Habitat Use, Phenology, and Gregariousness of the Neotropical Psocopteran Cerastipsocus sivorii (Psocoptera: Psocidae)

by

Gustavo S. Requena¹, Bruno A. Buzatto² & Glauco Machado³

ABSTRACT

A field account of the behavior and ecology of the gregarious and corticolous psocopteran Cerastipsocus sivorii is presented. The study was conducted from February to November 2003 on the campus of the Universidade Estadual de Campinas, state of São Paulo, southeastern Brazil. There was a strong positive correlation between the relative abundance of host tree species and their respective frequency of occupation by *C. sivorii*, suggesting that trees were used according to their availability in the study site. The phenology of C. sivorii is seasonal, with nymphs peaking in May and October, and teneral adults peaking in February, June, and October. The factors determining the variation in population density in psocopterans are poorly understood, but our data show that climatic variables, such as rainfall and temperature do not influence the phenology of C. sivorii. The individuals of C. sivorii remain together through the entire nymphal phase, resting, moving on the tree surface (mainly on bark, but occasionally on leaf petioles) and grazing in groups. Teneral adults within an aggregation usually dispersed a few days after molting. Nearly 50% of the aggregations had up to 90 individuals, but large groups presenting 240 individuals or more were also frequent, comprising 10% of all aggregations found in the field. When a moving aggregation encountered another one, they occasionally either interchanged individuals or merged into a single large group. More rarely, large aggregations divided into two groups. We suggest that gregariousness in C. sivorii is a behavioral strategy that confers protection against predation and reduces body water loss.

Keywords: Aggregation, Brazil, Cerastipsocinae, habitat selection, lifecycle, social behavior, selfish herd, urban ecology

¹Programa de Pós-graduação em Ecologia e Conservação de Recursos Naturais, Universidade Federal de Uberlândia, Uberlândia, MG, Brazil

²Programa de Pós-graduação em Ecologia, Universidade Estadual de Campinas, Campinas, SP, Brazil

³Museu de História Natural, Instituto de Biologia, Universidade Estadual de Campinas, CP 6109, CEP 13083-970 SP, Brazil Corresponding author; email: glaucom@unicamp.br

INTRODUCTION

The order Psocoptera comprises a group of insects with nearly 4,500 described species in 371 genera and 41 families (Lienhard & Smithers 2002). Psocopterans are recognized by their long antennae, membranous wings held roof-like over the abdomen, and body ranging from 1 to 10 mm in length (Mockford 1993). Most studies with psocopterans are taxonomic or deal with the biology of species with economic importance (e.g. Rees & Walker 1990; Wang *et al.* 2001; but see New 1987). Information on the ecology of species inhabiting trees, shrubs, and leaf litter is scarce and anecdotal, particularly for tropical species (see review in Thornton 1985). The great majority of published studies focus on the entire community of psocopterans, and detailed descriptions of the biology of individual species are generally neglected (e.g. Broadhead 1958; New 1970; Turner & Broadhead 1974; Baz 1991; but see Baz 1992; Broadhead & Wapshere 1966).

Psocopterans are present in a wide range of habitats, including human habitations. Some species occur in leaf litter, on rocks and inside caves, on herbs, grasses, and bark of trees, and a few species in moss. There are species living in bird, mammal, and termite nests, and some may even be found in the feathers and fur of living endothermic vertebrates (Thornton 1985). Habitat use is somewhat related to taxonomic groups so that representatives of certain families are exclusively associated with a specific type of substrate (Mockford 1993). Species of the family Mesopsocidae, for instance, are generally associated with open bark surfaces (Mockford 1993), whereas species of the families Prionoglarididae and Psyllipsocidae are primarily cave-dwellers (Thornton 1985).

The life cycle of most psocopterans involves an adult period of sexual inactivity (including the teneral period), courtship, copulation, oviposition, eclosion, and four to six nymphal instars (Mockford 1993). Phenology patterns vary greatly in the order; while most species overwinter as eggs in temperate regions (Broadhead 1958; Broadhead & Wapshere 1966; New 1970, 1991), in tropical and subtropical areas, species may occur as nymphs and adults throughout the year (Turner 1974; Turner & Broadhead 1974; Wolda & Broadhead 1985; New *et al.* 1991).

Some species are gregarious, forming mixed groups of winged or wingless adults and nymphs of various instars that congregate in damp areas (Daly *et al.*

1998). The role of gregariousness in psocopterans is unknown, though some authors suggest that this behavior is a strategy to reduce the effect of bark gleaning predators (New & Collins 1987). The genus *Cerastipsocus* (Psocidae: Cerastipsocinae) occurs throughout the Americas (Mockford 1981), and some species form large, dense groups that remain together after maturity, but disperse soon after adults lose tenerality (Mockford 1993). This paper provides a field account of the behavior and ecology of *Cerastipsocus sivorii*, with emphasis on habitat use, phenology, and gregariousness. This is the first detailed study on the autoecology of a neotropical psocopteran and one of the few to discuss the meaning of gregariousness in the order.

MATERIALS AND METHODS

Study site

The study was carried out on the campus of the Universidade Estadual de Campinas (22°49'S, 47°04'W), São Paulo state, southeastern Brazil. Annual rainfall in the site is about 1,360 mm and mean temperature is 20.6°C (data from the Instituto Agronômico de Campinas). The climate is seasonal, with a warm-wet season from September to April and a cold-dry season from May to August (more details on the study area in Vanini *et al.* 2000). Field observations were conducted on large lawns with sparse ornamental trees (including native and exotic species) among the buildings of the campus.

Behavioral and phenological data

Since *C. sivorii* occurs mainly on open-bark surfaces, 92 trees around the Biology Institute building were individually labeled and inspected *ad libitum* from March to July 2002. Further data were regularly taken once a month from February to November 2003, totaling nearly 100 h of fieldwork. Observations were generally taken in the morning (from 08:00 h to 12:00 h) or in the afternoon (from 14:00 h to 18:00 h), when individuals were active and could be observed without artificial light. Behavior was continually recorded when predation events or agonistic interaction were detected (cf. Martin & Bateson 1986). After predation events the individuals involved were collected for later identification. Voucher specimens were deposited at the Museu de História Natural (ZUEC) of the Universidade Estadual de Campinas and Museu de Zoologia (MZSP) of the Universidade de São Paulo, Brazil.

The bark of each tree was scanned from the ground to 2 m during approximately 90 s, and the number of nymphs and adults was counted. It was also recorded whether the individuals were isolated or aggregated and if they were under direct sun light or under shadow. Population size, considered as the total number of nymphs and teneral adults found per month in the 92 trees, and the number of aggregations found per month were correlated with both monthly rainfall and temperature using a Spearman rank correlation. The number of individuals per aggregation was compared between seasons using a Mann-Whitney test.

Habitat characterization

The 92 labeled trees were identified to species and trunk perimeter at breast height (PBH) was measured with a tapeline. These trees were ranked according to their relative abundance in the study site, from 1 (the least abundant) to 7 (the most abundant). Trees with the same number of individuals received the same ranking. The same procedure was used to rank the trees according to the number of individuals occupied by psocopterans. To test if individuals of C. sivorii select certain species as host trees, the data on the rankings of tree abundance and tree occupation were correlated using a Spearman rank correlation. A positive correlation indicates that the host trees are occupied in the same proportion as their relative abundance, whereas a negative correlation or no correlation suggest some kind of host tree preference. Additionally, the influence of the PBH on the probability of colonization by psocopterans was investigated using a simple logistic regression, in which PBH was the independent variable and the absence (0) or presence (1) of psocopterans on the trees were the dependent variables. PBH was also correlated with the total number of individuals found per tree during the entire study period using a Spearman rank correlation.

All labeled trees were classified in two discrete deciduousness categories: trees that lost the majority of their leaves in the cold-dry season were considered "deciduous" whereas trees that did not lose the majority of their leaves in any season were considered "perennial". A chi-square test was used to examine whether psocopterans occurred preferentially on any of these two deciduousness categories. This test was performed using only the aggregations of the dry-cold season because this is the period when deciduous trees

lose their leaves, and thus the psocopterans are exposed to sun incidence or rain on the bark.

RESULTS

Habitat use

From the 92 marked trees belonging to 39 species, 50 (26 species) were occupied at least once by individuals of *Cerastipsocus sivorii* during the study period (Table 1). There was a strong positive correlation between the relative abundance of host tree species and their respective frequency of occupation by psocopterans ($r_s = 0.71$; p < 0.001; n = 26 species). This suggests that the trees were used according to their availability in the environment. PBH did not affect the probability of psocopteran occurrence ($\chi^2 = 1.847$; n = 92; odds ratio = 1.007; p=0.174). Moreover, considering only the trees that were occupied at least once by psocopterans, there was no correlation between the total number of nymphs observed in those trees and PBH ($r_s = 0.060$; n = 50; p = 0.660). Finally, the frequency of occurrence of psocopterans on deciduous trees (46%) did not differ from that of non-deciduous trees (34.6%) ($\chi^2 = 1.207$; d.f. = 1; p = 0.272).



Fig. 1. Seasonal variation in the population of the psocopteran *Cerastipsocus sivorii* from February to November 2003 on the campus of the Universidade Estadual de Campinas, São Paulo State, Brazil. Dashed line = number of nymphs per tree; solid line = number of teneral adults per tree.

Table 1. List of trees present in the study site on the campus of Universidade Estadual de Campinas, São Paulo state, Brazil. The number of individuals of each species and the number of trees occupied at least once by the psocopteran *Cerastipsocus sivorii* are followed by their respective rankings in brackets. See text for details.

Trees	Number of individuals in the study site	Number of individuals occupied by psocopterans
ANACARDIACEAE		
Mangifera indica L.	1(1)	1(1)
ANNONACEAE	. ,	
Rollinia laurifolia Schltdl.	1 (1)	1 (1)
BIGNONIACEAE		
Tabebuia chrysotricha (Mart. ex DC.) Standl.	10 (6)	1 (1)
<i>Tabebuia heptaphylla</i> (Vellozo) Toledo	4(4)	2 (2)
<i>Tabebuia impetiginosa</i> Martius ex DC	3 (3)	0 (0)
Tabebuia sp.1	1 (1)	0 (0)
Tabebuia sp.2	1(1)	0 (0)
BORAGINACEAE		
<i>Cordia superba</i> Cham.	1 (1)	1 (1)
CLUSIACEAE		
Kielmeyera lathrophyton Saddi	2 (2)	1 (1)
COMBRETACEAE		
Terminalia argentea (Cambess.) Mart. & Zucc.	2 (2)	0(0)
EUPHORBIACEAE		
Joannesia princeps Vell.	1(1)	0 (0)
LAURACEAE	- (-)	
Nectandra megapotamica Spreng	2 (2)	2 (2)
FABACEAE	. (.)	<i>i</i> .
Adenanthera pavonina L.	1(1)	1 (1)
Albizia niopoides (Spruce ex Benth.) Burkart	2 (2)	2 (2)
Caesalpinia echinata Lam.	3 (3)	0 (0)
Caesalpinia peltophoroides Benth	5 (5)	3 (3)
Centrolobium tomentosum Guill. ex Benth.	4(4)	3 (3)
Cutoria faircouaiana R.Howard	1(1)	I(1)
Copaijera langsaorijit Dest.	2(2)	0(0)
Laga wind drieg (Voll Cone) Martine	1(1)	1(1)
Inga cyunarica (ven.Conc.) Martius	2(2)	2(2)
Low chosen the much langer and Hosel	$\frac{2}{2}$	0(0)
Machaerium nictitans (Vell Conc.) Benth	$1(1) \\ 1(1)$	0(0)
Myrawlan peruiferum (L) Harms	1(1) 1(1)	$\Gamma(1)$
Peltophorum dubium (Spreng) Taub	1(1) 18(7)	0(0)
Platycyamus regnellii Benth	10(7) 1(1)	10(4)
Platymiscium floribundum Vogel	1(1)	$\Gamma(1)$
Samanea tuhulosa (Benth) Barnehy & IW Grimes	1(1)	0(0)
MALVACEAE	1 (1)	0(0)
Eriotheca candolleana (K. Schum.) A. Robyns	3 (3)	2(2)
Pachira aquatica Aubl.	2(2)	$\frac{2}{1}$ (2)
MELIACEAE	- (-)	I (I)
<i>Cedrela fissilis</i> Vell.	2 (2)	1 (1)

Table 1. (continued) List of trees present in the study site at the campus of Universidade Estadual de Campinas, São Paulo state, Brazil. The number of individuals of each species and the number of trees occupied at least once by the psocopteran *Cerastipsocus sivorii* are followed by their respective rankings in brackets. See text for details.

Trees	Number of individuals in the study site	Number of individuals occupied by psocopterans
MORACEAE		
<i>Ficus luschnatiana</i> (Miq.) Miq. MYRTACEAE	2 (2)	1 (1)
Syzygium cuminii (L.) Skeels.	2 (2)	1 (1)
Syzygium jambos (L.) Alston RUBIACEAE	1 (1)	1 (1)
Genipa americana L. RUTACEAE	1 (1)	1 (1)
Citrus aurantifolia x reticulata VERBENACEAE	1 (1)	1 (1)
Callicarpa bodinieri Leveille	1 (1)	0(0)
Vitex montevidensis Cham.	1 (1)	1 (1)
TOTAL	92	50

Phenology

There was a marked seasonality in the number of individuals of *C. sivorii* found on trees throughout the year. The abundance is higher for nymphs in May and for teneral adults in June (Fig. 1). The number of nymphs decreased drastically in August and then increased again, reaching another peak in October (Fig. 1). For teneral adults there were two other peaks, one in October and another in February (Fig. 1). Nymphs occurred through the whole study period, whereas teneral adults were recorded from February to July and in October (Fig. 1). Teneral adults were always less abundant than nymphs, but they were particularly scarce in March and April (Fig. 1). Three females were observed ovipositing on terminal branches of trees in June 2003. Population size was not correlated with the mean monthly rainfall ($r_s = -0.046$; n = 10; p = 0.899) nor with the mean monthly temperature ($r_s = -0.224$; n = 10; p = 0.534).

Gregariousness

Nymphs of *C. sivorii* were always found in aggregations on the bark surface of trees. Some small aggregations were composed of nymphs of the same instar, but usually the larger aggregations were composed of nymphs in different instars and some teneral adults (Fig. 2). From a total of 167 aggregations,



Fig. 2. Aggregations of the psocopteran *Cerastipsocus sivorii* formed by nymphs of different instars and teneral adults.

27.5% were composed exclusively of nymphs and 72.5% were composed of both nymphs and teneral adults. The number of individuals per aggregation was similar between the cold-dry season (median = 90; range = 6 - 1172; n = 102) and the warm-wet season (median = 85; range = 14 - 623; n = 65) (U = 3452.5; p = 0.755). Nearly 50% of the aggregations had up to 90 individuals, but large groups presenting 240 individuals or more were also frequent, comprising 10% of all aggregations found in the field (Fig. 3). No association between the number of aggregations per month with rainfall (r_s = -0.036; p = 0.922; n = 10 months) and temperature (r_s = -0.270; p = 0.450; n = 10 months) was found.

The individuals of *C. sivorii* remain together through the entire nymphal phase, resting, moving on the tree surface (mainly on bark, but occasionally on leaf petioles) and grazing in groups (Fig. 4). Teneral adults within an aggregation usually disperse a few days after molting. Resting aggregations were found both on open areas of the trunk surface and inside bark fissures (Figs. 5, 6).



Fig. 3. Distribution of the number of individuals per aggregation of the psocopteran *Cerastipsocus sivorii* in the campus of the Universidade Estadual de Campinas, São Paulo state, Brazil.

The individuals of cohesive resting groups remain in a perpendicular position relative to the bark surface, grasping the substrate with their mouthparts, and making contact with other individuals (Fig. 5). For aging groups were observed grazing on crustose and foliaceous lichens with the individuals distributed more sparsely on the substrate (Fig. 4). Only 4.7% of all aggregations were found on sunny areas of the trees, and in most of them, the individuals were moving to shaded areas. While moving, the group became less cohesive, but all individuals walked toward the same direction. When a moving aggregation encountered another one, they occasionally either interchanged individuals or merged into a single large group (Fig. 7). More rarely, large aggregations divided into two groups.

Sixteen predation events were observed and the predators included: *Gastro-micans* sp. (Araneae: Salticidae) (n = 1), *Heza insignis* (Heteroptera: Reduviidae) (n = 1), *Ectatomma* sp. (n = 1), *Odontomachus* sp. (n = 11), *Pachycondyla* sp. (n = 1), and *Pseudomyrmex* sp. (n = 1) (Hymenoptera: Formicidae). In each event the predators consumed only one psocopteran. After predators contacted the aggregations, psocopterans dispersed fast, showing bursts of non-directional running. In most cases, the preyed psocopteran was captured



Fig. 4. Foraging group of the psocopteran Cerastipsocus sivorii grazing on lichens.

at the periphery of the aggregation or while fleeing alone. In one ant attack, different workers of *Odontomachus* sp. belonging to the same colony preyed upon 11 psocopterans in one aggregation. The first capture of an individual from the periphery of the aggregation caused the dispersion of the group, and the following ten captures were on fleeing individuals. Aggregations also rapidly dispersed upon the disturbance caused by blowing, but the individuals usually recomposed the group after 2 - 30 minutes. Some stray individuals, however, joined other aggregations nearby.

DISCUSSION

Habitat use

Most species of the families Psocidae, Mesopsocidae, and Pseudocaeciliidae are found mainly on bark and only rarely feed or oviposit elsewhere (New 1970). Thornton (1985) showed that different species of arboreal psocopter-



Fig.5. Individuals of the psocopteran *Cerastipsocus sivorii* resting on open bark. Note that most of them remain on a perpendicular position relative to the bark surface and maintain full body contact with neighbors.

ans present different degrees of host tree preference. In Europe, bark-living psocopterans show a clear ecological separation between species inhabiting coniferous and species inhabiting broad-leaf trees (Thornton 1985). Three closely related species of *Lachesilla* (Lachesillidae) are associated with *Syagrus* palms in the Brazilian Cerrado (New 1971). For many species, however, there is no indication of host tree preference, which seems to be the case for *Cerastipsocus sivorii*. This species was found in 67% of the tree species present in the study area, including some ornamental and/or exotic species (e.g. *Citrus aurantifolia*, Rutaceae). Since the diet of tropical species of psocopterans includes a greater variety of food items than the diet of temperate species (Broadhead 1958), food may be less important in influencing distribution patterns of bark psocopterans over different tree species in the tropics.



Fig.6. Individuals of the psocopteran Cerastipsocus sivorii resting inside a bark fissure.

There is little information on the influence of structural features of the host trees on the occurrence of bark-living psocopterans. Although Broadhead & Wapshere (1966) suggest that the bark texture of larch trees may account for the patterns of preference of two species of *Mesopsocus* (Mesopsocidae), no quantitative information was provided. Turner (1974) showed that denser foliage provides the psocopterans with greater protection from the rain. Finally, Baz (1995) suggests that the composition of psocopteran communities may be determined by the architectonic structure and taxonomical proximity of the host plants. In our study, features such as tree size (PBH) and deciduousness did not affect either the probability of occurrence or the density of *C. sivorii* nymphs on the host trees. Since nymphs of this species are unable to move from one tree to another (pers. obs.), the distribution pattern of individuals in the population is probably generated by ovipositing females, which do not seem to select host tree species.

Phenology

Temperate forest psocopterans typically have only one or two generations per year, with a long wintering dormant stage (eggs or nymphs, Turner 1974).



Fig. 7. Aggregation of nymphs of the psocopteran *Cerastipsocus sivorii* just after fusion. Note that on the left side of the picture there are large nymphs and on the right size the nymphs are smaller.

The peak of adult activity is generally restricted to the summer when adults mate and oviposit (Mockford 1993). The phenology of tropical psocopterans may be also seasonal, but different species have their peaks of adult activity at different times of the year; only a few species have a uniform distribution of adults over the year (Wolda & Broadhead 1985). Although our study focused mainly on nymphs, and not on flying adults, we found that the phenology of *C. sivorii* is highly seasonal. However, we did not find evidence that the variation in population density is related to climatic variables.

Nymphs of *C. sivorii* were present in the population year round, with two clear peaks of abundance, one at the beginning of the cold-dry season (May) and another at the beginning of the warm-wet season (October). The pattern



Fig. 8. Nymphs of the psocopteran *Cerastipsocus sivorii* on a roughened area of bark with many lenticels. On this type of substrate psocopterans are probably cryptic to visually oriented predators.

of occurrence of nymphs in different instars throughout the year suggests that reproductive activity in *C. sivorii* occurs continuously and the population is composed of individuals from different cohorts. Similar results were obtained for the corticolous caeciliusid *Valenzuela equivocatus* in a forested area in Jamaica (Turner 1974). For *C. sivorii*, teneral adults were present most part of the year, with a clear peak in June, one month after the higher peak of nymphs. Probably during this month adults disperse from the aggregations and mate. Indeed, the few observations on females ovipositing occurred in June 2003. There are two smaller peaks of teneral adults in the population, one in the early and another one in the late wet-warm season (October and February, respectively); we believe that they also correspond to reproductive periods of *C. sivorii*.

Gregariousness

As others species of the genus *Cerastipsocus* (Mockford 1993), *C. sivorii* forms large, dense aggregations that remain together after adulthood, but

disperse soon after adults lose tenerality. Some of the aggregations were composed strictly of individuals of the same instar, suggesting that they were primary groups of siblings resulting from large egg batches, as it has been previously observed with other species of the families Psocidae (subfamily Cerastipsocinae) and Myopsocidae (New & Collins 1987). However, we also found many mixed aggregations composed of individuals in different instars. As far as we know, this is the first record for psocopterans of aggregations with mixed instars, which sometimes may reach enormous numbers of individuals (more than 1,000). These aggregations are likely formed by individuals from different egg clusters. Our observations on different groups merging into a single larger aggregation support this hypothesis.

Although many species of psocopterans live in groups (Daly *et al.* 1998), most reports of such behavior are anecdotal and the role of gregariousness in the group remains largely unexplored. New & Collins (1987) suggest that group living in psocopterans may be a defensive strategy against bark gleaning predators, such as spiders, ants, and some birds. According to these authors, group living may confer defensive advantages for an individual psocopteran in three different ways. First, the nymphs are probably cryptic to predators since they superficially resemble a roughened area of bark (Fig. 2F) or a fructifying patch of lichens. Second, once a large visually-oriented predator has detected the group it might be alarmed by the jerky, cohesive movements of the group, perhaps mistaking the whole aggregation for a single organism. Finally, the sudden dispersal of the prey in all directions after the predator strikes is likely to be distracting, perhaps resulting in improved chances of survival for the individual nymphs. All these defensive advantages may apply to aggregations of *C. sivorii*.

The majority of the *C. sivorii* aggregations were composed of individuals in different instars, and they were probably large groups of non-relatives formed by the fusion of small groups of relatives. In a large group, an individual pso-copteran may decrease the risks of being predated due to the dilution effect (*sensu* Krebs & Davies 1993). Moreover, first instar nymphs may hide among larger individuals of other instars (see Fig. 6), avoiding the periphery of the aggregation, where predation seems to be highest (Hamilton 1971). Indeed, all events of predation observed in *C. sivorii* were directed towards marginal or isolated individuals. Immediately after a predation event, individuals of the

attacked aggregation rapidly dispersed, indicating a possible damage released pheromone (*sensu* Chivers *et al.* 1996) or mechanically-transmitted alarm mechanism, the so called "Trafalgar effect" (Treherne & Foster 1981).

Psocopterans are extremely sensitive to dehydration and some species maintain body water levels by absorbing water vapor when air humidity is 60% or above; below this level, more water is lost and the individual usually dies after some minutes (Devine 1982; Rudolph 1982; Rees & Walker 1990). Therefore, another role for psocopteran aggregations may be the reduction of water loss, as already demonstrated for other insects (review in Danks 2002). We suggest that the highly cohesive resting formation of *C. sivorii* groups, with individuals close together in a perpendicular position relative to the bark (Fig. 5), decreases the exposure to dry air and reduces individual water loss. Moreover, during dry days (relative humidity from 31 to 51%), individuals were commonly found crowded inside bark fissures (Fig. 6), which may confer additional protection against harsh climatic conditions. Avoiding direct sun light incidence precludes *C. sivorii* from dehydration. More than 95% of all aggregations of this species were found on shaded areas of the tree trunks.

In conclusion, we suggest that gregariousness in *C. sivorii* is a behavioral strategy that confers protection against predation and reduces body water loss. Since psocopterans are very appropriate model organisms to test hypothesis on the evolution of gregariousness in arthropods, we are now conducting behavioral experiments in order to understand the role of kin recognition on the dynamics of fusion and fission of aggregations. Additionally, we are investigating the putative chemical alarm communication between aggregated individuals upon disturbance promoted by predator attacks.

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