GA). Before use, a thin layer (0.5 cm) of fluon (Insect-a-Slip) (#2871B, Bio Quip Products, Inc., Rancho Dominguez, CA) was applied to the interior upper top of the portion cup to prevent the larva from crawling onto the lid and getting crushed when the lid was opened. To avoid static electricity, which impacted larval transfer when opening the lid for feeding, cardboard placement, and monitoring of development, the exterior wall of the cup was wiped with cotton cloth treated with a static guard (Static Guard, Alberto-Culver USA Inc., Melrose Park, IL). For larval rearing, newly laid eggs (<24 h old) were collected from the cheesecloth used in the adult oviposition cages. The cheesecloth was placed on top of the adult cage 24 h before the egg collection and then removed when it was time to collect eggs. Eggs were individually plucked by their stalks from the cloth using fine forceps and placed singly in portion cups and secured with lids. Approximately 0.2–0.3 g of *Ephestia kuehniella* Zeller (Lepidoptera: Pyralidae) eggs (purchased from Beneficial Insectary, Redding, CA, and stored in a freezer at −6°C) were placed in each cup as food for the hatched larva. The cups were arranged in batches of 30 in cup-trays (# 9040, Bio-Serv, Frenchtown, NJ). When the larva molted to the third instar, a piece of corrugated cardboard (1.5 by 1.5 cm) was provided as a substrate for pupation. Food was replaced two times a week until cocoon formation. Emerged adults from each species were released into their respective adult colonies. Each week, 60 eggs (≈24 h old) were collected and reared individually to the adult stage as described above, to maintain the colonies.

Rearing Lacewings for Egg Collection. Approximately 400 newly laid eggs (<24 h old) of each species were collected from the cheesecloths placed in *C. johnsoni* and *C. carnea* colony cages. The collected eggs were reared individually to obtain adult lacewings needed to produce eggs for life history studies. Emerged adults were reared in species-specific adult cages that were similar to the colony cages. Rearing procedures for the larvae and adults were similar to the colony-rearing procedures described above.

Development and Survival. Experimental eggs for life history measurements were collected from the cheesecloth covers that were newly placed 24 h before the egg collection. Collected eggs were placed individually in portion cups. The rearing procedure was similar to the colony larval-rearing procedure described above. There were 15 replicates per species, and each replicate consisted of six eggs. All experiments were conducted in an environmental growth chamber (Percival I-36LLVLC8, Percival Scientific Inc., Perry, NC) at 23°C, 60% RH, and a photoperiod of 16:8 (L:D) h. Cups were checked daily for egg hatch, larval and pupal development, and adult emergence. Mortality of each life stage was recorded. Larval stages were fed two times a week with *E. kuehniella* eggs (≈0.2–0.3 g/larva). When the larva reached the third instar, a piece of corrugated cardboard was added to the cup as a pupation substrate. The adult lacewings that emerged were sexed by observing the tip of the abdomen of each individual (Vogt et al. 2000). Sex ratio of the emerged adults was calculated as the percentage of females ([females/(males + females)] × 100%).

Emerged adults were placed individually in custom-made glass arenas covered with cheesecloth lids (15 by 15 cm) secured with rubber bands. These glass arenas consisted of a glass cylinder (Wheaton Glass Warehouse, Millville, NJ) standing on a glass plate (Cincinnati Gasket, Cincinnati, OH) (7.5-cm-diame-

ter by 6-cm-tall by 3.2-mm-thick glass cylinders and 9 by 9 cm and 2.3-mm-thick glass plates) and were used as experimental arenas in the adult reproduction and longevity experiments. To hold each cylinder upright on the glass plate, four aluminum strips (1 cm in width by 3 cm in length by 1.5 mm in thickness and bent to 90° angle) were glued with hot glue to the side of the lower exterior cylinder wall corresponding to the four corners of the plate. Small binder clips were used to hold the metal strips to the glass plate floor. Adult diet was provided to emerged adults as a thin layer spread on a piece of nonabsorbing cardboard material (2.5 by 5.5 cm) attached to the arena wall using a piece of reusable adhesive putty (DAP Bluestik, DAP products Inc., Baltimore, MD). All adults were provisioned with distilled water using a small (38 mm in diameter) piece of water-soaked cotton roll (Richmond Dental, Charlotte, NC) placed in a clear capless disposable microcentrifuge tube (1.7 ml; Cat. No. 20170-575; VWR International, LLC, Radnor, PA) attached to the bottom of the arena with a piece of putty.

Reproduction and Adult Longevity. Newly emerged virgin females and males from the above study (<24 h old) were used to determine reproductive capacity and longevity of *C. carnea* and *C. johnsoni*. Each female was paired with a newly emerged adult male of its own species. Fifteen paired females (replicates) per species were used in the experiment. All arenas were placed in an environmental growth chamber under controlled conditions as above. The preoviposition (number of days from adult emergence to oviposition) and oviposition (number of days from beginning to end of oviposition) periods, number of eggs laid, and adult mortality were recorded. Food and water was provided to adults (as mentioned above) three times a week until they died.

Intrinsic Rate of Increase. The intrinsic rate of increase (r_m) was calculated using the equation $r_m = 0.74 (\ln M_d)/T$, in which T is time from birth to onset of reproduction, M_d is the reproductive output per original female during a period equal to T, and 0.74 is a correction factor (slope of the fitted linear regression line) (Wyatt and White 1977). This equation was initially proposed for the estimation of the intrinsic rate of natural increase (r_m) of aphids and has been shown to be equally applicable to the calculation of r_m of tetranychid mites (Wyatt and White 1977). It was derived from the r_m calculation method of Birch (1948), which has been widely used to calculate r_m of many insect species (Lawo and Lawo 2011). It is a simple and convenient way of calculating the r_m when assessing life table parameters for insect species such as soft scales (Hemiptera: Coccidae) and phylloxera (Hemiptera: Phylloxeridae) with long life cycles (Amarasekare and Mannion 2011, Lawo et al. 2011). Although it is unknown whether this equation has been tested to calculate r_m of predatory insects, it has been tested for hymenopterous parasitoids and been proved that even though the parasitoids are biologically and ecologically different from aphids and mites, this equation can be applied to estimate their r_m with the minor changes of correction factor (Rongping and Smith 1993). In this study, we used the correction factor that was initially described by Wyatt and White (1977).

Age-structured matrix models of *C. carnea* and *C. johnsoni* were also developed using life history elements of survivorship, developmental rate, fecundity, and sex ratio to calculate the intrinsic rate of population increase (r_m). We used life history stages of egg, first to third instar, pupa (cocoon stage is referred to as pupal stage in this study, and it comprises both prepupal and pupal stages), preovipositing adult female, and ovipositing adult female to obtain the developmental time and survival of each life stage. Daily fecundity was obtained from eggs collected from adult females. Sex ratio was calculated from emerged adults. Pop Tools, an add-in for 32-bit PC versions of Microsoft Excel (version 97 and up) was used for the matrix model development and analyses (Hood 2011).

Statistical Analyses. The experiment was a completely randomized design. A one-way analysis of variance (ANOVA) was conducted using PROC MIXED for developmental time, survival, sex ratio, preoviposition and oviposition periods, fecundity, fertility, and egg viability (SAS Institute 1999). A two-way ANOVA was performed for adult longevity by gender (SAS Institute 1999).

Means were compared at $P \leq 0.05$ significance level (Least Square Means [LSMEANS] Test) for all experiments (SAS Institute 1999). Proportion of survival and sex ratio were arcsine square-root transformed to stabilize variances (Zar 1984) before ANOVA.

Insect Identification and Species Verification. Insect identification and species verification of C. *johnsoni* and *C. carnea* was provided by C. S. Henry of the University of Connecticut, Department of Ecology and Evolutionary Biology, Storrs, CT 06269.

Voucher Specimens. Voucher specimens of *C. carnea* and *C. johnsoni* were deposited in the entomology insect collection at Oregon State University, Mid-Columbia Agricultural Research and Extension Center, Hood River, OR 97031.

Results

Development. The life history stadia of these green lacewings include egg, three larval instars, and a pupal stage (cocoon stage is referred to as pupal stage in this study, and it comprises both prepupal and pupal stages). In this study, eggs hatched in ≈5–6 d. Developmental time of each larval instar was ≈3–4 d. The pupal stage had an 11–13 d developmental period. Egg to adult development time was ≈28–32 d.

There were significant differences in the developmental time of some of the life history stadia of *C. johnsoni* and *C. carnea* (Table 1). *C. carnea* had a significantly shorter developmental time for egg, first instar, and pupa than *C. johnsoni* (egg: $F = 14.01$; df = 1, 23; $P = 0.0011$; first instar: $F = 14.76$; df = 1, 23; $P = 0.0008$; pupa: $F = 8.82$; df = 1, 23; $P = 0.0069$). There was no difference between species in the developmental time of second and third instar larvae (second instar: $F = 2.62$; df = 1, 23; $P = 0.1193$; third instar: $F =$

Table 1. Mean number of days (±SEM) and survival (%) (±SEM) for each developmental stadium of *C. carnea* and *C. johnsoni*

Species	Stadia					Cumulative egg to adult
	Egg	First instar	Second instar	Third instar	Pupa	
Developmental Time (d) (mean ± SEM)[a]						
C. carnea	5.1 ± 0.0b	3.5 ± 0.1b	3.5 ± 0.1a	4.0 ± 0.1a	11.5 ± 0.2b	28.5 ± 0.3b
C. johnsoni	5.7 ± 0.2a	4.3 ± 0.1a	3.3 ± 0.1a	4.4 ± 0.3a	12.5 ± 0.2a	31.8 ± 0.5a
Survival (%) (mean ± SEM)[a]						
C. carnea	94.8 ± 5.2a	98.7 ± 1.3a	100.0 ± 0.0a	98.7 ± 1.3a	100.0 ± 0.0a	92.3 ± 5.2a
C. johnsoni	86.1 ± 5.7a	98.6 ± 1.4a	100.0 ± 0.0a	100.0 ± 0.0a	92.1 ± 3.5b	79.2 ± 6.8a

[a] Means within each developmental stadium for *C. carnea* and *C. johnsoni* followed by the same letters are not significantly different at $P > 0.05$ (LSMEANS Test).

1.95; df = 1, 23; $P = 0.1761$). Overall, *C. johnsoni* had a significantly longer (11.6%) egg to adult developmental time than *C. carnea* ($F = 39.5$; df = 1, 23; $P = 0.0001$).

Survival. Survival of eggs and the three larval stages was not different between *C. carnea* and *C. johnsoni* (Table 1). All *C. carnea* pupae were able to develop into adults compared with 92% of *C. johnsoni* pupae ($F = 5.83$; df = 1, 23; $P = 0.0241$). Egg to adult survival was not different between the two species ($F = 3.20$; df = 1, 23; $P = 0.0869$). Most of the larvae of both species survived to the next stadium, although only 86–95% of the eggs of either species survived to first instar. Egg survival impacted the egg to adult survival of both species.

Adult Sex Ratio. Adult sex ratio ([females/(males + females)] × 100%) was not significantly different between *C. carnea* and *C. johnsoni* ($F = 0.21$; df = 1, 23; $P = 0.6495$; Table 2).

Adult Longevity. Adult longevity was not species- or gender-specific ($F = 0.11$; df = 1, 33; $P = 0.7477$; Table 2).

Preoviposition and Oviposition Periods. *C. johnsoni* preoviposition period was ≈2 d longer than that of *C. carnea* ($F = 34.66$; df = 1, 25; $P = 0.0001$; Table 2). Oviposition periods were statistically the same for *C. carnea* and *C. johnsoni* ($F = 1.00$; df = 1, 24; $P = 0.3281$).

Lifetime Fecundity, Fertility, and Egg Viability. *C. carnea* had significantly higher fecundity than *C. johnsoni*, and lifetime fecundity of both species was >960 eggs per female ($F = 4.77$; df = 1, 19; $P = 0.0.0417$; Table 3). *C. carnea* also had higher lifetime fertility than *C. johnsoni* ($F = 5.98$; df = 1, 15; $P = 0.0273$). There was no significant difference in egg viability between the two species ($F = 0.43$; df = 1, 23; $P = 0.5168$).

Intrinsic Rate of Increase. The r_m of *C. carnea* and *C. johnsoni* using the equation $r_m = 0.74 (\ln M_d)/T$ were 0.161 and 0.132, respectively (Table 3). The r_m obtained from matrix models of *C. carnea* and *C. johnsoni* using Pop Tools software were 0.171 and 0.131, respectively (Table 3).

Discussion

This is the first comparative study on life history of *C. carnea* and *C. johnsoni* and provides new information on *C. johnsoni* development, reproduction, and survival. Results reveal similarities and differences in life history parameters of these two species and demonstrate that *C. johnsoni* shows strong fitness characteristics, indicating its suitability for use as a generalist predator.

Measurements of fundamental life cycle components are essential for understanding the population dynamics of *C. johnsoni.* Although we did not find significant differences between the two species for most life history fitness parameters, *C. carnea* seems to be more robust than *C. johnsoni* because of its significantly higher fitness characteristics, such as higher lifetime fecundity and fertility and shorter developmental time. These attributes may have contributed to the higher intrinsic rate of natural increase (*r*) of *C. carnea.* It is difficult to know whether the higher fecundity observed for *C. carnea* is a consequence of commercial rearing that results in selection for highly reproductive females when compared with recent field-collected and laboratory-reared *C. johnsoni* [e.g., as shown by Mohaghegh et al. (1999) and Oliva et al. (2011) in *Podisus nigrispinus* (Dallas) and lab-reared mosquitoes, respectively]. However, unlike *C. johnsoni*, *C. carnea* is a nomadic Palearctic species (Duelli 1981, Henry et al. 1993), so these differences in fitness

Table 2. Mean (±SEM) of sex ratio (%) (percentage of females), pre-oviposition and oviposition periods (d), and adult longevity (d) of *C. carnea* and *C. johnsoni*

Species	Sex ratio (%)[a,b]	Preoviposition period (d)[a]	Oviposition period (d)[a]	Adult longevity (d)[a,c]	
				Male	Female
C. carnea	54.4 ± 6.2a	4.2 ± 0.3b	45.6 ± 5.4a	59.4 ± 7.3a	51.7 ± 4.5a
C. johnsoni	47.4 ± 8.4a	6.6 ± 0.3a	52.4 ± 4.1a	68.3 ± 10.0a	65.1 ± 6.8a

[a] Means within each fitness parameter for *C. carnea* and *C. johnsoni* followed by the same letters are not significantly different at $P > 0.05$ (LSMEANS Test).
[b] Adult sex ratio (adults emerged from treated larvae) calculated as the percentage of females = ([females/(males + females)] × 100).
[c] Means between species and gender followed by the same letters are not significantly different at $P > 0.05$ (LSMEANS Test).

Table 3. Mean (±SEM) lifetime fecundity, lifetime fertility, and egg viability (%) of *C. carnea* and *C. johnsoni*

Species	Lifetime fecundity[a,b]	Lifetime fertility[a,c]	Egg viability (%)[a,d]	Intrinsic rate of increase (r_m)
C. carnea	1264.0 ± 99.5a	981.4 ± 92.5a	75.1 ± 3.3a	0.161[e] (0.171[f])
C. johnsoni	960.0 ± 97.2b	682.9 ± 76.9b	71.5 ± 4.7a	0.132[e] (0.131[f])

[a] Means within each fitness parameter for *C. carnea* and *C. johnsoni* followed by the same letters are not significantly different at $P > 0.05$ (LSMEANS Test).
[b] Lifetime fecundity = total number of eggs laid.
[c] Lifetime fertility = total number of eggs hatched.
[d] Egg viability (%) = [(Lifetime fertility/Lifetime fecundity) × 100].
[e] $r_m = 0.74 (\ln M_d)/T$ (T, time from birth to onset of reproduction; M_d, the reproductive output per original female during a period equal to T; and 0.74, correction factor).
[f] r_m calculated from the matrix model developed using Pop Tools.

parameters may simply be because of previously evolved species-specific attributes.

The r_m of *C. carnea* and *C. johnsoni* calculated from two different methods produced similar results. The calculated r_m for *C. carnea* agrees closely with the r_m calculated previously from a matrix model developed using Pop Tools (Hood 2011) in a life table response experiment to test side effects of pesticides on *C. carnea* (K.G.A. and P.W.S., unpublished data). Therefore, we are confident that the r_m value we obtained for *C. johnsoni* is as accurate as the r_m of *C. carnea.* Because ours is the first information available for r_m for *C. johnsoni*, we are unable to compare it with a reference value.

In this study, we found that the U.S. lacewing species *C. johnsoni* has the biological characteristics necessary to be a successful natural enemy similar to *C. carnea;* hence, releasing similar non-native sibling species in the western United States is perhaps neither required nor prudent. *C. johnsoni* and *C. carnea* belong to the *carnea* group because of their close resemblance to each other (Henry and Wells 2007). The *carnea* group has many cryptic lacewing species distributed throughout the world (Tauber and Tauber 1985, Henry and Wells 2007). Identifying biological species within the *carnea* group requires a combination of live insects, electronic equipment, and special training (Wells 1993, Henry and Wells 2007). Commercially purchased *C. carnea* can be a mixed species unless verified by special techniques. An alien lacewing species will not be an effective biological control agent if there is a native species that will do the same job just as well (Henry and Wells 2007). There is a risk involved in releasing *C. carnea* with common dangers of accidentally introducing other lacewing species and their establishment and reduction of closely related native species occupying the same niche (Henry and Wells 2007).

This laboratory experiment provides information needed to understand the life history of *C. johnsoni.* This information would be helpful in carrying out field studies to understand the field populations of *C. johnsoni.* With its high reproductive capacity, intrinsic rate of increase, egg viability that is similar to *C. carnea*, and ability to develop successfully in the laboratory, *C. johnsoni* has the characteristics and potential to be an efficient predator in the context of conservation biological control. These characteristics most likely contributed to *C. johnsoni's* abundance in the western United States (Henry 1993) where it is the most common green lacewing species collected from pear trees in Hood River, OR (K.G.A. and P.W.S., unpublished data). It also appears that *C. johnsoni* is a suitable candidate for mass-rearing and subsequent augmentative releases in western U.S. cropping systems.

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