# MOOSE-SNOWSHOE HARE COMPETITION DURING PEAK HARE DENSITIES

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Abstract: Browsing intensity by moose (Alces alces) and snowshoe hares (Lepus americanus) was measured in several habitat types during the peak and declining phases of the hare cycle to determine the degree of food and spatial overlap. During low population densities, hares remained in closed-canopy forest consisting of dense black spruce or willow-alder thickets, whereas moose foraged primarily in the more open early seral communities less than 20 years old. During the winters of high hare densities from 1970 to 1973, hares invaded the more open stands and consumed up to 100% of the available browse.

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Several studies have reported interactions between snowshoe hares (Lepus americanus) and potential food competitors, primarily cervids (Wolfe 1974, Telfer 1972, Dodds 1960). Over most of the species ranges, moose (Alces alces) and deer (Odocoileus spp.) utilize the same food sources as hares during the winter. Dodds (1960), working with moose and snowshoe hares in Newfoundland, recorded an overlap in use of food resources and competition for balsam fir (Abies balsamifera) and paper birch (Betula papyrifera). It is widely assumed, however, that food is usually not limiting to moose or hares and that competition occurs only during high population densities (Dodds 1960; Bookhout 1965; Telfer 1972, 1974).





Preferred winter browse for both hares and moose in interior Alaska include willows (Salix spp.), quaking aspen (Populus tremuloides), balsam poplar (Populus balsamifera), and paper birch (Cushwa and Coady 1976, Wolff 1978b). Several studies have been conducted on moose-snowshoe hare competition and most of these agree that hares feed on lower shrub and tree branches and moose on the upper (e.g., Coady 1973, J. Oldemeyer, U.S. Fish and Wildlife Service, Kenai, Alaska, personal communication). In Alaska, competition between moose and hares is usually prevented by habitat segregation with moose preferring the more open early seral communities and hares inhabiting dense black spruce (Picea mariana) or willow-alder (Salix-Alnus spp.) thickets which provide more cover. (LeResche et al. 1974, Wolff 1977).

Utilization of additional habitat types by snowshoe hares during population "highs" has been reported by Grange (1965) and Keith (1966). Competition for food and habitat does occur between moose and hares during the peak of the hare cycle when hares invade all habitat types (Wolff 1977). Browsing intensity by moose and hares was measured in several habitat types during the peak and declining phases of the hare cycle (620 hares/$km^2$ in 1971 to less than 20 hares/$km^2$ in 1975 (Wolff 1977:54)) to determine the degree of overlap in uses of food and habitat. Possible effects of this competition upon moose population dynamics are considered.

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## STUDY AREAS

Browsing intensity by moose and snowshoe hares was recorded at three study areas from 1972 through 1976. The Wickersham study area was located in taiga about 50 km northwest of Fairbanks, Alaska, and consisted of an area burned by a 1971 wildfire (6 000 ha) and an adjacent fairly homogeneous, continuous, 70-year-old, mature stand of black spruce. Prior to the 1971 wildfire, both areas supported similar plant communities dominated by black spruce with willow and alder shrubs in the understory. A 20-ha study site established in the unburned stand contained 4,316 (± S.E. 444) stems/ha of black spruce trees and saplings and 489 (± 16.2) shrubs/ha of willow (Salix scouleriana) (Wolff and Zasada 1979). Two 20-ha study sites were established in the burn; 1 in a willow stand and 1 in an aspen stand which contained new shoots of aspen sprouting from root suckers. The willow stand had about 400 shrubs/ha in 1971 and 1974. The aspen stand contained 198,375 aspen stems/ha in 1972 and 35,333 aspen stems/ha in 1974 (Table 1).

The Bonanza Creek and Tanana River areas were located about 20 km southwest of Fairbanks on recently deposited alluvium along the Tanana River. Each open habitat consisted of an early seral plant community which supported several species of willows, primarily S. alaxensis and S. novae-angliae, and smaller quantities of S. interior and balsam poplar. Each open area was adjacent to more mature stands of willow, alder, balsam poplar, and white spruce (Picea glauca) in a later stage of succession. These older stands were referred to as closed-canopy and offered more dense cover and protection from predators but less browse.



Table 1. Densities of twigs and shrubs and browsing intensities by moose and snowshoe hares from 1971 through 1976 at the six stands.

| Site | Year | Shrubs/ha (+S.E.) | Twigs/shrub (+S. E.) | Twigs/ha | % Browsing Intensity (±S.E.) Moose | Hares |
|---|---|---|---|---|---|---|
| Wickersham Burn | 1971-72 | ≈400 | - | - | 0 | 100[2] |
| Willow Stand | 72-73 | ≈400 | - | - | 0 | 100[2] |
| | 73-74 | 400(13.4) | 16.0(4.2) | 6,400 | 44(2.8)[1] | 3(0.4)[1,2] |
| | 74-75 | 452(15.0) | 43.8(3.8) | 19,797 | 45(2.1) | 0[1,2] |
| | 75-76 | 638(15.0) | 57.0(3.1) | 36,366 | 26[1] | 0 |
| Wickersham Mature | 71-72 | 489(16.2) | - | - | 0 | 100[2] |
| Spruce Stand | 72-73 | 489(16.2) | - | - | 0 | 100[2] |
| | 73-74 | 489(16.2) | 19.0(2.7) | 9,291 | 10(1.0)[1,5] | 50(2.6)[1,2] |
| | 74-75 | 489(16.2) | 19.0(2.7) | 9,291 | 8(0.7)[5] | 5(0.5)[1] |
| | 75-76 | 489(16.2) | 17.1(1.9) | 8,361 | 0[1] | 2(0.1)[2] |
| Bonanza Creek | 72-73 | - | - | - | 0 | 100[3] |
| Open Stand | 73-74 | - | - | - | 19(1.6)[1] | 40[1,2] |
| | 74-75 | 14,045(3,075) | 34(0.4) | 47,753 | 56(3.1)[1] | 0[1,2] |
| | 75-76 | 16,962(2,948) | 34(0.4) | 57,671 | 0[1] | 0 |
| Bonanza Creek | 71-72 | - | - | - | 0[3] | 100[2,3] |
| Closed Stand | 72-73 | - | - | - | 0[3] | 100[2] |
| | 73-74 | - | - | - | 0 | 100 |
| | 74-75 | - | - | - | 0 | 84(2.4)[1,2] |
| | 75-76 | 377(53)[4] | 1.0(0.1) | 377 | 0 | 20(1.0)[1,2] |
| Wickersham Burn | 71-72 | 198,375 | 1.0(0.1) | 198,375 | 0 | 100[2] |
| Aspen Stand | 72-73 | 119,114 | 2.1(0.1) | 250,139 | 0 | 100[2] |
| | 73-74 | 35,333 | 3.6(0.1) | 127,199 | 20(1.6)[1] | 30(2.1)[1] |
| | 74-75 | 28,945 | 4.0(0.2) | 115,780 | 19(1.4) | 7(0.9)[1,2] |
| | 75-76 | 19,776 | 5.1(0.2) | 100,858 | 12(0.9) | 0[1,2] |
| Tanana River | 71-72 | - | - | - | - | 100[3] |
| | 72-73 | - | - | - | 13(0.9) | 87(3.2)[1,2] |
| | 73-74 | - | - | - | 20(1.7) | 70(1.7)[2] |
| | 74-75 | 64,250(16,225) | 2.6(0.2) | 167,050 | 55(3.1)[1] | 0[1,2] |
| | 75-76 | - | - | - | 0[1] | 0 |

(1) Browsing intensity different from previous year (t-test $p<0.05$).

(2) Hare browsing intensity different from moose browsing intensity in same year ($p<0.05$).

(3) Estimated values, not quantified.

(4) Willows only; total stems or willow, alder, and poplar were ≈10,000/ha in all 5 years.

(5) Browse removed by moose was above reach of hares.

One 20-ha study site was established in each habitat type at Bonanza Creek and Tanana River. In 1974 the Tanana River site consisted of a 15-year-old stand which supported 64,250 stems/ha of browse plant species, primarily willows, and an adjacent 25-year-old stand of primarily alder. In 1974 the Bonanza Creek site consisted of an 8-year-old stand which supported 14,045 stems/ha of browse plant species and an adjacent 25-year-old stand with compositions similar to those of the Tanana River stands (Wolff 1976).

## METHODS

Browsing was measured at each site in May of each year from 1972 to 1976 (except the open stand at Bonanza Creek which was sampled from 1973 through 1976) by recording the number of browsed and unbrowsed twigs on all plants selected by use of the point-center-quarter method (Cottam and Curtis 1956) using 40 points (160 shrubs) in each site. A shrub consisted of all stems arising from a single base. Browse consisted of stems and branches of willows, aspen, and balsam poplar less than or equal to 3 mm in diameter between 50 and 120 cm above ground level (mean winter snow cover was between 50 and 70 cm). Browse within this range was available to both moose and hares. Browse above 120 cm was considered available only to moose. Browse production was determined by the Shafer (1963) twig-count method described by Wolff and Zasada (1979).

Snowshoe hares normally clip twigs up to 3 mm in diameter, and clip larger twigs only when food is scarce (Pease et al. 1979). Hares will occasionally clip stems up to 2.5 cm in diameter and eat the upper



twigs. The mean diameter at point of browsing for moose in these study areas was less than 4 mm (Wolff 1976, 1978a:136). Moose pellet counts were made in 40 circular plots (250 $m^2$) in each stand.

### Open-Closed Habitat Browse Transects

At the Bonanza Creek and Tanana River areas, 3 belt transects with dimensions of 25 cm x 30 m were sampled from the mature closed-canopy stands into the open willow stands in May 1975. Each transect was divided into 5 m intervals to record browsing by moose and hares in the closed-canopy stand, ecotone, and open stands. Snowfall and accumulation were recorded at weekly or monthly intervals at each site throughout the study.

## RESULTS

Snowfall began in mid-September each year with 50 cm accumulating by early December and between 50 and 70 cm remaining until late April (Wolff 1977:58). The physical properties of snow with respect to moose and hare movements in the forested regions of interior Alaska are fairly uniform from year to year (Coady 1974). Due to the mean winter snowline of approximately 70 cm during all winters and the low growth form of the willows, most browse was between 70 and 120 cm and available to both moose and hares (see below).

### Wickersham

The production of willow browse available to moose and hares in the willow stand at Wickersham was not recorded in 1971 through 1973, but in the winters of 1973-74, 1974-75, and 1975-76 was 8, 23, and 25 kg/ha,

respectively (Wolff and Zasada 1979). All browse in these stands was within the 50 to 120-cm height range from 1971 to 1974; from 1975 to 1976 about 20% was above 120 cm. All of the CAG browse in this stand was consumed by hares during the winters of 1971-72 and 1972-73; consumption by hares decreased to 3% during the winter of 1973-74, and to 0% from 1975 through 1976 (Fig. 1). The decrease in browsing intensity

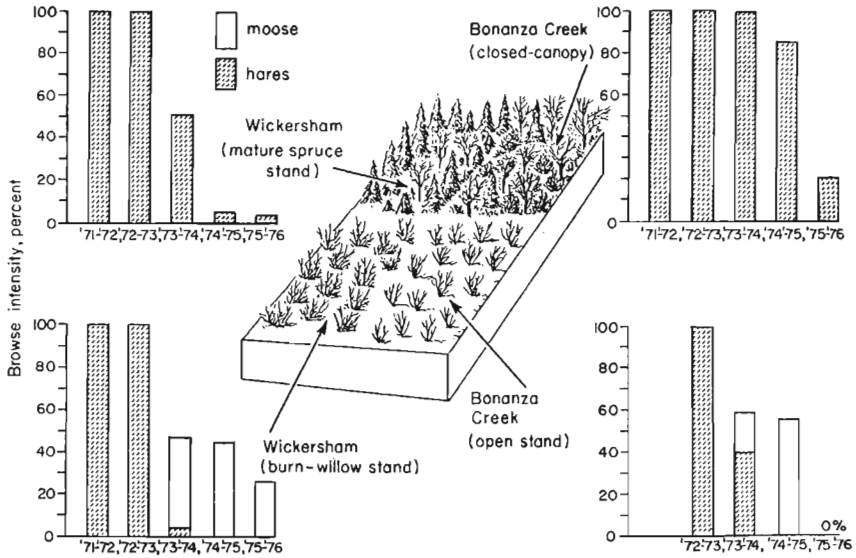


Figure 1. Browsing intensity as percent of available twigs browsed by moose and snowshoe hares between 50 and 120 cm above ground level at the Wickersham and Bonanza Creek closed-canopy and open stands from 1971 through 1976.

by hares coincided with a decline in the hare population. The hare population declined from a high of 624 hares/km$^2$ in 1971 to a low of 12 hares/km$^2$ in 1975 (Table 2, Wolff 1980). Browsing by moose was not evident until the winter of 1973-74, but from 1974 through 1976 it



varied from 26 to 45% (Fig. 1). No moose pellet groups were counted in the burned area from 1971 through spring 1973.

The amount of willow browse available to moose and hares in the adjacent unburned older spruce stand at Wickersham was about 5 kg/ha during all winters (Wolff and Zasada 1979). Browsing on willows by hares ranged from 100% in 1971-72 and 1972-73 to 2% in 1976 (Fig. 1), whereas browsing by moose was between 0 and 10% during all winters. The willow browse which was consumed by moose in the spruce stand was over 120 cm above ground level whereas all hare browsing was between 50 and 120 cm.

Browse utilization by hares and moose in the aspen stand was similar to that of the willow stand (Fig. 2). As browsing intensity by hares decreased following the population decline, browsing by moose increased.

## Bonanza Creek and Tanana River Study Sites

In the open stand at Bonanza Creek, available willow browse was 38 kg/ha in 1975 (Wolff 1976). All of the browse was consumed by hares in 1972-73 with consumption declining to 0% in 1974-75 (Fig. 1). At the Tanana River open stand approximately 20% of all browse less than 3 mm in diameter was over 120 cm above ground level during all years and was not available to hares. The Tanana River open stand consisted of 113 kg/ha of willow browse in 1975 (Wolff 1976:4); a similar decline in hare browsing was recorded over the same time period (Fig. 2b). Browsing was not quantified in these 2 stands in 1971-72, but qualitative observations indicated that hare usage of available browse was near 100%. No moose pellet groups were found in these areas following the winters of 1971-72 and 1972-73 which further supports these observations. Coady (1974) recorded moose browsing on 40 to 60-cm willows along the Tanana River in

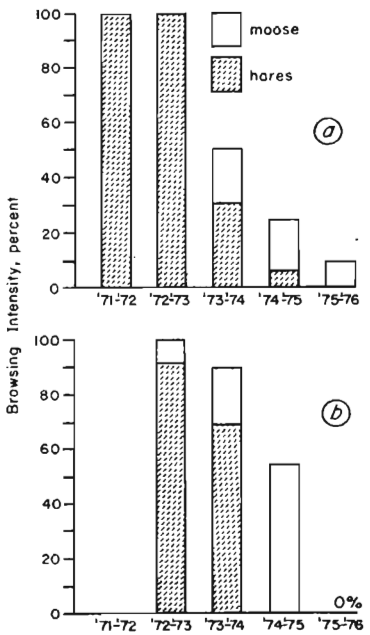


Figure 2. Browsing intensity as percent of available twigs browsed by moose and hares from 1972 through 1976 at: (a) the Wickersham aspen stand, and (b) the open stand at Tanana River.

fall and early winter 1972. However, my results suggest that by mid- to late winter hares moved into these areas and consumed all available browse within this height class.

Browsing by moose was not evident in either the Bonanza Creek or Tanana River sites during the peak of the hare cycle and did not become important until the winter of 1973-74. During the low phase of the hare cycle, browsing by moose in the open stands was about 55%. However, there was no evidence of moose browsing in either the Bonanza Creek or Tanana River stands during the winter of 1975-76.



Open-Closed Habitat Transect

In the Bonanza Creek closed-canopy stand in 1974-75, browsing by hares was 84%; it declined to 50, 10, and 0% at distances of 5, 10, and 20 m, respectively, from the stand (Fig. 3). Browsing by moose was 55%

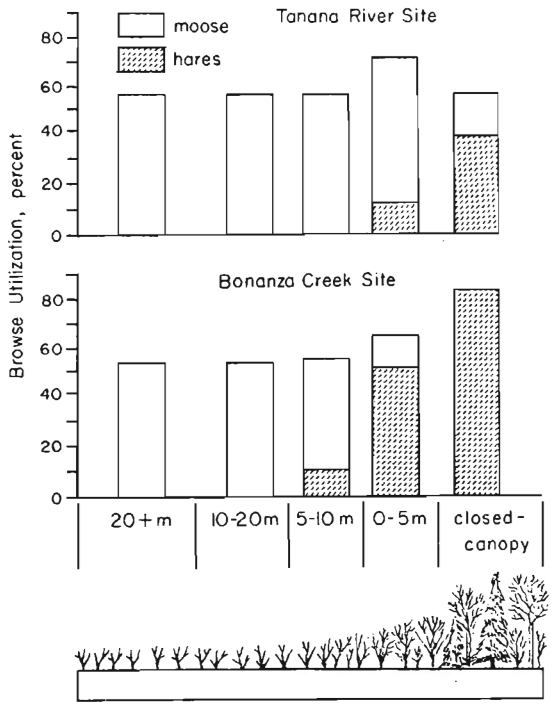


Figure 3. Browsing intensities by moose and snowshoe hares at Bonanza Creek and Tanana River in 1974-75 along a transect from the closed canopy into the open stand.

in the open stand and declined to 15% along the edge and 0% in the closed-canopy stand. These differences in browsing by moose and hares were significant ($p<0.05$). Along the ecotone at the 5- and 10-m distances,

both hares and moose were browsing on the same shrubs and at the same level.

A similar trend in habitat use by moose and hares from the closed canopy to the open stand was recorded at the Tanana River site, but here browsing intensity by hares was less in the closed-canopy stand than at the Bonanza Creek site (Fig. 3). The Tanana River closed-canopy stand was less dense and contained fewer browse plants than the closed-canopy stand at Bonanza Creek. On some of the taller shrubs at Tanana River, moose browsed at the 2- and 3-m level.

In all stands browsing by moose never exceeded 56% whereas during the peak of the hare cycle browsing by hares was at or near 100%. As browsing intensity by hares decreased concurrently with the population decline, browsing intensity by moose increased in the more open preferred winter habitat.

## DISCUSSION

Dietary overlap between moose and snowshoe hares provides a basis for potential competition between the two herbivores. This competition is usually prevented by habitat segregation with hares preferring dense cover and moose frequenting more open seral communities. During high hare densities, hares invade moose habitat which results in potential competition for food.

At the Bonanza Creek and Tanana River sites, snowshoe hares moved into the open 8- and 15-year-old stands from 1971 to 1974 and consumed from 40 to 100% of all available browse. In 1974-75, when the hare population was declining and below the food carrying capacity, hares remained in the closed-canopy habitats and moose moved into the open stands.





Winter moose densities in this region were low in 1975-76 and consequently browsing could vary greatly by the presence or absence of 1 or 2 moose in a specific area during a portion of the winter. Therefore, the absence of moose during this particular winter could be the result of chance and not necessarily exclusion.

In the willow and aspen stands at the Wickersham fire site, snowshoe hares removed 100% of available browse during the time of high hare population in the winters of 1971-72 and 1972-73. Browsing by hares in these burn areas declined after 1973 and browsing by moose increased.

Moose tend to use upland burns early in winter and move to the riverbottoms and lowlands in mid- and late winter (W. Gasaway, personal communication); consequently, competition for browse would not occur until late winter. Spring pellet counts from 1971 through 1973, however, indicated moose had not used the Wickersham burn nor the open stands at Bonanza Creek or Tanana River even in early winter. Personal observations at 2 other burn sites and 3 riverbottom sites showed a similar pattern of browse utilization.

During times of high hare populations, the only browse available to moose which hares cannot reach is 50 cm above snowline or about 120 cm above ground level. Even then, hares have been seen clipping stems 2.5 cm in diameter and consuming the upper branches of the fallen shrub. It is suggested that in late winter during years of high hare densities, moose are confined to habitats in which the browse is above reach of hares but still dense enough and of high quality to provide good winter range. These habitat types are characteristically greater than 12 years old, whereas in stands less than 12 years old, most of the browse is within reach of hares (this study and Wolff and Zasada 1979).

A snowshoe hare consumes 300 g of food per day (Pease et al. 1979) of which between 20 and 100% is woody browse (Wolff 1978b). Assuming a hare can survive on a diet of 20% hardwood browse (a conservative estimate), the hare population of 620 hares/km$^2$ (6.2 hares/ha) in 1971 would require 78 kg/ha of woody browse (390 kg/ha for all food) to survive the winter (6.2 hares/ha x 60g/day x 210 days = 78 kg/ha/winter/population). This is 1 to 4 times more woody browse than was available in any of these study areas (Wolff and Zasada 1979). With hares consuming their total available foods in the 50-120 cm range, there was little browse left for moose. Telfer (1978:641) noted that the amount of browse produced above 2.5 m on Elk Island near Edmonton, Alberta, was 10 to 27% or 10 to 18 kg/ha of total production. In this study and Wolff (unpublished), about 20% (between 4 and 20 kg/ha of total production) was above 2.0 m in stands greater than 12 years old. Habitats containing less than 20 kg/ha of woody browse is below optimal moose winter range (Wolff 1976; Milke 1968; J. Oldemeyer, personal communication). Consequently, even if hares could not exploit the upper 20 to 30% of browse, they lowered the overall habitat carrying capacity by removing 70 to 80% of the total biomass.

The effects of moose-hare competition on moose population dynamics are not known but some associations can be made. The moose population in interior Alaska declined from 1971 to 1975 (Coady 1976). The biggest decline occurred in 1970-71 when winter mortality approached 50% and a record low of 6 yearlings per 100 cows was recorded in the spring of 1971 in Game Management Unit (GMU) 20A south of Fairbanks (Coady 1976). The moose population in GMU 20A has continued to decline from an estimated high of 6,000 animals in 1970 to a low of about 2,500 animals in 1975 (Table 2). Coady proposed that severe winter conditions in 1970-71,





Table 2. Population densities of snowshoe hares near Fairbanks, Alaska, (Wolff 1980), and moose on the Tanana Flats (GMU 20A) (Adapted from Coady 1976). Densities of hares were probably comparable in both areas.

| Year | Number of moose on the Tanana Flats (GMU 20A) central Alaska | Number of hares/km$^2$ |
|---|---|---|
| 1970-71 | 6,000 | - |
| 1971-72 | 3,500 | 624 |
| 1972-73 | 3,000 | 312 |
| 1973-74 | 2,800 | 78 |
| 1974-75 | 2,500 | 12 |

hunting in 1970 to 1974, and wolf predation for 1970 to 1975 were primarily responsible for this decline.

The winter of initial moose decline coincided with the prepeak year in the hare cycle (Table 1). During the winter of 1970-71, and for the next 2 years, there was a food and spatial habitat overlap between moose and snowshoe hares. The record snowfall in 1970-71 limited moose movements and reduced available forage. Food competition with hares further limited food availability to moose during that winter and probably precipitated a greater die-off of moose than would have been the case if a low density of hares had existed. Although moose starvation was not recorded in this study the amount of browse consumed by hares resulted in a 70 to 80% reduction in carrying capacity on moose winter range in some areas.

High hare densities may have a long-range effect upon moose population dynamics not only by direct competition, but indirectly by providing an alternate prey species for wolves (Canis lupus) which feed largely on moose. With an abundant supply of food (hares and starving moose), it

is probable that the wolf population had a high survival rate and consequently increased in numbers (R. Stephenson, Alaska Dept. of Fish and Game personal communication and 1978). Since the crash of the hare population in 1974 (Table 2), wolves have relied entirely on ungulates, particularly moose, and thus have continued to depress the moose population (Stephenson 1978).

To summarize, the decline of the moose population in interior Alaska since 1970 was probably the result of a combination of overbrowsing, habitat deterioration, wolf predation, severe winters, and hunting (Coady 1976). In addition, the results of this study suggest for at least 2 to 3 years during the times of high hare population, moose may have been excluded from much of their preferred winter range by competition with hares. This competition may have affected moose distribution by forcing them into suboptimal habitats or to forage for a considerably reduced food source. More seriously, it could have increased winter moose mortality, particularly during winters of heavy snow accumulation and increased winter moose mortality. Moreover, high hare numbers probably contributed to increasing wolf numbers during and immediately following this critical period. It appears unlikely that there would be much interaction between moose and hares for the remaining 7 to 8 years of the hare cycle.

Although the role of hare competition in moose population dynamics has not been clearly documented, I feel the probability warrants consideration and should be examined more thoroughly in other regions under various habitat conditions.





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