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RELATIVE EFFECTS OF CLIMATE AND CROWDING ON WING POLYMORPHISM IN THE SOUTHERN GROUND CRICKET, *ALLONEMOBIUS SOCIUS* (ORTHOPTERA: GRYLLIDAE)

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ABSTRACT

Many factors determine the formation of flight wings in wing-polymorphic insects. Earlier studies on a cricket (*Gryllus firmus*) population producing spring and summer generations showed a declining frequency of macropterous, or long-winged, adults towards the end of a growing season. Numerous confounding factors can explain this seasonal decline, one of which is increasing mortality rates of juveniles that may otherwise emerge as macropterous adults. To test this hypothesis, we measured rates of juvenile mortality and adult macroptery in *Allonemobius socius* Scudder (Orthoptera: Gryllidae), an organism with a seasonal phenology similar to that of *G. firmus*. After rearing *A. socius* juveniles exclusively under "spring" versus "summer" conditions and at different population densities, we found that crickets reared in groups under "summer" conditions tended to emerge as macropters, with females being more likely than males to emerge long-winged. Juvenile mortality did not adequately explain the emergence pattern of macropters. Surprisingly, variation among families accounted for <1% of total variation in frequency of long-winged adults. Thus, seasonal climate, followed by population density, and then their interaction with each other appear to be the three major determinants of wing morph frequencies in *A. socius*. We discuss the possible adaptive significance of wing polymorphism in insects with respect to habitat persistence and mating success.

Key Words: migration, habitat persistence, polyphenism, crowding, wing dimorphism, plasticity

RESUMEN

Muchos factores determinan la formación de las alas de vuelo en insectos de alas polimórficas. Estudios anteriores sobre una población del grillo (*Gryllus firmus*) produciendo generaciones en la primavera y en el verano mostraron una frecuencia disminuyendo de adultos macrópteros, o de alas largas, acercándose al final de la estación de crecimiento. Numerosos factores componentes pueden explicar esta declinación estacional, uno de ellos es el aumento en la tasa de mortalidad de los juveniles que de otra manera emergerán como macrópteros adultos. Para probar esta hipótesis, nosotros medimos las tasas de mortalidad juvenil y la macropteria (el estado de alas largas) de los adultos en *Allonemobius socius* Scudder (Orthoptera: Gryllidae), un organismo con una fenología estacional similar a la de *G. firmus*. Después de criar los juveniles de *A. socius* exclusivamente bajo condiciones de "primavera" versus "verano" y en diferentes densidades de población, nosotros encontramos que los grillos criados en grupos bajo condiciones de "verano" tendían a emerger como macrópteros, y fué más probable que las hembras emergen con alas largas que los machos. La mortalidad juvenil no explicó adecuadamente el patrón de emergencia de los macrópteros. Sorprendentemente, la variación entre las familias contaba por <1% de la variación total en la frecuencia de adultos con alas largas. Así, el clima estacional, seguido por la densidad de la población, y después la interacción entre ellos parecen ser los tres mayores determinantes en la frecuencia de las diferentes formas de alas en *A. socius*. Nosotros discutimos el posible significado adaptivo derivado del polimorfismo de alas en insectos al respecto de la persistencia de habitat y el éxito en el apareamiento.

The independent evolution of wings among several animal taxa (Kingsolver & Koehl 1994) is due, in part, to the apparent benefits of flight. Flight-capable organisms can easily colonize pe-

ripheral areas of their current habitat, as well as migrate to more distant and, perhaps, novel environments in search of food and mates. By enhancing mobility and dispersal, flight undoubtedly

contributed to the remarkable diversification of insects (Roff & Fairbairn 1991; Rankin & Burchsted 1992; Kingsolver & Koehl 1994).

Developing and maintaining the flight apparatus, however, often carries a cost. For example, long-winged (or macropterous) females of the sand cricket, *Gryllus firmus*, reach reproductive age at a later date and have lower lifetime fecundities when compared to their short-winged counterparts (Roff 1990a). In the brown planthopper, *Nilaparvata lugens*, macroptery is associated with longer egg-to-adult development time and lowered male mating success (Novotny 1995). Such trade-offs between flight wings and other traits closely associated with fitness allows one to view flight ability as itself a fitness-determining trait along the same lines as growth rate and fecundity. Thus, not only is wing polymorphism interesting for its own sake, but also for its apparent ties to life history and life cycle evolution (Roff & Fairbairn 1991; Rankin & Burchsted 1992; Kingsolver & Koehl 1994; reviewed extensively in Dingle 1996).

Apart from being genetically determined (Masaki & Walker 1987; Mousseau & Roff 1989; Roff 1990a, 1990b), flight wings can develop in response to numerous environmental factors. For example, warm temperatures and long-day conditions typical of summer tend to produce macropterous adults, e.g., in crickets and grasshoppers (Tanaka 1978; see also Masaki & Walker [1987], and references therein) and in *Gerris* species (Vesäläinen 1978, in Dingle 1996). Conditions of crowding and food shortage also contribute to variation in the frequency of wing morphs in insect populations (Tauber et al. 1986; Walker 1987).

In their exhaustive survey of one population of the sand cricket, *Gryllus firmus*, Veazey et al. (1978) found that the frequency of macropterous adults caught in pitfall traps was lower in the summer than in the spring brood. However, such a pattern can be attributed to a number of confounding and interacting variables, including: (1) migration of flight-capable, macropterous adults away from the sampling site; (2) differential mortality of presumptive macropters and micropters, due perhaps to intraspecific competition for food or space; (3) increased predation by insectivores maturing later in the growing season; (4) shedding of flight wings by individuals that emerged earlier in the season as macropterous adults (though this phenomenon has not been reported for *G. firmus*); (5) a genetically fixed seasonal phenology for macropters and micropters, e.g. macropterous adults from only the spring brood always producing offspring that always emerge a year later (in the following spring) as long-winged adults; (6) the emergence of 2nd-generation, or summer brood, juveniles as short-winged rather than macropterous adults; and (7) a deficiency in the sampling methods used by Veazey et al.

(1978). Investigations since then have elaborated some of the genetic and physiological mechanisms that contribute to variation in *G. firmus* wing morph frequencies (Roff 1990a, 1990b; Zera et al. 1998). But surprisingly, very little empirical work has been done to tease out which ecological factors are most responsible for this pattern of naturally occurring wing polymorphism (cf. Roff 1994a; Crnokrak & Roff 1998).

The current study addresses the hypothesis that differential juvenile mortality explains variation in wing morph frequency in wing polymorphic insects (see Factor 2 above). Both spring and summer broods of the southern ground cricket, *Allanemobius socius* Scudder (Orthoptera: Gryllidae), occur at high densities throughout the southeastern region of North America, and experience a variety of seasonal temperatures and day-lengths associated with their widespread latitudinal and altitudinal distribution (Howard & Furth 1986; Mousseau & Roff 1989). Moreover, like *G. firmus*, both field and laboratory populations of *A. socius* produce a mixture of short- and long-winged adults, with the latter form also exhibiting variation in flight propensity (A.E.O., personal observation). Thus, *A. socius* is useful for investigating the genetic and environmental factors responsible for variation in wing morph frequencies in natural insect populations.

Materials and Methods

Cricket Stocks

All individuals used in this experiment were first-generation, laboratory-reared descendants of crickets caught as juveniles from a wet, grassy field adjacent to a greenhouse on the University of South Carolina—Columbia. Before the start of the experiment, all crickets and their eggs were incubated, reared, and maintained under conditions simulating a hot, summer day (31°C, 15 h day-length, >60% relative humidity) in Columbia, South Carolina, U.S.A. (Wood 1996). Voucher specimens have been sent to J. C. Morse of the Clemson University Arthropod Collection.

Experimental Design

Individually reared juveniles from 23 full-sibling families were housed in clear plastic petri plates (diameter = 100 mm) each provisioned ad libitum with pulverized cat chow, chopped carrots, water, and shredded unbleached paper towels for cover. Group-reared juveniles from 31 full-sibling families were housed in 9 × 9 × 8 cm clear plastic cages that were similarly provisioned. Left-over cat chow and carrots were changed every 2 to 3 days.

We used a double split-brood design, in which one-half of a cohort of newly hatched juveniles from each family was randomly assigned to a

“summer” (31°C, 15 h day-length) rearing environment, while the other half was reared in a “spring” (24°C, 11 h day-length) environment. Within a seasonal environment, group-reared juveniles were then assigned to either a high population density (14 to 21 juveniles per cage) or low population density (3 to 6 juveniles per cage) treatment. Among-family variation in maternal fecundity, egg-hatching rate, and juvenile survivorship precluded assignment of exactly equal numbers of individuals to replicate cages (in each population-density treatment). Because *A. socius* will consume dead conspecifics when available, we minimized scavenging by removing dead individuals without replacement. All surviving juveniles were reared to adulthood exclusively in the environment to which they were initially assigned.

Scoring Macroptery and Juvenile Survivorship

Only macropterous adults possess the ivory-colored flight wings that extend from beneath the beige-black tegmina, or outer wings (Fig. 1). We scored adults <3 d after the final molt as macropterous if they emerged with flight wings intact. In group-reared crickets, incidence of macroptery was then calculated as the number of macropterous adults divided by the total number of adults from a given replicate cage. Similarly,

incidence of macroptery in crickets reared in isolation was calculated as the number of macropterous adults divided by the total number of adults that were reared in petri plates within a given seasonal environment.

Juvenile survivorship of group-reared crickets was calculated as the number of emerging adults (regardless of wing morph) divided by the total number of nymphs from a given replicate cage. Similarly, juvenile survivorship for crickets reared in isolation was calculated as the total number of petri plates that yielded (long- or short-winged) adults divided by the original number of petri plates used to rear cricket nymphs individually.

Statistical Analyses

Because the macroptery data did not satisfy the normality assumptions for valid parametric analyses, we turned to a nonparametric, van der Waerden normal scores analysis to test for sex-specific differences in proportion of macropters for each treatment. We performed the NPAR1WAY procedure in SAS For Windows, Version 6.12 (SAS 1989). As discussed fully in Conover (1999), a van der Waerden analysis achieves asymptotic relative efficiency, or A.R.E. (~statistical power), comparable to that of para-

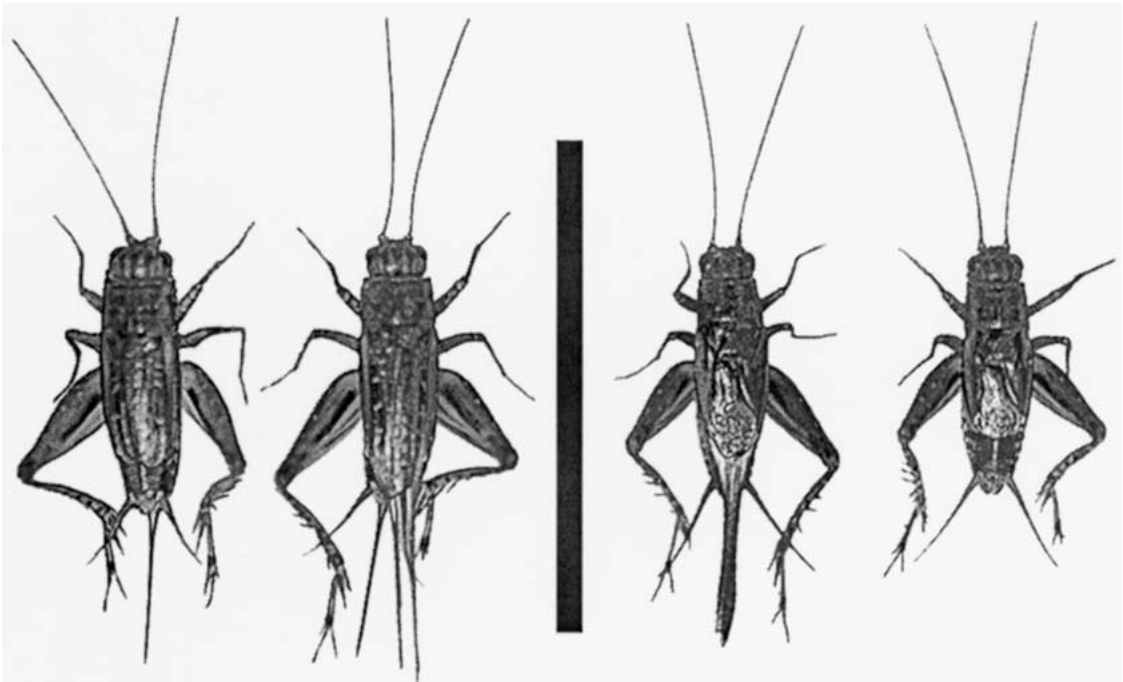


Fig. 1. Wing polymorphism in *A. socius*. Females are distinguished from males by the presence of a sword-like ovipositor protruding from the posterior end of the abdomen. Note the flight wings in long-winged adults—the two individuals flanking the vertical black bar—extend from beneath the darker tegmina (i.e., outer wings). Length of vertical black bar is 20 mm.

metric statistical tests, e.g., F-test, when data satisfy normality assumptions, and greater A.R.E. when data are non-normal. We adjusted the resulting probability values using the sequential Bonferroni method in order to maintain an experiment-wide Type I error rate of $\leq 5\%$ for all pairwise comparisons (Rice 1989).

We partitioned total variance in both the frequency of macropters and juvenile survivorship via the restricted maximum likelihood (REML) method available in the VARCOMP procedure of SAS for Windows 6.12 (SAS 1989). Although the VARCOMP procedure does not provide P-values for estimated variance components, it allows a quantitative description of importance of each biotic and abiotic factor to observed macroptery patterns in *A. socius*. The choice of REML as a method for estimating variances is justified by its common use in modern quantitative genetic studies, e.g., Shaw (1987), Meyer and Hill (1991), and Ferreira et al. (1999).

RESULTS

Compared to the spring rearing treatment, the summer rearing environment tended to produce a higher proportion of long-winged adults (Fig. 2). Differences in macroptery rates between the sexes appeared only at high population densities (Table 1), with more females than males emerging as long-winged adults (Fig. 2).

The largest contributing factor to variance in macroptery rates was juvenile rearing climate, followed by the interaction of rearing season with population density (Table 2). Family origin (nested within population density since not all of the families were represented in the population-density manipulations) contributed $<1\%$ to variance in macroptery rates (Table 2).

Juvenile survivorship was high across all rearing treatments. As expected, crickets reared in isolation had higher survival rates ($\sim 85\%$ in both spring and summer rearing environments) than those reared in groups, with high population densities resulting in the lowest survival rates (between 58-78%). At a given population density, juvenile survival rates were similar for both sum-

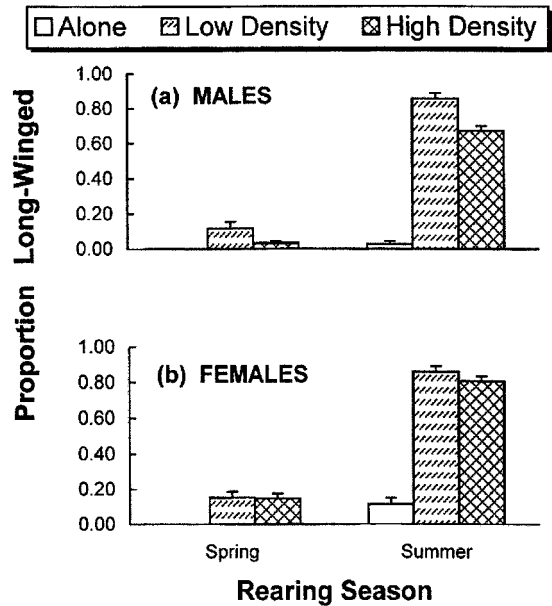


Fig. 2. The effects of rearing season and population density during juvenile development on mean (\pm SE) incidence of macroptery in *A. socius* males and females. All juveniles reared in isolation and under spring-like conditions emerged as short-winged adults.

mer and spring rearing conditions (Fig. 3), suggesting no effect of seasonal climate and no interaction between seasonal climate and population density on juvenile survivorship (Table 2).

We found that the largest contributors to variation in juvenile survivorship (aside from experimental error) were population density and family origin (Table 2). There were no significant interactions between either of these factors with rearing season.

DISCUSSION

Both seasonal climate and population density during juvenile development affect frequency of macropters in *A. socius*. In our study, high temperatures and long day-lengths typical of the summer

TABLE 1. EFFECT OF REARING ENVIRONMENT ON THE DIFFERENCE IN THE PROPORTION OF LONG-WINGED FEMALES TO LONG-WINGED MALES.

	Spring-reared ^a	Summer-reared
Reared alone ^b	N/A	4.739
Reared at low population density	1.569	0.001
Reared at high population density	13.692*	13.139*

^aNumbers are test statistics, T1, from a nonparametric van der Waerden one-way normal scores analysis (Conover 1999) with one degree of freedom.

^bAll juveniles reared alone under spring-like conditions emerged as short-winged adults.

*Statistically significant at experiment-wide $\alpha = 5\%$.

TABLE 2. RESTRICTED MAXIMUM-LIKELIHOOD VARIANCE-COMPONENTS ESTIMATION OF RELATIVE CONTRIBUTION TO INCIDENCE OF LONG-WINGED, EMERGING ADULTS AND TO JUVENILE SURVIVORSHIP.

Observed variance component	Incidence of macroptery	Juvenile survivorship ^a
(1) Rearing season	40.1%	0.9%
(2) Population density	12.2%	38.8%
(3) Family (population density) ^b	0.1%	21.5%
(4) Sex (population density, family) ^c	0.8%	N/A
Interaction of 1 and 2	25.5%	0.0%
Interaction of 1 and 3	1.1%	0.0%
Interaction of 1 and 4	1.1%	N/A
Error	19.1%	38.8%
Total	100%	100%

^aSex of newly hatched juveniles could not be determined non-invasively because secondary sexual traits appear only in the middle-to-late stages of development. Hence, variance in juvenile survivorship due to sex and to interaction between sex and rearing season cannot be estimated.

^bFamilies experienced both rearing seasons, but not all population-density treatments.

^cBecause a few families produced single-sex progeny, sex is nested within family, which in turn is nested within population density.

season led to greater numbers of macropterous males and females (Fig. 2; see comparable results in Tanaka 1978). Population density greatly compounded the effect of the summer rearing environment in producing macropterous adults, especially with crickets reared in groups (Fig. 2). At low population densities, the proportion of macropterous adults increased as climate changed from spring-to summer-like (Fig. 2; but see Walker 1987). At

high population densities, we found a reduced proportion of macropterous adults (Fig. 2), a result that may be due to intraspecific competition for space and nutrients (discussed in Walker [1987] and Zera & Tiebel [1988]).

Differences in juvenile survivorship among our rearing treatments do not adequately explain the variation in incidence of macroptery. Though juvenile survivorship appeared inversely related to population density in the rearing cages, the differences in juvenile survivorship among the population-density treatments were similar between spring- and summer-rearing treatments (Fig. 3), suggesting that seasonal climate had little effect on *A. socius* juvenile survivorship. More importantly, the pattern of juvenile survivorship did not parallel that of adult macroptery rates among treatment groups (Fig. 2). Thus, wing length variation in *A. socius* appears to be a response to seasonal climate and population rearing density (Fig. 2), and does not appear to reflect differences in juvenile survivorship.

The extent to which population density affects the timing of flight wing removal in *A. socius* is not known. It is possible that macropterous *A. socius* adults shed their flight wings <3 d post-eclosion, which would have introduced a downward bias in our method of scoring macroptery. In other words, the incidence of long-winged morphs in our high cage-density treatment may actually be higher than was observed in this study (Fig. 2). Notwithstanding this potential bias, the observed pattern of juvenile survivorship does not parallel that of macroptery rates.

Probabilistic models, e.g. in Roff (1975), “adaptive coin-flipping” of Kaplan and Cooper (1984), and “stochastic polyphenism” of Walker (1986), have been proposed to explain wing polymorphism in crickets and other flight-capable insects.

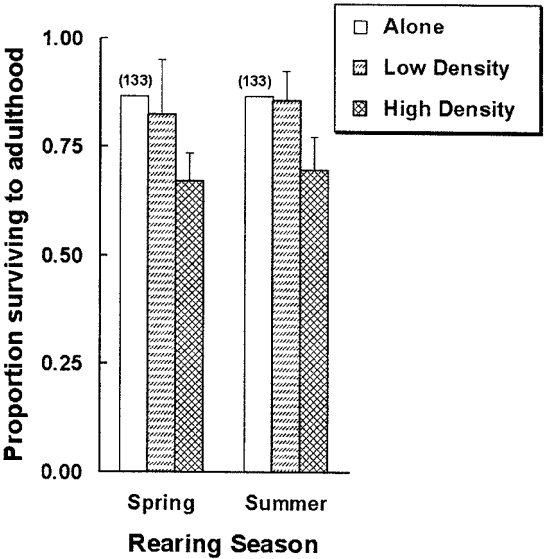


Fig. 3. Juvenile survivorship of *A. socius* at different rearing densities and seasonal climates. Column height represents the mean (\pm SE) proportion of newly hatched juveniles that eventually emerged as adults. Numbers in parentheses above each clear column indicates total number of individually reared *A. socius* juveniles scored for that treatment.

One simple prediction under probabilistic theory is that the proportion of long-winged adults will reflect the probability of those individuals experiencing a future environment that selects for flight. Unfortunately, the present results cannot confirm such predictions, nor can they validate probabilistic models in general because environmental variation in the wild (as experienced by *A. socius* juveniles of the parental generation in this study) would have been impossible to mimic in a laboratory setting. Critical tests of probabilistic models about macroptery may inevitably involve the use of more closely monitored rearing environments and isogenic lines.

The greater propensity of females than males to possess flight wings (Fig. 2) may be attributed, in part, to sex-specific reproductive behavior. In many crickets, sexually receptive females often travel some distance to locate the stationary, calling male (Loher & Dambach 1989). Presumably, the fitness gain from flight-aided mate-locating behavior more than compensates for the cost of developing the necessary flight apparatus in *A. socius* females.

Macroptery in male crickets, on the other hand, can impose a tremendous fitness cost in that macropterous males tend to be less successful than their short-winged counterparts in attracting females (Crnokrak & Roff 1995), although this has not been tested for *A. socius*. As well, male crickets probably have greater mating success when they remain in their natal habitat rather than fly to unknown destinations where mating opportunities may be scarce or absent (Walker 1986).

The greater incidence of macroptery in *A. socius* females than males might also reflect the role of habitat persistence in maintaining wing dimorphism (Denno et al. 1991; Roff 1994b). To the best of our knowledge, the field from which we collected crickets was watered daily and mowed every 3-6 wk during late-spring and throughout the summer months by campus grounds crew. The environmental disturbance caused by mowing could have augmented selection for late-summer dispersal, especially in female *A. socius*, since females can store sperm from previous matings. In such case, a female cricket has little reproductive "need" for males once she has reached the less affected periphery of her natal habitat. Thus, in patchy and temporary environments, natural selection might have acted to maintain the flight apparatus in a flight-capable female just long enough for her to escape a disturbed or deteriorating patch of habitat, and to colonize areas more conducive to oviposition and optimal development of her offspring during the regular growing season (Southwood 1962; Dingle 1996; Denno et al. 1991; Roff 1994b).

The apparent synergy between summer climate and moderate-to-high rearing density in producing long-winged *A. socius* suggests that, in

bivoltine populations, long-wingedness is more common in the 2nd generation than in the first. In the bivoltine life cycle of *A. socius*, the 1st generation is comprised of individuals that had survived the past winter as diapausing eggs and then hatched out in spring. These 1st generation juveniles develop to adulthood through spring and early summer, by which time they mate and produce non-diapausing eggs that hatch out immediately (Walker & Masaki 1989; Mousseau & Dingle 1991; Olvido et al. 1998). Thus, 2nd generation juveniles appear likely to experience the macroptery-inducing summer season, as well as higher population density resulting from the presence of 1st generation adults and other newly hatched 2nd generation juveniles. Experiments are under way to assess this prediction.

On the other hand, Veazey et al. (1976) showed that macroptery rates declined from summer through autumn in a Florida population of *G. firmus*. Proximate mechanisms that can explain such a pattern, e.g. predation pressure and migration of macropters from field sites, have yet to be fully explored in this and other insects.

In this current study, we found no evidence that would suggest differential juvenile survival affects macroptery rates in *A. socius*. That is, differences in wing morph frequencies between spring- and summer-reared full-siblings of *A. socius* are not likely due to differences in juvenile mortality, but instead may result from a response to seasonal climate and population density during juvenile growth. However, the generality of emergence patterns in *A. socius*, like in *G. firmus*, will require further and more detailed investigation of seasonal phenology in other wing polymorphic organisms.

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