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Source: Folia Zoologica, 62(1) : 59-66

Published By: Institute of Vertebrate Biology, Czech Academy of Sciences

URL: https://doi.org/10.25225/fozo.v62.i1.a9.2013

Wolf diet and its impact on the ungulates community in a new recolonized area of Western Alps: Gran Paradiso National Park

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Received 28 March 2012; Accepted 24 July 2012

Abstract. The aim of this study is to evaluate how wolves affected the prey community in a newly recolonization area of the Western Alps, the Gran Paradiso National Park (GPNP). Since 1960's, this portion of the Alps hosts a multi-specific wild ungulate community. It lived in absence of large predators for more than a century. In 2006 a couple of wolves re-established in GPNP and in summer 2007 the first reproduction was documented. The present study was conducted during the following two years. In term of biomass consumed (Bio%), Alpine chamois was the main prey of wolves in all seasons ($Bio\%_{Summer\ 2007}$ = 70.13; $Bio\%_{Winter\ 2007/2008}$ = 56.99; $Bio\%_{Summer\ 2008}$ = 67.52; $Bio\%_{Winter\ 2008/2009}$ = 36.35), while roe deer were intensely consumed during the adverse season ($Bio\%_{W2007/2008}$ = 23.05 %; $Bio\%_{W2008/2009}$ = 42.47 %). Although cervids were much less abundant than bovids in the area, they represented one of the main food items of wolves, possibly because of the strong habitat overlap and altitude use between predator and preys. Moreover, the minor adaptation of cervids to the Alpine environment compared to bovids could affect their vulnerability and thus the respective consumption of the different species during the adverse season.

Key words: *Canis lupus*, feeding habits, recolonization, Alpine environment

Introduction

The Alpine environment has been subject to severe alterations in the last century because of human activities and the inherent fragility of the extreme habitats. Specifically in Western Alps mammalian communities showed strong fluctuations: from the middle of the 19th century several ungulate species were threatened with extinction (*e.g.* Alpine ibex, *Capra ibex*) and all large carnivores were eradicated.
Since the foundation of Gran Paradiso National Park in 1922, the ungulate community started to recover its diversity and abundance also thanks to reintroduction projects carried out in the Alps. Since 1995 also wolves appeared in the region, but just during summer 2006 the stable presence of two wolves was confirmed in the area. After the first reproduction occurred in 2007, a pack of six wolves settled in Gran Paradiso National Park following 150 years of absence. Until the recolonization, wild ungulate population dynamics were regulated by physiological and environmental factors like disease, starvation, age and climate. In this environmental context, the recolonization of the area by large carnivores could strongly influence wild ungulate population dynamics.
Relations between wolf and its natural prey have been largely investigated in North America (Huggard 1993, Mech 1995, Peterson & Ciucci 2003, White & Garrott 2005) and in Central-Northern Europe (Okarma 1995, Okarma et al. 1998, Gade-Jørgensen & Stagegaard 2000, Jędrzejewski et al. 2000, 2002, Sidorovich et al. 2003, Kojola et al. 2004, Smietana 2005). In Italy, several studies on impact and dietary response were conducted in the Apennines (Meriggi et al. 1991, Patalano & Lovari 1993, Mattioli et al. 1995, Meriggi & Lovari 1996, Capitani et al. 2004, Mattioli et al. 2011). The topic was less investigated in the Alpine region because of its recent recolonization. The previous studies have been conducted just in Côtè d'Azur and Piedmont (Poulle et al. 1997, Gazzola et al. 2005, 2007, Marucco et al. 2008).
Therefore, the aim of the present study is to evaluate how the presence of the first reproductive wolf pack in

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the Gran Paradiso National Park could affect the local wild ungulate community by analysing the diet of wolves and their impact on the different prey species.

Material and Methods

The study was conducted in the Italian Western Alps, south-western portion of the Aosta Valley Region (45°35′34.19″ N; 7°12′34.17″ E). The study area covers 592 km^2, it is almost totally included within the Gran Paradiso National Park (GPNP). Altitude ranges from 1030 to 4061 m above sea level. Climate is continental with a prolonged snow cover period that runs from October-November to April-May, depending on altitude. At the lowest altitude broad-leaf forest of maples (*Acer pseudoplatanus*) and lime trees (*Tilia platyphyllos*) are present with discontinuous distribution. Coniferous forests constitute the main vegetation type from 1000 to 2300 m. Norway spruce (*Picea abies*) is a common species at the middle range of the sub-alpine level (1800-2000 m), while larch (*Larix decidua*) and Swiss stone pine (*Pinus cembra*) forests are present at the highest altitudes up to the highest sub-alpine level (2200-2300 m). Over 2300 m, Alpine meadows (*Carex* spp., *Festuca* spp., *Poa* spp.) and glaciers replace the forest. The study area is also characterised by abundant steep slopes, cliffs and stone ravines.

The wild ungulate community is constituted by two species of bovids: Alpine chamois (*Rupicapra rupicapra*) and Alpine ibex, by two species of cervids: roe deer (*Capreolus capreolus*) and red deer (*Cervus elaphus*), and by wild boar (*Sus scrofa*). Livestock is sporadically present: small flocks of sheep or goats and herds of cows are free-ranging on high pastures from May to October.

The study was conducted from May 2007 to April 2009. During this period the Aosta Valley Region (3263 km^2) was wholly monitored by the authors, Corpo Forestale della Valle d'Aosta and GPNP rangers to detect wolf presence. The wolf population was represented by a single pack of six wolves in 2007 and 2008 but during winter 2008-2009 the number decreased up to four individuals.

The wolf pack size was estimated by snow-tracking survey but also by direct observations. During the winter season, wolves were tracked in presence of fresh snow (24-48 hours after the snowfall) by several teams of operators in different portions of the study area. Once a wolf trail was found, it was followed until the number of individuals travelling along became distinguishable. The largest number of wolves was accepted as the size of the wolf pack in a certain season (following Jędrzejewski et al. 2000). Transects aimed to detect and collect wolf scats were monthly travelled on foot by the authors (total length = 1258 km per year) and GPNP rangers all over the study area crossing the different vegetation types and altitudinal ranges. The sampling effort was uniformly distributed over the whole study area. In presence of fresh snow we prioritized the portions of terrain with the higher probability of encountering the wolf trails. In absence of snow, we paid particular attention while checking crossroads and other potential marking spots to detect the scats (Llaneza et al. 2005). Every wolf scat detected along each transect and its proximities (*i.e.* both on trail and off trail) were collected to analyse the wolf diet.

Wild ungulates population abundance and structure were obtained by vantage-point counts for deer while Alpine ibex and Alpine chamois were censed by block counts; no data on wild boar population were available. Censuses were carried out in spring and in late summer by the Gran Paradiso National Park and Aosta Valley Regional Administration. Alpine chamois and Alpine ibex are the most abundant species followed by roe deer. Red deer is rather rare (Table 1).

Wolf feeding habits were assessed analysing 349 scats (153 from May 2007 to October 2008 and 197 from May 2008 to October 2009). Samples were washed and filtered through a 0.5 mm mashed sieve. Undigested prey remains, fruit and grasses were oven dried at 50 °C for 24 h. Prey remains were identified by comparison with a reference collection of mammal hairs. When necessary, hair microscopic characteristics (*cortex* and *medulla*) have been compared with atlases (Debrot et al. 1982, Teerink 1991).

The age class of ungulates found in wolf scats was determined by analysis of recognizable bone fragments, teeth, and macroscopic comparison of hairs (see Mattioli et al. 1995). Two age classes were distinguished for all species: juveniles (< 1 year of age) and adults (> 1 year of age). Determination of age by hairs was possible till the first moult (*i.e.* around October), after this only bone fragments were considered to discriminate young from adults. For wolf diet analysis two seasons were considered: May-October (summer), November-April (winter).

Besides scat-content analysis, we took into account 138 carcasses of ungulates consumed by wolves during the study period to determine species, age and gender of individuals consumed. Carcasses were detected by authors and GPNP rangers along transects

Table 1. Wild ungulate abundances.

Ungulate species	2007		2008	
	N individuals	%	N individuals	%
Alpine chamois	6051	68.29	6082	68.83
Alpine ibex	2176	24.56	2012	22.77
roe deer	582	6.56	697	7.89
red deer	51	0.57	44	0.49
Total	8860	100	8835	100

Table 2. Mean of live body mass referred to each food item.

	Average body mass (kg)		
	Adult	Juvenile (winter)	Juvenile (summer)
wild boar	60.0	22.5	8.0
roe deer	20.0	13.0	8.0
red deer	110.4	57.7	26.5
chamois	26.0	14.2	11.0
Alpine ibex	65.0	15.0	15.0
hare	3.0	-	-
rodents	0.03	-	-
sheep	66.8	-	-
goat	44.8	-	-
cattle	110.0	-	-

during summer and by tracking the wolves on snow during winter. We took into account exclusively carcasses bearing evidences of wolf predation.

Biomass ingested was estimated from relative volumes of remains for each scat. On the basis of a known relationship between the amount of mammalian prey biomass consumed and collectable scat produced, we used the biomass model of Weaver (1993): Y = 0.439 + 0.008 X. The dependent variable (Y) represents the biomass ingested per collectible scat, and the independent variable (X) is the live body mass (kg) of the prey species recovered in the scat. The number of samples used in calculating total biomass ingested was obtained by summing all relative biomass proportions of a given food type from scats where that food category had occurred (Floyd et al. 1979, Ciucci et al. 1996). Food items showing a percentage of biomass lower than five percent were considered accessories and not included in further analysis.

Live body mass of prey species (Table 2) needed to estimate wolf impact on the ungulate population were taken from several sources. Data about Alpine ibex and chamois have been obtained by calculating the mean body mass of individuals caught by GPNP rangers, those about cervids were taken from literature (Bassano et al. 1999). Values of average body mass of ungulates were reduced by 10 % for juveniles and 25 % for adults (Fuller 1989, Okarma 1992, Głowacinski & Profus 1997) on account of inedible and indigestible parts of their bodies (large bones, hairs and stomach).

A resample with replacement (bootstrap with 1000 permutations) was applied to the seasonal datasets of biomass values in order to calculate the 95 % confidence interval of our sample. Once we verified that the mean values calculated for the seasonal datasets were included in the 95 % CI, we compared those values with the mean values calculated for the seasonal datasets obtained by bootstrapping. Since the values were comparable, we used the mean values resulting from the bootstrapped datasets for the following analysis.

To estimate the total amount of biomass (expressed in kg) ingested by wolves we calculated the minimum food consumption rate based on the field metabolic rate (FMR) derived from Nagy's formula: FMR (kJ/day) = $2.58W^{0.862}$, where W is body mass in grams (Głowacinski & Profus 1997). We considered the body mass indicated by Gazzola et al. (2007) as the average body mass of the Italian wolf: 32 kg for the adults (> 1 year old) and 16 kg for young individuals. Energy requirements based on the field metabolic rate amounted to 2.6 kg of meat per day for an adult wolf and 1.4 kg for a young one.

Table 3. Wolf diet basing on scat-content analysis. Diet is expressed as percentage of biomass consumed at a seasonal scale and ninety-five per cent confidence interval (95% CI) for each food item ($N_{Summer\ 2007}$ = 42; $N_{Winter\ 2007-2008}$ = 111; $N_{Summer\ 2008}$ = 125; $N_{Winter\ 2008-2009}$ = 72).

Food items	2007-2008				2008-2009			
	Summer	95% CI	Winter	95% CI	Summer	95% CI	Winter	95% CI
Alpine chamois	70.13	56.22-81.97	56.99	47.95-65.85	67.52	59.63-76.01	36.35	26.92-49.01
roe deer	18.61	7.57-30.80	23.05	15.95-30.81	18.69	13.33-26.89	42.47	32.53-52.83
Alpine ibex	8.07	0.00-12.61	18.65	10.74-25.72	8.86	4.20-14.38	9.08	1.63-13.07
red deer	0.00	-	0.00	-	4.10	0.00-7.56	5.11	0.00-12.65
wild boar	0.00	-	0.00	-	0.82	0.00-2.38	1.75	0.00-3.66
sheep	3.19	0.00-9.00	1.31	0.00-3.93	0.00	-	1.98	0.00-5.80
goat	0.00	-	0.00	-	0.00	-	3.26	0.00-8.17
small mammals	0.00	-	0.00	-	0.00	-	0.26	-
Total	100.00		100.00		100.00		100.00	

Table 4. Pianka's index values, dietary niche overlapping on seasonal scale.

Pianka's index	Winter 2007-2008	Summer 2008	Winter 2008-2009
Summer 2007	0.98	1.00	0.82
Winter 2007-2008	-	0.98	0.88
Summer 2008	-	-	0.83

Table 5. Use of different age classes by wolves expressed as percentage of biomass consumed at seasonal scale ($N_{Summer\ 2007}$ = 42; $N_{Summer\ 2008}$ = 125).

Prey species	Summer 2007		Summer 2008	
	Juvenile	Adult	Juvenile	Adult
Alpine chamois	70.73	29.27	42.16	57.84
roe deer	45.27	54.73	75.20	24.80
Alpine ibex	100.00	0.00	72.42	27.58
red deer	-	-	22.06	77.94
wild boar	-	-	100.00	0.00

We calculated the seasonal biomass required by the pack based on the number of wolves we estimated for each season. In order to estimate the biomass consumed for each prey species and age class, the seasonal biomass required by wolves was shared among the different food items based on the proportion of use we measured by scat-content survey. The obtained values were divided by the mean body mass of each prey species to estimate the effective impact (expressed as the number of individuals consumed) of wolves on the ungulate population.

Differences between the observed seasonal use and the expected consumption of each prey species were verified using a chi-square test. All hypotheses were tested with a level of significance of $\alpha = 0.05$. Food niche breadths (*B*) were calculated after Levin's (1968) index for five main prey species (Alpine chamois, roe deer, Alpine ibex, red deer, wild boar). $B = 1/\Sigma P^2$ where *P* is the frequency of biomass of a particular prey item. Overlap of seasonal diets was determined using Pianka's (1973) index, it ranges in value from 0 (indicating no overlap between two seasons) to 1 (complete overlap).

Results

The bulk of wolf diet was represented by wild ungulates which constituted 94.7-100% (Min-Max) of biomass consumed for each season. Diet was made up of two main food items (*i.e.* Alpine chamois and roe deer). Levin's index (*B*) that we used to calculate food niche breath showed values ranging from 1.77 to 2.93 ($B_{Summer\ 2007} = 1.77$; $B_{Winter\ 2007\text{-}2008} = 2.40$; $B_{Summer\ 2008} = 1.99$; $B_{Winter\ 2008\text{-}2009} = 2.93$).

Red deer and Alpine ibex were secondary in diet of wolves while wild boar, domestic ungulates and small mammals never reached 5 % of the biomass consumed at seasonal scale and were considered accessory food items (Table 3). The dietary niche overlap among the four seasons was high: the only slight difference among seasons was due to winter 2008-2009 (Table 4).

We further investigated the use of different age classes of each prey species during summer seasons. Juveniles of all species appeared in the diet of wolves and sometimes they were consumed more than adults (Table 5).

Results obtained by the investigation on carcasses were similar to those resulted by scat-content analysis. Alpine chamois is the most consumed item (78.3 %) followed by roe deer (9.4 %) and Alpine ibex (5.8 %).

Table 6. Sex and age class of ungulates consumed by wolves basing on carcasses survey (NI = Not Identified).

Prey species	Sex			Age class			N
	%Male	%Female	%Sex NI	%Adult	%Juveniles	%Age NI	
Alpine chamois	35.19	10.19	54.63	37.04	7.41	55.56	108
Alpine ibex	75.00	25.00	0.00	75.00	0.00	25.00	8
roe deer	23.08	7.69	69.23	30.77	0.00	69.23	13
wild boar	50.00	0.00	50.00	50.00	50.00	0.00	2
Species ND	0.00	0.00	100.00	0.00	0.00	100.00	7

Table 7. Impact of wolves on the ungulate community, average seasonal impact and annual consumption expressed as percentage of the population censed in certain period.

Prey species	N individuals consumed/100 km²					Consumption %	
	Summer 2007	Winter 07/08	Summer 2008	Winter 08/09	Mean ± SD	2007-08	2008-09
Alpine chamois	23.79	16.61	17.69	8.03	16.53 ± 6.49	3.94 %	2.50 %
roe deer	7.02	7.53	8.60	12.69	8.96 ± 2.57	14.75 %	18.01 %
Alpine ibex	2.42	4.32	2.01	2.03	2.70 ± 1.10	1.83 %	1.19 %
red deer	0.00	0.00	0.27	0.24	0.13 ± 0.15	0.00 %	6.82 %
wild boar	0.00	0.00	0.23	0.12	0.09 ± 0.11	-	-

However the proportion of use of the different species and age classes was different: possibly because data obtained from carcasses tend to overestimate the use of larger prey species. Moreover, we observed a considerable percentage of individuals whose sex and age were impossible to determine (Table 6).

Between 2007 and 2009, wolf pack size ranged from 2 to 6 individuals. According to field metabolic rate calculated through Nagy's formula (Głowacinski & Profus 1997), food requirement ranges from 2.6 kg wolf^{-1} day^{-1} for an adult wolf (W = 32 kg) to 1.4 kg for a young one (W = 16 kg). Consequently, the seasonal requirement for the whole pack was 2152 ± 450 kg (mean ± SD) of meat and the daily consumption rate was 0.18 ± 0.03 prey items per wolf.

We found significant differences between the proportions of prey-categories consumed by wolves and those expected from the relative abundances of the different prey species ($X^2_{\text{Summer 2007}} = 88$; df = 3; $p < 0.01$; $X^2_{\text{Winter 2007-2008}} = 111$; df = 3; $p < 0.01$; $X^2_{\text{Summer 2008}} = 126$; df = 3; $p < 0.01$; $X^2_{\text{Winter 2008-2009}} = 420$; df = 3; $p < 0.01$). This evidence is emphasized by the annual consumption of the different prey species (Table 7). Despite the prevalence of Alpine chamois in terms of biomass consumed, the annual impact on its population was negligible. On the contrary, roe deer was proportionally most affected by wolf use.

Discussion

During the last century, the ungulate community in the Western Alps experienced a dramatic increase both in numbers and in species richness. This process resulted from changes in land use related to declining human activities in mountainous areas, from introduction of not-Alpine game species and from reintroduction of endangered Alpine species (*e.g.* Alpine ibex). Moreover, protected areas facilitated the recovery of wild ungulates providing shelter to expanding populations. As a result of the spreading, the region currently hosts abundant populations of Alpine species (*i.e.* Alpine chamois and Alpine ibex) that coexist with mounting populations of deer and allochthonous species like mouflon (*Ovis orientalis*) (Apollonio 2004, Carnevali et al. 2009).

Following the growth of prey populations and the banning of persecution, the wolf started to recolonize the Alpine area. The wolf was quite efficient in retaking terrain thanks to its abundance in the Apennine and its socio-ecological traits. Recolonization of Alps by Italian wolves proceeded from the west (Maritime Alps) to the east. The Aosta Valley is the eastern edge of the current wolf distribution in the Italian Alps. How the recolonization could affect local prey communities is not determined yet. The diet of opportunistic carnivores is generally connected to prey abundance, vulnerability and accessibility (Huggard 1993, Aryal et al. 2011). Several studies confirmed the preference of wolf for wild ungulates (Mech 1970, Voigt et al. 1976, Fritts & Mech 1981, Ballard et al. 1987, Smietana & Klimek 1993, Jędrzejewski et al. 2000, 2002, Gazzola et al. 2005, 2007, Mattioli et al. 2011) but the plasticity of its diet in relation to scarcity of natural prey is also well documented (Castroviejo et al. 1975, Boitani 1982, Salvador & Abad 1987, Meriggi et al. 1991, Patalano & Lovari 1993, Darimont 2002, Peterson & Ciucci 2003, Sidorovich et al. 2003).

The results presented in this study confirm wild ungulates as staple prey of wolves. The food niche breadth index calculated for the wolf pack ranged from 1.77 and 2.93 (min-max). These values were comparable to the results obtained by several studies carried out in Europe (Kübersepp & Valdmann 2003, Sidorovich et al. 2003, Andersone & Ozoliņš 2004, Nowak et al. 2005, Meriggi et al. 2011) and confirmed that wolves used few prey species despite the richness of the local ungulate community. In the present study we observed a slight increase of the wolf trophic niche breadth during winter, it could be due to the higher vulnerability of some prey species during the adverse season and the consequent increase in the use of those species by wolves.

We observed a seasonal shifting in the consumption of different prey items by wolf: consumption of roe deer increased during winter and decreased during summer while Alpine chamois showed an inverse trend in percentage of use. High consumption of roe deer during winter could be due to the lower adaptation of this species to mountainous snowy regions compared to Alpine bovids. Antipredator behaviour of roe deer in presence of deep snow and steep slopes is ineffective contrary to Alpine chamois that is well adapted to escape wolf predation in these environmental conditions. On the other hand, consumption of Alpine chamois increases during summer, in coincidence with the presence of vulnerable young individuals.

The seasonal shifting in the consumption of Alpine and not-Alpine prey species was observed also in other studies conducted in the Alps on feeding habits of wolf (Poulle et al. 1997, Gazzola et al. 2007, Marucco et al. 2008). In the Mercantour National Park (Côtè d'Azur – FR), mouflon is present with a stable population since its introduction in the 1970's. It represented the main prey species for wolves followed by Alpine chamois

(Poulle et al. 1997). The consumption of mouflon increased during winter and decreased during summer. The authors concluded that the trend in consumption could be due to the insufficient adaptation of mouflon to the Alpine environment. Gazzola et al. (2007) had similar results in Susa Valley (Piedmont – IT) where cervids represented the main part of total biomass ingested by wolves, particularly during winter. During summer, livestock was an important food item but Alpine chamois was the third most important food item in the area. Interesting data about the importance of cervids in the winter diet of wolves are provided by Marucco et al. (2008). Their study was conducted in Pesio Valley (Piedmont – IT) where the primary prey species of wolves during winter were roe deer and chamois. Also the red deer appeared in wolf diet and its consumption was relevant during winter 2001 despite its low density in the area.

We can hypothesize that wolves in the Alps tend to prey more intensively on not specifically adapted Alpine species, like deer and mouflon. Although the Alpine species were strongly consumed because of their abundance, the estimated impact on their population is not considerable and their densities should not vary in relation to wolf predation. Conversely, wolf predatory pressure was particularly high on not-Alpine species during the adverse season (Palmegiani & Apollonio 2011). The strong impact of wolves on these populations, jointly with harsh Alpine environment, could reduce the distribution and the abundance of these species in extreme Alpine environments.

Several studies conducted in the Apennine recognize wild boar as the main prey while deer were negatively selected by wolves (Meriggi et al. 1991, Mattioli et al. 1995, Meriggi & Lovari 1996, Capitani et al. 2004, Mattioli et al. 2011). The strong variability of wolf diets between areas is certainly related to prey availability, but also bio-physical features (*e.g.* topography, vegetation and climate) could influence the diet of wolves by affecting the vulnerability of prey species like roe deer.

Information obtained by analysing carcasses is comparable with that from scat-analysis but some differences emerged in the proportion of use among species. We realized that the estimated consumption of specific prey types depended on the method we used: using carcass surveys resulted in a higher estimate of consumption for large prey species and adults of each species compared to estimates derived from scat-content analysis. It could be due to the difficulty in finding remains of small individuals like roe deer and juveniles. Despite this, carcasses survey allowed us to observe a strong use of adult male individuals in Alpine chamois. This evidence could be related to the conditions of males during winter. In this season males are exposed to the physical stress related to the rut that can strongly affect their body conditions and consequently increase the vulnerability to predation of wolves.

The estimated impact on ungulate community shown in the present study is comparable with previous studies conducted in Central and Southern Europe (Jędrzejewski et al. 2002, Gazzola et al. 2007); most of the variation could be due to differences in average wolf bodymass and methodological approaches. The influence of wolves on ungulate populations is very difficult to evaluate, especially in complex European biocenoses, but basing on the results obtained we could assume that during winter wolves represented a compensatory cause of death for Alpine species like chamois. Although this species was the most consumed by wolves during the study period, its density held steady. At the contrary, not-Alpine species density (*e.g.* roe deer) could be affected by wolf presence in the long term as observed in several European biomes (Melis et al. 2009).

Acknowledgements

Our grateful thanks go to Aosta Valley Regional Administration for funding the present research and to Gran Paradiso National Park for availability and accommodation provided. Further we thank GPNP rangers and the Corpo Forestale della Valle d'Aosta for their precious support in monitoring activities.

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