FACTORS AFFECTING EPIZOOTICS OF WINTER TICKS AND MORTALITY OF MOOSE

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ABSTRACT: Die-offs of moose (*Alces alces*) associated with, or attributed to, winter ticks (*Dermacentor albipictus*) are widespread and have been reported since the early part of the last century. Extrinsic factors such as weather and vegetative structure, and host factors such as moose density and, indirectly, tick-induced damage to the hair coat, were examined in an attempt to predict related problems for moose. The proposal that warmer and shorter winters result in increased survival of adult female ticks dropping off moose in March and April, and increased tick populations on moose the following winter, was generally confirmed. Annual changes in hair damage and loss on moose, which are documented from the air, coincided with annual changes in numbers of ticks on moose, providing managers with a survey tool to monitor and estimate changing numbers of ticks. Tick numbers lagged 1 year behind moose numbers in Elk Island National Park over a 12-year period, and many moose died when numbers of both were high. Several widespread, concurrent die-offs suggest extrinsic influences play a role, possibly independent of moose density. The lack of objective and continuous data sets should guide future research efforts.

Die-offs of moose associated with, or attributed to, winter ticks are numerous and widespread across North America, having occurred since the early part of the last century (summarized by Samuel 2004). Almost all published and unpublished reports of such events indicate finding a certain number, sometimes few, often many, dead or dying moose covered with ticks. Tick-associated die-offs often are widespread and concurrent, involving many populations of moose in several-to-many jurisdictions. For example, the most recent widespread outbreaks of winter ticks, accompanied by losses of many moose, occurred in late winter and spring, 2002. There were reports from Isle Royale National Park, Minnesota, Maine, New Hampshire, and Vermont in the United States, and Alberta, Manitoba, Ontario, and Saskatchewan in Canada (Samuel et al. 2002, Peterson and Vucetich 2003, Samuel and Crichton 2003). Earlier

concurrent widespread die-offs occurred in late winter-spring, 1999 and 1992, and one across Alberta in 1982 (Samuel 2004).

Die-offs are often attributed to winter ticks, perhaps because ticks are obvious and numerous on dead and dying moose. Unfortunately, direct evidence of the lethal effect of winter ticks on moose populations is lacking. There is, however, good information from experimental and field studies (reviewed by Samuel et al. 2000) that, at the least, suggests that winter ticks are a significant factor in rapid declines of moose numbers. Other factors, such as moose numbers or density, habitat, weather, and predation, likely also play a role.

The objective here is to review factors potentially contributing to tick-related die-offs of moose using published literature, reports, and observations from central Alberta, particularly Elk Island National Park and vicinity;

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then, to assess specific factors or influences that might be used to predict epizootics of ticks and die-offs of moose. In an attempt to determine if various weather parameters might be predictive of moose die-offs, I examined parameters of snow cover and temperature at the time of 5 die-offs in Alberta, 2 of which (late winter-springs of 1982 and 1999) killed many moose. I also examined the feasibility of using tick-caused damage to the winter hair coat of moose as an indication of tick numbers as done by Wilton and Garner (1993) and others.

WEATHER

Several aspects of weather are potentially harmful to moose and ticks. For moose, depth of snow and length of severe cold, often in concert with condition of habitat, can be important (Mech et al. 1987, see logic in Vucetich and Peterson 2004). Snowfall was much above normal during 3 of 5 years of tick-related moose die-offs in central Alberta, including 50 cm above normal during the major die-off of moose in late winter-spring 1982 (Table 1). The winter-spring in 4 of 5 die-off years was colder than the 30-year average (Table 1). In particular, March and April 1982 and 2002, were much colder than the 30-year average.

For ticks, weather in autumn, when young ticks are on vegetation ambushing moose, and early spring, when female ticks are dropping from moose to lay eggs for the next generation of ticks, is critical for survival and transmission. Significant snowfall in early-to-mid October could bury tick larvae, thus potentially curtailing transmission to moose. That happened the week of October 14, 1991 at Elk Island National Park, near Edmonton Alberta, when approximately 45 cm of snow fell, burying most low vegetation (Aalangdong 1994). In autumn, particularly October, tick larvae tend to quest on low vegetation and ambush passing ungulate hosts (Drew and Samuel 1985). In 1991, minimum daily tem-

peratures at the park were below –10°C the last 10 days of October. The combination of snow that likely buried tick larvae and cold that inactivated or killed larvae (Drew and Samuel 1985, Aalangdong 1994), decreased potential transmission of ticks to moose by almost half in 1991 (Fig. 1). Unfortunately, it is impossible to estimate the effect of this snowfall on subsequent tick numbers on moose, because no moose were examined for ticks or tick-caused damage to the winter coat of hair (see below). There was no die-off of moose in the park or other parts of central Alberta that winter. There was also no moose die-off in winter 1991-1992 in the Peace River country of northwest central Alberta, where ticks often cause problems for moose (Pybus 1999). There was also no major snowfall or severe cold there in October 1991.

Weather in late winter-early spring, particularly related to snowfall and temperature the year before a moose die-off, is mentioned in literature as influencing tick survival and future numbers of ticks (e.g., Timmermann and Whitlaw 1992, Wilton and Garner 1993,
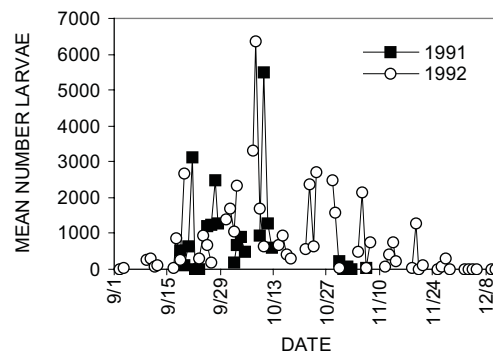

Fig. 1. Mean daily number of tick larvae recovered from vegetation in the Main Park area of Elk Island National Park, central Alberta. Larvae were collected by dragging 1-m² white flannel cloths (599 samples in 1991, 1,556 in 1992) along transects on vegetation 1 – 1.5 m in height 4 days each week at 4 sites. Transects were 2 km long and divided into eighty 25-m units of which 10 units were selected randomly for sampling (details in Aalangdong 1994; data from O. Aalangdong).

Table 1. Summary of weather characteristics that potentially impact moose and winter ticks during 5 moose die-offs in the Edmonton region (central Alberta).

Weather parameter	30-year average 1971-2000[1]	Year of late winter-spring die-off				
		1978[2]	1982[3]	1988[2]	1999[4]	2002[4]
Affecting moose:						
Total snowfall (cm)						
October – April[1]	115	79.9	164.8	49	132.2	129.8
Mean monthly temperature (°C)						
December – April[1]	-7.1	-8.5	-11.5	-4.1	-5.8	-8.5
Mean minimum monthly temperature (°C)						
December – April[1]	-12.8	-14.6	-17.9	-9.8	-13.4	-15.7
Mean temperature (°C)						
March[1]	-4.5	-3.6	-8.6	1.4	-5.9	-15
Mean minimum temperature (°C)						
March[1]	-9.9	-8.4	-14.7	-4.7	-10.8	-22
Mean temperature (°C)						
April[1]	4.3	4.7	-0.6	6	5.1	-2.1
Mean minimum temperature (°C)						
April[1]	-2.2	-0.5	-7	-2	-0.9	-7.5
Affecting ticks:						
Mean temperature (°C)						
March and March of year previous[1]	-4.5	-2.8	0.1	-5.1	-3.8	-2
Mean temperature (°C)						
April and April of year previous[1]	4.3	6.9	4.3	7	6.9	3.9
Mean minimum temperature (°C)						
March and March of year previous[1]	-9.9	-8.1	-5.7	-9.7	-8.8	-8.8
Mean minimum temperature (°C)						
April and April of year previous[1]	-2.2	-2.2	-2.9	-0.3	-0.1	-4.9
Snowfall (cm)						
October[1,5]	8	0	2.4	0.8	17.6	10
Snow depth (cm)						
end October[1,5]	1	0	0	0	0	4
Snow depth (cm)						
end March and end of March, year previous[1]	8	0	0	1	0	0

[1]Environment Canada, Edmonton International Airport.

[2]Only in Elk Island National Park.

[3]Throughout Alberta, including Elk Island National Park.

[4]Throughout Alberta, but not in Elk Island National Park.

[5]Preceding the winter–spring of die-off.

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DelGiudice et al. 1997). In general, the logic is that a warm late winter-early spring with low precipitation is conducive to survival and egg-laying of female ticks that drop from moose at that time. This results in above normal numbers of young ticks on moose the following autumn, possibly leading to die-offs of moose the subsequent winter. Data from Drew and Samuel (1986) appear to be the genesis of this logic. They put blood-fed, adult, female winter ticks in outdoor, screen-wire cages at Elk Island National Park at biweekly intervals from early March to late April-mid May, 1982 and 1983, and monitored for survival. Only 11% of ticks (same percentage, both years) put in cages on snow (i.e., before snowmelt) survived to lay eggs, while 73 and 55% of ticks put in cages on leaf litter (i.e., after snowmelt) in 1982 (~ 10 April) and 1983 (~ 24 April), respectively, survived. Drew and Samuel (1986) suggested that low survival prior to snowmelt in spring might be due to prolonged exposure to ambient temperatures at the snow surface that are below the tick's threshold for survival (~ minus 17°C). An extension of this idea is that snow depth or crusting of snow, which forms during the fluctuating temperatures in late March and April, prevents ticks from getting to the duff layer, and they die before laying eggs.

Drew and Samuel (1989) found that blood-fed adult female ticks dropped off moose from late February to early May, but the peak drop period was late March. So, what do the data indicate for late March preceding each of the 5 tick-related moose die-offs in the last 30 years; i.e., did female ticks drop on snow or leaf litter? The answer is that most ticks dropped on leaf litter (see bottom, Table 1). However, the context of these results is that, even though the 30-year average amount of snow on the ground at end March was 8.0 cm, there has been no snow on the ground at the end of March in 17 of 29 (65%) years, 1977-2005, in the Edmonton region. No snow tends to be "normal."

Warmer temperatures in March and April should result in higher survival of adult female ticks that have dropped from moose and, in general, it was warmer in March and April in years preceding die-offs (Table 1). Mean March and April temperatures were at or above the 30-year average 4 of 5 die-off years. Mean minimum temperatures in March were warmer than the 30-year average all 5 years, and minimum temperatures in April were at or above average 4 years; conditions good for tick survival and reproduction. In Ontario, Wilton and Garner (1993) saw more severe tick-induced hair damage and loss to moose in years following mean April temperatures above 3°C, suggesting that survival of ticks was good above and poor below this temperature. In the Edmonton region the 30-year, daily mean April temperature was 4.3°C.

Thus, these data indicate that colder-than-average winters in 4 of 5 die-off years, and extensive snow cover in 3 of 5 die-off years might have adversely affected moose in central Alberta. Further, ticks might have benefited from little or no snow on the ground and above normal temperatures during the drop-off period in March-April in all years preceding die-offs.

TICK NUMBERS AND
HAIR DAMAGE AND LOSS

In studies of moose and ticks at Elk Island National Park, hair loss correlated with rate of tick-induced self-grooming; i.e., moose that groomed more lost more hair (Mooring and Samuel 1999). In general, annual mean percent hair damage and loss coincided with annual mean number of winter ticks on moose (Samuel 2004) indicating that grooming was related to the number of ticks on moose. In a 10-year study in Algonquin Provincial Park, Ontario, damage to the winter hair coat of moose was used as an index of tick numbers on moose. Years with high numbers of moose carcasses generally coincided with years when hair damage was highest and vice versa

(Garner and Wilton 1993, Wilton and Garner 1993). However, a manager has few options to estimate trends in tick numbers. Estimating numbers of ticks on a sedated live moose is not reliable because there can be many thousands of ticks on this large mammal with a thick winter coat of hair, making counting impossible (personal observation). Counting ticks on dead moose is not an option because the digestion technique used to recover ticks, though accurate (Welch and Samuel 1989) is laborious.

An important management issue is whether data on annual hair damage/loss can provide an early warning of impending die-offs of moose. The answer might hinge on the accuracy of techniques used during aerial and ground surveys of moose to record tick-induced hair damage and loss. Hair damage and loss on moose can be quantified by ground or aerial survey in 2 ways: (1) use a digitizer to determine the percentage of the lateral silhouette of the torso with hair damage or loss from photographs or diagrams of lateral views of moose (see description of technique in Welch et al. 1990, and Samuel and Welch 1991); or (2) group moose subjectively into several categories of hair-loss severity (see photographs of categories in Samuel 1989, 2004). The first method takes more time because it demands either taking photographs, or making diagrams of hair damage of the lateral torso of moose. With some experience it is relatively easy to use the second method and assign moose to 1 of 5 categories of hair damage or loss: no damage to hair coat, slight (which is approximately 5 - 20% of winter hair broken or lost), moderate (~ 20 - 40%), severe (~ 40 - 80%), and ghost moose (> 80%).

Because grooming against ticks, and the resulting hair damage and loss, continues to late April (Welch et al. 1990), it is best to do surveys for hair damage as late in the season as possible. Unfortunately, moose managers must do their surveys well before mid-April taking advantage of snow and moose behavior.

However, annual surveys done earlier, preferably late February, can provide comparative trends in hair damage/loss, as long as they are done at approximately the same time each year (see Welch et al. 1990 and Samuel and Welch 1991 for temporal patterns of the progression of hair loss).

Hair damage and loss should coincide with tick numbers given that grooming against ticks by moose is proportional to tick bite; i.e., the more ticks present, the more blood-feeding by ticks, which results in more grooming and subsequent hair damaged or lost (Mooring and Samuel 1998). Wilton and Garner (1993) calculated a hair-loss severity index (HSI) to summarize category-type data (Fig. 2). The two methods, mean % hair loss and HSI, were compared using hair-loss data for moose from Elk Island National Park (Fig. 2). Yearly changes were parallel, in general, particularly so after the major die-off of moose in late winter-spring of 1982. The same was true for yearly change in HSI and tick numbers (Fig. 3) and yearly change in mean % damage to the winter hair coat and mean number of ticks (Fig. 4).

In summary, annual surveys of tick-caused damage to winter hair of moose, done as late as possible in the winter-spring season, provide good indication of numbers of ticks on moose. Unfortunately, more repetitive annual surveys are needed to determine if hair loss surveys are useful to predict moose population response in subsequent years (but see next paragraph on data currently being collected at Isle Royale National Park).

NUMBERS OF MOOSE

Samuel (2004) summarized a cascade of events, starting with increasing moose numbers that led to lethargic, ill, or dead moose. The cascade goes as follows: moose numbers increase in a local area; tick numbers increase; tick bite increases, which causes more itching and grooming; hair damage and loss increases; energy expended to grooming increases; blood
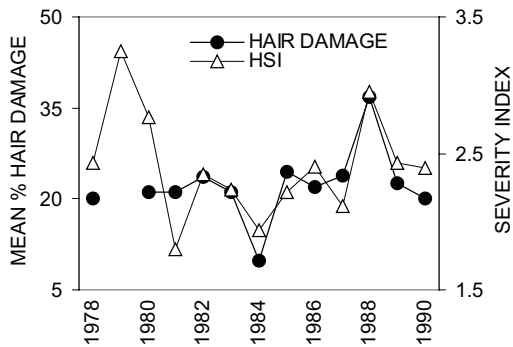
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Fig. 2. Comparison of mean % hair damage/loss and hair-loss severity index, two methods used to determine yearly changes in tick-caused damage to the winter hair of moose in Elk Island National Park. Categories of hair damage on 327 moose (variable numbers per year), observed from the air and ground, were used to calculate a Hair-loss Severity Index (HSI). Moose in categories were grouped subjectively as follows: no damage to hair coat of lateral torso (HSI class value = 1); slight damage (~ 5 – 20% of winter hair broken or lost) (HSI = 2); moderate damage (~ 20 – 40% broken/lost) (HSI = 3); severe damage (~ 40 – 80% broken/lost) (HSI = 4); and ghost moose (> 80% broken/lost) (HSI = 5). The frequency of moose in each category was multiplied by the appropriate class value and the sum divided by the total number of moose sampled for that time period. The second method involved diagrams of the hair damage on the lateral torso of 302 moose (variable numbers per year), surveyed from the air and ground, that were digitized for hair damage using methods in Samuel and Welch (1991).

loss increases; appetite and feeding by moose possibly suppressed; smaller energy reserves available for blood replacement and to support high rates of grooming; and increased cost of replacing heat energy lost through a damaged hair coat. All of this results in lethargic, ill, or dead moose. This cascade assumes that numbers of ticks track changes in moose numbers. Unfortunately, long-term data sets to test this assumption are scant because of the difficulty in monitoring a moose population for both moose numbers and tick numbers on an annual basis for many years; 12 years data were collected at Elk Island National Park

(Fig. 5). Currently, similar data are collected only at Isle Royale National Park where hair loss is monitored as an index of tick numbers (Delguidice et al. 1997, Peterson and Vucetich 2006).

Samuel and colleagues (see Samuel 2004) studied winter ticks in a closed system at Elk Island National Park in central Alberta, 1978-1996. The park is 195 km^2 in size, and surrounded by fences that prevent the large ungulates from leaving. It is dotted with numerous wetlands with aspen (*Populus* spp.) the dominant tree. Coyotes (*Canis latrans*) are the only resident large carnivore. The dynamics of the local ungulates were described by Blyth and Hudson (1987) and Blyth (1995). Some moose die-offs in the park were concurrent with die-offs of moose populations across central Alberta (Table 1), most recently in late winter-spring 1982, when tick-related die-offs occurred throughout Alberta. However, there was no major tick-mediated die-off in the park in 1999 (N. L. Cool, Parks Canada, Elk Island National Park, personal communication) when the province was experiencing major losses everywhere (Pybus 1999). Similarly, though die-offs occurred in local populations throughout much of Alberta in 2002, including central Alberta, there was no
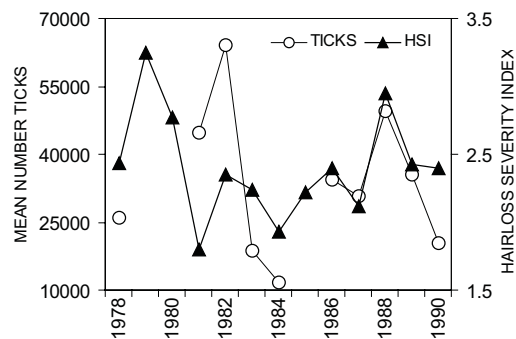

Fig. 3. Annual changes in mean number of winter ticks collected from digested hides and Hair-loss Severity Index (HSI) for moose from Elk Island National Park. Hides of 118 moose (variable numbers per year) were digested and ticks collected using techniques in Welch and Samuel (1989). See Figure 2 for information on HSI.
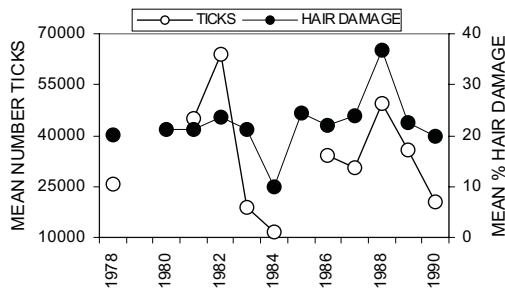
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Fig. 4. Annual changes in mean number of ticks collected from digested hides and extent of hair damage and loss in spring on moose, from Elk Island National Park. See Figures 2 and 3 for relevant information. Figure modified from Samuel (2004).

die-off in Elk Island National Park, though a die-off of about 150 moose occurred the next year in the Main Park area (N. L. Cool, Parks Canada, Elk Island National Park, personal communication).

Moose and tick numbers (and hair damage and loss, Fig. 4) were monitored in the northern part of the park (Main Park area, 136 km^2) in 1978-1990. In general, there was a lag of 1 year in tick numbers tracking moose numbers (Fig. 5). Die-offs occurred when moose densities approached 3 moose per km^2 and mean numbers of ticks on moose approached 50,000 – 60,000. Data for estimates of numbers of moose dying in some years are somewhat misleading because various forms of moose management were implemented when moose densities were high. For example, the park culled moose in some years (Blyth and Hudson 1987, Blyth 1995), and culls are included in the annual declines in moose density (Fig. 5). The number of culled moose in Main Park, where the tick research was done, cannot be separated from the estimates of moose dying naturally.

Culls were done in December 1977 and 1980 in an attempt to balance the moose population with estimated food resources. Nonetheless, Main Park suffered a number of natural, tick-mediated losses, including an estimated 100 moose in winter 1977 (Samuel

and Barker 1979), "extreme levels of mortality" (Blyth and Hudson 1987) in winter 1982, and smaller natural losses of moose in 1978, 1984, 1988, and 1989 (Blyth 1995). Chemical reproductive inhibition was administered to 59 adult females in Main Park in 1987, almost 25% of the mature cows (Blyth 1995), and 108 moose were shot from 1978-1990 for research on winter ticks.

Pybus (1999) summarized 1,130 occurrences involving moose in trouble or found dead (*n* = 311) during a winter (1999) of significant moose mortality in Alberta. Many reports (*n* = 1,035) involved winter tick-caused hair loss and indicated increasing occurrence with increasing density of moose. In summary, in spite of a mixture of somewhat subjective data sets, there appears to be a host-density component to tick numbers on moose. However, more reliable long-term data and objective studies are needed to ascertain this relationship.

VEGETATION STRUCTURE
Where a blood-fed, adult female winter tick drops from a moose in late winter-early spring, is where she must survive and produce offspring. Drew and Samuel (1986), Aalangdong (1994), and Aalangdong et al. (2001) found that different habitats in Elk Island Park, with different microclimatic conditions,
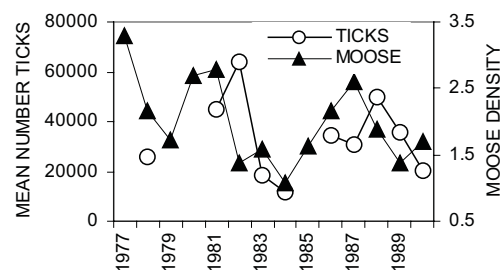

Fig. 5. Estimated density of moose (late fall, prior to implementation of management options; see text) and mean number of ticks collected from digested hides in Main Park area of Elk Island National Park. Figure modified from Samuel (2004).

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influence survival and reproduction of winter ticks. Aalangdong et al. (2001) put ticks in gauze bags ~ 2 cm beneath the litter in various habitat types in Elk Island National Park. All 3 habitat types with open canopies were more suitable for winter tick survival and production of larvae than the 4 habitat types with closed canopies. Thus, more ticks survived to produce eggs, and more eggs hatched to larvae, and the larvae survived longer, in habitat types with open canopies. The authors attributed this to mean monthly temperatures at ground level, which in summer were several degrees lower in all 4 'closed' habitats, than in 'open' habitats. These results might have broader implications and help explain why moose in parts of Alberta with open canopies, such as the aspen-rich Peace River country of northwest central Alberta, and the aspen parklands and southern edges of the boreal mixed wood forests of central Alberta, appear to suffer more from winter ticks than moose in more northerly spruce-dominated forests.

SUMMARY

Die-offs of moose are complex events that are probably mediated by several factors including winter weather, habitat conditions, density of moose, and winter ticks. The fact that some tick-associated declines in moose are concurrent in many populations in a number of areas suggests an "extrinsic influence" is involved (Delguidice et al. 1997). The hypothesis that weather in the form of shorter, warmer winters with less precipitation than usual results in more ticks the following year was generally confirmed. Intuitively, the scenario makes sense, but it is probably more complex than presented here. As Holmes (1995) states, "finding simple, consistent causes for complex biological phenomena" is wishful thinking. More rigorous analysis of climatic variables important to winter ticks in regions with moose die-offs (Delguidice et al. 1997, Vucetich and Peterson 2004) is needed, along with more long-term study of moose and tick numbers via monitoring of damage and loss to winter hair coat of moose; such monitoring is now done only at Isle Royale National Park. Assuming future climate change, minimum winter temperatures at high northern latitudes are expected to rise more than temperatures in other seasons (Intergovernmental Governmental Panel on Climate Change 1996). This will most certainly impact late winter-spring survival and development of off-host stages of ticks (Lindgren et al. 2000), in this case, winter ticks.

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