EFFECTS OF POPULATION DENSITY AND SELECTIVE HARVEST ON ANTLER PHENOTYPE IN SIMULATED MOOSE POPULATIONS

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ABSTRACT: We simulated moose (*Alces alces*) populations held either at or below carrying capacity (*K*) to determine the effect of population density on harvest rate and frequency of alleles favoring antler growth under a system of selective harvest. A stochastic model of density-dependent population growth was created to achieve stable populations at *K* with no hunting. Rates of mortality not associated with hunting were increased to simulate predation losses for a population held below *K*. The increased nutrition available to this lower-density population was assumed to result in larger age-specific antler size. Each population was subjected to a harvest plan that defined legal bulls as those with either a spike-fork antler as yearlings (small bulls) or with an antler spread of ≥50 inches (127 cm) as large bulls. Harvest, population composition, and frequency of alleles favorable to antler growth were monitored throughout the simulations. For the population held at *K*, the frequency of favorable antler alleles declined slightly from that obtained in the population with no hunting. When the population was reduced below *K*, harvest decreased and the proportion of small bulls in the harvest increased compared with the population at *K*. In the population below *K*, the frequency of favorable alleles declined steadily, likely to fixation for unfavorable alleles. Ratios of bulls:100 cows in the two harvested populations were similar but ratios of small:large bulls were changing, with the population at lower density exhibiting a higher proportion of small bulls prior to harvest. Under the conditions imposed by our model, increases in age-specific antler size associated with increased nutrition resulted in greater selection against alleles favorable for antler growth under a scenario of selective harvest. Changes in density of moose populations and resulting effects of nutrition on the potential for antler growth must be considered when predicting the outcome of antler-based selective harvests.

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Selective harvest of moose based upon antler size is a common management practice in Alaska and has been an effective management tool (Schwartz *et al.* 1992). This strategy permits harvest of bulls with either a spike or forked antler (hereafter referred to as small bulls) or having an antler spread of at least 127 cm (50 in; large bulls). Any bull having at least 3 tines on 1 brow palm also is legal to harvest. Such a harvest plan allows a moderate level of harvest while ensuring stability in the proportion of males in the population, and a greater mean age among males than does a plan in which any bull is legal to harvest. A modeling exercise demonstrated that this harvest plan also maintained allelic diversity among hypothetical loci coding for antler growth with the exception of alleles coding for numerous brow tines (Hundertmark *et al.* 1993).

The effect of environment on antler growth can be considerable, with estimates of up to 50% of variability in antler size attributable to the environment (Harmel 1983). At population densities below nutritional carrying capacity (*K*), cervids should exhibit larger age-specific body and antler size because of greater availability of nutritious forage to individuals (McCullough 1984). As the rate of antler growth changes in populations experiencing increasing nutrition, we hypothesize that the response of these populations to selective harvest also may change. Some managed populations of moose in Alaska are held near *K* because of hunting policies restricting harvest to males, and the population and genetic effects of selective harvest were evaluated only for populations at or near *K* (Hundertmark *et al.* 1993). Some populations in interior Alaska, however, are held at densities far below *K* because of predation (Gasaway *et al.* 1983, 1992). We conducted a modeling exercise to determine changes in genetic composition and harvest levels in a moose population held below *K* and compared our results with those from the model of populations at or near *K*.

METHODS

A stochastic population model (Fig. 1) reported originally by Thelen (1991) and modified by Hundertmark *et al.* (1993) was used to simulate harvests of different populations of moose at varying densities. The model simulated populations through annual cycles of births, summer mortality of calves, harvest, mating, and winter mortality of adults and calves. All adult mortality was registered in winter. Each animal in the population was characterized by age, sex, an antler genotype and phenotype.

Antler growth was assumed to be an age-dependent polygenic trait. Antler size conforms to a polygenic model because of the continuous variation seen within age classes (Futuyma 1986). In the model, 5 pairs of genes and environmental influences were assumed to contribute to a growth, or phenotype, score for antlers (SCORE). For each locus, there were 2 possible alleles: favorable and unfavorable, which contrib-

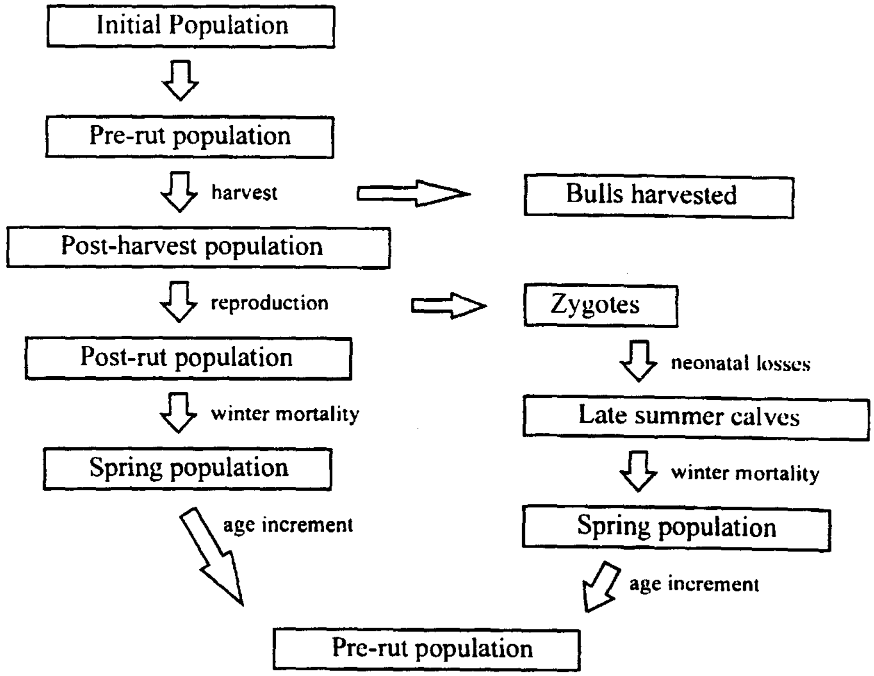

Fig. 1. Flow chart of the stochastic model.

uted 4 and 0 points to the score of the genotype, respectively. Thus, the score for antler growth varied from 0-40 (allele score x 2 alleles/locus x 5 loci). The model tracked the frequency of favorable antler alleles (Q_A). Environmental scores were generated randomly from a distribution with the same mean and variance as the scores for genotypes and 1 score was permanently assigned at birth to each male. The sum of an individual's genotype and environmental scores created its antler phenotypic score that determined age-specific antler size. We assumed a heritability of 0.5, which meant that the genotype and environmental scores were weighted equally. Williams *et al.* (1994) reported mean estimates of heritability between 0.42-0.47 for antler spread, main beam length, and number of antler points for white-tailed deer (*Odocoileus virginianus*). Unlike the prior exercise (Hundertmark *et al.* 1993) this model did not include an option to kill a bull legally if it had at least 3 brow tines on 1 antler. The hypothetical locus controlling expression of brow tines was considered independent of loci encoding for antler spread and we assumed that any effects attributable to genotype at that locus would be identical for either model.

Slower rates of antler growth in yearlings were expressed as spike-fork antlers. Antlers of this size were assumed to be present only in yearlings, and accounted for 60% of antlers in that age class in a population at or near *K* (Schwartz *et al.* 1992). All other bulls had palmated antlers that were characterized by a measurement of spread. Age-dependent antler spreads (Table 1) were assigned to the initial population based upon data from hunter check stations on the Kenai Peninsula. Maximum spreads occurred in animals 8-12 yrs old (Gasaway *et al.* 1987).

To simulate the effect of increased nutrition on antler phenotype resulting from the better nutrition available to a population below *K* (*sensu* McCullough 1979), we multiplied the antler score (phenotype score) by a variable that changed with population size. With a population $\leq$4,000 animals, antler scores were multiplied by 1.36. This value declined exponentially until it equaled 1.00 at a population of 10,000 moose (*K*). In this way, changes in environment caused changes in phenotype yet heritability remained at 0.5 throughout the simulation. The variation produced by this function was similar to the amount of variation observed in mean antler size among populations of moose in Alaska (Gasaway *et al.* 1987).

The initial population was created using estimates of age structure from a population from the northern Kenai Peninsula, Alaska (Schwartz *et al.* 1992). Individuals in the initial population were randomly as-

Table 1. Percentage of bulls, by antler spread, in 4 age classes from the northern Kenai Peninsula, Alaska, used as the starting population in this modeling exercise.

	Antler spread			
Age(yrs)	Spike/fork	<91 cm	≥91 and <127 cm	≥127 cm
1.5	60	25	15	0
2.5-3.5	0	25	60	15
4.5-5.5	0	0	60	40
≥6.5	0	0	5	95

signed genotype scores. Survival rates of females were based upon those reported for the northern Kenai Peninsula by Bangs *et al.* (1989) but were adjusted slightly to produce a stationary population. Survival rates of calves in summer and winter were 0.55 and 0.40, respectively. Annual rates of survival of females older than calves were 0.88 (yearling), 0.95 (2-5 years), 0.90 (6-10 years), 0.85(11-12 years), 0.80 (13-14 years), 0.70 (15-16 years), 0.60 (17 years), 0.45 (18 years), 0.25 (19 years), and 0.0 (20 years). Determination of individual survival was a stochastic process involving comparison of a randomly-generated number with the appropriate survival rate. Survival rates for males were based upon those of females but were reduced by an exponential decay function in which antler-size-dependent survival (ASDS) for bulls decreased as it aged and its antler size increased. The function determining antler growth score was represented by the equation:

$$ASDS = 1 - [(SCORE - DECLINESCORE)/60]^2,$$

where SCORE is the phenotype score, and DECLINESCORE is an age-dependent value that reflects the score at which survival begins to drop. Values for DECLINESCORE of calves and yearlings were 40, and for bulls aged 2-7 were 20, 16, 12, 8, 6, and 4, respectively. For bulls ≥ 8 years the value of DECLINESCORE was 2. We assumed that mortality would increase as a function of antler size because the energy required to produce and carry large antlers, as well as that required to achieve and maintain dominance during rut would place large-antlered animals in a greater energy deficit during winter compared with smaller-antlered animals. Such an outcome is common among rutting males in cervids (Bowyer 1981, 1991). With these assumptions, the initial ratios of all bulls and large (>127 cm antler spread) bulls:100 cows were 80 and 34, respectively.

Based upon data from the moose population on the Kenai Peninsula (Alaska Dept. of Fish and Game, *unpubl. data*) we assigned a harvest rate equal to 50% of all legal bulls. We did not assume a relationship between the age of the bull and a learned ability to avoid hunters, unlike the model developed for elk (*Cervus elaphus*) by Thelen (1991).

Reproductive rates (calves/cow/yr) at *K* were 0.0 for calves, 0.22 for yearlings, 1.27 for ages 2-15, 0.14 for ages 16-19, and 0.0 for age 20 (Schwartz and Hundertmark 1993). To produce these rates in the model for the population at *K* we assumed that 12% of yearlings would produce single calves, 5% would produce twins, and 83% would produce no offspring. Respective values for other age classes were 63%, 32%, and 5% for ages 2-15 yrs, and 8%, 3%, and 89% for ages 16-19 yrs To simulate changes in productivity associated with changes in population density relative to *K* we increased the twinning rate as density decreased (Franzmann and Schwartz 1985). For populations not at *K*, the twinning rate was determined by multiplying the twinning rate at *K* by the ratio of population size at *K*:current population size. The sex ratio of offspring at birth was 1:1 (Schwartz and Hundertmark 1993).

To simulate a moose population held below *K* by predation, we increased mortality rates for all sex-age groups as population size increased. Likewise we simulated additional mortality with little increase at a population size of 4,000 and with an exponential increase until it accounted for an additional 5.6% at or above *K* (10,000 animals).

Because our model was stochastic, we conducted 10 simulations of each scenario, from which we generated means and standard deviations of estimates of population and genetic composition. The original modeling exercise (Hundertmark *et al.* 1993) tracked populations for 50 years, but we extended the model to 100 years in this effort. Estimates of population composition and allele frequencies (Q_A) were generated from the initial population (year 0) and at 5-year intervals to year 100. The simulation of no harvest in a population at *K* (Model A) conducted by Hundertmark *et al.* (1993) was compared with simulations of selective harvest in a population at *K* (Model B), and selective harvest in a population held below *K* by predation (Model C). Comparisons between new simulations and Model A were necessarily limited to the first 50 years because of the length of simulations conducted by Hundertmark *et al.* (1993), and are reported here to facilitate comparison with that earlier effort. Comparisons between the current 2 models included data from the entire 100-year simulations.

Differences in final estimates of parameters between any 2 simulations were tested with a *t*-test; all comparisons were tested simultaneously and Bonferonni adjusted probabilities were reported (Wilkinson *et al.* 1996). Differences in parameters among all simulations were tested with ANOVA. *Post-hoc* tests among means within ANOVA were conducted with Bonferonni comparisons (Wilkinson *et al.* 1996).

The effects on model results of changes in heritability and different harvest criteria were discussed by Hundertmark *et al.* (1993) and Thelen (1991). Thelen (1991) also documented the response of the original model to changes in assumptions concerning genetic control of antler growth and in parameters controlling population dynamics. We believe that the model is robust with respect to perturbations in these basic functional relationships.

RESULTS

Population size after 50 years differed among the populations ($F_{2,27}$ = 1,350, $P <$ 0.0001). Both harvested populations had significantly fewer animals than the unhunted population (Model A) and Model C (with predation) had significantly fewer animals than Model B (hunting at *K*). Both populations subjected to hunting (B and C) declined initially as hunting was instituted (Fig. 2a). The population under Model B recovered from this decline as density-dependent processes brought the total size back toward *K* where the population stabilized. The population under Model C stabilized at approximately 7,000 animals, representing an equilibrium between the greater rates of mortality and increased productivity associated with better nutrition.

Percent declines in Q_A (frequency of favorable alleles) over the first 50 years for Models A, B, and C were 1.1, 5.4, and 15.5, respectively (Table 2). Estimates of Q_A in year 50 differed significantly ($F_{2,27}$ = 503.4, $P <$ 0.0001) among the 3 models, with selective harvest in Model C causing the greatest decline. In the 2 models involving selective harvest (B and C), allele frequencies continued to decline steadily but at different rates through the 100 years of the simulation (Fig. 2b).

Total harvest under both models decreased for the first 10 years, primarily because the population was unhunted prior to year 1. After year 10, harvest increased initially prior to becoming stable for Model B, whereas it decreased slowly for Model C (Fig. 2c). By year 50, the mean harvest of small bulls under Model C was significantly less than under Model B (t = 8.35, 18 df, P < 0.0001; Table 2). Mean harvest of large bulls also was less under Model C (t = 10.68, 18 df, P < 0.0001; Table 2). Moreover, the proportion of spike-fork yearlings in the harvest differed between the 2 scenarios (B and C). Under both models, the proportion of spike-fork yearlings increased concomitant with the decrease in harvest in the first

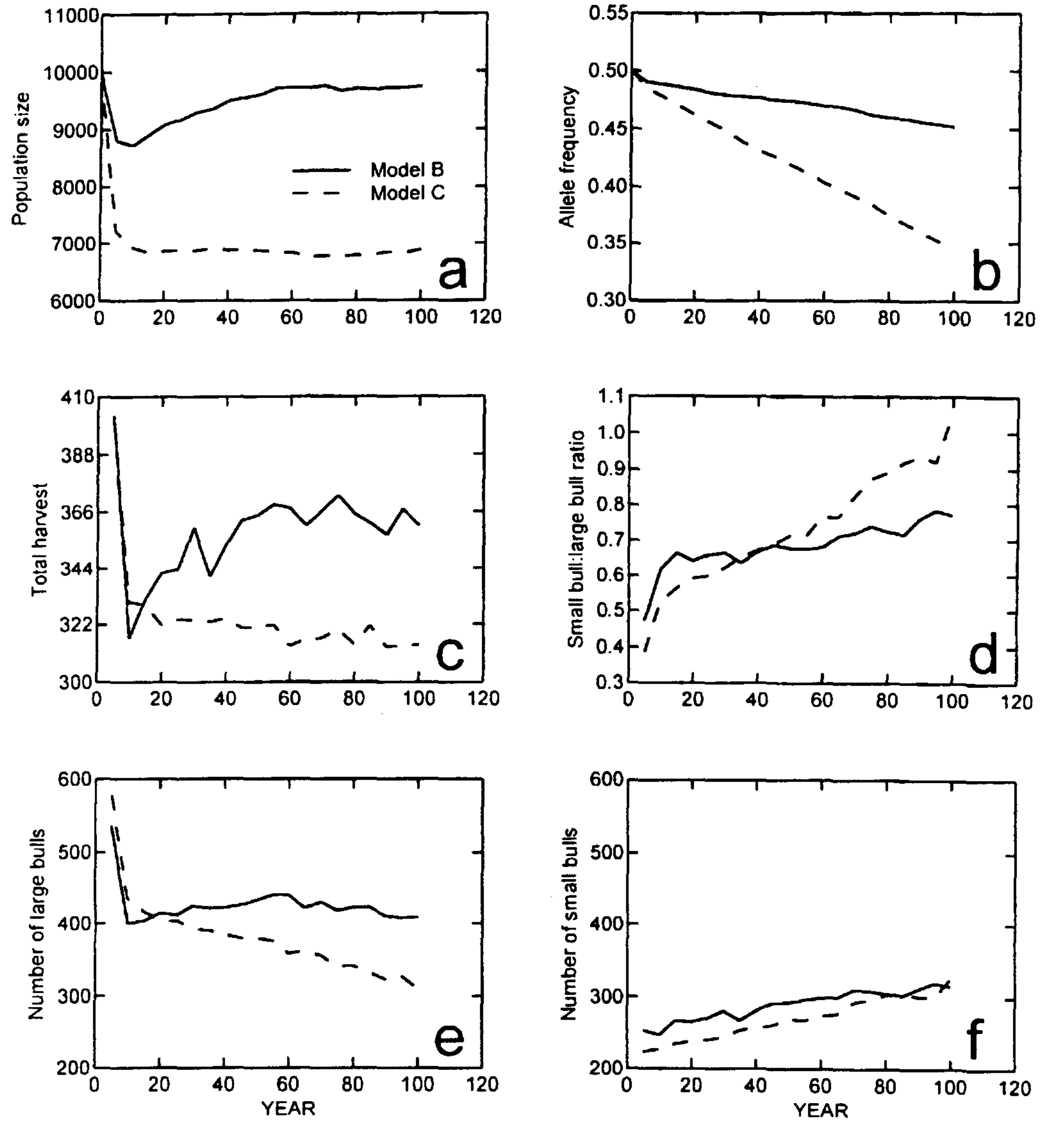

Fig. 2. Temporal changes in (a) total population size; (b) frequency of favorable antler alleles; (c) total harvest; (d) small bull:large bull ratio prior to hunting; (e) number of large bulls in the population prior to hunting; and (f) number of small bulls in the population prior to hunting for simulated moose populations subjected to either harvest Model B (harvest at *K*) or C (harvest below *K*). Data represent means of 10 simulations.

decade; this reflected the harvest of abundant large bulls in the previously unhunted populations. Subsequently, the small bull:large bull ratio in the population prior to harvest increased slightly under Model B, but increased at a faster rate under Model C (Fig. 2d). By year 100, spike-fork yearlings represented 44% of the harvest under Model B, whereas they represented 52% of the harvest under Model C, compared with an approximate 30% share of the harvest initially.

Ratios of bulls:100 cows of hunted populations after 50 yrs were reduced significantly ($F_{2,27}$ = 2,800, $P < 0.0001$; Table 2) from that of the unhunted popula-

Table 2. Population parameters of simulated moose populations at year 50. Data for Model A taken from Hundertmark *et al.* (1993). Values represent means (SD) of 10 simulations. Harvest data are means of years 30-50 of the simulations.

Model	Frequency of favorable alleles	Population size	Harvest of small (spike/fork) bulls	Harvest of large (> 127 cm spread) bulls	Number of bulls per 100 cows	Number of large bulls per 100 cows
A	0.490^{A}	9956^{A}	0	0	79.4^{A}	33.5^{A}
	(0.0033)	(167)			(1.65)	(1.2)
B	0.470^{B}	9457^{B}	140^{a}	210^{a}	43.4^{B}	4.4^{B}
	(0.0024)	(166)	(3)	(3)	(0.88)	(0.3)
C	0.420^{C}	6805^{C}	126^{b}	195^{b}	37.2^{C}	5.1^{C}
	(0.0079)	(90)	(4)	(3)	(1.09)	(0.5)

^{A,B,C} Means within a column differ significantly (ANOVA and Bonferroni *post hoc* comparisons).

^{a,b} Means within a column differ significantly (t-test).

tion and differed significantly from each other although this latter difference may have no practical biological significance for management. Moreover, these ratios were well above the objective level of approximately 30 bulls:100 cows (Schwartz *et al.* 1992). Ratios of large bulls:100 cows also differed among the simulations ($F_{2,27} = 4{,}592$, $P < 0.0001$), with hunting causing a marked decrease. At 50 years, the low-density population had a significantly higher ratio of large bulls:100 cows than did the hunted population at K (Table 2).

The most notable difference in composition between the 2 hunted populations was the decrease in the number of large bulls in Model C (Fig. 2e). After the initial decrease in the first decade, numbers of large bulls increased slightly under Model B and stabilized. Under Model C, numbers of large bulls continued to decrease. After 100 years, large bull:100 cow ratios for Model B (4.2; SD=0.32) and Model C (4.5; SD=0.41) did not differ ($t = -1.75$, 18 df, $P = 0.097$), but the ratio of the population in Model C was expected to continue to decline. The number of spike-fork yearlings in each population increased at relatively constant rates (Fig. 2f). Thus, the proportion of spike-fork yearlings in the harvest under Model C initially was less than that under Model B, but increased at a faster rate and was greater than that in Model B by year 50 (Fig. 2d).

DISCUSSION

We caused an increase in expression of antler size via increased nutrition in a population in which density was decreased relative to K. This increase in phenotype initially caused an increase in the proportion of large bulls in the population (relative to a population at K) and a decrease in the proportion of spike-fork yearlings. These changes were short-lived, however, as changes in harvest of these groups caused changes in allele frequencies. Specifically, the decrease in number of spike-fork yearlings available for harvest caused a decrease in selection against unfavorable antler alleles. Under the original simulations conducted by Hundertmark *et al.* (1993), the harvest of animals with inferior genotypes (i.e., spike-fork yearlings) balanced the harvest of animals with superior genotypes (i.e., large bulls) and acted to stabilize allele frequencies over time. In the current simulation, more inferior animals grew palmated antlers as yearlings because of better available nutrition and thus were protected from harvest. This caused an increase in the frequency of unfavorable antler alleles and a corresponding decrease in the frequency of favorable ones. Moreover, animals with superior genotypes would, due to increased nutrition, spend less time in the protected class of animals and would thus obtain less of an opportunity to mate. The outcome of these changes in phenotype was an increase in selection pressure against favorable alleles and a consistent decrease in the proportion of bulls in the population with antler spreads $\geq$127 cm.

McCullough (1984) demonstrated that trophy harvest from a white-tailed deer herd was higher when both males and females were harvested. He argued that reducing population density below *K* caused an increase in nutritious forage and a corresponding increase in age-specific antler size. The absolute decrease in number and harvest of large bulls in Model C (with predation) seemingly runs counter to this idea, but McCullough (1984) was considering harvest as a random process whereas we harvested males based on antler size. Harvest based on antler size always decreased the frequency of favorable antler alleles compared with random harvest in previous simulations (Hundertmark *et al.* 1993).

Changes in antler size were gradual in this simulation and likely would escape detection for a number of years. Ultimately, however, there would be adequate time to detect and rectify the observed problems. Managers should monitor ratios of large:small bulls in their post-hunt surveys and in their harvest reports. Any significant and lasting change in this ratio not accounted for by changes in population density would likely indicate potential changes in genetic composition in the population.

We assumed that *K* did not change throughout the simulations; this assumption is unlikely to hold in many populations. Nonetheless, our results are informative because they demonstrate that alleles controlling antler growth are subject to a continuum of selective force ranging from balancing selection at or near *K* to selection against favorable alleles below *K*. This information is particularly relevant to moose populations in Alaska that are being considered for intensive management (Hundertmark and Schwartz 1996).

This exercise illustrates the contribution of environment to antler growth and the possible effect, given our assumptions, that this may have on management of moose populations by selective harvest. The relative position of the population with respect to *K* will determine the success of selective-harvest management. The trends observed in this simulation were dramatic only when extended many years into the future, allowing time to detect and rectify problems. The true relationships between nutrition and expression of antler size in moose needs to be documented before real effects of selective harvest can be more thoroughly assessed.

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