

NOTE

Generation Time in Structured Populations

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ABSTRACT: Generation time is an intuitively simple concept, but for structured populations there are multiple definitions and no general understanding of how they relate to each other. François Bienvenu and Stéphane Legendre, in their note “A New Approach to the Generation Time in Matrix Population Models,” appearing in the June 2015 issue of *The American Naturalist*, introduced a new measure of generation time T_a , the average time between birth events in an ancestral lineage, and derived the remarkably simple formula $T_a = \lambda(v^T w)/(v^T F w)$ for any matrix model, where F is the fecundity matrix, v is reproductive value, and w is stable population structure. Here I generalize their formula and interpretations of T_a to a continuous or continuous-discrete population structure and derive similar formulas for three other established generation time measures: average parent age across all births at one time (\bar{A}) and mean parent age at birth events for a cohort (μ_i) or generation (T_c). The new formulas reveal that these differently defined measures are unexpectedly often identical in value and clarify when they differ.

Keywords: generation time, integral projection model, matrix model, structured population.

Introduction

Generation time is an important feature for characterizing a species' life history and for understanding the timescales of response to perturbations and natural selection. The concept of generation time is intuitively simple, but for structured populations there are many different definitions and no general understanding of how they relate to one another (Caswell 2001, sec. 5.3.5).

Bienvenu and Legendre (2015) introduced a new measure of generation time T_a for structured populations: the average time between birth events in an ancestral lineage going from daughter to mother to grandmother and so on, ad infinitum, an idea they credit to Lloyd Demetrius. They derived the remarkably simple formula

$$T_a = 1 + \frac{v^T S w}{v^T F w} = \lambda \frac{v^T w}{v^T F w}. \quad (1)$$

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Here S and F are the survival and fertility matrices, respectively, of a matrix population model with projection matrix $A = S + F$, λ is the dominant eigenvalue of A , v is reproductive value, and w is stable age/stage distribution (dominant left and right eigenvectors of A). Moreover, Bienvenu and Legendre (2015) showed that T_a is exactly equal to a “complex and hard to interpret” (p. 834) formula for a seemingly different definition of generation time: the mean parent age for all offspring born at one time, when the population is at the stable distribution w (Cochran and Ellner 1992).

Here I generalize Bienvenu and Legendre's (2015) results and then derive new, unexpected relationships among the existing measures of generation time. The generalization is showing that equation (1) holds for general discrete-time-structured population models, including integral projection models (IPMs); this is true for both of its interpretations (average time between birth events and mean parent age). The general IPM framework (Ellner and Rees 2006) can model a wide range of structured populations in discrete time, including continuous variation in size; age or stage structure; sex structure; cross-classification by age and size; and classification that changes over the life cycle (e.g., seeds classified by burial depth, adults by size and age). General IPMs require a new analysis because Cochran and Ellner (1992) used the times between visits to a state (which do not exist in general for IPMs), and Bienvenu and Legendre (2015) used a finite Markov chain on the set of links in the life-cycle graph corresponding to S . Bienvenu and Legendre's (2015) approach and calculations are formally valid for IPMs but hit a mathematical obstacle that I could not get past (proving directly that the chain on the infinite set of possible transitions is ergodic, i.e., that it invariably converges to a unique stationary distribution). The approach here is simpler and avoids that obstacle. As a side benefit, it implies that the chain on transitions is ergodic, which is useful because that chain has other applications (Bienvenu et al. 2017).¹

The relationships among generation time measures are found by deriving formulas like equation (1) for other measures. Cochran and Ellner (1992) described T_a as “mean age

1. I thank F. Bienvenu for pointing out the implication.

of the parents of offspring produced in the current time period" (p. 354), a standard measure of generation time. But that is not quite true. Their complex formula, and thus T_a , are the weighted mean parent age when births are weighted by reproductive value of the newborn, rather than the more conventional equal weighting of all births (e.g., Caswell 2001, p. 130). I derive a formula similar to (1) for mean parent age \bar{A} , when births are weighted in any way, and similar formulas for two forward-looking measures of generation time, the mean age at birth events for all individuals in a cohort (μ_1 ; Caswell 2001, sec. 5.3.5) or a generation (T_c ; Steiner et al. 2014).

Surprisingly, given their different biological meanings, in a stable population ($\lambda = 1$), these four measures coincide if offspring are weighted by reproductive value in \bar{A} and μ_1 . Moreover, the generation time measure T_R (defined by $\lambda^{T_R} = R_0$ for $\lambda \neq 1$, where R_0 is the net reproductive rate) converges to this common value as $\lambda \rightarrow 1$. Under the common assumption that offspring state at birth is independent of parent state, the forward-looking measures μ_1 and T_c are always equal, and the backward-looking measures T_a and \bar{A} are always equal; if, moreover, the population is stable, these four measures always coincide for any offspring weighting (while T_R is undefined). Thus, substantial differences between measures can occur only in a rapidly increasing or decreasing population or with strong parent-offspring trait correlations.

The key ideas are a simpler representation of ancestral lineages and a method to compute mean parent age for a set of newborns. The math in the main text is the minimum needed for those; details are in the appendixes (apps. A–D are available online).

Assumptions, Background, and Notation

I consider a population of individuals classified by individual-level state variable z in some bounded set \mathbf{Z} . In matrix population models, \mathbf{Z} is a finite set of points representing discrete ages, stages, or size classes. Here I consider the case of a basic continuous-state IPM (Easterling et al. 2000; Coulson 2012), where \mathbf{Z} is an interval (or rectangle, cuboid, etc. in higher dimensions), but all formulas and results hold much more generally (see app. A).

The population state is described by the distribution function $n(z, t)$, such that

$$\int_A n(z, t) dz \quad (2)$$

is the number of individuals whose z value lies in A at time t . When z is a state vector, $z = (z_1, z_2, \dots, z_m)$, dz is shorthand for $dz_1 dz_2 \dots dz_m$. The population dynamics

$$n(z', t+1) = \int_{\mathbf{Z}} K(z', z) n(z, t) dz \quad (3)$$

are specified by kernels $K(z', z) = F(z', z) + S(z', z)$, where F represents state- z' offspring at time $t+1$ produced by state- z parents at time t , and S represents state- z individuals surviving from t to $t+1$ and transitioning to state z' (S is often called P in the IPM literature). Here F and S are assumed to be continuous on $\mathbf{Z} \times \mathbf{Z}$, and $n(z, t)$ is continuous on \mathbf{Z} for all t . The kernels are assumed to be time invariant (otherwise, generation time would vary from generation to generation) and power positive (Ellner and Rees 2006), so there is a dominant eigenvalue $\lambda > 0$, with strictly positive left and right eigenvectors v and w . The model as written is density independent, but F and S could be the kernels of a density-dependent model evaluated at an equilibrium, in which case λ must equal 1.

Formulas for mean parent age are derived using the identity

$$I + 2M + 3M^2 + 4M^3 + \dots = (I - M)^{-2} \quad (4)$$

(Cochran and Ellner 1992; Ellner et al. 2016). This holds if a population having M as its kernel or matrix (i.e., $n(t+1) = Mn(t)$) decreases exponentially to zero in the long run (technically, if M has norm < 1). I assume this holds for S and for $M = S/\lambda$ (i.e., the population with kernel $F + S$ would grow at a slower exponential rate or decrease at a faster exponential rate, if reproduction were eliminated). I use matrix-like notation so that formulas suggest computer code in matrix languages like MATLAB and R. Here $f^T g$ denotes the inner product $\int_{\mathbf{Z}} f(z)g(z)dz$, Kf means $\int_{\mathbf{Z}} K(z', z)f(z)dz$, and $f^T K$ means $\int_{\mathbf{Z}} f(z')K(z', z)dz'$. Expressions like $v^T Fw$ are unambiguous because $(v^T F)w = v^T (Fw)$. Be warned, many numerical calculations (such as $h \times \text{sum}(f \times g)$ for $f^T g$ by midpoint rule) include bin-width (h) factors that the notation omits.

Mean Time between Birth Events in an Ancestral Lineage

Bienvenu and Legendre (2015) derived formula (1) by representing an ancestral lineage as a backward-in-time finite Markov chain on the set of links in the life-cycle graph corresponding to S . But with a continuum of states, to make the mathematics tractable, I construct a simpler representation of ancestral lineages. I do this by expanding the individual state to include individuals' age class a , with $a = 1$ for new recruits and $a = 2$ for everyone else. In an online review of Bienvenu and Legendre (2015), Kisdi (<https://f1000.com/prime/725454928>) also used this state space but still considered the chain on links. Here I use the same logic as Bienvenu and Legendre (2015) but apply it to an ancestral chain on expanded states. Birth events are signaled by the individual's state having $a = 1$. The frequency of birth events is the stationary probability that $a = 1$, and the inverse of that frequency is the average time between birth events, T_a .

The population is described by state distributions $n_1(z, t)$ on the set Z_1 of possible z values for new recruits and $n_2(z, t)$ on the set Z_2 of possible z values for older individuals. Because w is strictly positive, $Z_1 = \{z : Fw(z) > 0\}$ and $Z_2 = \{z : Sw(z) > 0\}$. Let $\mathbf{z} = (z, a)$ denote a point in this expanded state space.

The transition kernel on the expanded state space also involves F and S , but they are separated so that new recruits (from F) go into $(Z_1, 1)$, while survivors (from S) go into $(Z_2, 2)$. The transition kernel is therefore

$$\mathbf{K}(\mathbf{z}', \mathbf{z}) = \begin{pmatrix} F(z', z) & F(z', z) \\ S(z', z) & S(z', z) \end{pmatrix} \begin{matrix} (z', 1), z' \in Z_1, \\ (z', 2), z' \in Z_2 \end{matrix} \quad (5)$$

with the matrix multiplication interpretation that

$$\begin{pmatrix} K_{11} & K_{12} \\ K_{21} & K_{22} \end{pmatrix} \begin{pmatrix} n_1 \\ n_2 \end{pmatrix} = \begin{pmatrix} K_{11}n_1 + K_{12}n_2 \\ K_{21}n_1 + K_{22}n_2 \end{pmatrix}.$$

To derive the transition kernel for the ancestral chain, first note that

$$w^* = \begin{pmatrix} Fw(z), z \in Z_1 \\ Sw(z), z \in Z_2 \end{pmatrix} \quad (6)$$

is the stable distribution for (5) (i.e., a right eigenvector with eigenvalue λ). It can be verified directly that $\mathbf{K}w^* = \lambda w^*$, but this can also be understood intuitively. If the population (on the original state space) is at the stable distribution w , then its distribution next year is λw , also a stable distribution. On the expanded state space, the distribution next year consists of Fw in Z_1 and Sw in Z_2 , which is w^* .

Transition probabilities for the ancestral chain now follow from Bayes's theorem. The reverse-time transition probability from \mathbf{z} to \mathbf{z}_p (parent or prior state) equals the (forward-time) contribution of \mathbf{z}_p to \mathbf{z} divided by the total at \mathbf{z} now, when the distribution of the previous state was w^* . For example, the individuals at $(z, 1)$ now come from fecundity of $(Z_1, 1)$ individuals ($F(z, z_p) \times Fw(z_p)$ if last year's population was at w^*) and fecundity of $(Z_2, 2)$ individuals ($F(z, z_p) \times Sw(z_p)$). The total population now is λw^* , which is $\lambda Fw(z)$ for $(z, 1)$. Using the same logic for $(z, 2)$ individuals, the transition kernel for the ancestral chain is

$$\mathbf{R}(\mathbf{z}_p, \mathbf{z}) = \begin{pmatrix} \frac{F(z, z_p) \times Fw(z_p)}{\lambda Fw(z)} & \frac{S(z, z_p) \times Fw(z_p)}{\lambda Sw(z)} \\ \frac{F(z, z_p) \times Sw(z_p)}{\lambda Fw(z)} & \frac{S(z, z_p) \times Sw(z_p)}{\lambda Sw(z)} \end{pmatrix} \begin{matrix} (z_p, 1), z_p \in Z_1, \\ (z_p, 2), z_p \in Z_2. \end{matrix} \quad (7)$$

The definitions of Z_1 and Z_2 imply that the denominators in all four subkernels are positive. I verify in appendix B that \mathbf{R} defines a Markov chain.

It can be directly checked that a right eigenvector for \mathbf{R} , with eigenvalue 1, is given by

$$w_a = \frac{1}{\lambda v^T w} \begin{pmatrix} v(z) \times Fw(z) \\ v(z) \times Sw(z) \end{pmatrix}. \quad (8)$$

Here w_a integrates to 1, so it is a stationary distribution. Moreover, (i) w_a is the unique stationary distribution of the ancestral chain, and (ii) it gives the long-term frequency of different states in the ancestral chain starting from any individual (these are proved in app. B). The frequency of birth events is therefore $\int_{Z_1} w_a(z) dz = (v^T Fw) / (\lambda v^T w)$, implying (as in Bienvenu and Legendre 2015) that the mean time between birth events is $(\lambda v^T w) / (v^T Fw)$, which is equation (1).

Mean Age of Parents

I now generalize the second interpretation of T_a by computing the mean parent age, \bar{A} , for all offspring born at one time when the population is at its stable distribution. The definition of mean parent age is offspring-centric: each newborn is (effectively) asked, "How old is your mother?" so the age of one parent can occur multiple times in the calculation of \bar{A} .

Being in stable distribution means $n(t) = C\lambda^t w$ for some $C > 0$ ($n(t)$ is short for the function $n(\cdot, t)$); we can take $C = 1$ by redefining Cw as w). The offspring produced by the year- t population and added as new recruits in year $t + 1$ are then

$$b(t) = Fn(t) = \lambda^t Fw. \quad (9)$$

To compute mean parent age, $n(t)$ is subdivided by age. The year t population consists of new recruits plus survivors, $n(t) = b(t - 1) + Sn(t - 1)$; partitioning $n(t - 1)$ the same way and continuing gives

$$\begin{aligned} n(t) &= b(t - 1) + Sb(t - 2) + S^2b(t - 3) + \dots, \\ &= \underbrace{\lambda^{t-1} Fw}_{\text{age 1}} + \underbrace{\lambda^{t-2} SFw}_{\text{age 2}} + \underbrace{\lambda^{t-3} S^2 Fw}_{\text{age 3}} + \dots \end{aligned} \quad (10)$$

Note, new recruits are assigned age 1. A new recruit now whose parent was a new recruit last year therefore has a parent of age 1. This is the sensible choice for calculating generation time, because it gives annuals a generation time of 1.

The total number of births from the year- t population is $\mathbf{e}^T b(t) = \lambda^t \mathbf{e}^T Fw$, where $\mathbf{e}(z) \equiv 1$. The births from age- a parents (eq. [10]) account for the following fraction of total births:

$$\frac{\mathbf{e}^T F \lambda^{t-a} S^{a-1} Fw}{\lambda^t \mathbf{e}^T Fw} = \frac{\mathbf{e}^T F(S/\lambda)^{a-1} Fw}{\lambda \mathbf{e}^T Fw}, \quad a = 1, 2, \dots \quad (11)$$

Using equation (4) and the fact that $Fw = (\lambda I - S)w$ because $(F + S)w = \lambda w$, the mean parent age is

$$\begin{aligned}\bar{A} &= (\lambda \mathbf{e}^T F w)^{-1} [\mathbf{e}^T F (I + 2(S/\lambda) + 3(S/\lambda)^2 + \dots) F w], \\ &= (\lambda \mathbf{e}^T F w)^{-1} [\mathbf{e}^T F (I - (S/\lambda))^{-2} F w], \\ &= (\lambda \mathbf{e}^T F w)^{-1} [\lambda^2 \mathbf{e}^T F (\lambda I - S)^{-2} F w], \\ &= \lambda \frac{\mathbf{e}^T F (\lambda I - S)^{-1} w}{\mathbf{e}^T F w}.\end{aligned}\quad (12)$$

All offspring count equally in equation (12), but we can also consider a weighted average parent age $\bar{A}(q)$ in which type- z offspring are given weight $q(z) \geq 0$. The only change is that \mathbf{e}^T is replaced by q^T in numerator and denominator. Even equal weighting ($q = \mathbf{e}$) values some births more than others, because offspring that die before their first census are not counted. But if we do not count those offspring, should we count ones so small that they probably will not survive to breed? This reasoning suggests that we should weight offspring by their expected contribution to future population growth, that is, by reproductive value v (Cochran and Ellner 1992). Then because $\lambda v^T = v^T (F + S)$ implies $v^T F = v^T (\lambda I - S)$, (12) becomes

$$\bar{A}(v) = \lambda \frac{v^T F (\lambda I - S)^{-1} w}{v^T F w} = \lambda \frac{v^T w}{v^T F w} = T_a, \quad (13)$$

as shown by Bienvenu and Legendre (2015) for matrix models.

Mean Age at Birth Events

The measures T_a and \bar{A} look backward from current newborns, to when their parent was born or to all birth events in their ancestral lineage. Others look forward from current newborns, to births where they are the parent. Starting with a cohort of newborns (assigned age 1) with state distribution $n_1(z)$, generation time μ_1 is defined as the mean parent age at offspring production over all offspring produced by the cohort. Total offspring from cohort members at age 1 are $\mathbf{e}^T F n_1$, those from cohort members at age 2 are $\mathbf{e}^T F S n_1$, and so on.

The value of μ_1 depends on the initial cohort, n_1 . The conventional choice is a birth cohort in a stable population; that is, $n_1 = Fw$. Then proceeding as in equation (12), the mean parent age at offspring production is

$$\mu_1 = \frac{\mathbf{e}^T F (I - S)^{-2} F w}{\mathbf{e}^T F (I - S)^{-1} F w}. \quad (14)$$

As with \bar{A} , it is useful to consider $\mu_1(q)$ in which offspring are weighted by $q(z) > 0$; this is given by equation (14), with \mathbf{e} replaced by q in the numerator and denominator.

Steiner et al. (2014) chose n_1 to be the state distribution at birth for all individuals in a single generation. That dis-

tribution is proportional to the dominant right eigenvector c of the next-generation kernel $G = F(I - S)^{-1}$ (Caswell 2001, sec. 5.3.4), under the assumption (in force from now on) that G is uniformly power positive and therefore has a positive dominant eigenvalue (the net reproductive rate R_0). Offspring are weighted by cohort reproductive value d , the dominant left eigenvector of G . The resulting generation time measure is

$$T_c = \frac{d^T F (I - S)^{-2} c}{d^T F (I - S)^{-1} c} = \frac{d^T (I - S)^{-1} c}{d^T c}. \quad (15)$$

Choosing $q = d$ and $n_1 = c$ was not arbitrary; indeed Steiner et al. (2014) showed that T_c is the optimal measure of reproductive timing for approximating population growth rate $r = \log \lambda$ in terms of R_0 and the reproductive schedule.

When Do the Measures Coincide and Differ?

The formulas derived above, of the Bienvenu and Legendre (2015) type, are useful for understanding when and why the different measures of generation time are equal or different. Bienvenu and Legendre (2015) showed that $T_a = \bar{A}(v)$. But there are many other connections, especially for stable populations ($\lambda = 1$) or under the common assumption that offspring state is independent of parent state.

Formally, offspring state is independent of parent state if

$$F(z', z) = c_1(z') m^T(z). \quad (16)$$

Here $m(z)$ is per capita fecundity of a state- z parent, and $c_1(z')$ is the offspring state distribution. Ellner et al. (2016) call this exact mixing at birth. Exact mixing at birth would generally not hold if the state z includes (or is) genotype, breeding value, or location, all of which produce positive correlations between offspring and parent states. Otherwise, barring evidence to the contrary, exact mixing at birth has often been assumed (Ellner et al. 2016), especially for plant populations where new recruits cannot be assigned to particular parents.

Stable populations ($\lambda = 1$) are also relevant empirically because a majority of populations for which long-term counts are available exhibit aperiodic (and seemingly random) fluctuations about their mean, rather than cycles, chaos, or a long-term trend (Kendall et al. 1998; Louca and Doebeli 2015). Average demographic rates for those populations would therefore imply $\lambda \approx 1$.

The relationships among generation time measures are summarized in table 1; the derivations are in appendix D. The spade equalities hold because weighting offspring by q is equivalent to weighting parents by the mean q of their offspring, which is equal across parents when there is exact mixing at birth. The dagger equalities hold for the same reason plus the fact that annual and generational birth cohorts are

Table 1: Relationships among the generation time measures

Measure	General case	Exact mixing at birth	Stable population
$\bar{A}(q)$		♣	
$\bar{A}(v)$	§	♣	♣
T_a	§	♣	♣
$\mu_1(q)$		†	
$\mu_1(v)$		†	♣
T_c		†	♣

Note: Within each column, all measures with the same symbol are always equal in value under the condition in the column heading. In addition, T_R , defined by $\lambda^{T_R} = R_0$ for $\lambda \neq 1$, converges to the common value of the clubs measures as $\lambda \rightarrow 1$. The q denotes an arbitrary nonnegative offspring weighting function; v is relative reproductive value, the dominant left eigenvector of the kernel $K = F + S$. “Exact mixing at birth” means that the distribution of offspring states z at birth is the same for all parents. “Stable population” means that the dominant eigenvalue of K is $\lambda = 1$. Generation time measures are \bar{A} (mean age of the parent for all births at one time, when offspring of state z are given relative weight $q(z)$), T_a (mean time between birth events in an ancestral lineage), $\mu_1(q)$ (mean age at birth events for all individuals in a cohort with offspring weighted by q), and T_c (mean age at birth events for all individuals in a generation, when offspring are weighted by cohort reproductive value d).

both multiples of the offspring state distribution c_1 . Thus, with exact mixing at birth, the two backward-looking measures coincide ($\bar{A}(q) = T_a$) and the two forward-looking measures coincide ($\mu_1(q) = T_c$), for any offspring weighting. The stable population equalities (and the approximation $T_R \approx T_a$ for $\lambda \approx 1$) follow from relationships among v , w , c , and d in stable populations (see app. D). Thus, in a stable population with exact mixing at birth, all four defined measures coincide: $T_a = T_c = \bar{A}(q) = \mu_1(q)$ for any $q \geq 0$.

Discussion

I have studied the five main previously defined generation time measures for structured populations. The measures have different definitions and biological interpretations, so there is no obvious reason why any two of them should ever be equal for a population. Surprisingly, several or all of them often coincide exactly (table 1).

What do we learn from this? First, that differences among the measures result from two kinds of symmetry breaking: between past and future, when $\lambda \neq 1$, and between offspring of different parents, when there are parent-offspring correlations. Unless a population is far from stable or has strong parent-offspring correlations, all measures will be similar and there is no need to decide which is most meaningful.

But in (for example) an expanding population with evolutionary dynamics, the measures may diverge, and different measures may be appropriate for different questions. The measures T_a and $\bar{A}(q)$ define generation time by looking

back to current individuals’ ancestors. Consequently, they may be most relevant for identifying the time period over which selection would have acted to make current individuals different from their ancestors. If $\bar{A}(q)$ varies substantially depending on q , it means different groups of current newborns have parents born (on average) at substantially different times. In an evolving population, especially with time-varying selection, this might imply that the different groups of current newborns are genetically different. Conversely, T_c and μ_1 are relevant for identifying the turnover time to the immediate descendants of current individuals, which is the time required for major changes in heritable traits.

The results for stable populations (table 1) also provide support for the argument that average parent age should be computed with offspring weighted by reproductive value v . Cochran and Ellner (1992) gave no rigorous justification for weighting by v , and their similar proposal for calculating R_0 proved to be incorrect (Caswell 2001), so some skepticism about weighting by v is justified. My results show that weighting by v brings \bar{A} and μ_1 into closer alignment with generation time measures T_a , T_c , and T_R having independent biological justifications.

Finally, equality of T_a and $\bar{A}(v)$ tells us something about ancestral lineages. The time between two birth events in an ancestral lineage is the parents’ age at the later birth event. Thus, T_a is the unweighted average parent age at the birth events encountered on any ancestral lineage. We have seen that $\bar{A}(v)$ is average parent age when parents are weighted by average offspring reproductive value, which is proportional to the reproductive value of the parent. Thus, the ancestors of current individuals are a biased sample of past populations (as we would expect), where the bias is exactly proportional to state-dependent reproductive value.

Acknowledgments

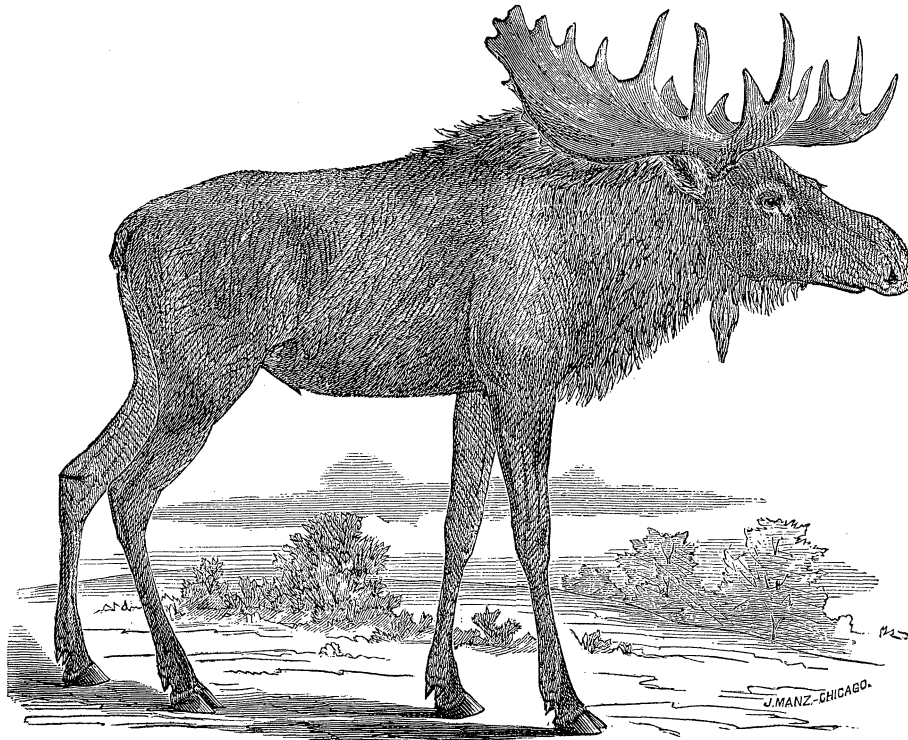
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“But, quite seriously, we would urge the double delight that all sportsmen and hunters may experience, if, instead of ending their interest in game with killing it, they would capture animals and birds, and study them.” From the review of Caton’s *Deer of America* (*The American Naturalist*, 1877, 11:354–358).