

Michael G. Loso · Daniel F. Doak

## The biology behind lichenometric dating curves

Received: 14 March 2005 / Accepted: 1 September 2005 / Published online: 20 October 2005  
© Springer-Verlag 2005

**Abstract** Lichenometry is used to date late-Holocene terminal moraines that record glacier fluctuations. Traditionally, it relies upon dating curves that relate diameters of the largest lichens in a population to surface ages. Although widely used, the technique remains controversial, in part because lichen biology is poorly understood. We use size-frequency distributions of lichens growing on well-dated surfaces to fit demographic models for *Rhizocarpon geographicum* and *Pseudophebe pubescens*, two species commonly used for lichenometry. We show that both species suffer from substantial mortality of 2–3% per year, and grow slowest when young—trends that explain a long-standing contradiction between the literatures of lichenometry and lichen biology. Lichenometrists interpret the shape of typical dating curves to indicate a period of rapid juvenile “great growth,” contrary to the growth patterns expected by biologists. With a simulation, we show how the “great growth” pattern can be explained by mortality alone, which ensures that early colonists are rarely found on the oldest surfaces. The consistency of our model predictions with biological theory and observations, and with dozens of lichenometric calibration curves from around the world, suggests opportunities to assess quantitatively the accuracy and utility of this common dating technique.

**Keywords** Alaska · Lichen biology · Lichenometry · *Pseudophebe pubescens* · *Rhizocarpon geographicum*

### Introduction

Lichens dominate many early successional environments, yet their population dynamics remain a mystery. In laboratories, biologists have made progress towards understanding the basic physiology of some species, but field studies are challenged by slow growth rates, by the resemblance of dead lichens to living ones, and by the difficulty of documenting colonization by sexual or asexual propagules. This is particularly true in recently deglaciated terrain, where cold, dry conditions limit lichen growth rates to the order of millimeters per decade, but also where lichen ecology is of pressing importance for geologists practicing lichenometry, a dating technique that uses lichen measurements to provide minimum ages for geomorphic landforms (e.g., Innes 1985; Noller and Locke 2000).

Because it is one of the only techniques suitable for dating moraines that record late-Holocene glacier fluctuations, lichenometry is increasingly used in research projects that document past and contemporary climate change. The inferred rates at which landscapes respond, both biologically and physically, to these climatic changes are hence dependent upon the accuracy and precision of lichenometric dates. Despite the technique’s broad usage, however, lichenometry remains statistically suspect, hampered by the persistent uncertainties about basic lichen demography and undermining confidence in the inferred relationships among climate change, glacier behavior, and biological succession.

As traditionally practiced, lichenometry relies upon calibrated dating curves that relate diameters of the largest—and presumably oldest—lichens in a series of populations with the known ages of surfaces where those populations reside (examples include gravestones, stone buildings and bridges, and independently-dated glacier moraines). Lichenometric dating curves commonly

Communicated by Jim Ehleringer

M. G. Loso (✉)  
Department of Earth Sciences, University of California,  
Santa Cruz, CA 95062, USA  
E-mail: mloso@alaskapacific.edu  
Tel.: +1-907-3340970  
Fax: +1-907-5624276

*Present address:* M. G. Loso  
Department of Environmental Science, Alaska Pacific University,  
Anchorage, AK 99508, USA

D. F. Doak  
Department of Ecology and Evolutionary Biology,  
University of California, Santa Cruz, CA 95062, USA

assume a predictable shape: the slope of largest lichen size versus surface age is initially steep and decreases over time. The interpretation of this shape is disputed (Aplin and Hill 1979; Clayden et al. 2004). Lichenometrists call the steep portion of such curves the period of “great growth” (Beschel 1973; Bull and Brandon 1998; Karlén and Black 2002), implicitly asserting that these calibration curves reflect highest radial growth rates in the smallest lichens. Lichen biologists, however, argue on both theoretical (Childress and Keller 1980) and experimental (Armstrong 1976; Proctor 1977; Hill 1981; Clark et al. 2000) grounds that growth rates of individual lichens should be lowest in small thalli, increasing asymptotically towards a more or less constant rate as the curvature of the thallus rim diminishes. That the debate persists illustrates our generally poor understanding of the biological processes that govern lichen population dynamics, that give rise to lichenometric data, and that are necessary to understand before we can quantify errors associated with the technique.

Generally, practitioners of lichenometry use only the largest lichens to measure surface ages. Here, we argue that the sizes of these largest lichens, and especially the probabilities of finding them, are functions of the size frequency distribution of a population. The shape of that distribution is determined not only by individual growth rates, but also by rates of colonization and survival. These rates, and their variability, are driven by biological processes that are poorly known and thus typically ignored, as demonstrated by the persistent misinterpretation of lichen calibration curves as simple time-integrals of growth rate. In this sense, the debate over great growth reflects a deeper failure to consider the biological processes that govern lichen population dynamics, give rise to lichenometric data, and are necessary to quantify errors associated with the technique’s assumptions and its application. Others have noted the need for incorporation of biological reality into lichenometric dating techniques (Innes 1985; McCarthy 1999), but to date few geologists or biologists have estimated even basic rates of recruitment or mortality.

To address this gap in our understanding, we measured thousands of lichen thalli to generate full population size–frequency distributions for two lichen species growing on a series of well-dated surfaces. Treating the distribution from each surface as a snapshot of the development of a single population, we then use maximum likelihood techniques to determine best-fitting colonization, growth, and survival rules. The model fitting techniques we employ have not been used by lichen biologists before, but they were designed to yield robust inferences about the dynamics and life histories of difficult to study species (Doak and Morris 1999; Monson et al. 2000). This approach to studying lichen population dynamics has the particular advantage of relying upon size–frequency distributions, which are more readily obtainable from the cryptic, slow-growing lichen species favored by lichenometrists than are direct measurements of colonization growth, or survival.

## Methods

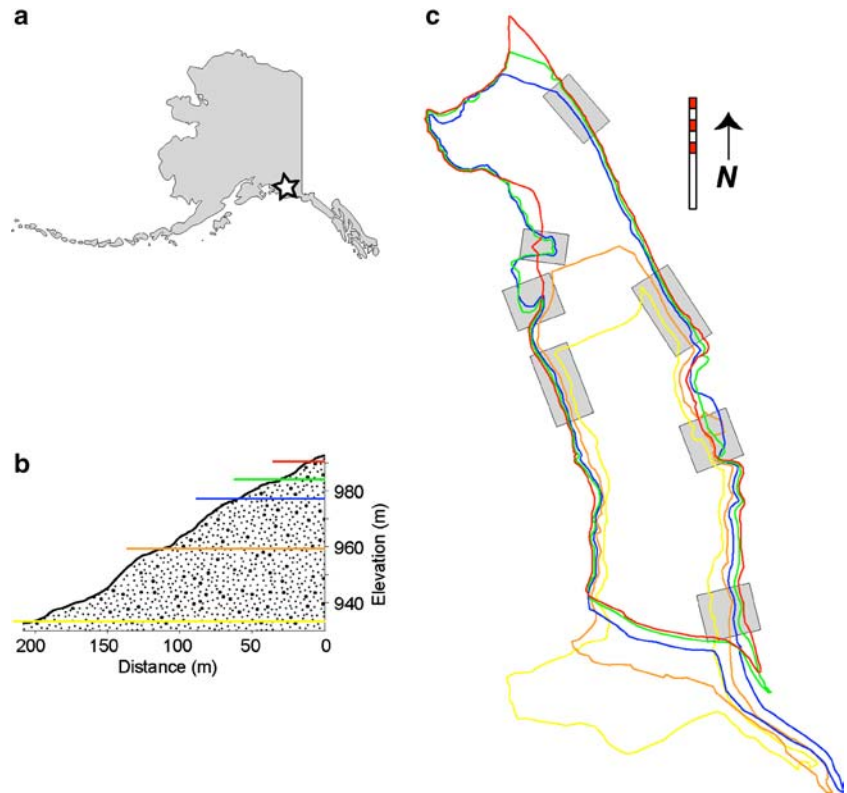
In the summers of 2002 and 2003, we measured lichens growing on unshaded upper surfaces (slopes  $< 20^\circ$ ) of stable granitic and gneissic boulders (rocks with major axis  $> 15$  cm) exposed by episodic shoreline regression at Iceberg Lake, an ice-dammed lake in the eastern Chugach Mountains of Alaska (Fig. 1). At each sampling site, surface age was equated with abandonment age of the next higher shoreline; ages of these shorelines ( $\pm 5$  year) were previously determined from stratigraphy of annually varved lacustrine sediments (Loso et al. 2004), independently verified by  $^{14}\text{C}$  and  $^{137}\text{Cs}$ . These dated events allowed us to group the lichens into four distinct populations with exposure ages ranging from 45 to 177 years old.

We measured diameters of all individuals encountered (not just the largest) of two species: *Rhizocarpon geographicum* (L.) DC., the slow growing, long-lived, and widely distributed saxicolous crustose lichens used most commonly for lichenometric dating, and *Pseudophebe pubescens* (L.) Choisy, a prostrate fruticose lichen that grows faster and more abundantly at Iceberg Lake than *R. geographicum*. Major and minor axes of sampled boulder and bedrock surfaces were measured to the nearest centimeter, and major axes of all lichens  $> 1$  mm were measured with digital calipers to the nearest 0.1 mm. We never measured lichens growing in contact with other lichens of the same species, but thallus density was generally low on the surfaces we examined and intraspecific competition was therefore assumed to be minimal. On four surfaces of ages  $t$  (where  $t_{1-4}$  are the surface ages dictated by shoreline abandonment dates, [45, 135, 168, 177] years), the total numbers of thalli measured ( $n_{1-4}$ ) were [185, 703, 348, 439] for *R. geographicum* and [269, 891, 1,100, 1,059] for *P. pubescens*. Total sampled areas ( $a_{1-4}$ ) were [151, 48, 22, 29]  $\text{m}^2$ .

For analysis and modeling, we combined *R. geographicum* data in 2 mm size classes and *P. pubescens* data in 4 mm size classes. In all populations of both species, we found very few individual lichens in the smallest size class. We attribute this rarity to undercounting of extremely small thalli. Therefore, although the model adds new colonists as “infants” with a diameter of 0.1 mm, we ignored the smallest size class when fitting model results to the data. Following Calkin and Ellis (1980), we also excluded from the analysis eight anomalous individuals that were  $> 20\%$  larger than the next largest thallus in their respective populations. We assume these thalli grew on boulders washed in from higher (older) surrounding surfaces, a presumption partially corroborated by the observation that three of these eight grew on the same boulder.

We developed and tested multiple demographic models to explain observed trends in population structure. Simulating lichen colonization, growth, and mortality in annual timesteps, each model run produced five multinomial probability distributions: the distribution of

**Fig. 1** Map of study site showing paleoshorelines of Iceberg Lake, Alaska. **a** Shows location within Alaska (*star*). Shorelines are shown in typical profile view (**b**), and in map view (**c**). Oldest shoreline (*red polygon*) was abandoned in 1825 AD. Subsequent lake lowering events abandoned shorelines in 1834 (*green*), 1867 (*blue*), 1957 (*orange*), and 1999 AD (*yellow*). Surface/population ages of lichen sampling sites (*shaded rectangles*) were assumed to equal the abandonment age of the immediately adjacent upslope paleoshoreline. Scale bar for map is 1 km long



lichen sizes among size classes  $i$  at each of four time intervals  $t$ , and the distribution of total population sizes among time intervals  $t$ . Because the model does not track population density explicitly, the latter distribution compared temporal patterns of relative population size between the model and the data. Predicted population sizes were adjusted to account for unequal sampling efforts among the four real populations. For each function tested, best-fitting parameters were selected to minimize the relative negative log-likelihood (NLL) of the model, given the data,

$$\text{NLL} = -\sum_{t=1}^4 \sum_{i=1}^{\max} y_{t,i} \ln(\psi_{t,i}) - \sum_{t=1}^4 n_t \ln(v_t a_t)$$

where  $y_{t,i}$  are numbers of lichens in size class  $i$  at time interval  $t$ ,  $\psi_{t,i}$  are modeled probabilities for each class and time,  $n_t$  are the total population size at a given interval,  $v_t$  are modeled probabilities of population size, and  $a_t$  are sampling areas. For each set of parameters, we used one-dimensional likelihood profiles to calculate confidence limits (Hilborn and Mangel 1997).

We used the Akaike information criterion (AIC) and associated AIC weights to select the best-supported functional forms (Burnham and Anderson 2002). In the first round of testing, each vital rate was fit by a logistic function of a single independent variable: colonization by population size, and growth and survival by thallus size. In these models, the function

$$\text{rate} = c \frac{\exp(fn)}{1 + \exp(fn)}$$

was used, where  $c$  is a constant and  $fn$  is either a linear or quadratic function of the independent variable. The logistic function was used first because it is very flexible, and thus prevented us from dictating a priori the general shape of the function. As the preferred general shape of each function emerged, we next tested additional non-logistic functions that used the same independent variables. AIC weights dictated the most parsimonious model; that is, the one that best-fit the data with the fewest fitted parameters. In a final round of testing, we added additional independent variables to the previously selected functional forms, but found no marginal improvement in model fit.

## Results

Trends in the measured size–frequency distributions of both species (Fig. 2) are consistent with those found in other studies (Benedict 1967; Lindsay 1973; Innes 1983). The oldest surfaces have the largest lichens, as expected, although there is a significant absolute difference in size between the two species: *R. geographicum* reaches a maximum diameter (on the oldest surface) of  $\sim 26$  mm, while in the same area *P. pubescens* grows to a larger maximum diameter of  $\sim 102$  mm. Qualitatively, the distributions of both species exhibit similar trends. Relatively small lichens dominate surfaces of all ages, including the oldest, and large lichens are always rare. Population densities of both species (normalized to account for differing sample sizes, Fig. 2) increase from the youngest to the 168 year old surface, but decline slightly on the oldest surface.

To infer the demographic processes responsible for these measured distributions, we independently tested hundreds of possible models for each species. Of the models tested, functional forms of the best ten models for each species are shown in Table 1; these top ten models garner greater than 99% of all AIC support (Burnham and Anderson 2002). The best-supported models are fairly simple, with the best models tested requiring only six and four fitted parameters for *R. geographicum* and *P. pubescens*, respectively (Table 2). For both species, these models explain survival and growth rates as functions of individual thallus size and explain colonization (we do not distinguish between sexual and asexual reproduction) as a function of existing population size.

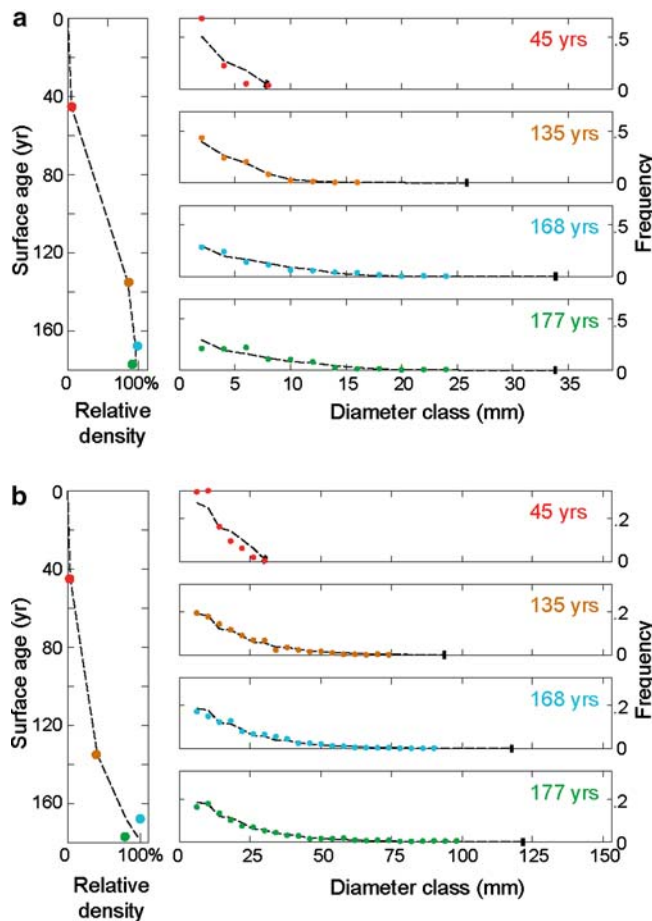
The simplest and most robust prediction of the best-fit models is that both species undergo steady mortality of a few percent per year (Table 2). For the size–frequency distributions we observed, AIC weights provide

virtually no support for any model that excludes lichen mortality. Equally importantly, the survival rates (1–mortality) predicted by our favored models are steady through time and tightly constrained. The annual survival probabilities, with 95% confidence intervals from a likelihood ratio test, are  $0.967 \pm 0.001$  for *R. geographicum* and  $0.979 \pm 0.003$  for *P. pubescens*. The cumulative probability of any single thallus living beyond ~200 years is consequently quite low (*P. pubescens* < 2%, *R. geographicum* < 1%; Fig. 3c). In the case of *R. geographicum*, the model-fitting process provides substantial support (0.240, compared with 0.655 for the best model; Table 1) for an alternate model that differs from the favored model primarily in its treatment of mortality. This second-best model has survival rates increasing slightly with lichen size (not plotted, but beginning at 0.955 for small lichens and approaching 0.990 at the size, by extrapolation, of a 300 year old thallus-model), but the cumulative survival probability (after 200 years) remains < 1%.

Maximum growth rates are broadly consistent with those found by other investigators in Alaska (Denton and Karlén 1973; Miller 1973): 0.21 mm/year for *R. geographicum* and 0.72 mm/year for *P. pubescens* (Table 2). More importantly, the favored models for both species reveal growth rates that are lowest in the smallest thalli, increasing rapidly towards a steady maximum rate that is attained while the individual thallus is still quite small: 2–3 mm diameter (Fig. 3b). This result, although chosen by a model-fitting process that made no a priori assumptions about growth patterns or rates, is precisely the one expected by lichen biologists (Childress and Keller 1980).

The most significant functional difference between the models of the two species lies in the function used to describe temporal patterns of colonization rates (Table 2). A three-parameter logistic function models *R. geographicum* colonization rates as increasing rapidly before diminishing slightly with increasing population size at the end of the model run (Fig. 3a). In contrast, a one-parameter inverse negative exponential function has *P. pubescens* colonization increasing more gradually and still climbing when the model run ends at 185 years. There is another difference in colonization between the two species, readily apparent in the field. *P. pubescens* thalli are two to four times more common than *R. geographicum* on surfaces of all ages, demonstrating a significant difference in their absolute colonization rates. Still, the best-fit colonization functions imply that both species share one important demographic feature—a dependence of colonization rate upon preexisting population size, which ensures that the earliest colonization is very slow and hence easily mistaken for a colonization “lag” after exposure of a new surface.

Conspicuously, these models provide no support for a period of juvenile great growth. With a simple numerical experiment, we tested a possible alternative explanation for the common shape of lichenometric calibration curves. We used the best-fit model to simu-



**Fig. 2** Data and model results for both lichen species. For **a** *R. geographicum*, and **b** *P. pubescens*, the panel at right shows size–frequency distributions on surfaces of four known ages, and the panel at left shows evolution of population density over time. Density is normalized so that the highest density observed equals 100%. In both plots, colored dots are binned data measured at Iceberg Lake, and dashed lines are simulation results based upon the best-fitting demographic model. Black rectangle shows the size class of the largest simulated lichen for each population

**Table 1** Best supported functional forms used in models of demography for *R. geographicum* (above) and *P. pubescens* (below)

Colonization <sup>c</sup>	Survival <sup>d</sup>	Growth <sup>e</sup>	$k^a$	NLL <sup>b</sup>	AIC	$\Delta$ AIC	AIC weight
log 2	C	-1/exp	6	4278.39	8568.78	0.00	0.655
log 2	log	-1/exp	7	4278.40	8570.79	2.01	0.240
log 2	C	C	5	4281.30	8572.60	3.82	0.097
log 2	S-log	-1/exp	8	4281.04	8578.07	9.29	0.006
log	C	-1/exp	5	4285.51	8581.01	12.23	0.001
log	C	C	4	4287.76	8583.51	14.73	0.000
log	S-log	-1/exp	7	4286.88	8587.76	18.98	0.000
-1/exp	C	C	3	4323.26	8652.52	83.74	0.000
-1/exp	S-log	-1/exp	6	4322.38	8656.76	87.97	0.000
-1/exp	C	-1/exp	4	4328.86	8665.72	96.94	0.000
-1/exp	C	-1/exp	4	10354.34	20716.67	0.00	0.919
-1/exp	log	-1/exp	5	10356.40	20722.80	6.13	0.043
-1/exp	C	C	3	10358.83	20723.66	6.99	0.028
-1/exp	S-log	-1/exp	6	10356.81	20725.62	8.95	0.010
log 2	C	-1/exp	6	10396.72	20805.43	88.76	0.000
log 2	C	C	5	10399.90	20809.79	93.12	0.000
log	C	C	4	10412.47	20832.95	116.27	0.000
log	S-log	-1/exp	7	10419.84	20853.67	137.00	0.000
-1/exp	log 2	-1/exp	6	10428.80	20869.59	152.92	0.000
-1/exp	0M	C	2	10485.55	20975.10	258.43	0.000

<sup>a</sup> $k$  is the number of fitted parameters

<sup>b</sup>Measures of model support include negative log-likelihood (NLL), Akaike information criterion (AIC), differences between each model and the best-fit model ( $\Delta$ AIC), and AIC weights

<sup>c</sup>Colonization rules: *-1/exp* negative inverse exponential on population size, *log* logistic on linear population size, *log 2* logistic on quadratic population size

<sup>d</sup>Survival rules: *C* fitted constant, *log* logistic on linear thallus diameter, *log 2* logistic on quadratic thallus diameter, *S-log* logistic on linear thallus diameter scaled to prevent immortality, *0M* no mortality

<sup>e</sup>Growth rules: *C* fitted constant; *-1/exp* negative inverse exponential on thallus diameter

late development of large lichen populations, and then sampled 100, 1,000, and 10,000 individuals from these populations (to represent different levels of search effort) at 10-year intervals (to represent differing surface ages). The entire simulation was repeated 1,000 times, and the average largest lichen size is plotted as a function of surface age. For the three levels of search effort, the simulations represent lichenometric calibration curves constructed by increasingly industrious lichenometrists (Fig. 3d). As surface age increases, a similar result is predicted for both species: all three curves fall off from what we would expect to find if we sampled an infinite number of lichen and hence always found a lichen that colonized in the first year of surface exposure and never died. Slow initial colonization and ongoing mortality ensure that this will rarely happen. Instead, large lichens

are rare, become rarer through time, and hence are rarely found. As noted by others (Innes 1984; McCarroll 1994), search effort has a strong influence on the result, with larger samples yielding larger “largest lichens.” Even the largest sample sizes, however, yield a typical great growth type curve that is a function of the interaction of mortality and sampling efficiency, rather than of real lichen growth rates or patterns.

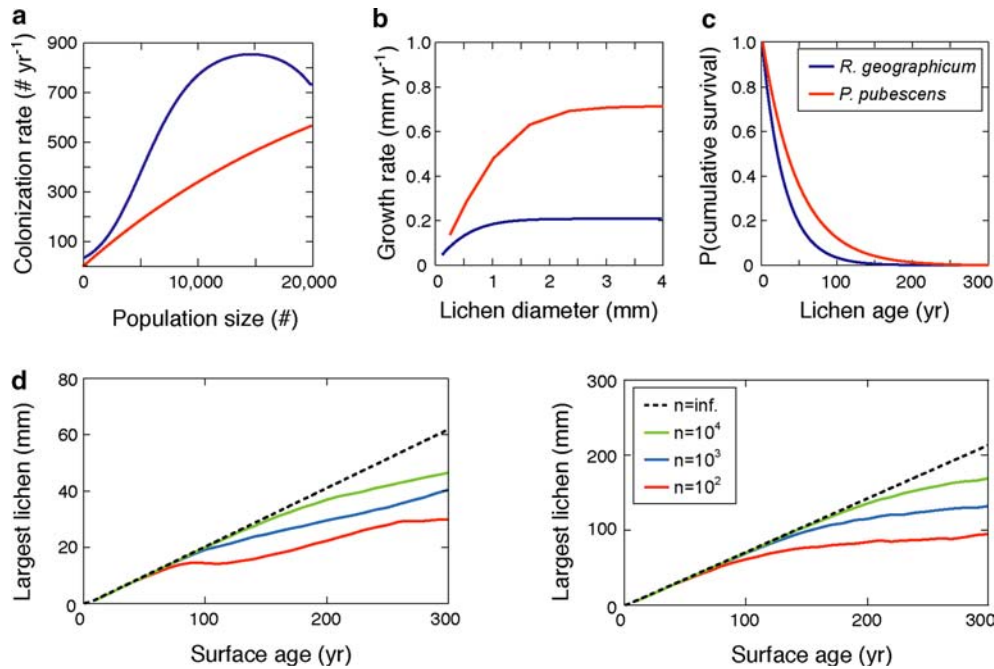
## Discussion

It is encouraging that two independent model-fitting processes, using separate datasets, converge upon simi-

**Table 2** Fitted parameters of the best demographic models

Structure	<i>R. geographicum</i>	<i>P. pubescens</i>
Colonization	$1,000 \times \left[ \frac{\exp(a_1 + a_2 n - a_3 n^2)}{1 + \exp(a_1 + a_2 n - a_3 n^2)} \right]$	$1,000 \times \left[ 1 - \exp\left(\frac{-n}{a_1}\right) \right]$
Growth	$a_4 \times \left[ 1 - \exp\left(\frac{-d}{a_5}\right) \right]$	$a_2 \times \left[ 1 - \exp\left(\frac{-d}{a_3}\right) \right]$
Survival	$a_6$	$a_4$
Parameters	<i>R. geographicum</i>	<i>P. pubescens</i>
$a_1$	-3.35	23,917
$a_2$	0.00075	0.7148
$a_3$	-0.000000027	0.4667
$a_4$	0.2084	0.9790
$a_5$	0.4000	-
$a_6$	0.9665	-

Fitted parameters  $a_1$ : $a_k$ ,  $n$  population size,  $d$  thallus diameter (mm)



**Fig. 3** The biology behind lichenometric dating curves. **a–c** Rates of colonization, growth, and cumulative survival estimated for *R. geographicum* (blue lines) and *P. pubescens* (red lines) populations at Iceberg Lake. Note that growth rates of both species (**b**) are lowest in the smallest lichens, as biologists predict. **d** The expected result, from many simulations, if a lichenometrist randomly sampled the population described by this demography and plotted the largest lichen found on surfaces of increasing age. Simulation

results for *R. geographicum* at left, *P. pubescens* at right. Dotted black line shows the largest possible thallus in an infinitely large sample. Mortality ensures that large lichens are extremely rare on old surfaces, so in practice the largest lichen increasingly falls off from this theoretical maximum as sample size decreases, giving rise to the “great growth” pattern found in most lichenometric dating curves

lar results. The two lichen species we studied share demographic patterns that include mortality of a few percent per year, maximum growth rates that are attained after a period of slow juvenile growth, and colonization rates that increase rapidly in response to growth of the initially small population. We do not argue that the life histories of *R. geographicum* and *P. pubescens* are identical, nor that they are the same everywhere in their circumboreal distributions. But the similar, biologically-defensible rules that emerged from our independent analyses of the size-frequency distributions of these two cryptic lichen species suggest that the population dynamics of lichens may not be as anomalous as often assumed.

Like most other organisms, mortality plays a significant role in shaping even the youngest lichen populations. This is not as obvious as it may first appear, in part because lichen mortality is rarely observed: dead lichens are difficult, for the casual observer, to distinguish from physiologically dormant ones. More importantly, crustose lichens like *R. geographicum* are known and valued by lichenometrists for their long maximum lifespans, which have been inferred (on the basis of lichen size) to reach several thousands of years (Denton and Karlén 1973; Savoskul and Zech 1997). This seemingly indefinite lifespan has been used by some researchers to justify the assumption that mortality is thus irrelevant (Topham 1977; Innes 1983). But while

these lichens may indeed be capable of very long lives, our analysis shows that they are always at substantial risk of mortality (more than 1% per year). In other words, these lichens can grow very old, but only if they are repeatedly lucky enough to escape the extreme weather events, diseases, overturned rocks, and other unknown factors that make the largest, oldest lichens relatively uncommon.

The lichen populations commonly used in lichenometric studies consequently have important dynamical behavior, with fairly rapid population turnover and substantial reductions in the initial cohorts that are targeted by traditional lichenometry. This suggests a new interpretation of lichenometric calibration curves. Their convex upward shape is typically understood as evidence for a gradual reduction in growth rate after some period of “great growth.” Instead, we argue that on progressively older surfaces, the initial colonists are increasingly rare, diminishing the probability that the largest lichen found by a lichenometrist will actually be a member of that initial cohort. This argument emerges directly from our results, and is consistent not only with dozens of lichenometric calibration curves from around the world, but also with experimental data and biological theory.

For the still-numerous practitioners of lichenometry, this provides an immediate opportunity: the ability to bracket lichenometric dates with confidence intervals.

The probability of finding a given largest lichen is dependent upon patterns and rates of colonization, growth, and survival, and also, importantly, on sample size. We have shown that modestly-sized datasets can be combined with simple models to estimate these parameters. Application of these techniques to larger, more diverse datasets will improve lichenometric dating and, equally important, will provide greater insights into the basic biology of these important organisms, including interspecific differences, vital rate variability, and late lifespan behaviors.

**Acknowledgements** We acknowledge with thanks the partial support from the National Science Foundation, the Geological Society of America, and the Lawrence Livermore National Laboratory. Thanks to R. Anderson, S. Anderson, M. Booth, J. Jolliffe, K. Smith, G. Stock, D. Thompson, and Rusty for their field assistance. Logistical and technical support was kindly provided by the Limnological Research Center, St. Croix Watershed Research Station, LLNL CAMS facility, UNAVCO, VECO, Wrangell Mountain Air, Wrangell Mountains Center, and Wrangell-St. Elias National Park. All research described in this paper was done in compliance with the laws of the United States and the state of Alaska.

## References

- Aplin PS, Hill DJ (1979) Growth analysis of circular lichen thalli. *J Theor Biol* 78:347–363
- Armstrong RA (1976) Studies on the growth rates of lichens. In: Brown DH, Hawksworth DL, Bailey RH (eds) *Lichenology: progress and problems*. Academic, London
- Benedict JB (1967) Recent glacial history of an alpine area in the Colorado front range, USA. 1. Establishing a lichen growth curve. *J Glaciol* 6:817–832
- Beschel RE (1973) Lichens as a measure of the age of recent moraines. *Arctic Alpine Res* 5:303–309
- Bull WB, Brandon MT (1998) Lichen dating of earthquake-generated regional rockfall events, Southern Alps, New Zealand. *Geol Soc Am Bull* 110:60–84
- Burnham KP, Anderson DR (2002) *Model selection and multi-model inference: a practical information-theoretic approach*. Springer, Berlin Heidelberg New York
- Calkin PE, Ellis JM (1980) A lichenometric dating curve and its application to Holocene glacier studies in the Central Brooks Range, Alaska, USA. *Arctic Alpine Res* 12:245–264
- Childress S, Keller JB (1980) Lichen growth. *J Theor Biol* 82:157–165
- Clark BM, Mangelson NF, St. Clair LL, Rees LB, Bench G, Southon JR (2000) Measurement of age and growth rate in the crustose saxicolous lichen *Caloplaca trachyphylla* using  $^{14}\text{C}$  accelerator mass spectrometry. *Lichenologist* 32:399–403
- Clayden SR, Pentecost A, Dawson RJM (2004) Growth of the lichen *Rhizocarpon lecanorinum*, with comments on Aplin-Hill and lichenometric curves. *Symbiosis* 37:379–394
- Denton GH, Karlén W (1973) Lichenometry: its application to Holocene moraine studies in southern Alaska and Swedish Lapland. *Arctic Alpine Res* 5:347–373
- Doak DF, Morris WF (1999) Detecting population-level consequences of ongoing environmental change without long-term monitoring. *Ecology* 80:1537–1551
- Hilborn R, Mangel M (1997) *The ecological detective: confronting models with data*. Princeton University Press, Princeton
- Hill DJ (1981) The growth of lichens with special reference to the modeling of circular thalli. *Lichenologist* 13:265–287
- Innes JL (1983) Size frequency distributions as a lichenometric technique: an assessment. *Arctic Alpine Res* 15:285–294
- Innes JL (1984) The optimal sample size in lichenometric studies. *Arctic Alpine Res* 16:233–244
- Innes JL (1985) Lichenometry. *Prog Phys Geogr* 9:187–254
- Karlén W, Black J (2002) Estimates of lichen growth-rate in northern Sweden. *Geogr Ann* 84:225–232
- Lindsay DC (1973) Estimates of lichen growth rates in the maritime Antarctic. *Arctic Alpine Res* 5:341–346
- Loso MG, Anderson RS, Anderson SP (2004) Post-Little Ice Age record of coarse and fine clastic sedimentation in an Alaskan proglacial lake. *Geology* 32:1065–1068
- McCarroll D (1994) A new approach to lichenometry: dating single-age and diachronous surfaces. *Holocene* 4:383–396
- McCarthy DP (1999) A biological basis for lichenometry? *J Biogeogr* 26:379–386
- Miller GH (1973) Variations in lichen growth from direct measurements: preliminary curves for *Alectoria miniscula* from eastern Baffin Island, N.W.T., Canada. *Arctic Alpine Res* 5:333–339
- Monson DH, Doak DF, Ballachey BE, Johnson A, Bodkin JL (2000) Long term impacts of the Exxon Valdez oil spill on sea otters, assessed through age-dependent mortality patterns. *Proc Natl Acad Sci* 97:6562–6567
- Noller JS, Locke WWI (2000) Lichenometry. In: Noller JS, Sowers JM, Lettis WR (eds) *Quaternary geochronology: methods and applications*. American Geophysical Union, Washington DC, pp 261–272
- Proctor MCF (1977) The growth curve of the crustose lichen *Buellia canescens* (Dicks.) De Not. *New Phytol* 79:659–663
- Savoskul OS, Zech W (1997) Holocene glacier advances in the Topolovaya Valley, Bystrinskiy Range, Kamchatka, Russia, dated by tephrochronology and lichenometry. *Arctic Alpine Res* 29:143–155
- Topham PB (1977) Colonization, growth, succession and competition. In: Seaward MRD (eds) *Lichen ecology*. Academic, London, pp 31–68