Negative indirect effects of an avian insectivore on the fruit set of an insect-pollinated herb

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Though an abundance of research has focused on direct interactions between birds and plants, relatively few studies have reported on indirect interactions. Of those reports, all have focused on positive indirect effects of birds on plants through predation of plant natural enemies. We conducted an observational study along the Middle Rio Grande in New Mexico to determine if avian aerial insectivores had a negative, indirect impact on insect-pollinated plants through predation of insect pollinators. We found considerable taxonomic overlap, at the order and family level, between insects visiting sweet clover (*Melilotus officinalis*) and those eaten by cliff swallows (*Hirundo pyrrhonota*). We found a significant negative relationship between proximity of sweet clover to cliff swallow breeding colonies and sweet clover fruit set during the cliff swallow nestling period. The apparent effect of cliff swallows was strongest within 200 m of breeding colonies (approximately 50% reduction in fruit set) and decreased nonlinearly to a distance of approximately 400 m. Finally, we found that the clover fruit set gradient disappeared after the nestling period, when chicks had fledged and the colony was abandoned.

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Direct interactions between birds and plants have been well studied. Birds are known to play important roles as pollinators (Regal 1982, Jordano 1987), seed dispersers (Temple 1977, Hutchins and Lanner 1982, Wheelright 1988, Wenny and Levey 1998), seed predators (Castro et al. 1999, Howe and Brown 1999), and herbivores (Clout and Hay 1987, James and Burney 1997, Perrow et al. 1997). These direct interactions have been shown to affect plant population dynamics and community structure, as well as the evolution and expression of plant life histories and morphologies (Brown and Kodric-Brown 1979, Paige and Whitham 1985, 1987, Murray et al. 1994, Bruneau 1997).

Economic ornithologists of the late 19th and early 20th centuries suggested indirect interactions between birds and plants (Judd 1901, Beal 1904, 1907, McAtee 1911), though it is only recently that these relationships

have been quantified. It has since been shown that bird predation of invertebrate herbivores can lead to decreased herbivory and increased growth in desert grasses (Bock et al. 1992), deciduous trees (Marquis and Whelan 1994, Sipura 1999, Murakami and Nakano 2000, Strong et al. 2000, Sanz 2001, Lichtenberg and Lichtenberg 2002), and intertidal algae (Wootton 1995). These studies have illustrated how birds have a positive indirect effect on plants through predation of plant natural enemies. We have not encountered studies that have quantified the indirect effects of birds on plants through predation of plant mutualists. In particular, we are aware of no studies that have quantified the negative indirect effects of birds on plants through the predation of insect pollinators.

In this study, we examine the hypothesis that avian aerial insectivores, through predation of aerial insect

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pollinators, have a negative, indirect impact on the fruit set of insect-pollinated plants. We studied the fruit set of a monocarpic herb, sweet clover (*Melilotus officinalis*), as a function of distance from cliff swallow (*Hirundo pyrrhonota*) colonies during the swallow nestling period and after fledging. We hypothesized that cliff swallows would have a negative, indirect effect on sweet clover fruit set. We predicted that this effect would be strongest near the colonies and during the nestling stage.

Material and methods

Study system

We investigated the indirect effects of insectivorous birds on sweet clover fruit set at three different cliff swallow colonies along the Middle Rio Grande in Albuquerque, New Mexico U.S.A. The colonies were located approximately 10 m above the ground on the sides of bridges where Central Avenue, Montaño Road, and Paseo del Norte cross the river (Fig. 1). Each of the three bridges was separated from the next nearest bridge by approximately 6 km. The number of active nests per colony ranged from approximately 100 to 200. Barn swallows (*Hirundo rustica*) and black pheobes (*Sayornis nigricans*) were two other aerial insectivores nesting concurrently
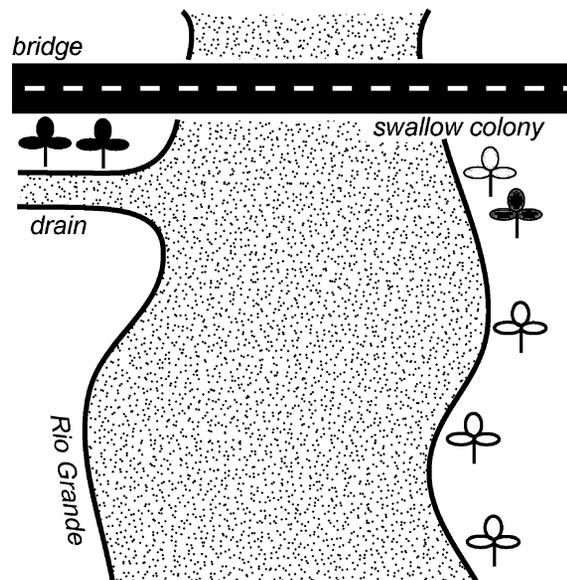

Fig. 1. Generalized diagram of one of three cliff swallow colonies along the Middle Rio Grande, Albuquerque, New Mexico, USA. The diagram depicts a swallow colony located on the side of a bridge, the river (stippled area), and the sweet clover individuals (clover-shaped symbols). Empty and gray-shaded clover symbols represent locations of plants used for the distance effect component. Gray-shaded symbols represent plants used for the bridge-effect and distance effect component. Solid clover symbols represent locations of plants used for the bridge effect component.

on the bridges; these species comprised <5% of the total birds present. At the colonies, the Rio Grande is approximately 100–200 m wide and is bordered by early succession meadows, mid-succession willow (*Salix exigua*) and salt-cedar (*Tamarix chinensis*) shrublands, and late succession Russian olive (*Elaeagnus angustifolia*) and cottonwood (*Populus deltoides*) forests. Our study was focused on sweet clover in the early-succession meadows along the river's edge.

Sweet clover is a 0.3–2.6 m tall, monocarpic, annual or biennial herb introduced to North America from Eurasia as early as 1664 (Turkington et al. 1978). On average, 50 small, white or yellow, perfect flowers are borne on each of 40–80 racemes (Coe and Martin 1920). In New Mexico, the species produces flowers from May through October. Each flower produces one mature fruit, typically with one seed (Turkington et al. 1978), within 10 days of fertilization (Coe and Martin 1920). Flowers that are not pollinated wither and blow away within 5 days (Coe and Martin 1920). Sweet clover pollen is self-compatible. However, in some populations plants experimentally restricted from insect visitation have very low fruit set compared to insect-visited plants (Coe and Martin 1920). Sweet clover flowers are known to be visited by a wide variety of insects from the orders Hemiptera, Neuroptera, Coleoptera, Lepidoptera, Diptera, and Hymenoptera (Coe and Martin 1920).

Cliff swallows are 24 g passerine birds that breed throughout North America during the summer, and range from southern Brazil to southern Argentina during the winter (Brown and Brown 1995). Cliff swallows are highly social. They live in colonies of 10–3500 nests, with 200–300 nests being most common (Brown and Brown 1995). Cliff swallows are opportunistic aerial insectivores, with prey size ranging from small midges (4 mm) to large grasshoppers (4 cm). Dissection of food boluses has demonstrated that cliff swallows consume a wide variety of insects from the orders Ephemeroptera, Odonata, Orthoptera, Hemiptera, Homoptera, Neuroptera, Coleoptera, Lepidoptera, Diptera, and Hymenoptera (Brown and Brown 1995, 1996).

Study components

Our field and laboratory efforts were divided into five main components. The first task was to determine if insect visitation was necessary for pollination to occur in the local population of sweet clover (hereafter "visitor effect" component). The second objective was to determine which insect taxa were visiting the sweet clover at our study sites, and if the cliff swallows were eating those taxa ("visitor and diet identification" component). The third, and primary, objective was to investigate fruit set of sweet clover at different distances from the cliff

swallow colonies during the swallow nestling period ("distance effect" component). Preliminary observations suggested that fruit set near colonies was indeed relatively low. To explore whether low fruit set near bridges was caused by a plant's proximity to a colony or to a bridge, we designed the "bridge effect" component. The fifth objective was to learn if relatively low fruit set near colonies disappeared after the swallow nestling stage, when parents and their young have dispersed from colonies ("swallow presence/absence" component).

Sweet clover selection

There are several factors besides a shortage of pollinators that can lead to reduced pollination and fruit set in plants. Factors affecting pollination include the quantity and quality of nectar and pollen (Young and Stanton 1990, Real and Rathcke 1991), flower position on plant (Kearns and Inouye 1993), overall plant size (Dudash 1991, Groom 1998), plant density within a patch (Schmitt et al. 1987, Kunin 1993, Bosch and Waser 2001), and the characteristics of the landscape surrounding a patch (Kunin 1993, Agren 1996, Groom 1998, Cunningham 2000). Several of these pollination-related factors are affected by the water and nutrient content of soil. Soil quality can also affect fruit set after pollination has occurred; several studies have shown that fruit abortion rates are higher in lower quality soils (Galen 1985). We designed our sweet clover sampling to reduce the confounding effects of these factors. We only studied plants in early-succession meadows, in sandy, floodplain soil, within 3 m of the river's edge. We studied plants that were 1.5–2.0 m tall and had 3–5 conspecific neighbors within a 5 m radius. We removed neighboring plants when necessary to achieve the desired neighborhood density. Weeding was conducted early in the growing season, before sweet clover reproduction began. Once a focal individual was found, we systematically selected three branches for study: the upright main stem, the uppermost branch pointing towards the river, and the uppermost branch pointing away from the river.

Fruit set quantification

Sweet clover fruit set was quantified by determining the number of flower scars and developing fruits on racemes using a stereo dissecting scope. Fruit set was calculated as: fruit set = (the number of developing fruits/(the number of developing fruits + the number of flower scars)) × 100. Throughout the manuscript, we report fruit set as a percentage ±1 SD unless otherwise noted.

Visitor effect

We selected 25 plants from a sweet clover population located 1 km north of the Central Avenue swallow colony during the third week of June 2002. On each plant, we chose 2 racemes, both located on the same branch and both with unopened flower buds. One randomly selected raceme was covered with a green mesh bag (hereafter "exclosure racemes"; Kearns and Inouye 1993). Bags were made of polyester, had a mesh spacing of 0.33 mm, and were tied around the base of the exclosure raceme using brown embroidery thread. Embroidery thread was also tied to the base of a nearby, bagless raceme (hereafter "control racemes"). We collected exclosure and control racemes during the second week of July 2002, after all flowers had a chance to be pollinated, petals had fallen off, and fruit development had begun. Fruit set per raceme was calculated as described in the fruit set quantification section. We used a two-sample randomization test (Manly 1991) to look for statistically significant differences between fruit set of exclosure and control racemes because measures were not normally distributed and were frequently equal to zero for the exclosure treatment.

Visitor and diet identification

We collected insects that were observed on open sweet clover flowers near the Central Avenue and Paseo del Norte cliff swallow colonies. Visitors were sampled on 3 different occasions during the cliff swallow incubation and nestling periods. Insects were collected with a sweep net, pinned, and identified to family in the laboratory using a stereo dissecting scope and published keys (Bland and Jaques 1978, Borror et al. 1981).

We collected cliff swallow fecal samples from directly below nests at the Central Avenue colony. Samples were collected on 3 occasions during the cliff swallow nestling period and were stored in vials containing 90% ethanol. In the laboratory, feces were placed into a petri dish, taken apart with a probe, and viewed under a stereo dissecting scope. The presence of insect orders or families was determined by inspection of insect body parts and comparing them to reference specimens, published keys, and photographs (Bland and Jaques 1978, Borror et al. 1981, Ralph et al. 1985). More detailed taxonomic analysis of visitors and diet was not conducted due to the difficulty of identifying insect fragments below the family level.

Distance effect

We examined fruit set of sweet clover individuals at varying distances from the Central Avenue (n = 40 plants), Montaño Road (n = 40), and Paseo del Norte

(n = 20) cliff swallow colonies (Fig. 1). We selected individual plants during the first week of July 2002 and tied brown embroidery thread on 3 branches where all racemes had unopened flower buds. All racemes on each of the three branches were collected during the third week of July 2002, after all flowers had ample chance to be pollinated, petals had fallen off, and fruit development had begun. When collecting racemes, we measured the distance of the plant to the nearest active nest of the colony using a laser range finder with an accuracy of ±1 m. Fruit set per raceme was calculated as described in the fruit set quantification section. Seven racemes per plant were randomly selected to calculate mean fruit set for each individual. We used nonlinear regression to model the effect of distance to cliff swallow colony on sweet clover fruit set because we expected the effect of swallows to decrease with distance. For each colony, we computed the asymptotic regression function: fruit set = $a - bc^{distance}$ (Zar 1999). In the context of this study, a represented the asymptotic level of fruit set, b represented the effect of cliff swallows on fruit set at 0 m from the colony, and c represented the rate at which the function reached the asymptote. We assessed the statistical significance of the model for each site individually with an F-test that compared the full models with reduced, mean-only models (Zar 1999).

Bridge effect

While conducting the distance effect component at the Montaño colony, we sampled racemes from 6 sweet clover plants that were located within 30 m of the bridge, but 100–110 m from the nearest cliff swallow nest (hereafter "bridge-effect plants"; Fig. 1). Bridge-effect plants were pooled with 8 distance-effect plants that were within 30 m of the bridge and within 30 m of active cliff swallow nests (Fig. 1). Bridge-effect plants were growing within 3 m of open water, an ephemeral drainage ditch (Fig. 1); plants, branches, and racemes were selected as described in the sweet clover selection section. Fruit set per plant was calculated as described above in the distance-effect section. We predicted a positive relationship between distance to swallow colony and sweet clover fruit set for this pool of 14 plants if foraging swallows caused relatively low fruit set near colonies. Conversely, we predicted no relationship between distance to colony and fruit set if proximity to a bridge caused relatively low fruit set near colonies. We modeled fruit set as a simple linear function of distance from the colony because the maximum distance was only 110 m, and an asymptotic function was unnecessary. We determined the statistical significance of the model using an F-test.

Swallow presence/absence

During summer 2003, we studied sweet clover fruit set on plants growing 20–450 m from the Paseo del Norte swallow colony, both during the cliff swallow nestling stage (n = 9) and after parents and young had dispersed (n = 10). Focal plants and racemes were selected as described above. Nestling stage racemes had flowers in bloom during the swallow nestling stage and were collected after all chicks had fledged. Post-fledging racemes were collected 2 weeks later. Mean fruit set was determined per plant as described in the distance effect section. If foraging swallows were responsible for low fruit set near colonies, then we predicted a positive relationship between distance to colony and fruit set during the nestling stage, and no relationship between these two measures after the colony was abandoned. We modeled and tested the relationship between fruit set and colony distance during each swallow-breeding stage as described above in the bridge-effect section.

Results

Visitor effect

We found that sweet clover along the Middle Rio Grande was indeed able to self-pollinate. However, while self-pollination was possible, it did not occur often. Fruit set was only 6 ± 6% on exclosure racemes, compared to 44 ± 23% on control racemes. This 7-fold increase in fruit set indicated that insect visitation was important for sweet clover reproduction in this system. The two-sample randomization test indicated that this difference was highly significant (P < 0.001).

Visitor and diet identification

The visitor and diet identification component of this study indicated upper-level taxonomic overlap between the insects visiting sweet clover and those consumed by cliff swallows (Table 1). Forty-six percent of the families observed visiting sweet clover during this study have been reported as cliff swallow prey (Brown and Brown 1996), and 29% of the families consumed by cliff swallows during this study have been previously identified as sweet clover visitors (Coe and Martin 1920).

Distance effect

We found that during the nestling period, sweet clover fruit set and a plant's distance from a cliff swallow colony were positively related at the Paseo del Norte

Table 1. Visitors of *Melilotus officinalis* and prey of *Hirundo pyrrhonota* observed during this study.

Observed visitors	Observed prey
	Orthoptera[1]
Hemiptera[1,2]	Hemiptera[1,2]
	Lygeidae
	Homoptera[1]
Coleoptera[1,2]	Coleoptera[1,2]
Curculionidae[1]	Curculionidae
	Chrysomelidae[2]
Lepidoptera[1,2]	Lepidoptera[1,2]
Pieridae[2]	
Diptera[1,2]	Diptera[1,2]
Simuliidae[1]	Schizophora[2]
Tephritidae[1]	
Tachinidae[1,2]	
Hymenoptera[1,2]	Hymenoptera[1,2]
Scoliidae[1]	Ichneumonoidea
Vespidae[1,2]	Brachonidae
Sphecidae[2]	Chalcidoidea
Colletidae	Formicidae[1]
Halictidae[1,2]	Apidae[1,2]
Andrenidae	
Megachilidae[2]	
Apidae[2]	

[1]taxa reported by Brown and Brown (1996) to be part of *Hirundo pyrrhonota* diet.
[2]taxa reported by Coe and Martin (1920) to be visitors to *Melilotis officinalis*.

($r^2 = 0.40$, $F_{3,16} = 5.59$, $P = 0.008$), Moñtano ($r^2 = 0.43$, $F_{3,36} = 13.70$, $P < 0.001$), and Central ($r^2 = 0.22$, $F_{3,36} = 5.16$, $P = 0.005$) study sites. Figure 2 illustrates the asymptotic relationships, where fruit set increased with distance from the colonies and then eventually leveled off.

Bridge effect

We found a significant positive relationship between distance to a cliff swallow colony and fruit set in the pool of 6 bridge-effect and 8 distance-effect plants at the Montaño study site ($r^2 = 0.36$, $F_{1,12} = 6.84$, $P = 0.02$; Fig. 2). This positive relationship occurred in spite of the fact that the bridge-effect plants were growing within 30 m of the bridge.

Swallow presence/absence

We found that during the nestling stage, there was a significant positive relationship between fruit set and colony distance at the Paseo del Norte study site ($r^2 = 0.47$, $F_{1,7} = 6.21$, $P = 0.04$; Fig. 2). Once the swallow chicks had fledged and the colony was abandoned, the relationship between fruit set and colony distance disappeared ($r^2 = 0.05$, $F_{1,8} = 0.45$, $P = 0.52$).

Discussion

Given that breeding adult cliff swallows harvest 14.7 kJ hr^{-1} (Brown and Brown 1995) and forage 7.5 hr d^{-1} (Withers 1977), and that the caloric value of insects is roughly 25 kJ g^{-1} (dry mass, Karasov 1990), a swallow colony with 150 nests could consume more than a half-million 5 mm insects per day. We hypothesized that, even if a small fraction of these insects were pollinators, this consumption could drive an indirect, negative interaction between cliff swallows and sweet
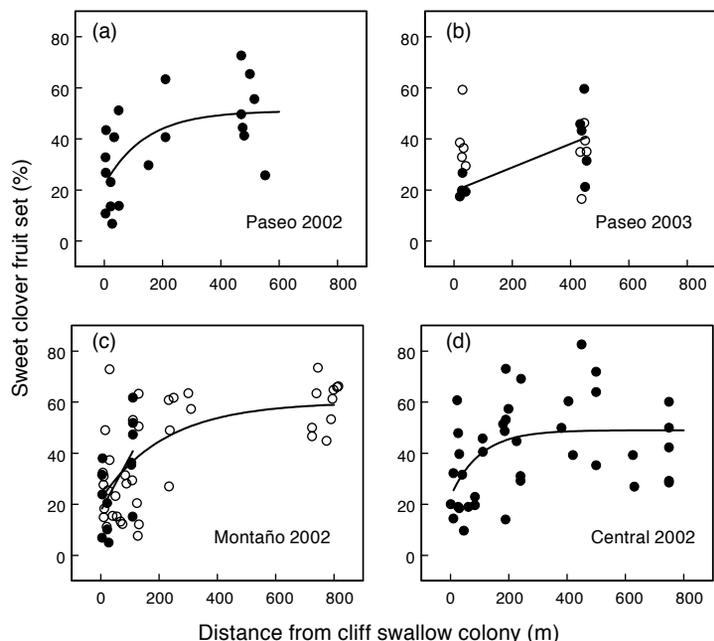

Fig. 2. Graph of sweet clover fruit set as a function of distance from three cliff swallow colonies: (a) during the 2002 nestling period at the Paseo del Norte colony; (b) during the 2003 nestling period (filled circles and line) and post-fledging period (empty circles) at the Paseo del Norte colony; (c) during the 2002 nestling period along transects perpendicular to the Montaño bridge (open circles and curved line) and along transects parallel to the bridge (filled circles and straight line); and (d) during the 2002 nestling period at the Central Avenue colony.

clover. We hypothesized that the indirect effect of swallows on sweet clover would be measurable during the nestling stage, when swallow foraging is relatively intense near their colonies. Consistent with our hypotheses, observational data collected during our study showed that sweet clover fruit set was significantly lower near cliff swallow colonies during the nestling period. The asymptotic regression model calculated for the Montaño study site estimated average fruit set to be 28% at 40 m from the colony, compared to 54% at 400 m. Evidence for an indirect, negative relationship virtually disappeared after 400 m; fruit set at 800 m from the colony was predicted to be 59%.

We were concerned that the distance effect observed during the swallow nestling period could have been generated by factors associated with growing near bridges, other than a swallow-induced reduction in insect pollinators. For instance, bridges may interrupt wind patterns and cause lee-side insect pollinator aggregations (Brown 1988); bridges may fragment habitat and affect insect pollinator movement (Cunningham 2000); abiotic conditions that influence sweet clover condition such as exposure to sun and soil characteristics could differ with proximity to bridges; and finally, sweet clover seed predators may preferentially inhabit areas around bridges. However, the bridge-effect component conducted at the Moñtano study site showed that sweet clover near bridges but far from swallows had significantly higher fruit set than sweet clover near bridges and near swallows. Through this comparison, we were able to separate the effects of the bridge and the swallow colony, and show that low fruit set near swallow colonies during the nestling period was not likely to be caused by bridges, per se.

We did not directly demonstrate that insect pollinator abundance was reduced near cliff swallow colonies during the nestling period. Instead, we inferred this through the observed reduction in sweet clover fruit set close to the colonies. This required us to assume (1) that the density of foraging swallows is higher nearer the colonies and (2) that the foraging swallows consume sweet clover pollinators. The first assumption is supported by personal observations and those of other researchers who have reported that cliff swallows forage relatively close to their colonies during the nestling period, frequently over surrounding fields (Brown and Brown 1996). The second assumption is supported at the family and order level by literature on cliff swallow diets (Brown and Brown 1996) and sweet clover pollinators (Coe and Martin 1920) and by the results of our visitor and diet identification studies (Table 1). Note that 46% of the families observed visiting sweet clover at our study site are reported to be cliff swallow prey, and 29% of the families observed in the cliff swallow fecal samples collected at our study site are reported to be sweet clover visitors. One superfamily – Apoidea, which is known (Coe and Martin 1920) to be an important pollinator of sweet clover – was both found in cliff swallow feces and observed visiting sweet clover at our study sites.

An experimental study, where cliff swallows are excluded from randomly selected bridges, would provide the strongest test of our hypothesis. This was not possible in our system, so we relied on an observational study and duly acknowledge the shortcomings of this design. We took advantage of swallow phenology, and the fact that sweet clover blooms throughout the growing season, to look for evidence of pollen limitation when swallows were present and absent from the colony. We found that sweet clover fruit set was much higher in far plots than in near plots while the colony was occupied and swallows were feeding young. In contrast, fruit set in near and far plots was nearly identical after young had fledged and the colony was abandoned. These results further implicate the cliff swallows as being the main drivers of the reduced sweet clover fruit set observed near the colonies during the nestling stage.

It is well known that aerial insectivores often prey on insect pollinators. Our data provide support for the hypothesis that predation by aerial insectivores can lead to reduced fruit set in plants. However, the magnitude of the effect may depend upon the degree of pollen limitation inherent in the local system. For example, if there is an abundance of pollinators in the system, then aerial insectivore predation may not impact plant fruit set. However, if insect pollinator abundance is already low, then aerial insectivores may have a relatively large impact on plant fruit set. Thus the effects of aerial insectivores on fruit set could vary across sites or across time at a single site as pollinator numbers fluctuate.

We found observational evidence for negative, indirect effects of cliff swallows on sweet clover at locations where bird abundance was particularly high, and during the nestling stage of the breeding season, when energetic demands and foraging intensities were also particularly high. While our study was conducted in a somewhat artificial, model system, we note that there are several avian taxa that are both colonial breeders and insectivorous (e.g. bee eaters, swifts, and other swallows). Thus the relationships between birds and plants observed during this study might be observed in other natural systems. Future studies could investigate (1) variation in pollen limitation in relation to aerial insectivore density and life cycle stage, and (2) the degree to which insectivore-induced pollen limitation effects the distribution, abundance, phenology, and morphology of plants.

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