

## Quantification of Resources

### PREDATION BY BIRDS AND ANTS ON TWO FOREST INSECT PESTS IN THE PACIFIC NORTHWEST

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*Abstract.* We used artificial stocking techniques, specialized prey-census methods, and selective enclosures and sticky barriers to identify and quantify bird and ant predation on Douglas-fir tussock moth (*Orgyia pseudotsugata*) and western spruce budworm (*Choristoneura occidentalis*). Fourteen species of birds preyed on tussock moth larvae. We observed losses of 0.08 larvae/m<sup>2</sup>/day. Six species of birds preyed on tussock moth pupae, among which we observed 6–47% losses from predation. Bird predation was implicated in reductions of 43–71% in egg survival.

Birds and foliage-foraging ants were the dominant predators of budworm larvae and pupae. Predation was studied using bird enclosures around tree branches 2–20 m above the ground, and around entire 9-m-tall trees. Sticky barriers kept ants off branches or trees. When enclosures or sticky barriers were used to protect larvae from predation, 2–15 times as many budworm survived to the pupal stage. At high larval densities survival of protected larvae was about double that of unprotected larvae. At low densities survival was 10–15 times higher among protected larvae. Predation was influenced by crown stratum; ants were most effective in lower strata, and birds excelled higher in the crown. Survival of pupae protected by branch-cages and sticky barriers was four times higher than unprotected pupae.

Predatory ants and many of the insectivorous birds identified in this study are influenced by the availability of standing or down dead wood, or stumps. Forest plans that provide for retention and recruitment of snags or logs can affect the ability of stands to support populations of these beneficial predaceous birds and ants.

*Key Words:* Predation; insectivorous birds; predaceous ants; enclosure techniques; Lymantriidae; Tortricidae.

The two most important forest-defoliating insects in the Pacific Northwest are the Douglas-fir tussock moth (*Orgyia pseudotsugata*) and the western spruce budworm (*Choristoneura occidentalis*). Their preferred host species are Douglas-fir (*Pseudotsuga menziesii* var. *glauca*) and grand fir (*Abies grandis*). Outbreaks of either species often extend over hundreds of thousands and even millions of hectares. In this paper we summarize studies that describe the population behavior of the tussock moth and budworm, and consider management strategies for preventing or minimizing damage; we also review studies of the possible role of predation in the dynamics of these two important pests. The methods used to identify and quantify predation included specialized prey-census methods, artificial stocking techniques, and selective enclosures and sticky barriers.

#### STUDIES ON DOUGLAS-FIR TUSSOCK MOTH

##### *Population dynamics*

Before starting the predation studies, we had monitored populations of the tussock moth near

Crater Lake, Oregon, for several years (Mason and Torgersen 1987). For sampling, we used a pole-pruner and basket to collect tussock moth stages on 45-cm, mid-crown, branch tips (Paul 1979). Branch tips are roughly triangular, so area was calculated as the product of length and width divided by two. Tussock moth density was expressed as the number of larvae, pupae, or egg masses/m<sup>2</sup> of foliage (Mason 1979). The samples showed that average population density declined over 90% between the early larval stage and the pupal stage late in the season. We knew what proportion of these stages were parasitized, but we could not account for the disappearance of larvae and pupae.

##### *Identifying predation*

*Larval stocking trials.* To identify the causes of these losses, we stocked lower crown branches of host trees with known numbers of larvae. Under one set of branches were drop-trays to catch larvae falling from the foliage. A sticky, polybutene substance prevented escape. Larvae on another set of branches were protected by fine-mesh nylon bags to prevent predation or other losses. By the end of larval development, losses

of larvae on the unprotected branches were eight-fold higher than on branches protected by mesh bags. We had not actually observed predation or the source of these losses, which we attributed to “arthropod predation,” based on the mangled appearance of the dead larvae, “dispersal” when larvae fell to the tray, and “disappearance.” Disappearance of small, early larvae was attributed to spiders and predatory insects that left unidentifiable remains. Disappearance of large, late larvae was suspected to be caused by birds (Mason and Torgersen 1983).

To confirm our suspicions regarding bird predation on larvae and to quantify possible predation on pupae and egg masses, we continued artificial stocking trials using tussock moth larvae and, later, pupae and egg masses. The next set of larval stocking trials consisted of cohorts of five larvae each, placed on clusters of four branches with drop-trays below. Each of the three clusters of branches was observed for 4 or 5 hours every third day from a blind about 10 m away. Before each observation period branches were examined for missing larvae, which were replaced as necessary. Foraging visits and observations of apparent predation by birds were recorded. The observer counted the larvae on the branch and in the tray after each visit by a potential predator to confirm predation or dislodging of the prey. We directly observed nine species of birds eating tussock moth larvae, and recorded “suspected” predation by 14 others. In the latter cases birds visited trial branches and appeared to be foraging. Immediately after they departed, one or more larvae had disappeared. Late in the season, after some larvae had pupated, six bird species were also observed preying on pupae (Table 1).

Predation of stocked larvae was expressed as loss per exposure day. The daily loss rate was used to compare mortality between exposure periods of different lengths and examine the relation between predation rates and bird densities. For the 2840 exposure days when 228 stocked larvae disappeared, we calculated a mean, daily, larval loss rate of 0.08/m<sup>2</sup>. We tested differences in mean loss per exposure day among periods, sites, and sites by period. The analysis showed that peak losses occurred during 1–7 August, followed by a general decline in losses toward the end of the season (Fig. 1). Losses of larvae were closely correlated with the total number of about 30 species of birds classed as high-potential predators of tussock moth. Simple correlation analysis indicated that estimated bird density accounted for about 78% ( $r = 0.885$ ,  $P < 0.01$ ) of the variation in loss rate (Torgersen et al. 1984b).

Kendeigh (1970) suggested that birds generally seek prey of a size that produces a food value at

TABLE 1. AVIAN SPECIES OBSERVED OR SUSPECTED OF PREYING ON DOUGLAS-FIR TUSSOCK MOTH LARVAE AND PUPAE (TORGERSEN ET AL. 1984B)

Species	Number of prey	
	Larvae	Pupae
<b>Observed predation</b>		
Dark-eyed Junco ( <i>Junco hyemalis</i> )	4	3
Red-breasted Nuthatch ( <i>Sitta canadensis</i> )	3	1
Mountain Chickadee ( <i>Parus gambeli</i> )	3	1
Golden-crowned Kinglet ( <i>Regulus satrapa</i> )	2	1
Western Tanager ( <i>Piranga ludoviciana</i> )	2	—
Nashville Warbler ( <i>Vermivora ruficapilla</i> )	1	1
Black-headed Grosbeak ( <i>Pheucticus melanocephalus</i> )	1	—
Black-capped Chickadee ( <i>Parus atricapillus</i> )	1	—
Chipping Sparrow ( <i>Spizella passerine</i> )	1	—
Subtotal	18	7
<b>Suspected predation</b>		
Red-breasted Nuthatch ( <i>Sitta canadensis</i> )	10	—
Dark-eyed Junco ( <i>Junco hyemalis</i> )	7	—
Ruby-crowned Kinglet ( <i>Regulus calendula</i> )	6	1
Bushtit ( <i>Psaltriparus minimus</i> )	5	—
MacGillivray's Warbler ( <i>Oporornis tolmiei</i> )	5	—
Yellow-rumped Warbler ( <i>Dendroica coronata</i> )	3	—
Chestnut-backed Chickadee ( <i>Parus rufescens</i> )	2	—
Lincoln's Sparrow ( <i>Melospiza lincolni</i> )	2	—
Pine Siskin ( <i>Carduelis pinus</i> )	2	—
Veery ( <i>Catharus fuscescens</i> )	2	—
Wilson's Warbler ( <i>Wilsonia pusilla</i> )	2	—
Cassin's Finch ( <i>Carpodacus cassinii</i> )	1	—
Solitary Vireo ( <i>Vireo solitarius</i> )	1	—
White-crowned Sparrow ( <i>Zonotrichia leucophrys</i> )	1	—
Subtotal	49	1
Total	67	8

least equal to the energy expended for locating and consuming it. Tussock moth larvae apparently do not reach this size—that is, about fourth instar—until late July or early August. The rate of larval loss from the stocked branches was probably influenced by the number of available large tussock moth larvae in the natural population. The observations of Curio (1976), who suggested that birds maintain search images of preferred prey during certain periods, could account for the onset of heavy predation losses. In

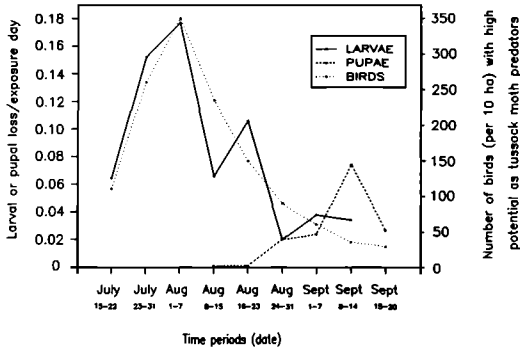


FIGURE 1. Tussock moth larvae and pupae lost per exposure day, and density (per 10 ha) of known or presumed avian predators of the tussock moth, by period, from 15 July to 14 September 1977, Fort Klamath, Oregon (from Torgersen et al. 1984b).

this study, such losses appeared to coincide with the presence of large larvae and peak bird density when birds were foraging both for themselves and for their young.

Rates of predation on stocked branches were higher than those in the natural population. Losses were also higher than those estimated for stocked larvae in a previous study at the same location, where larvae that disappeared or dropped off the foliage were not replaced (Mason and Torgersen 1983). Natural tussock moth larval density was less than  $0.05/m^2$  at the time of this study, so that density on stocked branches (about  $20/m^2$ ) was considerably higher than natural densities. Even so, we saw no patterns of losses suggesting that birds or other predators were returning to the trial branches and systematically taking most or all the stocked larvae (Torgersen et al. 1984b).

**Pupal stocking trials.** The larval stocking study suggested that avian predation might also be a significant mortality factor among tussock moth pupae. To quantify predation, we stocked pupae in the same and one other Oregon site, and at two California sites. Cocooned pupae were produced in the laboratory (Thompson and Peterson 1978) and individually wired to the underside of foliated branches of white fir (*Abies concolor*) to simulate naturally occurring pupae. Pupae were stocked, one to a tree, on branches about 2 m above the ground. Trees were spaced at about 10-m intervals according to the method and plot design described by Torgersen and Mason (1979). We stocked 46–136 pupae at each site for 1–6 years, for a total of 11 place-years.

Two types of predation were observed: either the entire cocoon was missing, leaving only the attachment wire, or, more commonly, the cocoon was torn open and the pupa was missing

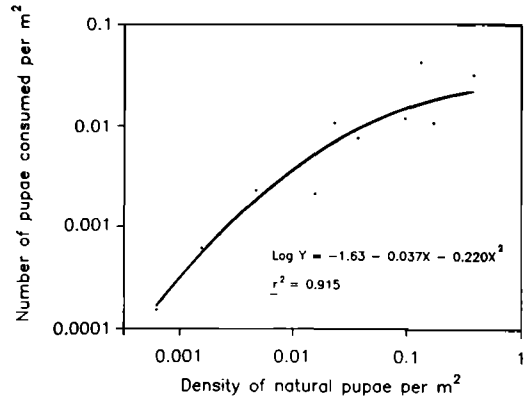


FIGURE 2. Relation of the number of pupae consumed to density of natural Douglas-fir tussock moth pupae. Data from sites near Placerville, California, and Fort Klamath and Malin, Oregon (from Torgersen et al. 1983).

or only fragments of it remained. When the entire cocoon was missing, or the cocoon was torn open and the pupa was missing, we presumed avian predation. Subsequent observations indicated that some of the predation in which only pupal fragments remained was caused by ants (*Camponotus* probably *modoc*). Pupal mortality of this kind was also observed by Dahlsten and Copper (1979).

Predation of stocked pupae varied from about 6–49% and was inversely correlated ( $r = -0.725$ ;  $P < 0.05$ ) with the estimated density of naturally occurring pupae. In terms of absolute numbers, the maximum number of pupae consumed by predators was less than  $0.1/m^2$ . Density of natural pupae at each site was estimated directly by sampling branches for cocoons (Mason 1977, 1987a). With increasing prey density, the absolute number of pupae preyed on (natural prey density times percent predation) increased, but at a decreasing rate to a maximum of about  $0.04/m^2$ . This occurred at a natural pupal density of  $0.13/m^2$  (Fig. 2).

**Egg-mass stocking trials.** In sampling tussock moth egg masses, we noticed that some masses and associated cocoons had been disturbed. Some cocoons seemed to have only a partial complement of eggs, and the remaining portion of the egg mass and the cocoon were tattered. Dahlsten and Copper (1979) suggested that avian predators might account for such partial, tattered egg masses. They also reported predation on egg masses by Mountain Chickadees.

We undertook a stocking study to examine the incidence of both partial loss and complete removal of egg masses at nine sites in Oregon, Idaho, and California. From 1977 to 1981, we

collected predation data on these sites for a total of 17 plot-years. Overwintering losses of entire egg masses, presumably from predation, were 5–33% and averaged about 14%. Among surviving egg masses, about two-thirds lost some eggs, and more than half lost about 50% of their eggs. Analyses showed that among the masses that remained in the spring, only about 60% of the original egg complement survived. Thus, in combination, partial predation and complete removal of egg masses resulted in reductions in egg survival of 43–71%, averaging about 52%.

We attributed major egg losses to predation by resident, foliage-gleaning birds. The capture of a Red-breasted Nuthatch in a snap-trap baited with an egg mass, and individual observations of a Dark-eyed Junco and a Nashville Warbler preying on egg masses partly verified our suspicions.

One observation was made of a foliage-foraging ant (*Camponotus* probably *modoc*) pulling apart an egg mass and carrying off an egg (Torgersen and Mason 1987). Dahlsten and Copper (1979) also suggested that ants might be preying on eggs.

*Avifaunal censuses.* The patterns of predation we observed in the artificial stocking trials may be correlated with avian density or species composition, or with other unknown factors influenced by habitat differences among the sites. Unfortunately, we do not have comparative avifaunal censuses for all sites, but censuses were done on the Oregon sites during the 1977 field season. Avian species composition and density/10 ha were determined from nine straight-line censuses (Emlen 1971) from mid-July to mid-September. These censuses indicated that six of the known avian predators of larvae, pupae, or eggs—Red-breasted Nuthatches, Mountain Chickadees, Dark-eyed Juncos, Golden-crowned Kinglets, Black-capped Chickadees, and Nashville Warblers—numerically dominated the area.

Because larvae, pupae, and egg masses were installed only on lower crown branches, the predation we recorded does not necessarily represent that occurring in other strata. However, we think our values provide a relative index of avian predation on the Douglas-fir tussock moth. They also suggest that such predation is an important component among the mortality factors that keep numbers of this pest low for long periods (Mason and Torgersen 1987).

## STUDIES ON WESTERN SPRUCE BUDWORM

### *Population dynamics*

*Budworm sampling.* In 1979 we began studies to examine budworm population behavior. Four

study sites were established in the upper Methow River valley in northcentral Washington. In 1980 we added two study sites about 50 km away on the Okanogan Highlands. Sampling for larvae, pupae, and egg masses was done much as described for the tussock moth. Density of each stage was expressed as number/m<sup>2</sup> of foliage based on insect counts and measurements of foliage (Srivastava *et al.* 1984).

Because of our studies on the tussock moth, we were interested in the role birds might have in the population dynamics of the budworm. The literature also suggested that birds were a potentially important source of mortality.

### *Selective exclusion methods on branches*

*Identifying predation on larvae.* The first set of exclusion trials was done on the three population sampling sites in northcentral Washington in 1979. Our first experimental design used 3/4-m<sup>3</sup>, single-branch enclosures with frames of 13-mm polyvinylchloride (PVC) pipe covered with 1-cm × 2-cm polypropylene garden mesh. The enclosures were placed on branches of Douglas-fir and grand fir at about 2 m and 5 m above the ground (Campbell *et al.* 1981). These branches were compared with unprotected control branches at the same heights, but accessible to all predators. The enclosures were installed when budworm larvae had completed spring dispersal and bud- and needle-feeding had begun. Protected and control branches were left undisturbed until all larvae had pupated, when surviving pupae were counted to compare predation among treatments.

Budworm survival was about twice as high on protected branches as on unprotected branches. Survival was significantly higher on protected branches at 2 m, but not at 5 m. Most of the differences, however, were accounted for by two of our three study sites. On these two sites, survival on protected branches was about triple that on unprotected ones. Differences in predation were possibly related to differences in natural budworm densities among the sites. The two sites where survival among treatments was pronounced had budworm densities of about 16/m<sup>2</sup>; the site where no significant difference was discernible had a density of about 32/m<sup>2</sup> (Torgersen and Campbell 1982).

*Assessing ant predation on pupae.* Because we were interested in processes that might maintain sparse budworm populations, we chose an additional Washington study site in 1979, where host trees showed little evidence of either prior defoliation or current budworm activity. We stocked branches with clipped twigs containing pupae inside their web shelters. Fine wire was

used to attach the twigs to trial branches. Because numerous colonies of a potentially predaceous ant (*Formica haemorrhoidalis*) inhabited this site, half of the trial branches had a sticky barrier applied to the base of the branch to prevent access by ants. Equal numbers of treatment and control branches in the same whorl were stocked with 5, 10, or 20 pupae at 2 m and 5 m.

Where no barrier had been applied, 84% of the stocked pupae were missing or reduced to fragments after three days, whereas only 8% were missing or in fragments on branches protected by a barrier. Few direct observations of predation by ants were made in 1979, but in repeat experiments in 1980 we observed nearly 100 instances of ants investigating or eating stocked budworm pupae. Other work in our study sites in 1981 and 1982 identified nine species of ants that preyed on budworm pupae (Youngs and Campbell 1984).

*Assessing bird predation on pupae.* Five branches each were stocked with 5, 10, or 20 pupae at 2 m and 5 m; each branch was protected from predation by birds by a single-branch enclosure. Every branch with an enclosure was accompanied by three unprotected control branches in the same whorl and stocked with the same number of pupae.

About 98% of the pupae installed on the control branches disappeared or were reduced to fragments after 12 days, vs. 84% on branches protected from birds ( $P < 0.001$ ). The status of pupae on protected branches at 2 m differed only slightly from those at 5 m ( $P < 0.05$ ). The relatively small differences emphasized the possible importance of predaceous ants.

*Selective enclosure trials.* We conducted further experiments to clarify the roles of birds vs. ants as predators of pupae (Campbell and Torgersen 1982). Treatments and a control were randomly assigned to equal numbers of branches stocked with 5, 10, or 20 pupae. We used both sticky barriers and whole-branch enclosures, or sticky barriers alone to exclude both ants and birds, or only ants at 2 m and 5 m.

Survival of budworm pupae was nearly four times higher (49% vs. 13%) on branches with both birds and ants excluded than on unprotected branches. Survival on branches with ants excluded was about three times higher than on controls (36% vs. 13%). Analysis of survival among treatments between crown strata was more complicated. Apparently the sticky barriers offered the pupae little or no protection on branches at 2 m. Occasionally, we watched ants drop from one branch to another, and enough ants may have fallen from higher branches to those at 2 m to confound results on branches with sticky barriers, whether in enclosures or not.

#### *Exclusion trials on whole trees*

*Selective enclosure methods for whole trees.* Results from the single-branch enclosures prompted us to design enclosures for whole trees up to 9 m tall. In 1980, enclosure trials were done on two sites in northcentral Washington and four sites near McCall, Idaho. In 1981, we established four sites near Seely Lake and Potomac in northwestern Montana, where we conducted both population sampling and enclosure trials. In northeastern Oregon, we established five sites for population sampling, only two of which were used for enclosure trials.

Our experimental design was expanded to include four treatments: birds excluded, ants excluded, both excluded, and neither excluded. At each site on grand fir, Douglas-fir, or both, the four treatments were completely randomized, and each treatment was done twice. Birds were excluded by polypropylene garden net attached to a 9-m-tall hexagonal framework of 13-mm PVC pipe reinforced with wooden  $2 \times 4$ 's (Campbell et al. 1981). Ants were excluded from treatment trees by applying a 50-cm-wide sticky barrier below the base of the live crown. These trials were installed after completion of spring budworm dispersal and before budworm emergence from the host shoots. The enclosures were removed after adult moth emergence. Hence, insects in enclosures were protected during the interval from instar IV to adults.

Beginning density in each trial site was determined from samples of 45-cm branch tips from the upper, middle, and lower crown thirds of the trial trees and 25 additional trees in the site. Plot density based on this sample was determined from equations developed by Srivastava et al. (1984). At the end of the developmental period—that is, when most budworm moths had emerged—the trial trees were dissected. Every branch of each treatment tree was removed. The foliated area of every third, fourth, or fifth branch (depending on the year of study) was calculated, and all pupal remains were counted. Posttreatment density based on dissection of trial trees was expressed as number of surviving budworm per square meter of foliage.

The results of the 1980 trials in Washington and Idaho indicated that at the lowest initial budworm density—about  $1.7/\text{m}^2$ —10 to 15 times as many budworms survived on trees protected from both birds and ants as on control trees. Even when density was high, about  $25/\text{m}^2$ , survival continued to be fully twice as high on the doubly protected trees as on the controls. In the 1981 trials in Montana and Oregon, a similar strong inverse relation was apparent between budworm density and the effects of birds and ants. This

predation was consistently adequate to reduce survival to about 5% in populations with budworm densities near  $1/m^2$ . When birds and ants were excluded, survival increased to about 40%. Birds and ants displayed different patterns of predation among crown strata of the trial trees. Ants were most effective in the lower third of the crown; birds were most effective in the upper third (Campbell and Torgersen 1983b, Campbell 1987).

At the lower densities, in both years and all areas, birds alone or ants alone were usually sufficient to greatly dampen the high survival observed when both groups were excluded. In fact, the contribution of either birds or ants largely compensated for the absence of the other guild in the single exclusions. Little or no evidence of further mortality was found after birds and ants were excluded. Thus, during the period from early foliage-feeding larvae through the pupal stage at the densities where we worked, other mortality-causing factors played minor roles (Campbell and Torgersen 1983a).

*Single-branch exclusions in tall trees.* Based on the apparent differences in predation by birds or ants among crown strata, we hypothesized that birds would continue to be important budworm predators even in trees much taller than 9 m, and that ants would play a decreasing role as tree height increased. Accordingly, we attempted to test our hypothesis on higher branches in tall trees. Because whole-tree exclusions were out of the question, we used single-branch exclusions at two sites in Montana at about 2 m and 20–25 m above the ground in Douglas-fir and Engelmann spruce (*Picea engelmannii*). The sites had widely different budworm densities ( $0.28/m^2$  and  $23.1/m^2$ ). A truck-mounted, 27-m hydraulic lift was used to install and remove exclusions, apply sticky barriers, and stock branches with pupae. Pupae were individually wired to branch tips, five to a branch.

Results paralleled those on smaller trees. Across all treatments, predators had relatively minor effects on the high-density site, confirming that predation of both the budworm and the tussock moth by ants, birds, or both was inversely related to insect density (Campbell et al. 1983, Torgersen et al. 1983). On the site with low natural budworm densities, mortality among pupae on both high and low branches protected from birds and ants was about 40%, as compared with 72% on controls. Birds appeared to be more effective predators than ants high in the trees, but were

about equally effective in low branches. These results left little doubt that birds and ants, separately or together, were at least as effective predators on high branches of old-growth trees as on branches or trees up to 9 m tall (Campbell and Torgersen 1983b).

*Identification of avian predators.* In concurrent studies designed to observe and identify avian predators on several of our study sites, Langelier and Garton (1986) and Garton (1987) identified several species of birds that were eating the budworm. Observations and stomach analyses confirmed that about two dozen species of birds were preying on the budworm in these sites. Half of these were also on our list of bird predators of the Douglas-fir tussock moth.

## CONCLUSIONS

These studies showed that insectivorous birds and foliage-foraging ants are major predators of two of the most important forest insect pests in the Pacific Northwest. Management-induced habitat changes can influence the abundance and diversity of these predators and other natural enemies of these pests. For example, forest plans that provide for retention and recruitment of snags can affect the ability of stands to support populations of predaceous birds and ants. Almost all of the ants, and many of the birds that prey on the tussock moth and the budworm, are influenced by the availability of standing or downed dead wood. Even birds that are not cavity nesters will use snags for foraging, perching, roosting, or singing.

The need to reduce damage to forests from insect pests suggests that managers view these and other natural enemies as a resource to be conserved and enhanced. One of the great challenges for land-management professionals today is to use new knowledge to broaden their perspectives and expand their management alternatives to maintain and improve forest health. We hope the results reported here will focus more attention on the beneficial role of natural enemies of insect pests in forest ecosystems.

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