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Aversive or Attractive? The Effects of Skunk Oil on Predator Behavior

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ABSTRACT: The oil produced by the anal glands of the striped skunk is known to be a strong deterrent to potential predators. However, it is also a common ingredient in many trap lures, especially those for carnivores such as the coyote. This paradoxical nature of skunk oil being both attractive and aversive has yet to be investigated, leaving a gap in the understanding of how predators of skunks respond to visual and olfactory information. In this project, camera traps with baited skunk models with either black-and-white or brown pelage were deployed in natural areas around Southern California in order to study the effects of skunk oil and pelt coloration on predator behavior. Our study found scented models were less likely to be visited, indicating an avoidance of the oil and its scent.

KEY WORDS: anal gland, aposematism, *Canis latrans*, carnivore, coyote, *Mephitis mephitis*, olfaction, striped skunk, urban ecology

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INTRODUCTION

Surviving in urban environments presents unique challenges to wildlife, often requiring adjustment to activity times, food and habitat preferences, and breeding seasons, among many other aspects of the species' biology and ecology (Jokimäki et al. 2011). Typically, animals able to exploit a wide range of food items acclimate more easily to life in an urban environment than specialist species, as they are easily able to take advantage of the wide range of potential food items that a city could present. Species that possess plastic behavioral responses to predators, as well as plastic foraging strategies, tend to be the species that are found most commonly in urban environments. Furthermore, shifting active and foraging times from diurnal to nocturnal allows animals to reside within cities while minimizing the potential for interaction with humans. In order to study how urban animals adapt to their environments, we investigated the effects of different olfactory and visual information on the behavioral ecology of urban carnivores.

The coyote (*Canis latrans*) is an exemplary case of an animal adjusting its behaviors and biology in response to having taken up residence within urban environments throughout North and South America. Coyotes now commonly reside within many urban areas, including Los Angeles, New York City, and Chicago, among many other large cities. First, cities provide many of the coyote's natural food sources – fruits, vegetables, and rodents – as well as anthropogenic food sources such as pet food and food waste (Gehrt 2007). The coyote's generalist diet combined with the range of foods available within a city has aided in the acclimation of coyotes to life within a city. Further, in non-urban environments, coyotes have been reported as being diurnal and nocturnal, but in cities they tend towards nocturnality though this effect is not consistent among locales (Clark 2011). Finally, coyotes are able to den in locations completely lacking green space, which doesn't appear to hinder their reproductive abilities (Grinder and Krausman 2001).

Few studies, however, have investigated how carnivores, specifically coyotes, adjust their hunting behavior in response to available olfactory, visual, and auditory information (or a combination thereof). By studying how the removal of one type of sensory information influences an animal's response to prey or food, we are able to determine which sensory modalities are the most relied upon during hunting or foraging. Understanding what modality is most relied upon can provide information as to which modality would be the most beneficial to exploit when developing management programs or deterrent technologies. In a series of laboratory studies, Michael Wells (Wells 1978, Wells and Lehner 1978) recorded the time coyotes took to locate prey when one or more sources of information (visual, olfactory, and auditory) were not available. The removal of visual and olfactory information together resulted in the largest increase in search time, indicating these two senses to be the most relied upon when approaching prey or carrying out hunting behaviors. Few other experimental studies have been conducted to illuminate how coyotes use their senses while hunting.

The reliance upon visual information by predators was demonstrated by Hunter (2009) in a study investigating the behavior of wild carnivore predators – including coyotes, gray foxes (*Urocyon cinereoargenteus*), raccoons (*Procyon lotor*) and other species – approaching taxidermy models shaped like a skunk (*Mephitis mephitis*) or a gray fox and with either black-and-white skunk pelage or fox pelage. Animals were more cautious when approaching the black-and-white models, spending more time pausing when approaching, as well as less likely to approach skunk-shaped models regardless of color. The natural wariness related to black-and-white coloration indicates predators are able to adjust their approach behavior in response to the visual signal from a potentially dangerous prey item, a wariness that could be used in the creation of a deterrent. There is still a large gap in the knowledge, however, of how coyotes and mammalian predators in general use olfaction, a sense arguably as important as vision, during approach to potential prey or food.

The skunk's noxious spray, used as a last-resort defense to repel predators, is an odor as recognizable as its pelt coloration. Oddly, skunk anal glands are a common ingredient in many carnivore lures typically used to attract coyotes to traps (Bullard et al. 1983, Turkowski et al. 1983). Despite this, skunk carcasses have been encountered in which everything except the anal glands had been consumed by scavengers (T. S., pers. observ.), probably coyotes, which could indicate an aversion to and avoidance of the oil contained within these glands. Indeed, coyotes are so wary of a skunk's spray that skunks have been known to deter coyotes without spraying (Walton and Lariviere 1994). An understanding of how predators use both olfactory and visual signals, specifically the olfactory and visual signals from a skunk, and how those senses are used during approach to potential prey could provide valuable information about the predatory behavior of carnivores. This information could be valuable when developing novel repellents and deterrents.

Our research aimed to investigate the interaction between visual and olfactory prey information on predatory/scavenging behaviors in urban coyotes and other urban mammals. Models created from black-and-white or brown pelts, along with skunk oil collected from live animals, were used to assess the behavior of mammalian carnivores *in situ* to determine potential effects of pelt coloration and noxious odor on approach behavior. We hypothesized that pelt coloration and odor both affect predator approach behavior. If the skunk oil was acting as an attractant, we predicted two potential effects on behavior: 1) models with oil added to the bait would have higher visitation rates than those without oil, or 2) skunk oil would act as an attractant to investigate, but a deterrent to consumption due to its noxious nature. If instead the oil was acting as a component of the skunk's warning signal, then we predict the models with oil would have the lowest visitation rate, and the models with skunk oil and the black-and-white pelt coloration would have the lowest visitation rates of all models.

METHODS

Study Locations

Experiments were conducted at Portuguese Bend Reserve, Los Cerritos Wetlands, Seal Beach National Wildlife Reserve, El Dorado Nature Center, and Frank G. Bonelli Regional Park from January to August 2015. All locations had documented coyote presence prior to data collection.

The Portuguese Bend Reserve in Ranchos Palos Verdes, CA, located at 33.75°N, -118.36°W, was used for data collection between January 13 and February 14, 2015 for a total of 23 nights. Habitat consists of coastal riparian and sage scrub bordered by human residences (Barbour et al. 2007). This location is open to the public and saw the most human activity of the sites used. Camera and models were located in open areas not obstructed by brush.

Los Cerritos Wetlands (33.76°N, -118.09°W), located on the border of Los Angeles and Orange Counties in Long Beach and Seal Beach, CA, is a tidal salt marsh bordered by residences and is not open to the public. This site was sampled between February 19 and May 31, 2015 for a total of 33 nights. Vegetation is dominated by mule fat (*Baccharis salicifolia*) and black mustard (*Brassica nigra*).

Seal Beach National Wildlife Refuge (33.76°N, -118.07°W) in Seal Beach, CA, was sampled between April 17 and June 25, 2015 for a total of 30 nights. This location is also a tidal salt marsh, which is being replanted with native vegetation. As it is enclosed by the Seal Beach Naval Weapons Station, this site is not open to the public and is highly restricted. Cameras were located in an open area currently under restoration.

The sampling area used at El Dorado Nature Center (33.80°N, -118.09°W), in Long Beach, CA, was not open to the public and has not been developed or restored. The habitat at this location most resembles coastal riparian scrub. This location is bordered by the San Gabriel River and is surrounded by a large open area park complex. Data collection occurred here between June 19 and August 21, 2015 for a total of 41 nights.

Frank G. Bonelli Regional Park (34.09°N, -117.79°W), in San Dimas, CA, was sampled for 16 nights between June 23 and August 11, 2015. This location is a developed open-area park intended for human recreation. Cameras were placed within a sparsely wooded area on the edge of the park.

Animal Models

Models were created by attaching tanned skunk pelts, either left as the natural black-and-white or dyed brown, to a 26 × 9-cm PVC pipe. A clear 8.5 × 7-cm acrylic tray was attached to the dorsal surface of the model 2 cm from the end of the pipe at what would be considered the posterior of the animal. Brown pelts were created by bleaching natural skunk pelts with Clairol® Basic White Lightener (P&G-Clairol Inc., Stamford, CT) and Salon Care™ 40 Volume Crème Developer (Sally Beauty Holdings Inc., Denton, TX) and then dyed brown using Ion™ Color Brilliance™ Permanent Liquid Hair Color in Dark Blonde (Arcadia Beauty Lambs LLC, Reno, NV) and Salon Care™ 10 Volume Crème Developer. Tails were propped up in a neutral position using wire, and the models were staked to the ground to prevent removal by visiting animals.

Camera and Model Protocol

For each night of data collection, 6 Bushnell Trophy Cam™ trail cameras (Bushnell Outdoor Products, Overland Park, KS) were attached to green T-posts 40 cm above the ground and 200 cm from an animal model or control station. This placement resulted in videos having the model at the bottom center of the field of view, with a maximum visible distance of 24 m extending at a 55°-angle from the camera. Camera stations were established a minimum of 50 m apart, with the exception of El Dorado Nature Center. Due to the small size of this location, cameras were placed a minimum of 25 m apart. All camera locations were in open areas free of obstruction. Cameras were deployed approximately one hour before sundown. Two brown animal models, two black-and-white skunk models, and two control stations were deployed nightly (see Table 1 for a listing of model and scent types). One of each model or control type contained bait scented with dilute skunk oil. After models were placed, but prior to bait placement, the model and surrounding 50-cm radius was sprayed with Scent Killer® Gold™ (Wildlife Research Center Inc., Ramsey, MN) in an attempt to remove the scent left from handling the models and control for any influence the presence of human scent may have. After spraying to remove scent, the bait was placed into the tray at the rear of the model while wearing nitrile exam gloves to minimize any transfer of odor onto the model.

Table 1. Model color and scent types deployed.

Model Color	Model Scent
Control (no pelt)	-
Control (no pelt)	+
Brown	-
Brown	+
Black-and-white	-
Black-and-white	+

All models and control stations contained 40 g of Chicken of the Sea® canned tuna in water (Chicken of the Sea Int'l., Mt. Olive, NJ) and 40 g of Gravy Train® canned dog food (Big Heart Pet Brands, Orrville, OH). Oil from skunk anal glands from skunks at Bonelli Park was collected then diluted in a 1:5 ratio with canola oil. Canola oil was used, as it is a stable and neutrally-scented and flavored oil that is safe for consumption (Przybylski 2001). Models or control stations designated as scented stations had 2 drops of dilute skunk oil added. While models were not in the field, all models designated as scented models were stored in a ScentLok® tote bag (ScentLok Technologies, Muskegon, MI) to avoid potential spread of the oil and smell to unscented models. Dilute skunk oil was kept at -20°C in a UV-proof bottle to minimize potential decay of the oil components.

The morning following deployment, cameras and models were collected no sooner than one hour post sunrise. Upon collection, an estimate of the percentage of bait consumed during the night was recorded for each model, along with any additional observations such as change in positioning of the model, missing model, etc. Bait was immediately removed from the model, and trays were cleaned with a dilute bleach solution to remove any remaining odor (Wood 1999).

Following a deployment, videos were transferred from the cameras' SD cards onto an external hard drive and sorted into folders denoting the video's study location, camera site, date, and model. Additionally, videos containing animals that potentially approached the models were sorted into a separate folder.

Visitation Analyses

An animal present on the video was considered as visiting the model if 1) the animal paused and directed its attention to the model, or 2) the animal decreased it distance from the model during the duration of the video. Unless obvious markings or other physical characteristics of the animal(s) present in the videos indicated otherwise, visitations to models by the same species occurring within 10 minutes were considered as one approach to the model (Hunter 2009). To test for differences in visitation frequencies within species, a χ^2 goodness-of-fit test was used for each species visitation to individual model types as well as color and scent types. If the camera did not record any videos, including videos during deployment or collection, that model was not considered as deployed and was not included when calculating expected frequencies. All statistical analyses were completed using IBM SPSS Statistics v. 23 (IBM Corp., Armonk, NY).

To test if certain camera locations were visited more or less frequently due to their location potentially being close to a common travel route or near a denning location, a χ^2 goodness of fit test was used to analyze any preference for camera location.

RESULTS

A total of 222 visits were made to the models over a grand total of 748 camera trap nights. Visits were made by the following species: Virginia opossums (*Didelphis virginiana*), raccoons, domestic dogs (*Canis lupus familiaris*), juvenile and adult coyotes, skunks, turkey vultures (*Cathartes aura*), great horned owls (*Bubo virginianus*), common crows (*Corvus brachyrhynchos*), and domestic house cats (*Felis catus*). Table 2 contains visit frequencies by each species at each field location.

Animals showed no preference for any camera location at Portuguese Bend in Palos Verdes, Los Cerritos Wetlands, Seal Beach National Wildlife Refuge, or Frank G. Bonelli Park. However, there was a preference to visit camera locations 2 and 4 at El Dorado Nature Center when all species visits were accounted for ($\chi^2 = 19.972$, df 5, $p = 0.001$). This effect was mainly accounted for by the high number of visitations by juvenile coyotes and opossums to these stations.

Table 3 contains visitation frequencies by all animals to model types. Combining all species visitations, there was no difference in visitation rates to models types ($\chi^2 = 7.159$, df 5, $p = 0.209$). See Tables 4a-g for observed and expected visitation frequencies to model scent and color types for each species.

Accounting for both adult and juvenile coyote visitations (see Tables 4a-c), an unequal proportion of visits were made to different model types, with more than expected visitations to black-and-white unscented models, and fewer than expected visits to control scented and black-and-white scented models ($\chi^2 = 19.584$, df 5, $p = 0.001$). This effect is mainly due to frequent visitations to black-and-white unscented models by juvenile coyotes in addition to rare visitations to brown scented models ($\chi^2 = 19.061$, df 5, $p = 0.002$). However, when only adult coyote visitations are considered, this effect is no longer seen ($\chi^2 = 4.973$, df 5, $p = 0.419$). Within all coyote visitations, there was no difference in visitation based on color type ($\chi^2 = 3.477$, df 2, $p = 0.176$), a result also seen when considering adult ($\chi^2 = 0.079$, df 2, $p = 0.961$) visitations separately. Juvenile coyotes did show a non-significant trend for visiting black-and-white models more than expected ($\chi^2 = 5.824$, df 2, $p = 0.054$). For all

Table 2. Visitation rates by each species at each of the five field locations.

	Portuguese Bend, Palos Verdes	Los Cerritos Wetlands	Seal Beach Natl. Wildlife Refuge	El Dorado Nature Center	Frank G. Bonelli Park
Coyote	9	4	3	37	3
Raccoon	11	0	1	2	28
Skunk	10	0	0	10	10
Opossum	0	0	0	43	0
Domestic Dog	3	0	0	0	37
Bird Species	2	4	2	0	0
Domestic Cat	0	0	0	0	2

Table 3. Predator visitations made to model types.

	Control, No Scent	Control, With Scent	Brown, No Scent	Brown, With Scent	Black-and-White, No Scent	Black-and-White, With Scent
Coyote	11	5	7	8	21	4
Raccoon	6	2	10	10	10	4
Skunk	4	9	3	4	2	8
Opossum	12	8	7	5	9	2
Domestic Dog	8	11	3	8	5	6
Bird Species	0	1	0	3	2	2
Domestic Cat	0	0	2	0	0	0

Tables 4a-g. Visitations to model color and scent types. Top cells indicate observed visitation frequencies; bottom cells indicate expected visitation frequencies.

Table 4a. All visitations made by coyotes to model types.

	No Scent	Scent
Control	11	5
	(9.4)	*(9.1)*
Brown	7	8
	(9.5)	*(9.4)*
Black-and-white	21	4
	(9.5)	*(9.0)*

Table 4b. Visitations to model types made by adult coyotes.

	No Scent	Scent
Control	5	1
	(3.2)	*(3.1)*
Brown	4	3
	(3.2)	*(3.2)*
Black-and-white	5	1
	(3.2)	*(3.0)*

Table 4c. Visitations to model types made by juvenile coyotes.

	No Scent	Scent
Control	6	4
	(6.8)	*(3.2)*
Brown	3	5
	(5.4)	*(2.6)*
Black-and-white	16	3
	(12.8)	*(6.2)*

Table 4d. Visitations to model types made by raccoons.

	No Scent	Scent
Control	6	2
	(5.0)	*(3.0)*
Brown	10	10
	(12.4)	*(7.6)*
Black-and-white	10	4
	(8.7)	*(5.3)*

Table 4e. Visitations to model types made by opossums.

	No Scent	Scent
Control	12	8
	(7.2)	*(7.0)*
Brown	7	5
	(7.3)	*(7.2)*
Black-and-white	9	2
	(7.3)	*(6.9)*

Table 4f. Visitations to model types made by skunks.

	No Scent	Scent
Control	4	9
	(5.0)	*(4.9)*
Brown	3	4
	(5.1)	*(5.0)*
Black-and-white	2	8
	(5.1)	*(4.8)*

Table 4g. Visitations to model types made by dogs**.**

	No Scent	Scent
Control	8	11
	(6.9)	*(6.7)*
Brown	3	8
	(7.0)	*(6.9)*
Black-and-white	5	6
	(7.0)	*(6.6)*

coyote visitations combined (both adult and juvenile visitations), coyotes visited unscented models more than expected ($\chi^2 = 7.955$, df 1, $p = 0.005$). This effect remains when adult and juvenile coyote visitations are analyzed separately (Adult: $\chi^2 = 3.981$, df 1, $p = 0.046$; Juvenile: $\chi^2 = 4.162$, df 1, $p = 0.041$).

Raccoons did not show a difference in visitation rates for model types ($\chi^2 = 8.201$, df 5, $p = 0.146$). The raccoons did show a non-significant trend of visiting the brown models more than expected, with fewer visits than expected to the control models ($\chi^2 = 4.908$, df 2, $p = 0.086$). There was no difference in visitation rates to models based on scent ($\chi^2 = 2.072$, df 1, $p = 0.150$).

Visitations by opossums were not different among model types ($\chi^2 = 7.840$, df 5, $p = 0.165$). There was no difference in visitations to model color types ($\chi^2 = 3.454$, df 2, $p = 0.178$). A non-significant trend for visiting unscented stations more than expected was observed ($\chi^2 = 3.526$, df 1, $p = 0.060$).

Skunks did not visit any model type at a different rate than expected ($\chi^2 = 8.757$, df 5, $p = 0.119$). All color types were visited at a similar rate ($\chi^2 = 1.901$, df 2, $p = 0.387$), but skunks visited scented models significantly more than expected ($\chi^2 = 5.193$, df 1, $p = 0.023$).

Dogs did not show a difference in visitation rates to models ($\chi^2 = 6.007$, df 5, $p = 0.305$). Additionally, visitations to model colors were not significantly different ($\chi^2 = 3.195$, df 2, $p = 0.202$) and visitations to scented and unscented models were not different ($\chi^2 = 2.275$, df 1, $p = 0.132$).

DISCUSSION

We found that skunk oil is acting as a deterrent to both predators and competitors, as evidenced by preference to visit unscented models. Coyotes and opossums both preferentially visited unscented models, but raccoons did not display this same preference. This result could be due to skunk oil acting as a long-range olfactory signal to warn potential predators of its presence, and would explain why model color did not significantly affect visitation rates for most animals. Model color, being a short-range signal, would not have been available to the animal until approach was already underway and the camera had already captured the animal's presence. Visitations by raccoons, unlike coyotes and opossums, did not seem to be influenced by the presence of the oil. They did, however, preferentially visit brown models and black-and-white models that were not scented. Thus, both predators and some competitors may be relying upon the longer range olfactory signal indicating the presence of a skunk, in order to avoid potentially negative interactions. Additionally, skunks may use some aspects of the oil for interspecific communication, as skunks preferentially visited scented models. Evaluation of the behavior during approach will provide further information as to the interaction of olfactory and visual signals on predator behavior.

The juvenile coyotes that visited the black-and-white unscented models may have been initially attracted by the conspicuous pelage, and without being paired with the odor of skunk oil, the model may not have been recognized as a potentially dangerous prey item. Since juveniles may not have had previous experience with skunks, both the visual and olfactory aspect of the skunk's warning signal may be needed initially to deter potential predators, after which only one aspect, the odor or the pelage, is needed. While all color types were visited equally by coyotes, evaluation of the behavior during visitation has yet to be analyzed, which could reveal differences in approach tactics between color types as seen by Hunter (2009). The avoidance of scented models by adult and juvenile coyotes indicates the oil is acting as a deterrent to investigation.

The efficacy of carnivore lures containing skunk oil could be a result of using the entire anal gland in the lure, or the skunk oil could be reacting with other ingredients in the lure to create an attractive odor. Further, the use of the entire anal gland in lures could result in a carrion odor, which is inherently attractive to many vertebrate species and actively used by scavengers when foraging (DeVault et al. 2004). Using the entire anal gland in the lure could result in the release of pheromones that indicate the animal has been injured. The release of alarm pheromones upon injury has been well documented in fish (Smith 1992), with some alarm pheromones known to attract secondary predators in order to disrupt the primary predator from continuing its attack (Chivers et al. 1996). Mice and other mammals are known to release alarm signals when stressed or under attack, but the release of pheromones solely upon injury, and not from stress, has not been documented (Dulac and Torello 2003).

It should be noted that Scent Killer® Gold™ may not entirely remove all human scent. However, all study areas had at least semi-regular human presence, and thus animals in the surrounding area would most likely be habituated to any scent that was potentially left behind at the models. It is possible that despite keeping the scented and unscented models in separate containers while they were not deployed oil could have been transferred between models. However, the amount of oil potentially transferred between model types would have been minute, considering the oil used was already diluted.

Intraguild competition driven by dietary overlap between skunks, raccoons, and opossums (Azevedo et al. 2006) is evidenced by the avoidance of all scented models by opossums, as well as an avoidance of all black-and-white scented models by raccoons. Competitors may be using long-range olfactory abilities to recognize skunk oil as an indicator of a potentially dangerous competitor, and thus avoiding areas where the scent is present. The similar visitation frequencies to all model colors by skunks could indicate that skunks do not view raccoons or opossums as competitors, since the skunks are able to avoid costly interactions due to their noxious spray. Skunks preferentially visiting scented models could be a result of this study partly taking place during February and March, the skunk's breeding season (Verts 1967). The oil from the skunk's anal gland could be used for interspecific communication or mate attraction, though the skunk's oil is not known to play any role in sexual signaling, unlike in other carnivores. Further investigation into the variation of skunk oil compounds and its potential uses in interspecific signaling could provide useful information for management of skunks.

Domestic dogs did not show a preference for model color or scent, and this could be a result of behavioral modification during domestication. The predatory behaviors of dogs have been altered extensively compared to the wild type ancestor (Coppinger and Coppinger 2001), such that the same signals that result in a wild canid avoiding skunk oil could no longer be present or active. Anecdotal evidence suggests there is variation in dogs' reactions to skunks and skunk spray, with many of the accounts describing an attraction to the odor despite spraying events, and some describing an active aversion to it (Anonymous 1840, Anonymous 1888, Anonymous 1903, Cuyler 1924). It is not known if the causes for these differences in reaction to skunks are due to learning events or alterations in the dogs' behavior that occurred during domestication.

An analysis of domestic cat visitations was not completed due to the small sample size (n = 2). Investigation as to how domestic cats rely upon visual and olfactory information during approach to a prey item would be a valuable line of investigation due, to the large impact of feral cats on island ecology and biodiversity (Nogales et al. 2013) and the need for effective control and management plans.

While skunk oil is not a practical deterrent to use near human residences, there is the potential for using skunk oil as a deterrent to coyotes, raccoons, opossums, and other mesopredators for agricultural pest control. The use of black-and-white models and skunk oil, paired with additional deterrents such as startling noises and other aversive strategies, possibly could be used to develop multi-modal non-lethal management systems for coyotes and other mesopredators. Laboratory studies with chicks (*Gallus gallus domesticus*) have demonstrated an increase in avoidance learning when the defensive signal exploits multiple senses, though this effect has not been studied in mammals (Siddall and Marples 2008). Indeed, the presence of model competitors that exploit multiple sensory systems could mimic an increase in intraguild competition among mesopredators. An increase in perceived competition, while potentially not as effective as mimicking the presence of a predator, may slow trophic cascades caused by mesopredator release that frequently occur within urban environments or environments in which an apex predator has been removed (Prugh et al. 2009). Slowing or halting the trophic cascades that occur in the absence of an apex predator could potentially relieve some predation pressure on native prey species, providing an opportunity for population expansion and recovery.

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