Rolling stones gather moss: Movement and longevity of moss balls on an Alaskan glacier

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Abstract:

Glaciers support diverse ecosystems that are largely comprised of microbial life. However, at larger, macroscopic scales, glacier moss balls (sometimes called “glacier mice”) develop from impurities in the ice and represent a relatively rare biological phenomenon. These ovoid-shaped conglomerations of dirt and moss are only found on some glacier surfaces and provide key habitats for invertebrate colonization. Yet, despite their development and presence being widely reported, no targeted studies of their movement and longevity have been conducted. This knowledge gap is particularly important when considering the degree to which glacier moss balls may represent viable, long-term biotic habitats on glaciers, perhaps complete with their own ecological succession dynamics. Here, we describe the movement and longevity of glacier moss balls on the Root Glacier in southcentral Alaska, USA. We show that glacier moss balls move an average of 2.5 cm per day in herd-like fashion, and their movements are positively correlated with glacier ablation. Surprisingly, the dominant moss ball movement direction does not align with the prevailing wind nor downslope directions; instead, we propose that it depends on the dominant direction of solar radiation. We also show that glacier moss balls are relatively long-lived, with a lifespan in excess of 6 years and annual survival rates similar to large vertebrates. Finally, we observed moss ball formation on the Root Glacier to occur within a narrow, low albedo stripe downwind of a nunatuk, a potential key source of moss spores and/or fine-grained sediment that interact to promote their formation.

Keywords: cryobiology, glacier mice, glacier biology, jokla-mys, Root Glacier, Wrangell-St. Elias National Park

Introduction:

Glaciers have long been overlooked as important components of global biodiversity, but it is now clear that they host thriving, multi-trophic ecosystems (Anesio and Laybourn-Parry 2012), supporting taxa from microbes to vertebrates (Rosvold 2016; Dial et al. 2016; Hotaling et al. 2019; Hotaling et al. 2017b). Most biological activity on glaciers occurs within surface ice where microorganisms take advantage of nutrients that are either wind-delivered or generated *in situ* (Hotaling et al. 2017b). In addition to a nutrient input, impurities on the glacier surface can drive the development of at least two potential "hotspots" of biological diversity on glaciers: well-studied cryoconite holes (depressions in the ice surface caused by local melt, Anesio et al. 2017) and glacier moss balls (ovular conglomerations of moss and sediment that move on the glacier surface, Coulson and Midgley 2012).

Under the right conditions, a small piece of rock or other impurity can set in motion the formation of a glacier moss ball [also referred to as "jokla-mys" (Eythórsson 1951), "glacier mice" (e.g., Coulson and Midgley 2012), or "moss cushions" (e.g., Porter et al. 2008)]. On a local scale, glacier moss balls are typically distributed with some degree of local clustering (e.g., ~1 glacier moss ball/m^2; Fig. 1). While more immobile moss aggregations have been observed on glaciers elsewhere (e.g., East Africa, Uetake et al. 2014), true glacier moss balls appear to be particularly rare, having only been described on a few geographically disparate glaciers in Alaska (Shacklette 1966; Heusser 1972), Iceland (Eythórsson 1951), Svalbard (Belkina and Vilnet 2015), and South America (Perez 1991). Many different moss species have been found in glacier moss balls (Shacklette 1966; Heusser 1972; Perez 1991; Porter et al. 2008), suggesting that they are not dependent on specific taxa, but instead their development is likely driven by the interaction of suitable biotic (e.g., availability of moss spores) and abiotic (e.g., growth substrate) factors. However, the specific steps and timeline underlying glacier moss ball genesis remains unclear.

An intriguing aspect of glacier moss balls, and one that is almost certainly partially responsible for their "glacier mice" namesake, is their movement. Though the speed and direction of glacier moss ball travel has not been studied, it has been posited that they move by inducing the formation of an ice pedestal, then rolling or sliding off of it (Porter et al. 2008). Moss balls first reduce local albedo by shielding the ice beneath them from sunlight and locally reducing the ablation rate. As the surrounding ice melts, the glacier moss ball is left on an elevated pedestal. Eventually, a threshold is reached where the moss ball falls from its pedestal and the process begins anew, potentially including a “flip” of the moss ball that exposes what was previously their underside (Porter et al. 2008). However, the speed and direction of moss ball movement has not been tested, though it has been suggested that their movements generally track the downslope direction of their local habitat (Porter et al. 2008).

Where they do occur, glacier moss balls contribute to glacier biodiversity by offering a thermally buffered, island-like habitat on the glacier surface that can host a wide array of invertebrates (Coulson and Midgley 2012). On Icelandic glaciers, moss balls contain invertebrate communities dominated by springtails (Collembola), tardigrades (Tardigrada), and nematodes (Nematoda; Coulson and Midgley 2012). While an array of potential food resources are available on glacier surfaces (Hotaling et al. 2017b), these are typically only exploited by invertebrates on the margins of glaciers (e.g., springtails, spiders, grylloblattids) because suitable on-glacier habitat is lacking (Mann et al. 1980). Glacier moss balls may therefore provide key habitable islands on the glacier that facilitate wider resource exploitation versus glaciers without moss balls (Coulson and Midgley 2012). It is also possible that glacier moss balls, which have not been shown to be inhabited by larger predatory insects (e.g., grylloblattids) may provide prey refuge that are sufficiently removed from the typical foraging areas of their predators. Either way, it is clear that glacier moss balls represent important habitat for glacier-associated fauna yet basic aspects of their ecology (e.g., longevity and movement) are unknown.

In this study, we took an integrated behavioral ecology and geophysical approach to the study of glacier moss balls to answer three basic questions about their life history: (1) What is the lifespan of a glacier moss ball? (2) How quickly do they move and is their movement idiosyncratic or herd-like? (3) Are the movements of glacier moss balls linked to the ablation of the glacier itself? The answers to these questions have implications for invertebrate fauna in glaciated ecosystems, nutrient cycling (both directly via moss ball decomposition and indirectly as supporting habitat for biotic communities), and feedback between glacier moss balls and local ablation rates. Beyond biotic interactions and ecosystem dynamics, glaciers are rapidly receding worldwide (Gardner et al. 2013; Larsen et al. 2015; Roe et al. 2017) and their diminished extents will almost certainly affect the persistence of glacier moss balls on local and global scales. Thus, it is important to better understand these unique micro-ecosystems before their habitats are lost.

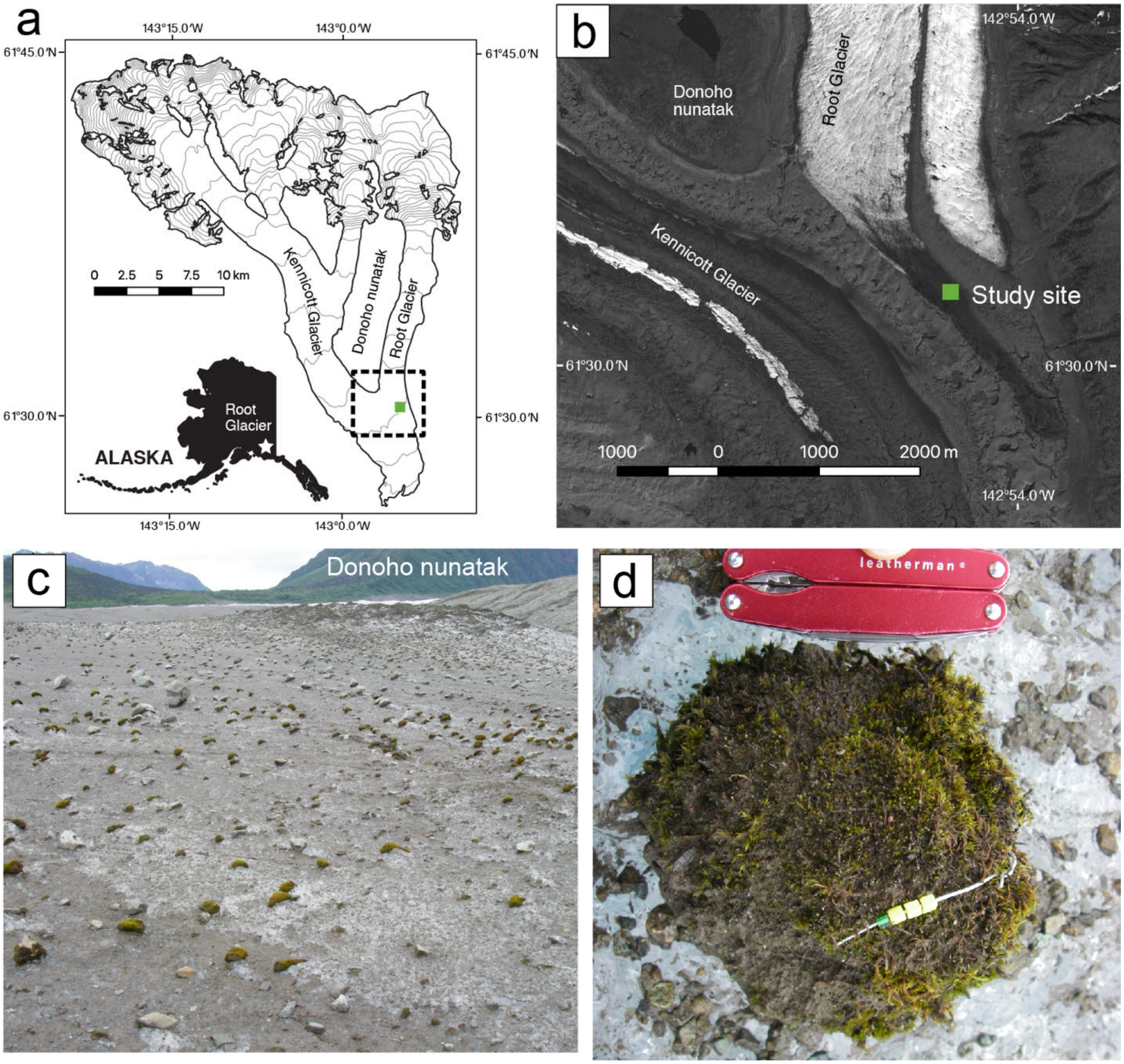

Fig. 1. a) Our study site (solid green square) on the Root Glacier in southcentral Alaska, USA, within Wrangell-St. Elias National Park. Contour lines are spaced every 100 m in elevation. The dashed square represents the field of view shown in panel (b). The inset map shows the location of the Root Glacier (white star) within Alaska. b) Satellite image of the study site (green square) showing the confluence of the Root and Kennicott Glaciers with the Donoho nunatak to the northwest. The image was recorded on 19 June 2013. c) A landscape view looking northwest of the study site dotted with glacier moss balls. d) A close-up view of a glacier moss ball with the type of bracelet tag used in this study.

Materials and methods:

Study area

We conducted fieldwork over four years (July, 2009 - July, 2012) on the lowest portion of the Root Glacier, a major tributary to the Kennicott Glacier, in the Wrangell Mountains in Wrangell-St. Elias National Park, Alaska, USA (Fig. 1a). Our study area (61.5076° N, 142.9172° W, ~700 m elevation) spanned a ~15 x ~40 m (600 m^2) area of glacier ice selected for its especially high concentration of moss balls. The site has a gentle slope, dipping 3° east-northeast (N75°E) and is found between two medial moraines (Fig. 1b), each ~100 m away. Moss ball concentrations decrease both up- and down-glacier and are absent from the coarse-grained (> 5 cm) rock that covers the adjacent medial moraines.

We estimated the proportion of fine-grained sediment cover on the ice within our study area by applying image processing techniques in the Python package scikit-image (Van der Walt et al. 2014) to two vertical photographs taken of representative ice surfaces. Pixel brightness contrasts between ice and sediment are most distinct within the blue band of the red-green-blue images, so we differentiated between sediment (dark pixels) and ice (bright pixels) by binarizing the blue band with Otsu's thresholding method. We then performed a morphological opening to diminish the influence of light-colored sediment grains set within the otherwise dark sediment cover. Finally, we quantified the areal sediment cover as being approximately equal to the number of dark colored pixels relative to the total number of pixels in the binarized images.

Mark-recapture

During the summer of 2009, we tagged 30 glacier moss balls with a bracelet identifier (Fig. 1d). Each bracelet consisted of a unique combination of colored glass beads (~2-3 mm in diameter) threaded on aluminum wire. Bracelets were threaded through the moss ball center and pulled snug so as to not protrude beyond the moss ball's exterior and interfere with movement. We returned eight times during the 2009 season to re-survey moss balls and record their movements. We followed up our initial surveys with annual visits from 2010-2012. During each survey, we visually inspected in and around the core study area multiple times in an effort to recapture moss balls. As part of this process, we visually inspected each moss ball in the area for any sign of a bracelet tag. After inspection, we replaced each moss ball in the exact location and orientation as it was found.

Moss ball movement and glacier ablation

We assessed moss ball movement over 54 days in 2009. As benchmarks for their movement, we installed three ~1.3 cm PVC tubes into the glacier. Each stake was drilled ~60 cm into the glacier. Stakes were installed in a triangle that spanned the study area and served two purposes. First, the stakes provided a reference against which the location of each moss ball was measured. Second, they allowed us to measure glacier ablation (i.e., the distance the ice surface moves vertically down) over the same study period so we could test for links between moss ball movement and the rate of glacier ablation.

To track glacier moss ball movement, we measured the distance between re-identified moss balls and each of the reference stakes for each visit to the site. Next, for each moss ball, we calculated three independent positions within our field site--one for each of the three pairs of reference stakes. We assigned the location of a surveyed moss ball to the mean of these three relative positions and constructed a location covariance matrix for each measurement, to assign uncertainties to surveyed locations. After diagonalizing the covariance matrix, we identified the size (eigenvalues) and orientation (eigenvectors) of an uncertainty ellipse around each mean location. Major and minor axes of the uncertainty ellipse were defined as twice the square root of the eigenvalue lengths, such that each error ellipse represented a 2σ error window. Thus, assuming independent, normal errors, we are 95% confident that the true location of each moss ball fell within its error ellipse. While we used stakes for most of the measurement period, we were forced to switch to washers (~5 cm in diameter) laid flat on the ice surface later in the season, during a period when we were unable to drill the benchmark stakes sufficiently deep to avoid melting out between visits to the study area. Before transitioning from benchmark stakes to washers, we tested the stability of the washers to ensure that they did not slide over the ice surface. Over a 5-day period, we did not detect significant washer movement (outside of 2σ uncertainty). Final measurements (11 August 2009) and calculations were made relative to the washers.

For the purposes of quantifying glacier ablation, the height of each stake above the local ice surface was re-measured during each visit and periodically re-drilled into the ice as necessary. Ablation reported in this study is the mean ice surface lowering rate calculated for each of the three stakes. As an assessment of ablation uncertainty, we also calculated the maximum deviation of any single stake's ablation rate from the overall mean.

Longevity

We sought to understand how long glacier moss balls survive, particularly across individual seasons. We hypothesized that moss balls might survive better or worse in some years due to variation in environmental conditions (e.g., precipitation, freeze-thaw cycles) or random chance (e.g., a crevasse opening within a key area). Furthermore, we wanted to know not only how likely we are to detect glacier moss balls, given that they had persisted within the study area, but also if our detection probability varies among years. To do this, we fit capture-recapture models of annual survival to each glacier moss ball included in the study. Because moss balls were individually marked but were not equipped with radio-transmitters or other devices which would allow us to know their ultimate fates, we applied Cormack-Jolly-Seber (CJS; Lebreton et al. 1992) survival models. These CJS models develop a “capture history” of each moss ball to estimate apparent survival (i.e., the probability that an individual is in the population at time *i* and still in the population at time *i*+1) and probability of detection if they persisted within our study area. Survival estimates from CJS models only represent apparent survival because emigration cannot be estimated from survival data with unknown fates (i.e., we did not know if a tagged moss ball had disaggregated, lost its identifying bracelet, or was no longer in the study area). Therefore, our estimates of apparent survival are likely to underestimate true survival (e.g., a moss ball might have lost its bracelet or moved out of the study site). In addition, CJS models also account for imperfect detection, which in our case would be if a moss ball persisted within our study area but was overlooked.

Using our individual moss ball annual detection data (1 = detected, 0 = not detected), we fit four competing CJS survival models, including the null model [no effect of year on apparent survival (□) or detection probability (*p*); Model 1)], an effect of year on □ (Model 2), an effect of year on *p* (Model 3), or an effect of year on both □ and *p* (Model 4). We then selected the model(s) best supported by our data using Akaike’s information criterion (AIC; Akaike 1998), adjusted for small sample size (AICc; Hurvich and Tsai 1989). Our model selection approach was based on model likelihoods and models were penalized for extra parameters to favor parsimony.

Finally, we calculated the average life expectancy of a glacier moss ball. To do this, we used annual survival rates based on life-table analysis (Deevey Jr 1947; Millar and Zammuto 1983), in which average life expectancy was calculated as -1/ln(Annual Survival Rate). Because this estimation of life expectancy is quite sensitive to annual survival rate, we calculated it for both the lowest annual survival rate and the mean annual survival rate. Thus, the true average life expectancy might be substantially greater than the conservative values estimated here. This framework for estimating average life expectancy does not account for potentially higher or lower mortality rates when glacier moss balls are first forming or nearing the end of their lifespans.

Results:

Study area

Our study area was located on a “bare ice” glacier surface, between two medial moraines covered by coarse-grained, angular, rock debris. However, two types of sediment distinguish the study area surface from what would be considered clean, pure, water ice. First, glacier moss balls were found amidst gravel and small boulders (< 30 cm diameter), spaced every ~1 m. Second, the ice surface within the study area has an unusually pervasive, fine-grained sediment cover, ~1-3 mm thick, which partially blankets the otherwise bare ice. Image processing indicated that this fine sediment covers approximately 70% of the study area surface. This low albedo sediment cover is visible in all inspected satellite imagery of the site and first appears at lower concentrations emerging from cleaner ice ~1 km northwest of the study site (Fig. 1b). Down-glacier of the study site, the low albedo region extends ~1.7 km as a ~300-m-wide, rounded finger that spans adjacent medial moraines, in a manner consistent with wind-deposited dust, draping over underlying geomorphic features. Therefore, we interpreted the southeast (135°) trend direction of this low albedo finger to be the prevailing, down-glacier, katabatic wind direction.

During the 26 days of glacier ablation measurements, the ice surface lowered by 1.91 m due to melt and sublimation. Ablation rates ranged from 5.8-9.6 cm per day (cm/d) between measurement times, and averaged 7.3 cm/d.

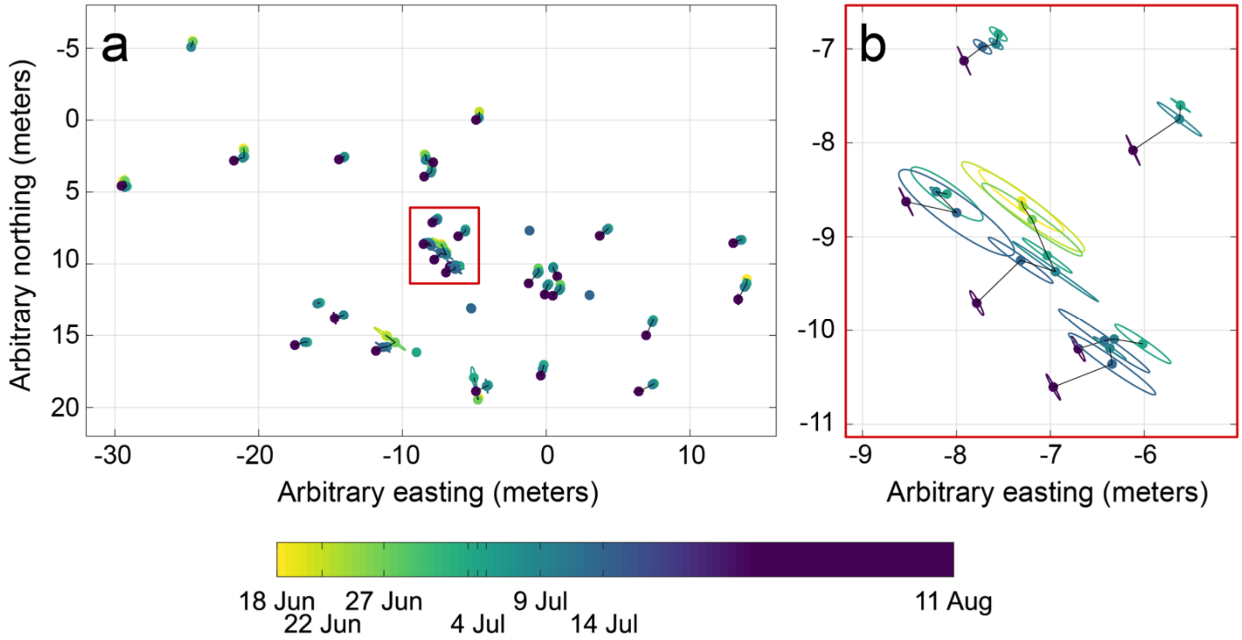

Fig. 2. (A) Locations of surveyed glacier moss balls throughout the survey period. Most likely locations of each moss ball are shown with small filled circles relative to an arbitrary, local grid system. Ellipses surrounding each moss ball indicate 2 uncertainty (i.e., 95% confidence) of their location. Thin black

lines connect consecutive surveyed locations for individual moss balls. The red rectangle identifies the location of the large-scale view in panel (B). (B) A zoomed in view of movement patterns for six glacier moss balls (red square in A), showing their similar azimuths.

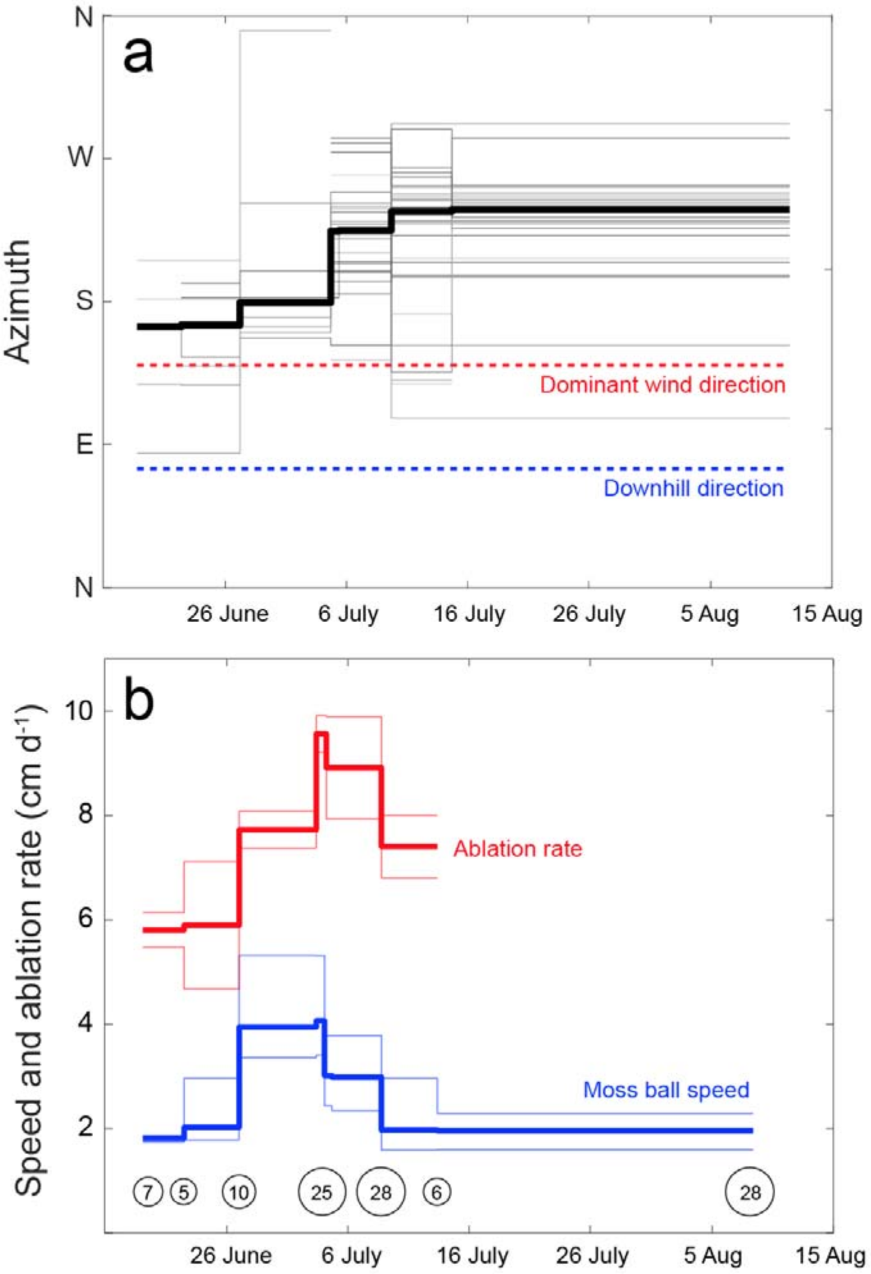

Fig. 3. (A) A comparison of glacier moss ball movements versus the dominant wind (dashed red line) and downslope (dashed blue line) directions. Direction of each moss ball's motion between measurement times is shown with thin gray lines, while the bold black line indicates the median direction of all glacier moss ball movements. (B) Glacier moss ball movement versus ablation rate. Median ablation rate is indicated with a bold red line, while the mean +/- the maximum absolute deviation from the mean are shown with thin red lines. The median speed of glacier moss balls is shown with the bold blue line, while the 25th and 75th percentile speeds are shown with thin blue lines. Numbers in circles along the bottom of the plot represent the number of moss balls surveyed at each timepoint (single measurements not indicated).

Movement

Glacier moss ball movements varied systematically over the study period, with increases and decreases that coincided with changes in direction (Figs. 2-3). Median moss ball speed was 2.5 cm/d, but their rates varied widely throughout the season. The median speed started at 1.8 cm/d in late June, increased to 4.0 cm/d at the start of July, then slowed to 2.0 cm/d during late July/early August. The maximum observed speed for any glacier moss ball was 7.8 cm/d during the 5-day period from July 9-14 (excluding two outlier speeds that were more than 8 interquartile ranges greater than the median, 14.2 and 21.0 cm/d, and which were based upon particularly uncertain moss ball positions). The interquartile range of moss ball speeds was approximately 50% of the median speed; thus, these observed increases and decreases in speed reflect changes in the entire population of moss balls.

The direction of glacier moss ball movements was not random. Rather, glacier moss balls underwent clear changes in their direction of motion (i.e., azimuth) throughout the summer season (Fig. 3a). While individual moss balls moved in many directions, when viewed in aggregate, azimuths of the population clearly cluster over time. Early in the season, median moss ball motion was south-southeast (165°) but over the ensuing weeks azimuths progressively increased, such that at the end of the measurement period the median azimuth was west-southwest (240°; Fig. 3a).

Considering speeds and azimuths together, we see the moss ball population initially moving at 2 cm/d to the south for 9 days, then the group nearly doubles its speed to 4 cm/d while deviating slightly to the right (towards the west). After a week at these maximum speeds, speeds drop by 25% to 3 cm/d while also deviating 45 degrees further towards the west for five days. During the next 5-day measurement period, speeds drop further, back to 2 cm/d while the azimuths turn another 10-15 degrees further west. Over the final 28-day measurement period, the azimuths remain stable, while speeds continued to fall. This decrease in speed is apparent in the decline of the upper quartile of speeds, despite our not making sufficient new measurements to influence the median speed.

Our fine-scale movement and ablation data allowed us to compare glacier moss ball speeds and azimuths with potential drivers of their motion. The southern and western directions of moss ball movement are clearly distinct from both the prevailing wind direction as inferred from the dust plume (towards the southeast) or the downhill direction of the gently sloping ice surface (towards the east-northeast; Fig. 3a). Instead, we find more rapid moss ball speeds are associated with more rapid ablation; an ordinary least squares model between ablation rate and speed indicates that, on average, for every 1 cm of surface ablation, the glacier moss balls move horizontally 0.34 cm (Fig. 3b). However, the relationship between ablation rate and speed is relatively weak ($R^2 = 0.40$). It should also be noted that during the course of our study, participants in a program hosted by the Wrangell Mountains Center, McCarthy, Alaska, visually confirmed the posited primary movement method described by Porter et al. (2008), when a glacier moss ball was observed rolling off its elevated pedestal and inverting in the process.

Table 1. Apparent survival models for glacier moss balls tested in this study with their corresponding Akaike's Information Criterion scores that have been adjusted for small sample sizes (AICc). Relative AICc scores (ΔAICc) model weight are also given. Lower ΔAICc and higher model weight indicate greater support for a given model. Model components: probability of detection (p), apparent survival (ϕ).

Model	Description	AICc	ΔAICc	Weight
1	Null; No year effect on p or ϕ	107.09	1.56	0.26
2	Year effect on ϕ	105.53	0	0.58
3	Year effect on p	108.92	3.39	0.10
4	Year effect on both p and ϕ	110.25	4.72	0.05

Table 2. Estimates of the apparent survival (ϕ) and detection probability (p) of glacier moss balls for the two best-fit models. Parentheses after estimates indicate 95% confidence intervals.

Model	Parameter	Estimate
1	p	0.84 (0.70-0.92)
	ϕ	0.86 (0.75-0.93)
2	p	0.82 (0.69-0.91)
	ϕ (2009-2010)	0.74 (0.55-0.87)
	ϕ (2010-2011)	0.98 (0.27-0.99)
	ϕ (2011-2012)	1.0 (0.99-1)

Longevity

We initially tagged 30 glacier moss balls in 2009. We subsequently recaptured 18 moss balls each in 2010, 2011, and 2012 (although this was not the same 18 moss balls each year). Recapture rates for individual glacier moss balls were highly variable with some never seen again after the first year (n = 8) and others detected every year (n = 13). The best-fit survival model included differing apparent survival (□) among years, but with constant detection probability (p; Model 2; Table 1). This model received 58% of AICc weight, compared to 26% for the null model (Model 1), and less than 10% for the other models (Models 3 & 4; Table 1). The average annual rate of apparent survival, □, based on the null model, was 0.86 [95% confidence interval (CI) = 0.75-0.93], and the average detection rate was 0.84 (95% CI = 0.70-

0.92). When parameterized by year, the annual apparent survival rate ranged from 0.74 in 2009-2010 to 1.0 in 2011-2012 with a particularly large 95% CI for 2010-2011 (Table 2; Fig. 4).

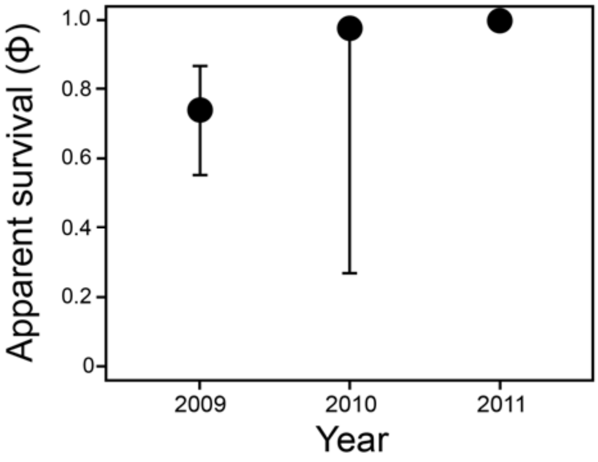

Fig. 4. Estimates of apparent moss ball survival (□; dark circles) with 95% confidence intervals (thin dark lines) from model 2, the best-fit model, which included a year effect on □. Year-long, bracketed time intervals labeled on the x-axis are identified by their starting year. For instance, apparent survival for 2009-2010 is shown as 2009.

Our detection rate estimates may underestimate actual glacier moss ball survival for several reasons. First, at least four glacier moss balls lost their marking bracelet after the first year because we found the marking bracelet on the ice, separate from a moss ball. Second, another moss ball partially obscured its bracelet by growing to cover the beads, but we were able to detect a single bead and then delicately “excavate” the bracelet. Since we did not destructively search glacier moss balls that did not have an obvious bracelet, it is possible that additional instances of lost marking bracelets or growth to cover beads may have impacted our detection. Third, between 2009 and 2010, two tagged moss balls fell inside of a shallow crevasse within the study area. The two crevasse-bound glacier moss balls persisted, and likely continued to photosynthesize and grow to some capacity for the remainder of the study. We continued to check crevasses in the study area carefully, but some moss balls could have fallen into deeper crevasses, or into shallow crevasses in a way that obscured their markings, and therefore persisted without detection.

Our estimate of average life expectancy varied depending on whether the lowest overall or mean annual survival rate were used. If using the lowest annual survival rate (0.74), average life expectancy was 3.3 years (95% CI = 1.67-7.18). However, we expect this life expectancy to be biased low to some extent, because we were only able to estimate apparent survival (e.g., some insecure tags fell off moss balls that likely still persisted). If using the mean annual apparent survival rate across the entire study (0.86), average life expectancy rose to 6.63 years (95% CI = 3.48-13.78), although this may be biased high because we did not tag any new moss balls in years 2 and 3 (2010 and 2011), but simply re-captured existing (and therefore high survival probability) glacier moss balls. When thinking of lifespan, it is relevant to note that we also observed a glacier moss ball split roughly in half during the course of the study along its intermediate axis. The moss ball had become elongated and essentially pulled apart. This mechanism may contribute to both keeping glacier moss balls ovular as well as a form of cloning, propagating new moss balls on the landscape.

Discussion:

Glacier moss balls are intriguing components of glacier ecosystems that integrate physical (e.g., debris cover) and ecological (e.g., invertebrate colonization) factors into a unique habitat type. Glacier moss balls have a global distribution, with colonies identified in Iceland, North and South America, and Asia (Eythórsson 1951; Heusser 1972; Perez 1991; Porter et al. 2008; Coulson and Midgley 2012) and more dispersed moss aggregations on glaciers have been described from an even broader area (e.g., Uganda, Uetake et al. 2014). Previous studies have revealed a great deal about glacier moss ball biology (e.g., their invertebrate colonizers, Coulson and Midgley 2012) yet their movement and longevity has remained unknown. It has been speculated that glacier moss ball movement patterns likely follow the general downward slope of the glacier (Porter et al. 2008) and that they represent an ephemeral habitat type on glaciers, a factor that may limit colonization by specific invertebrate taxa (e.g., spiders; Coulson and Midgley 2012). Our results do not align with these predictions of movement and longevity. Rather, we show that glacier moss balls, at least on a relatively gently sloped Alaskan glacier, exhibit relatively quick (2.5 cm/d) herd-like movements that do not align with the downward slope of the glacier nor the dominant wind direction. Glacier moss balls are also relatively long-lived with a mean lifespan of more than 6 years.

Movement

On the Root Glacier, glacier moss balls move relatively quickly (~2.5 cm/d) in similar general directions and at similar general speeds. Directions of motion do not align solely with either the downhill direction nor the direction of the prevailing wind. The rate of glacier moss ball movements is also positively correlated, albeit weakly, with overall glacier ablation (Fig. 3b). It appears likely that the dominant direction of solar radiation, which melts exposed ice surrounding glacier moss balls more rapidly than the insulated ice below them (Porter et al.

2008), is the major force driving glacier moss ball movement. However, the relative contributions of gravity in the downslope direction versus solar radiation is almost certainly dependent on glacier steepness. Porter et al. (2008) posited a considerable effect of gravity on glacier moss ball movement for a relatively steep (9.6°) Icelandic glacier which contrasts with our much flatter study area on the Root Glacier (~3°). Still, regardless of steepness, differential melt patterns create pedestals that glacier moss balls rest upon and, eventually, enough ice melts below the moss ball causing it to fall and potentially flip (Porter et al. 2008). Assuming glacier moss balls are, on average, ~10 cm in their intermediate axis, and their only means of movement is melt-induced flipping driven by pedestal emergence at the rate of 6-9 cm/d, their rates of movement would imply each glacier moss ball flips every ~2-4 days. However, we cannot rule out alternative modes of glacier moss ball movement. Many glacier moss balls have one side that is flattened and commonly faces down, while the other, more rounded and vegetated side faces skyward (Shacklette 1966). Given this orientation, an alternative scenario is that glacier moss balls also move by basal sliding over the wet glacier surface below.

One movement-related question remains puzzling: why do the azimuths of glacier moss balls appear to shift simultaneously throughout the summer season, resulting in the moss ball “herd” synchronously changing directions (Fig. 3a)? They begin the season moving generally south and slowly transition towards the west. Given their independence from the dominant wind direction and downhill direction of the glacier, we can speculate that a slow shift in the dominant direction of solar radiation or shifting weather patterns during summer drives this pattern. Perhaps the weather transitioned from clear mid-day skies during late June and early July (associated with the most rapid motion and southerly azimuths), to a different weather pattern in late July consisting of morning clouds and afternoon sun, that drives enhanced ablation on the west sides of moss balls, and therefore preferential rolling towards the west. Furthermore, the interaction between rate of movement and ablation may depend additionally on the degree to which the dominant solar radiation and downslope directions align. If they are in the same direction, glacier moss balls should move rapidly, downslope, towards the sun. However, if melt is being driven from a direction perpendicular to the downslope direction, then glacier moss balls will move considerably less per unit melt.

Longevity

Glacier moss balls show considerable potential to persist across multiple years as stable ecological units. On average, 86% of the marked glacier moss balls included in this study survived annually which translates to a lifespan of more than 6 years. This longevity is on par with large, long-lived vertebrates (e.g., adult female ungulates in typically have annual survival probabilities ≥ 0.85; Gaillard and Yoccoz 2003; Gaillard et al. 1998). Thus, with high rates of survival across multiple years, and relatively high detection rates, we consider glacier moss balls to be long-lived, rather than ephemeral, glacier features. Unlike living individual organisms which can show senescence as they age (e.g., Loison et al. 1999), moss ball survival rates are unlikely to decline with time in the traditional sense, nor are they likely to exhibit density dependence in survival (e.g., Festa-Bianchet et al. 2003), however the factors that control disaggregation may be the most important factor for moss ball longevity. At any rate, the temporal stability of individual moss balls on the glacier surface means that they likely exist for long enough to develop complex biotic communities, a fact supported by the distinctive invertebrate communities inhabiting moss balls (Coulson and Midgley 2012). However, the degree to which geographic location (e.g., distance to a glacier margin), and not persistence, influences invertebrate colonization remains to be tested.

The limited scope of our mark-recapture data collection precludes us from drawing conclusions about the inter-annual drivers of moss ball apparent survival. However, we can highlight potential factors that may influence it. First, it is possible that glacier moss balls moved more frequently out of the study area in one year versus others, perhaps due to exceptionally clear skies (and thus higher rates of glacier ablation). Second, we observed a number of fragmented moss balls. This fragmentation may be part of normal glacier moss ball growth trajectories, too frequent or intense freeze thaw cycles, perhaps as a product of moss ball water content, or some other as yet unknown factor. It is also unclear at what rate fragmented glacier moss balls continue to move and grow, eventually developing back into mature, ovoid, full-sized moss balls. If glacier moss balls did survive within our study area, they had an 84% probability of being detected in a given year. This indicates that our bracelet and colored beads marking scheme was relatively successful. However, for future studies, more robust marks should be considered. One possibility is the use of passive integrated transponder (PIT) tags which are commonly used for mark-recapture studies of a variety of organisms (e.g., fish; Castro-Santos et al. 1996), and allow researchers to scan study organisms electronically rather than rely on visual ID.

Genesis, growth, and disaggregation

Our combined movement and longevity analyses allow us to add new speculation about patterns of glacier moss ball growth as well as additional evidence for previous hypotheses regarding their genesis and disaggregation (e.g., Heusser 1972; Perez 1991). In terms of growth, our documentation of glacier moss balls rolling over a fine-grained, wet, sedimentary substrate is consistent with growth through the adherence of fine-grained sediment to an existing moss ball. When a moss ball rolls from its elevated pedestal, sediment grains stick to the moss (or potentially to the cohesive sediment itself). We visually observed such “dirty” moss on some glacier moss balls in our study area. As the moss itself grows, this adhered sediment may then become integrated within the fibrous material, increasing the size of the glacier moss ball. Field observation of moss growth over and around our identification bracelets indicates that several millimeters of growth can occur within years. However, the observation that most bracelets were not engulfed by sediment accumulation and moss growth during our four-year study period suggests an upper limit on moss ball growth. Consistent with a greater than 6-year lifespan, moss ball growth to an observed size of 10 cm must take years, and given the conservative nature of our longevity estimates, potentially much longer.

Understanding year-to-year moss ball growth, however, does not explain moss ball genesis, nor disaggregation. It is well-established that fibrous moss provides the skeletal structure that allows moss balls to be cohesive, ovoid structures. A source of moss spores is there essential for initial glacier moss ball genesis (in our study, putatively, the Donoho nunatak). The question, then, is how glacier moss balls begin to grow in the first place, and on what substrate. (Eythórsson 1951) suggested that a “stone kernel” is likely at their centers. However, later investigations (e.g., Shacklette 1966; Gremmen 1982) found mixed results that largely reflected a consensus that there is no general rule about rock cores at the center of glacier moss balls. Our exploratory testing of moss balls also indicated that some, but not all, moss balls contained a ~1-cm gravel “kernel” at their centers. Potentially, these kernels, with adhered fine-grained sediment, provide a growth substrate for initially wind-deposited moss spores. In our study area, the co-occurrence of moss balls with an unusually extensive, fine-grained “plume” of sediment cover (Fig. 1b) aligns with a similar observation by Heusser (1972) for the Gilkey Glacier in southeastern Alaska, USA. The fine-grained sediment may be essential proto-soil for moss ball growth and may explain the unusual density of moss ball occurrence at our study area. The origin of this fine-grained sediment is unknown, but in satellite imagery (Fig. 1b), it appears to originate from the ice itself. It may be a volcanic ash layer emerging from the ice after being carried down from the high, volcanic, Wrangell Mountain peaks. Once moss growth initiates, the moss itself, and the abundant moisture of the ablating glacier surface, may provide the necessary cohesion for the incipient moss ball formation, and continued growth thereafter.

In this study, we identified very few glacier moss balls greater than ~15 cm on their long axis. Generally, moss balls appear to rarely exceed ~10 cm except for rare cases in Alaska where they have been reported up to 18 cm (Heusser 1972; Benninghoff 1955). Why glacier moss balls in Alaska appear to grow larger than elsewhere in the world remains an open question but, regardless of location, there appears to be some size limiting process within the moss ball lifecycle at work. Shacklette (1966) suggested that the tensile strength of moss stems may be the key factor controlling their size. Exceeding this tensile limit appears to occur when the moss ball major axis grows too great relative to the intermediate axis. For instance, when a moss ball becomes too elongated, subtle variations in ice surface topography may lead the two ends of a moss ball to move in different directions, leading to a tear in the middle when the moss ball's tensile strength is exceeded. We observed such a tearing-in-two of a long, linear moss ball during the course of our study. Again, while this process applies an upper-limit to moss ball size it also circles back to inform questions regarding the presence or absence of a rock kernel. If the upper size limit is reached and a moss ball splits, only one of the two remaining moss balls involved in this "cloning" process will retain the gravel kernel. This may explain why a number of moss balls do not appear to have any coarse-grained rock at their cores.

Conclusions

Since their first description nearly 75 years ago (Eythórsson 1951), a general understanding of the physical and biological composition of glacier moss balls and their ecological role as drivers of small-scale ecosystem development has been established. In this study, we extended this previous work to quantify the movement and longevity of glacier moss balls on an Alaskan glacier. In light of these results, we discussed a potential life cycle for moss balls. We showed that glacier moss balls move relatively quickly, at a rate of centimeters per day, and that moss balls within the surveyed colony speed up, slow down, and change direction in synchrony. This finding suggests that moss ball motion is controlled by some broadly applied external forcing. However, for our study, this external forcing was surprisingly not solely associated with either the wind or downslope direction. Instead, the glacier moss ball movement patterns we observed likely depend on a combination of the intensity of glacier ice ablation, the direction of solar radiation, and the physical surface of the glacier (i.e., the downslope direction). Future studies that take a similar mark-recapture approach to the study of glacier moss ball movements on multiple glaciers throughout the world, including a range of steepness, will shed important light on the general nature of their movements.

We also showed that glacier moss balls are long-lived, with an average life expectancy of more than 6 years, on par with many relatively long-lived vertebrates (e.g., large mammalian herbivores, Gaillard and Yoccoz 2003). This potential for glacier moss balls to act as relatively stable, long-term ecological units further confirms their potential to act as key habitat for invertebrates. Coulson and Midgley (2012) previously described invertebrate colonization of glacier moss balls and suggested that a lack of Enchytraeidae and Aranea may be the result of the ephemeral nature of moss balls in glacier habitats. Our results contrast with this assumption. Instead, we postulate that selective invertebrate colonization of glacier moss balls may depend instead on their geographic locations and their frequent movements or, as Coulson and Midgley (2012) noted, may simply reflect the variable dispersal capacities of potential colonizers.

Given the importance of microbial diversity to carbon cycling (Anesio et al. 2009), ecosystem function (Anesio et al. 2017; Hotaling et al. 2017a; Hotaling et al. 2017b), and even albedo (Ganey et al. 2017), future efforts to understand the microbial ecology of glacier moss balls could shed important light on their ecological role in glacier ecosystems. Like cryoconite, the granular, darkly pigmented dust that accumulates on the surface of glaciers and drives hotspots of biological activity and microbial diversity (Cook et al. 2016), glacier moss balls may have similar value at the ecosystem scale. Indeed, glacier moss balls may act as reservoirs of microbial diversity, seeding and re-seeding a glacier surface with key, colonizing microbial life as they move around its surface.

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