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EFFECTS OF VISIBLE SIGNS OF CONTAGIOUS ECTHYMA ON MASS AND SURVIVAL OF BIGHORN LAMBS

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ABSTRACT: External signs of contagious ecthyma became common in a population of Rocky Mountain bighorn sheep (*Ovis canadensis*) in Alberta, Canada, after it attained high density. Between 1990 and 1993, we studied effects of this disease on mass gain and survival of lambs. Prevalence and severity were independent of lamb sex. Lambs with large sores and scabs gained less mass than other lambs and were lighter the following spring as yearlings. There was no significant effect of the disease upon lamb survival, and contagious ecthyma did not appear to play a primary role on the dynamics of the study population.

Key words: Bighorn sheep, *Ovis canadensis*, contagious ecthyma, body mass, survival.

INTRODUCTION

The importance of disease on population dynamics long has been recognized (Anderson and May, 1978). There have been several studies of parasites in birds where marked hosts of known infection status were monitored (Richner et al., 1993; Weatherhead et al., 1993), but few investigations have been conducted on wild mammals, and these have focused mostly on macroparasites (Folstad et al., 1989; Festa-Bianchet, 1991; Arnold and Lichtenstein, 1993). Most studies of the effects of parasites upon growth and survival of wild ungulates have relied on information from dead animals (Leader-Williams, 1982; Demarais et al., 1983; Messier et al., 1989; Mulvey and Aho, 1993), because live mammals are difficult to capture and observe, and few diseases or parasites can be monitored without killing the host.

Among sexually dimorphic mammals, males are generally more susceptible to parasites than females, and younger animals are more susceptible than older animals (Folstad et al., 1989; Festa-Bianchet, 1991; Gulland and Fox, 1992). Young males appear to be more susceptible than young females to resource shortages (Clutton-Brock et al., 1985), perhaps because males maximize growth to the detriment of body reserves. In bighorn sheep (*Ovis canadensis*) and in many other polygynous

ungulates, the reproductive success of males depends mostly on body and horn size, because access to mates is determined by male-male combat (Geist, 1971). Festa-Bianchet (1989) suggested that young bighorn males are more vulnerable than females to parasites and pathogens. Young males had a higher mortality rate than young ewes during a pneumonia epizootic (Festa-Bianchet, 1989), and more lungworm larvae were found in the feces of male than of female lambs and yearlings (Festa-Bianchet, 1991).

Our objective was to determine the effects of a viral disease, contagious ecthyma, on bighorn sheep lambs. This disease is not normally considered lethal and its external lesions are readily observable (Samuel et al., 1975), but there is no information on whether it affects growth or survival of wild hosts. We predicted that the prevalence and severity of the disease would be greater in males than in females, and that the disease would lower the growth of affected individuals and increase mortality.

Contagious ecthyma (CE), otherwise known as orf or pustular dermatitis, can affect several wild ungulates, including bighorn sheep (Lance et al., 1981), Dall sheep (*Ovis dalli*) (Smith et al., 1982), mountain goats (*Oreamnos americanus*) (Blood, 1971; Samuel et al., 1975), chamois (*Rupicapra rupicapra*), Himalayan thar

(*Hemitragus jemlaicus*) (Kater and Hansen, 1962), steinbock (*Raphicerus campestris*), musk ox (*Ovibos moschatos*), and reindeer (*Rangifer tarandus*) (Kummeneje and Krogsrud, 1979). Lance et al. (1983) induced experimental infections in mule deer (*Odocoileus hemionus*), white-tailed deer (*O. virginianus*), pronghorns (*Antilocapra americana*), and wapiti (*Cervus elaphus*).

METHODS

We evaluated bighorn sheep at Ram Mountain, Alberta, Canada (52°25'N, 115°45'W, elevation 1082 to 2173 m). Descriptions of the study area and the methods used to capture, mark, and monitor individual sheep are summarized in Jorgenson et al. (1993b) and L'Heureux et al. (1995). Over 90% of the bighorns on Ram Mountain have been individually marked since 1975, and most are recaptured at least twice each summer. The mountain is separated from the main Rocky Mountain range by about 30 km of coniferous forest. Bighorn sheep on Ram Mountain migrate seasonally to different sections of the mountain, but much of the mountain is used year-round and there are no well-defined seasonal ranges. Data reported here were collected from 1990 to 1993, when the population in mid-June averaged 217 sheep (95 ewes, 52 rams, 22 yearlings, and 48 lambs), more than twice the number (average of 102 sheep) present in 1978 to 1981 during a ewe removal experiment (Jorgenson et al. 1993b). Lambs were captured in a corral trap from early June to early October (mean = 1.5 captures/lamb, for 208 captures). All lambs captured were individually marked with colored plastic streamers attached to numbered metal ear tags. By matching each lamb (marked or unmarked) with its mother during observations of suckles, we estimated that we caught 79% of the lambs seen alive each year. All ewes were individually marked, and once we had established reproductive status for each ewe (suckling a lamb or without lamb), the number of matches gave us the total number of lambs. When lambs were recaptured the following year as yearlings, the plastic streamers were replaced with Allflex plastic ear tags for males and canvas collars for females. We weighed captured lambs with a spring scale to the nearest 125 g, and checked all individuals for lesions around the hooves, lips and nose. Some lesions were small superficial scabs whereas other were inflamed, oozing clear liquid, pus, or blood. Contagious ecthyma was confirmed in a skin biopsy collected

from a lamb in 1993. A pox virus was observed via negative stain electron microscopy (D. K. Onderka, pers. comm.).

We based our field diagnoses entirely on the presence or absence of visible lesions. In 1990, lambs were classified as either affected by CE or not affected, regardless of the severity of lesions. From 1991 to 1993, we scored CE lesions on a four-point scale according to the following criteria: negative (0), no visible lesions; mild (1), superficial scabs; moderate (2), dry blood and scabs; and severe (3), open, bleeding sores. To analyze data for lambs that were scored differently at different captures, we used the highest score. We also noted the size and location on the body of scabs and sores.

We were interested in the potential effects of CE upon mass gain. Because lambs were captured at different dates, we adjusted mass to 15 September, near the end of the trapping season. Lambs gained mass linearly during summer (L'Heureux, 1993). For lambs that were caught twice or more ($n = 59$), we used the individual linear rate of mass gain of each lamb to adjust its mass to 15 September. For other lambs ($n = 26$), we adjusted body mass using sex- and infection-specific linear regression equations obtained from pooling all captures of lambs of a given sex and infection status (visible signs or no visible signs). To increase the accuracy of adjusted mass, only lambs weighed within 50 days of 15 September were included. Lambs that died before 15 September were excluded.

We also adjusted individual masses to 15 June, to see whether lambs that later developed lesions were lighter than other lambs early in the season. Most lambs were born in late May (Festa-Bianchet, 1988), and by 15 June they were 2 to 3 wk of age. We chose 15 June because, although we started trapping in late May, we caught few lambs until the second week of June. Because more lambs were caught within 50 days of 15 September than within 50 days of 15 June, our sample of early-season mass measurements was smaller than our sample for late summer.

To adjust individual body mass to the following 5 June for lambs born in 1991, we used individual mass gain rates of yearlings in 1992. All yearlings were caught two to five times in 1992 and individual rates of mass gain were available to adjust their mass. Linear regressions were used, because yearlings gained mass linearly (L'Heureux et al. 1995).

We analyzed effects of CE on lamb body mass adjusted to 15 June and 15 September with three-way analysis of variance (ANOVA), including year and lamb sex as factors. All statistical procedures followed Sokal and Rohlf

TABLE 1. Severity and location of contagious ecthyma lesions in 105 bighorn sheep lambs at Ram Mountain, Alberta, Canada, 1991 to 1993.

Location	Severity of lesions			Total
	Mild	Moderate	Severe	
Feet only	17 (16%) ^a	5 (5%)	5 (5%)	27 (26%)
Mouth only	11 (10%)	1 (1%)	0 (0%)	12 (11%)
Both feet and mouth	15 (14%)	11 (10%)	10 (10%)	36 (34%)
Total	43 (41%)	17 (16%)	15 (14%)	75 (71%)

^a Number (percent) with a particular lesion.

(1981) and all probability values were two-tailed. Because in 1990 CE signs were only recorded as present or absent, we performed an analysis with data from 1990 to 1993 including only two levels of CE severity, followed by an analysis of data from 1991 to 1993 with four levels of CE severity. We used G-tests to determine if CE prevalence varied as a function of sex or affected survival to one year. To test for sex differences in CE severity, we assigned values of zero to three for severity as described, and compared lambs of different sex with Mann-Whitney *U*-tests.

RESULTS

Occasional cases of CE (less than one per year) were noticed at Ram Mountain before 1990, but no detailed records were kept. In 1990, the disease was common among all sex-age classes. After 1990, the disease was prevalent among lambs (Table 1) but signs were absent in older sheep.

The CE prevalence was 74% for male lambs ($n = 57$) and 65% for females ($n = 68$); it did not vary significantly by sex ($G = 1.28$, $df = 1$, $P > 0.2$). Disease severity on a scale of 0 to 3 also did not vary with lamb sex (z -transformation of Mann-Whitney *U*-test = 0.37, $P = 0.7$) and averaged 1.2 for both males and females (Table 2).

There were no significant between-year differences in severity, based on a Kruskal-Wallis ANOVA.

Lambs that had CE lesions during summer were not lighter than other lambs at an early age. The effects of CE prevalence on 15 June body mass were not significant, according to analyses of variance including year and sex effect, either when the data were analyzed according to CE presence (1990 to 1993; $F_{1,37} = 1.004$, $P = 0.32$) or according to CE severity (1991 to 1993; $F_{3,29} = 0.904$, $P = 0.45$). Lambs that never had signs of CE had mean (\pm SD) weights of 8.7 ± 2.2 kg ($n = 12$) on 15 June, and lambs that developed CE lesions weighed 8.0 ± 1.8 kg ($n = 31$).

Over the summer, pooling all captures from all years of the study, male lambs that had no signs of CE gained mass (in kg) according to the equation $y = 4.2 + 0.20x$, where y is the gain in kg and x is the number of days since 25 May. Male lambs with signs of CE gained mass according to the linear equation $y = 4.8 + 0.16x$, while the equation for mass gain by female lambs was $y = 5.9 + 0.20x$, regardless of infection status.

TABLE 2. Severity of contagious ecthyma lesions in bighorn sheep lambs at Ram Mountain by year and sex.

Lesion severity	1991		1992		1993		Total	
	Males	Females	Males	Females	Males	Females	Males	Females
Negative	9	8	1	3	1	6	11	17
Mild	13	7	3	6	7	8	23	21
Moderate	4	3	5	4	1	1	10	8
Severe	4	5	0	2	2	2	6	9
Total	30	23	9	12	11	17	50	55

In 1990 to 1993, lambs affected by CE were lighter in September than unaffected lambs ($F_{1,73} = 5.35$, $P = 0.02$). Mid-September mass also varied with lamb sex ($F_{1,73} = 7.76$, $P = 0.007$) and year ($F_{3,73} = 4.00$, $P = 0.01$), and there was a significant interaction of year and CE status ($F_{3,73} = 3.97$, $P = 0.01$); thus the relationship between CE and September mass was not consistent among years (Fig. 1). When we separated lambs (1991 to 1993) according to four classes of disease severity, lamb mass apparently decreased as the severity of lesions increased ($F_{3,55} = 4.64$, $P = 0.006$). September mass in 1991-1993 varied according to lamb sex ($F_{1,55} = 8.25$, $P = 0.006$) and year of study ($F_{2,55} = 6.27$, $P = 0.004$).

The comparison of mass adjusted to 5 June 1992, when lambs born in 1991 were 1 yr old, provided evidence that yearlings affected by CE as lambs were lighter ($\bar{x} \pm \text{SD} = 26.9 \pm 3.1$ kg, $n = 13$) than other yearlings (31.0 ± 2.3 kg, $n = 6$; ANOVA including sex effects: $F_{1,16} = 8.53$, $P = 0.01$).

In 1990 and 1991, CE prevalence was not related to survival from October to 1 yr of age: 13 of 22 lambs without lesions and nine of 20 lambs with lesions survived ($G = 1.27$, $df = 1$, $P > 0.2$). In 1992, most lambs were born 2 to 3 wk later than in other years, and of 24 lambs alive in late September, only five survived the winter. Thus, we did not include the 1992 cohort in analyses of survival. The five survivors in spring 1993 were females that had been affected by CE as lambs: three mildly, one moderately, and one severely; this latter yearling disappeared in June 1993.

DISCUSSION

The CE virus enters its host through skin abrasions (Bruner and Gillespie, 1973), and CE produces lesions on lips, udders, hooves and vulvae. Most lesions start as discrete reddened swellings, followed by pustules and ulcers in 3 or 4 days (Robinson and Balassu, 1981). Lesions

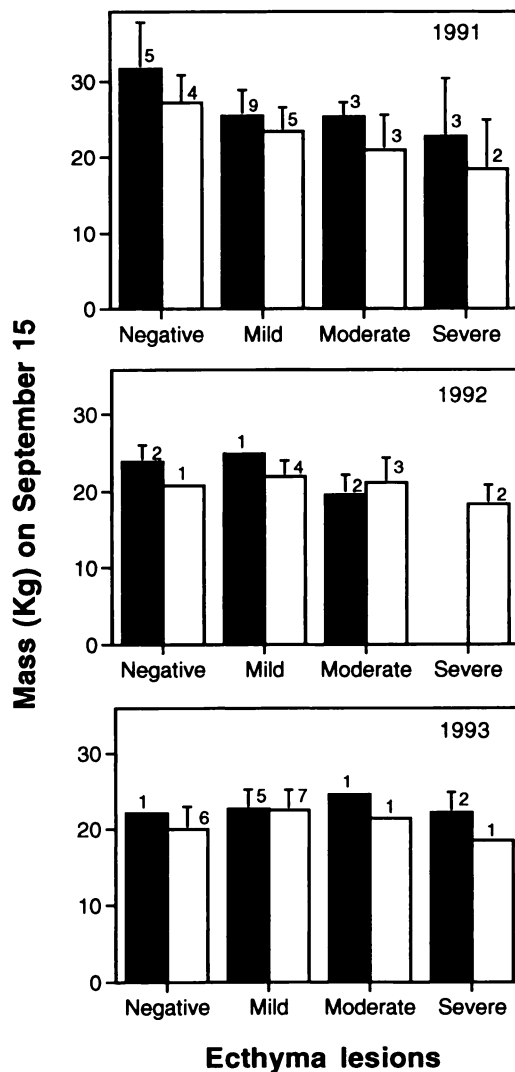


FIGURE 1. Body mass (mean + SD) adjusted to September 15 for bighorn sheep lambs at Ram Mountain, Alberta, Canada, 1991 to 1993, as a function of severity of contagious ecthyma lesions. Numbers above histograms are sample size. Black bars are for male lambs, open bars are for female lambs.

usually disappear in 2 to 4 wk (Yirrell et al., 1989).

Our field research was based entirely upon visible signs of CE. We did not collect blood samples and have no data on the seroprevalence of the virus. We also assumed that the information collected at capture was representative of a lamb's CE lesions during the summer. Except for very

severe lesions and bleeding sores, it was not possible to monitor CE in free-ranging lambs during behavioral observations. We could not estimate how long CE lesions remained visible, or whether their severity affected the time during which they were evident. Our data may underestimate CE prevalence, but are representative of what might be available to wildlife managers from capture operations. Our study is a first attempt to assess the long-term effects of CE in individually recognizable bighorn sheep.

Contrary to our prediction, we did not observe a difference in susceptibility of lambs to CE by sex. Contagious ecthyma was associated with smaller mass of lambs in late summer, although the negative effect of CE on lamb mass was not consistent between years. Because there were no significant differences in body mass of affected and unaffected lambs in early summer, it is likely that CE interfered with body growth during summer. Sheep that had been affected as lambs were lighter than unaffected sheep as yearlings; thus, we propose that CE could have long-term effects on the development of affected individuals.

Blood (1971) suggested that sores on the udder may make nursing uncomfortable, so that affected mothers may nurse their offspring less frequently than non-affected mothers. Lambs infected on the mouth may transmit the infection to their mothers during suckling. In the Ram Mountain population, however, few cases of CE involved severe lesions near the mouth (Table 1). From 1991 to 1993 we did not observe any signs of CE on udders, although these were seen (but not systematically recorded) in 1990. Apparently, adult sheep developed immunity to CE after the 1990 all-age epizootic.

Only 15% of lambs had severe lesions on the legs. It is likely that severely affected individuals experienced pain in walking and may have spent more time laying down, thereby reducing their forage intake. It appeared that some lambs with

severe lesions on the legs were limping, but behavior of most affected lambs was not superficially different from that of non-affected lambs.

The Ram Mountain bighorn population more than doubled after ewe removals were ended in 1981. Visible CE lesions became prevalent only at very high density when the population had evidence of low resource availability, such as smaller horn size of males and later age of primiparity in females (Jorgenson et al., 1993a, 1993b). High density likely increased intraspecific competition and may explain the sudden epizootic of CE in 1990. Leader-Williams (1982) reported that the prevalence of mandibular infection in reindeer increased with population density, possibly because of lower resource availability. When population density is high, animals may suffer from the cumulative effects of social and environmental stress, leading to an increase in susceptibility to disease. Stressed individuals may be less resistant to infections. The late birth of lambs in 1992 and the small mid-September body mass of lambs in 1992 and 1993 (Fig. 1) possibly also resulted from high population density. In another bighorn population, Festa-Bianchet (1988) found that the proportion of late-born lambs increased with ewe density.

Despite a negative effect on body mass, lamb survival was not significantly related to CE prevalence or severity. Nfi (1991) reported that despite very high prevalence of CE in other ruminants, varying between 70% and 100%, mortality was usually less than 2% and was often related to secondary infections.

In conclusion, the high prevalence of CE in bighorn sheep lambs at high population density was associated with reduced summer mass accumulation, but the relationships between CE and lamb mass were not consistent among years and the presence of visible CE lesions was not associated with an increase in lamb mortality. Therefore, CE does not appear to play a primary role in affecting the population

dynamics of this population. The negative relationship between CE and body mass, however, is evidence that CE ultimately may depress the survival or the reproductive success of affected individuals. Further monitoring of individuals with known levels of infection as lambs is necessary to determine the long-term impacts of this disease on population dynamics.

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LITERATURE CITED

- ANDERSON, R. M., AND R. M. MAY. 1978. Regulation and stability of host-parasite population interactions. I. Regulatory processes. *Journal of Animal Ecology* 47: 219–247.
- ARNOLD, W., AND A. V. LICHTENSTEIN. 1993. Ectoparasite loads decrease the fitness of alpine marmots (*Marmota marmota*) but are not a cost of sociality. *Behavioral Ecology* 4: 36–39.
- BLOOD, D. A. 1971. Contagious ecthyma in Rocky Mountain bighorn sheep. *The Journal of Wildlife Management* 35: 271–275.
- BRUNER, D. W., AND J. H. GILLESPIE. 1973. Hagan's infectious diseases of domestic animals. Cornell University Press, Ithaca, New York, pp. 936–939.
- CLUTTON-BROCK, T. H., S. D. ALBON, AND F. E. GUINNESS. 1985. Parental investment and sex differences in juvenile mortality in birds and mammals. *Nature* 313: 131–133.
- DEMARAIS, S., H. A. JACOBSON, AND D. C. GUYNN. 1983. Abomasal parasites as a health index for white-tailed deer in Mississippi. *The Journal of Wildlife Management* 47: 247–252.
- FESTA-BIANCHET, M. 1988. Birthdate and survival in bighorn lambs (*Ovis canadensis*). *Journal of Zoology* 214: 653–661.
- . 1989. Survival of male bighorn sheep in southwestern Alberta. *The Journal of Wildlife Management* 53: 259–263.
- . 1991. Numbers of lungworm larvae in feces of bighorn sheep: Yearly changes, influence of host sex, and effects on host survival. *Canadian Journal of Zoology* 69: 547–554.
- FOLSTAD, I., A. C. NILSSEN, O. HALVORSEN AND J. ANDERSEN. 1989. Why do male reindeer (*Rangifer t. tarandus*) have higher abundance of second and third instar larvae of *Hypoderma tarandi* than females? *Oikos* 55: 87–92.
- GEIST, V. 1971. Mountain sheep: A study in behavior and evolution. University of Chicago Press, Chicago, Illinois, 383 p.
- GULLAND, F. M. D., AND M. FOX. 1992. Epidemiology of nematode infections of Soay sheep (*Ovis aries* L.) on St Kilda. *Parasitology* 105: 481–492.
- JORGENSEN, J. T., M. FESTA-BIANCHET, M. LUCHERINI, AND W. D. WISHART. 1993a. Effects of body size, population density and maternal characteristics on age of first reproduction in bighorn ewes. *Canadian Journal of Zoology* 71: 2509–2517.
- , ———, AND W. D. WISHART. 1993b. Harvesting bighorn ewes: Consequences for population size and trophy ram production. *The Journal of Wildlife Management* 57: 429–435.
- KATER, J. C., AND N. F. HANSEN. 1962. Contagious ecthyma in wild thar in the South Island. *New Zealand Veterinary Journal* 10: 116–117.
- KUMMENEJE, K., AND J. KROGSRUD. 1979. Contagious ecthyma (ORF) in reindeer (*Rangifer tarandus*). *The Veterinary Record* 105: 60–61.
- LANCE, W. R., W. ADRIAN, AND B. WILDHALM. 1981. An epizootic of contagious ecthyma in Rocky Mountain bighorn sheep in Colorado. *Journal of Wildlife Diseases* 17: 601–603.
- , C. P. HIBLER, AND J. DEMARTINI. 1983. Experimental contagious ecthyma in mule deer, white-tailed deer, pronghorn and wapiti. *Journal of Wildlife Diseases* 19: 165–169.
- LEADER-WILLIAMS, N. 1982. Relationship between a disease, host density and mortality in a free-living deer population. *Journal of Animal Ecology* 51: 235–240.
- L'HEUREUX, N. 1993. Effect du sexe et d'une maladie virale sur le développement social et physique des jeunes mouffons des Rocheuses (*Ovis canadensis*). M.Sc. thesis, Université de Sherbrooke, Sherbrooke, Québec, Canada. 92pp.
- , M. LUCHERINI, M. FESTA-BIANCHET, AND J. T. JORGENSEN. 1995. Density-dependent mother-yearling association in bighorn sheep. *Animal Behaviour* 49: 901–910.
- MESSIER, F., M. E. RAU, AND M. A. MCNEILL. 1989. *Echinococcus granulosis* (Cestoda: Taeniidae) infections and moose-wolf population dynamics in southwestern Quebec. *Canadian Journal of Zoology* 67: 216–219.
- MULVEY, M., AND J. M. AHO. 1993. Parasitism and mate competition: Liver flukes in white-tailed deer. *Oikos* 66: 187–192.
- NFI, N. A. 1991. Soremouth in sheep and goats at

- the Mankon Animal Research Station, Cameroon. *Revue d'Elevage et de Médecine Vétérinaire des Pays Tropicaux* 44: 141–142.
- RICHNER, H., A. OPPLIGER, AND P. CHRISTE. 1993. Effect of an ectoparasite on reproduction in great tits. *Journal of Animal Ecology* 62: 703–710.
- ROBINSON, A. J., AND T. C. BALASSU. 1981. Contagious pustular dermatitis (ORF). *Veterinary Bulletin* 51: 771–782.
- SAMUEL, W. M., G. A. CHALMERS, J. G. STELFOX, A. LOEWEN, AND J. J. THOMSEN. 1975. Contagious ecthyma in bighorn sheep and mountain goats in Western Canada. *Journal of Wildlife Diseases* 11: 26–31.
- SMITH, T. C., W. E. HEIMER, AND W. J. FOREYT. 1982. Contagious ecthyma in an adult Dall sheep (*Ovis dalli dalli*) in Alaska. *Journal of Wildlife Diseases* 18: 111–112.
- SOKAL, R. R., AND F. J. ROHLF. 1981. *Biometry*. Freeman, San Francisco, California, 859 pp.
- WEATHERHEAD, P. J., K. J. METZ, G. F. BENNETT, AND R. E. IRWIN. 1993. Parasite faunas, testosterone and secondary sexual traits in male red-winged blackbirds. *Behavioral Ecology and Sociobiology* 33: 13–23.
- YIRRELL, D. L., H. W. REID, M. NORVAL, AND S. E. M. HOWIE. 1989. Immune response of lambs to experimental infection with orf virus. *Veterinary Immunology and Immunopathology* 22: 321–332.

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