

The Moose of Isle Royale: An Unnatural Condition?

Samuel V. Scarpino^{1,+}, Rafael F. Guerrero², and Philip V. Scarpino³

¹Santa Fe Institute, Santa Fe, New Mexico, USA

²Department of Biology, Indiana University, Bloomington, IN, USA

³Department of History, Indiana University-Purdue University Indianapolis, Indianapolis, IN, USA

+address correspondence to scarpino@santafe.edu

Dead and dying moose were frequently found lying in the heavy snow along the lake shores from January until Spring.

-Paul F. Hickie, Isle Royale Moose Studies 1936

1 The now iconic moose of Isle Royale National Park arrived on the island sometime between
2 1910 and 1915 (Hickie, 1936; Murie, 1934). Prior to that period there is no evidence of moose
3 in either naturalist reports or in the archaeological history of the island (Murie, 1934; Scarpino,
4 2011). Early naturalists—while observing the moose during their first 20 years on the island—
5 noted both their dramatic expansion, and equally dramatic population crash in the 1930s, see
6 Figure 1. Around 1950, and just as the moose were rebounding, wolves crossed a frozen Lake
7 Superior and began what is now one of our most emblematic predator/prey systems (Peterson,
8 1995). Recently, the wolves on Isle Royale appear headed for local extinction (Mlot, 2015).
9 Calls to repopulate the island have renewed the vigorous debate surrounding what is and
10 what is not wild about Isle Royale (Scarpino, 2011; Cronon, 1996; Nelson & Callicott, 2008;
11 Cronon, 2003; Peterson, 1999).

12 Folklore surrounding the arrival of Isle Royale's moose speculated that they either swam or
13 crossed over the ice from mainland Canada (Murie, 1934). However, prior to the two-hundred
14 observed in 1915, no moose were recorded on the island and a detailed accounting of the fauna
15 on Isle Royale conducted during 1905 did not report any moose (Adams *et al.*, 1909). Given
16 the large numbers observed in 1915, the relatively narrow time-period in which they arrived,

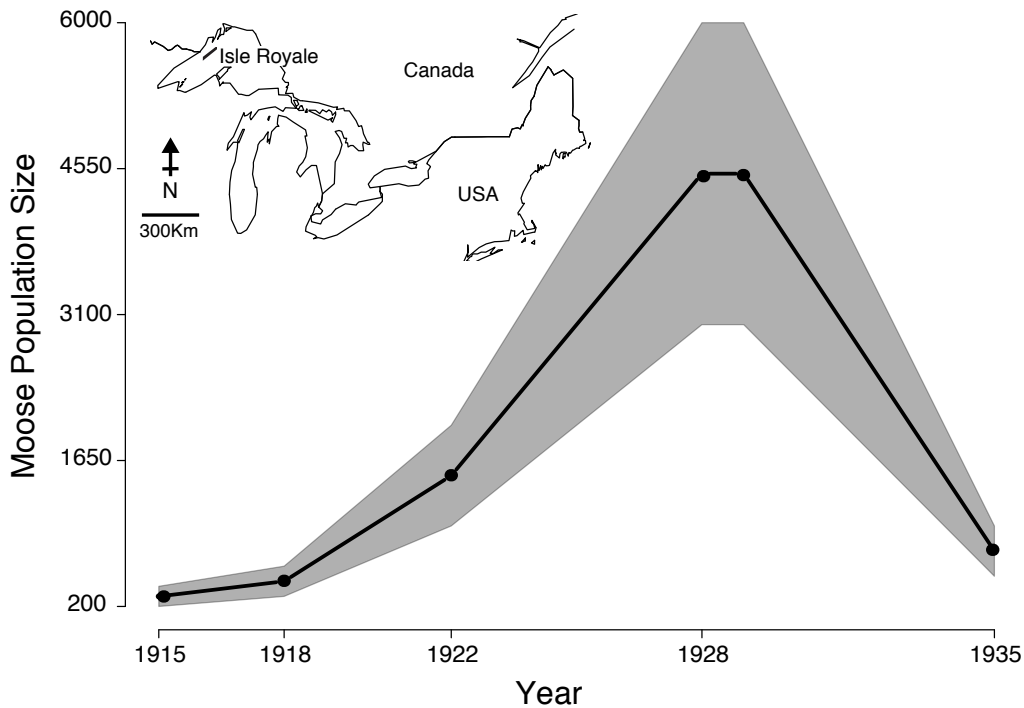


Figure 1. The early population dynamics of moose on Isle Royale. Estimates of moose population size were taken from early naturalist reports of Isle Royale (see map for the island’s location). The points indicate the average trend and the shaded region represents the reported discrepancy. The lower bound of the shaded region represents the actual value reported in the literature and were used for model fitting.

17 and that moose are solitary animals, e.g. in Minnesota their group sizes rarely exceed seven
18 individuals (Peek *et al.*, 1974), one might question the belief that they swam or walked on to
19 the island (Scarpino, 2011). In fact, the website for Isle Royale National Park now reports
20 that, “Cultural evidence has suggested that a private citizen’s group may have intentionally
21 stocked the moose onto the island for the purposes of recreational hunting (NPS, 2015).” To
22 better evaluate the competing hypotheses surrounding the moose’s arrival on Isle Royale, we
23 fit standard ecological models to data on moose population size from 1915 to 1929. With these
24 models, we estimated the most likely: 1) year of immigration; 2) founder population size; and
25 3) yearly population growth rate.

26 Our results suggest that for a logistic growth model, between 40 and 90 moose must have

27 arrived between 1913 and 1914 and subsequently grew at a yearly rate of 0.36–0.43, see
28 Figure 2a. Given that mainland moose near Isle Royale typically live in densities around two
29 moose per square mile (Peek *et al.*, 1971, 1974), this would require all of the moose in between
30 20 & 45 square miles to band together and travel to Isle Royale. The best-fit exponential
31 growth models required even larger founder population sizes (Figure 2b). Although our
32 estimated growth rate from the logistic model is nearly three times greater than post crash
33 estimates of moose population growth on Isle Royale, see (Messier, 1994), they are in line
34 with estimates of a reindeer population on St. Paul Island, Alaska, USA, which similarly
35 experienced an environment without competitors, predators, human hunting, and with nearly
36 unlimited resources (Scheffer, 1951).

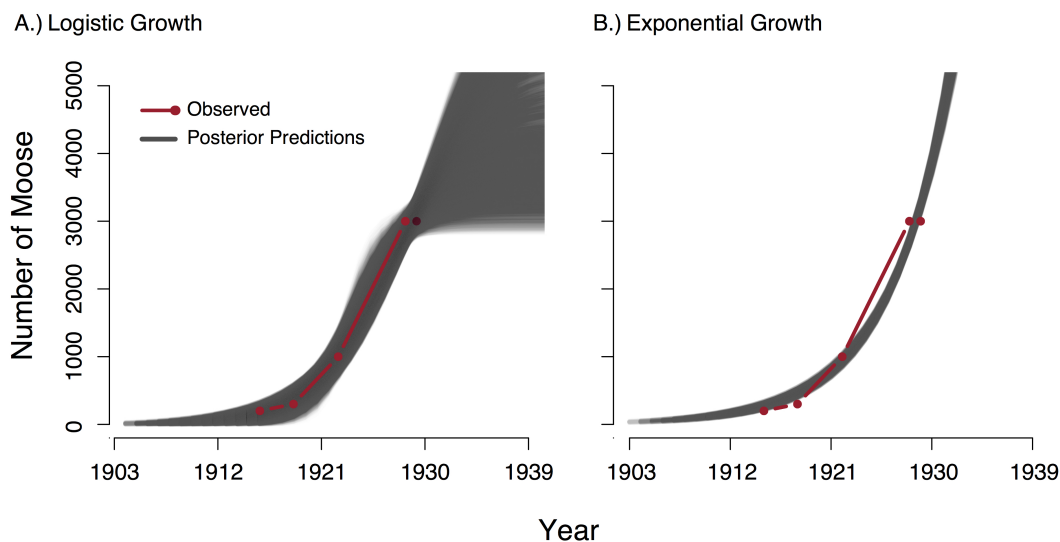


Figure 2. Best-fit growth models for the Isle Royale moose. All parameter sets that were within 6% absolute error were used to plot the moose's population trajectory (black lines) from: A.) the logistic growth model and b) the exponential growth mode. The observed data used for model fitting are in red.

37 The population fluctuations observed in the moose of Isle Royale are less dramatic than
38 those seen in the deer population crash on the Kaibab Plateau in Arizona, a crash that was
39 largely the result of United States Forest Service management practices (Binkley *et al.*, 2006).
40 In 1906, the population of deer on the Kaibab Plateau was only a few thousand, by 1921 it had

41 ballooned to over 100,000, and only a few later the deer were headed rapidly towards local
42 extinction. This population increase and crash resulted from the removal of biotic regulation
43 on deer populations; specifically, the interruption of natural fire cycles and the U.S. Forest
44 Service policy of predator reduction (Binkley *et al.*, 2006).

45 In *The Wolves of Isle Royale*, Rolf Peterson points out similarly problematic management
46 issues on Isle Royale: “Thus the NPS [National Park Service] policy of maintaining ‘native’
47 species cannot clearly guide us in our quandary. In an ironic blend of tradition and history,
48 one might argue that neither the wolf nor the moose are purely ‘native’ species at Isle Royale.”
49 Peterson continues his critique of the National Park Service’s non-interventionist policy,
50 stating, “Passive observation, can be an easy policy that doesn’t require much expense or
51 ecological understanding; perhaps that explains some of its appeal. But our national parks
52 deserve better than rote adherence to tradition.”

53 Our results provide insight into the early dynamics of the moose population on Isle
54 Royale and represent one of the only estimates of large ungulate population growth in the ab-
55 sence of biotic regulation. Clearly, more population modeling—in combination with population
56 genomic studies of mainland and island moose—would provide greater insight into the origin
57 of Isle Royale’s moose. However, when coupled with the emerging cultural evidence, we must
58 conclude that the moose on Isle Royale may have been introduced by humans. If true, we
59 encourage the National Park Service to re-evaluate its decision not to intervene and save the
60 wolves, and also how they value all of the human cultural resources in our Park system.

61 **Acknowledgements**

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63 **Methods, Data, and Posteriors**

64 **Models and Inference**

65 When populations are self-limiting, their dynamics can be modeled using logistic growth equa-
66 tions. When considering only a single-species, the following differential equation completely
67 describes its population growth over time t :

$$\frac{dP}{dt} = rP\left(1 - \frac{P}{K}\right)$$

68 where P is the population size, r is growth rate, and K is the maximum sustainable
69 population size, i.e. the carrying capacity.

The solution for the population size P after a certain amount of time t , $P(t)$, with an initial condition that at time $t = 0$ the population had P_0 individuals is:

$$P(t) = \frac{KP_0e^{rt}}{K + P_0(e^{rt} - 1)}$$

70 For exponential growth, i.e. growth without a carrying capacity, the corresponding equation
71 for the population size as a function of elapsed time is:

$$P(t) = P_0(1 + r)^t$$

72 We estimated the parameters of both models from data using a non-linear least squares
73 algorithm coded in the R programming language (R Core Team, 2015). To better explore the
74 uncertainty around these estimated values, we performed Approximate Bayesian Computation
75 using broad, uniform priors over all parameters (Beaumont *et al.*, 2002). Both models were fit
76 to the lower bound on the observed moose population size, clearly a conservative assumption
77 with regard to our conclusions.

78 **Data**

79 Data were taken from early naturalist reports on Isle Royale as summarized in Paul F. Hickie's
80 1934 manuscript, "Isle Royale moose studies," see Table 1.

Year	Observed Number of Moose
1915	200
1918	300
1922	1000
1928	3000–5000
1929	3000–5000
1935	200–500

Table 1. Observed Numbers of moose on Isle Royale 1915 - 1935 as reported in (Hickie, 1936)

81 **Posteriors**

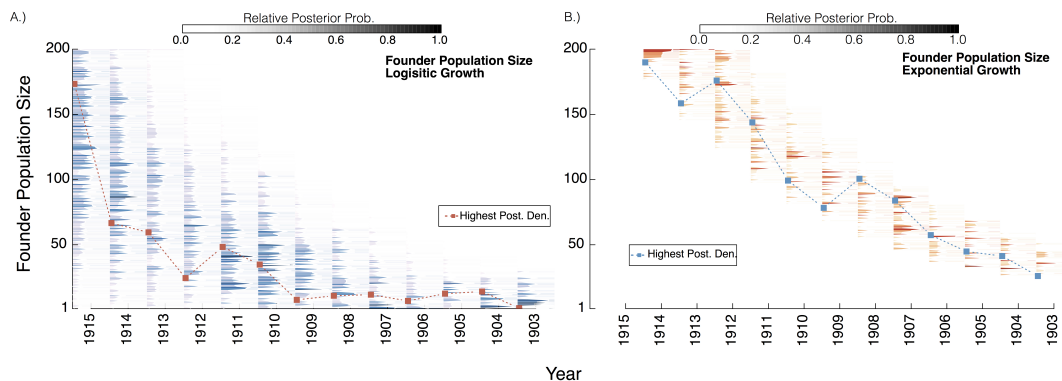


Figure 3. Posterior distribution of the founder population size. The posterior distribution of founder population size is plotted as a function of immigration year for: A.) the logistic growth model and B.) the exponential growth model. All parameters producing fits with 6% absolute error or less were retained, with darker colors indicating progressively better fits.

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