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

2 **glacier**

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16

17 **Abstract:**

18 Glaciers support diverse ecosystems that are largely comprised of microbial life. However, at

19 larger, macroscopic scales, glacier moss balls (sometimes called "glacier mice") can develop

20 from impurities on ice surfaces and represent a relatively rare biological phenomenon. These

21 ovoid-shaped conglomerations of dirt and moss are only found on some glacier surfaces and

22 provide key habitats for invertebrate colonization. Yet, despite their development and presence

23 being widely reported, no targeted studies of their movement and persistence across years

24 have been conducted. This knowledge gap is particularly important when considering the

25 degree to which glacier moss balls may represent viable, long-term biotic habitats on glaciers,

26 perhaps complete with their own ecological succession dynamics. Here, we describe the

27 movement and persistence of glacier moss balls on the Root Glacier in southcentral Alaska,

28 USA. We show that glacier moss balls move an average of 2.5 cm per day in herd-like fashion,

29 and their movements are positively correlated with glacier ablation. Surprisingly, the dominant

30 moss ball movement direction does not align with the prevailing wind or downslope directions,

31 nor with any dominant direction of solar radiation. After attaining a mature size, glacier moss

32 balls persist for many years, likely in excess of 6 years. Finally, we observed moss ball

33 formation on the Root Glacier to occur within a narrow, low albedo stripe downwind of a

34 nunatuk, a potential key source of moss spores and/or fine-grained sediment that interact to
35 promote their formation.
36
37 **Keywords:** cryobiology, glacier mice, glacier biology, jokla-mys, Root Glacier, Wrangell-St.
38 Elias National Park
39
40 **Introduction:**
41   Glaciers have long been overlooked as important components of global biodiversity
42 (Stibal et al. 2020), but it is now clear that they host thriving, multi-trophic ecosystems (Anesio
43 and Laybourn-Parry 2012), supporting taxa from microbes to vertebrates (Rosvold 2016; Dial et
44 al. 2016; Hotaling et al. 2017a; Hotaling et al. 2019). Most biological activity on glaciers occurs
45 within surface ice where microorganisms take advantage of nutrients that are either wind-
46 delivered or generated *in situ* (Hotaling et al. 2017a). In addition to a nutrient input, impurities on
47 the glacier surface can drive the development of at least two potential "hotspots" of biological
48 diversity on glaciers: well-studied cryoconite holes (depressions in the ice surface caused by
49 local melt, Anesio et al. 2017) and glacier moss balls (ovular conglomerations of moss and
50 sediment that move on the glacier surface, Coulson and Midgley 2012).
51   Often a small piece of rock or other impurity sets in motion the formation of a glacier
52 moss ball [also referred to as "jokla-mys" (Eythórsson 1951), "glacier mice" (e.g., Coulson and
53 Midgley 2012), or "moss cushions" (e.g., Porter et al. 2008)]. On a local scale, glacier moss
54 balls are typically distributed with some degree of local clustering (e.g., ~1 glacier moss ball/m^2;
55 Fig. 1). While immobile moss aggregations have been observed on glaciers elsewhere (e.g.,
56 East Africa, Uetake et al. 2014), true glacier moss balls appear to be particularly rare, having
57 only been described on a few geographically disparate glaciers in Alaska (Shacklette 1966;
58 Heusser 1972), Iceland (Eythórsson 1951), Svalbard (Belkina and Vilnet 2015), and South
59 America (Perez 1991). Many different moss species have been found in glacier moss balls
60 (Shacklette 1966; Heusser 1972; Perez 1991; Porter et al. 2008), suggesting that they are not
61 dependent on specific taxa, but instead their development is driven by the interaction of suitable
62 biotic (e.g., availability of moss spores) and abiotic (e.g., growth substrate) factors. However,
63 the specific steps and timeline of glacier moss ball genesis remains unclear.
64   An intriguing aspect of glacier moss balls, and one that is almost certainly partially
65 responsible for their "glacier mice" namesake, is their movement. It has been posited that moss
66 balls move by inducing the formation of an ice pedestal, then rolling or sliding off of it (Porter et
67 al. 2008). Under this process, moss balls first reduce local albedo by shielding the ice beneath

68 them from sunlight and locally reducing the ablation rate. As the surrounding ice melts, the

69 glacier moss ball is left on an elevated pedestal. Eventually, a threshold is reached where the

70 moss ball falls from its pedestal and the process begins anew, potentially including a "flip" of the

71 moss ball that exposes what was previously their underside (Porter et al. 2008). Though the

72 speed and direction of moss ball movement has not been measured, though it has been

73 suggested that their movements generally track the downslope direction of their local habitat

74 (Porter et al. 2008).

75   Where they occur, glacier moss balls contribute to glacier biodiversity by offering a

76 thermally buffered, island-like habitat on the glacier surface that hosts an array of invertebrates

77 (Coulson and Midgley 2012). On Icelandic glaciers, moss balls contain invertebrate

78 communities dominated by springtails (Collembola), tardigrades (Tardigrada), and nematodes

79 (Nematoda; Coulson and Midgley 2012). While many potential food resources are available on

80 glaciers (Hotaling et al. 2017a, 2020), these are typically only exploited by invertebrates on the

81 margins (e.g., springtails, spiders, grylloblattids), likely because suitable on-glacier habitat is

82 lacking (Mann et al. 1980). Glacier moss balls may therefore provide key habitable islands on

83 the glacier that facilitate wider resource exploitation versus glaciers without moss balls (Coulson

84 and Midgley 2012). It is also possible that glacier moss balls, which have not been shown to be

85 inhabited by larger predatory insects (e.g., grylloblattids) may provide prey refuge that are

86 sufficiently removed from the typical foraging areas of their predators. Either way, it is clear that

87 glacier moss balls represent important habitat for glacier-associated fauna yet basic aspects of

88 their ecology (e.g., longevity and movement) are unknown.

89   In this study, we took an integrated behavioral ecology and geophysical approach to the

90 study of glacier moss balls to answer three basic questions about their life history: (1) How long

91 do mature glacier moss balls persist on the landscape? (2) How quickly do they move and is

92 their movement idiosyncratic or herd-like? (3) Are the movements of glacier moss balls linked to

93 the ablation of the glacier itself? Answers to these questions have implications for invertebrate

94 fauna in glaciated ecosystems, nutrient cycling (both directly via moss ball decomposition and

95 indirectly as supporting habitat for biotic communities), and feedback between glacier moss

96 balls and local ablation rates. Beyond biotic interactions and ecosystem dynamics, glaciers are

97 rapidly receding worldwide (Gardner et al. 2013; Larsen et al. 2015; Roe et al. 2017) and their

98 diminished extents will almost certainly affect the persistence of glacier moss balls on local and

99 global scales. Thus, it is important to better understand these unique micro-ecosystems before

100 their habitats are lost.

101

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. Glacier surface speeds here are slow, typically 0.05 to 0.15 m d^{-1} during summer (Armstrong et al. 2016). Several, narrow (<1 cm wide) and stagnant crevasses (manifesting as closed, linear, surface depressions) cross our study area, but did not significantly disrupt the otherwise consistent slope of the site. 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). We focused our efforts on "mature" moss balls that had reached at least ~10 cm in length on their longest axis and were ovoid with no obvious morphological irregularities. 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

4

136   recapture moss balls. As part of this process, we visually inspected each moss ball in the area

137   for any sign of a bracelet tag. After inspection, we replaced each moss ball in the exact location

138   and orientation as it was found.

139

140   *Moss ball movement and glacier ablation*

141   We assessed moss ball movement over 54 days in 2009. As benchmarks for their

142   movement, we installed three ~1.3 cm PVC tubes into the glacier. Each stake was drilled ~60

143   cm into the glacier. Stakes were installed in a triangle that spanned the study area and served

144   two purposes. First, the stakes provided a reference against which the location of each moss

145   ball was measured. Second, they allowed us to measure glacier ablation (i.e., the distance the

146   ice surface moves vertically down) over the same study period so we could test for links

147   between moss ball movement and the rate of glacier ablation.

148   To track glacier moss ball movement, during each site visit, we measured the distance

149   between re-identified moss balls and each reference stake with a flexible, fiberglass measuring

150   tape, pulled taught between the moss ball center and reference stake. Next, for each moss ball,

151   we used trilateration to calculate three independent positions within our field site—one for each

152   of the three pairs of reference stakes. We assigned the location of a surveyed moss ball to the

153   mean of these three relative positions and constructed a location covariance matrix for each

154   measurement, to assign uncertainties to surveyed locations. After diagonalizing the covariance

155   matrix, we identified the size (eigenvalues) and orientation (eigenvectors) of an uncertainty

156   ellipse around each mean location. Major and minor axes of the uncertainty ellipse were defined

157   as twice the square root of the eigenvalue lengths, such that each error ellipse represented a 2σ

158   error window. Thus, assuming independent, normal errors, we are 95% confident that the true

159   location of each moss ball fell within its error ellipse. The size of each error ellipse thus accounts

160   for potential errors including failure to pull the tape completely tight in the face of katabatic winds

161   or long measurement distances, or inconsistent identification of moss ball centers. While we

162   used stakes for most of the measurement period, we were forced to switch to washers (~5 cm in

163   diameter) laid flat on the ice surface later in the season, during a period when we were unable

164   to drill the benchmark stakes sufficiently deep to avoid melting out between visits. Before

165   transitioning from benchmark stakes to washers, we tested the stability of the washers to ensure

166   that they did not slide over the ice surface. Over a 5-day period in early August, we did not

167   detect significant washer movement (outside of 2σ uncertainty). Only the final measurements

168   (11 August 2009) and calculations were made relative to the washers. From moss ball position

169   data, we calculated mean speeds and azimuths (travel directions) between position

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170   measurements for each moss ball. Moss ball velocities are reported relative to a reference

171   frame that travels with the ice surface, into which the reference stakes were drilled and onto

172   which washers were placed. Velocities are therefore unaffected by bulk glacier motion.

173   To quantify glacier ablation, the height of each stake above the local ice surface was re-

174   measured during each visit and periodically re-drilled into the ice as necessary. Ablation

175   reported in this study is the mean ice surface lowering rate calculated for each of the three

176   stakes. As an assessment of ablation uncertainty, we also calculated the maximum deviation of

177   any single stake's ablation rate from the overall mean.

178   We assessed the potential for East/West asymmetry in the direction of incoming solar

179   radiation as a control on the direction of moss ball movement using a time series of solar

180   radiation from a Remote Automatic Weather Station (RAWS) located 15 km up-glacier from our

181   study site and approximately 500 m higher in elevation. The RAWS site, at Gates Glacier

182   (https://wrcc.dri.edu/cgi-bin/rawMAIN.pl?akAGAT), is located on a ridge above the Kennicott

183   Glacier and records incoming solar radiation and other meteorological variables every hour. To

184   evaluate the relative levels of solar energy arriving at our field site before and after solar noon,

185   we integrated each afternoon's solar radiation and subtracted each morning's integrated solar

186   radiation from it, thus arriving at a daily metric of the morning/afternoon solar energy

187   asymmetry. Values near 0 indicated equal amounts of energy arriving during mornings and

188   afternoons, positive values indicated more solar energy during the afternoons than mornings,

189   and negative values revealed more incident energy during the mornings.

190

191   *Persistence*

192   We sought to understand how long mature glacier moss balls persist on the landscape,

193   particularly across years. We hypothesized that mature moss ball longevity might vary due to

194   differences in environmental conditions (e.g., precipitation, freeze-thaw cycles) or random

195   chance (e.g., a crevasse opening within a key area). Furthermore, we wanted to know not only

196   how likely we are to detect glacier moss balls, given that they had persisted within the study

197   area, but also if our detection probability varies among years. To do this, we fit capture-

198   recapture models of annual survival to each glacier moss ball included in the study. Because

199   moss balls were individually marked but were not equipped with radio-transmitters or other

200   devices which would allow us to know their ultimate fates, we applied Cormack-Jolly-Seber

201   (CJS; Lebreton et al. 1992) survival models. These CJS models develop a "capture history" of

202   each moss ball to estimate apparent survival (i.e., the probability that an individual is in the

203   population at time i and still in the population at time i+1) and probability of detection if they

204 persisted within our study area. Survival estimates from CJS models only represent apparent
205 survival because emigration cannot be estimated from survival data with unknown fates (i.e., we
206 did not know if a tagged moss ball had disaggregated, lost its identifying bracelet, or was no
207 longer in the study area). Therefore, our estimates of apparent survival are likely to
208 underestimate true survival (e.g., a moss ball might have lost its bracelet or moved out of the
209 study site). In addition, CJS models also account for imperfect detection. In our case, if a moss
210 ball persisted within our study area but was overlooked.
211   Using our individual moss ball annual detection data (1 = detected, 0 = not detected), we
212 fit four competing CJS survival models, including the null model [no effect of year on apparent
213 survival (ϕ) or detection probability (p); Model 1)], an effect of year on ϕ (Model 2), an effect of
214 year on p (Model 3), or an effect of year on both ϕ and p (Model 4). We then selected the
215 model(s) best supported by our data using Akaike's information criterion (AIC; Akaike 1998),
216 adjusted for small sample size (AICc; Hurvich and Tsai 1989). Our model selection approach
217 was based on model likelihoods and models were penalized for extra parameters to favor
218 parsimony.
219   Finally, we calculated the average life expectancy of a mature glacier moss ball. To do
220 this, we used annual survival rates based on life-table analysis (Deevey Jr 1947; Millar and
221 Zammuto 1983), in which average life expectancy was calculated as -1/ln(Annual Survival
222 Rate). Because this estimation of life expectancy is quite sensitive to annual survival rate, we
223 calculated it for both the lowest annual survival rate and the mean annual survival rate. Thus,
224 the true average life expectancy might be substantially greater than the conservative values
225 estimated here. This framework for estimating average life expectancy does not account for
226 variable mortality rates when glacier moss balls are first forming or nearing the end of their
227 lifespans.
228
229 **Results:**
230 *Study area*
231   Our study area was located on a "bare ice" glacier surface, between two medial
232 moraines covered by coarse-grained, angular, rock debris. However, two types of sediment
233 distinguish the study area surface from what would be considered clean, pure, water ice. First,
234 glacier moss balls were found amidst gravel and small boulders (< 30 cm diameter), spaced
235 every ~1 m. Second, the ice surface has an unusually pervasive, fine-grained sediment cover,
236 ~1-3 mm thick, which partially blankets the otherwise bare ice. Image processing indicated that
237 this fine sediment covers approximately 70% of the study area surface. This low albedo

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238   sediment cover is visible in all inspected satellite imagery of the site and first appears at lower

239   concentrations emerging from cleaner ice ~1 km northwest of the study site (Fig. 1b). Down-

240   glacier of the study site, the low albedo region extends ~1.7 km as a ~300-m-wide, rounded

241   finger that spans adjacent medial moraines, in a manner consistent with wind-deposited dust,

242   draping over underlying geomorphic features. Therefore, we interpreted the southeast (135°)

243   trend direction of this low albedo finger to be the prevailing, down-glacier, katabatic wind

244   direction. During the 26 days of glacier ablation measurements, the ice surface lowered by 1.91

245   m due to melt and sublimation. Ablation rates ranged from 5.8-9.6 cm per day (cm d^{-1}) between

246   measurement times and averaged 7.3 cm d^{-1}.

247

248   *Movement*

249   Glacier moss ball movements varied systematically over the study period, with increases

250   and decreases that coincided with changes in direction (Figs. 2-3). Median moss ball speed was

251   2.5 cm d^{-1}, but their rates varied widely throughout the season. The median speed started at 1.8

252   cm d^{-1} in late June, increased to 4.0 cm d^{-1} at the start of July, then slowed to 2.0 cm d^{-1} during

253   late July/early August. The maximum observed speed for any glacier moss ball was 7.8 cm d^{-1}

254   during the 5-day period from July 9-14 (excluding two outlier speeds that were more than 8

255   interquartile ranges greater than the median, 14.2 and 21.0 cm d^{-1}, and which were based upon

256   particularly uncertain moss ball positions). The interquartile range of moss ball speeds was

257   approximately 50% of the median speed; thus, these observed increases and decreases in

258   speed reflect changes in the entire population of moss balls.

259   The direction of glacier moss ball movements was not random. Rather, glacier moss

260   balls underwent clear changes in their direction of motion (i.e., azimuth) throughout the summer

261   season (Fig. 3a). While individual moss balls moved in many directions, when viewed in

262   aggregate, azimuths of the population clearly clustered over time. Early in the season, median

263   moss ball motion was south-southeast (165°) but over the ensuing weeks azimuths

264   progressively increased, such that at the end of the measurement period the median azimuth

265   was west-southwest (240°; Fig. 3a).

266   Considering speeds and azimuths together, we see the moss ball population initially

267   moving at 2 cm d^{-1} to the south for 9 days, then the group nearly doubles its speed to 4 cm d^{-1}

268   while deviating slightly to the right (towards the west). After a week at these maximum speeds,

269   speeds drop by 25% to 3 cm d^{-1} while also deviating 45 degrees further towards the west for five

270   days. During the next 5-day measurement period, speeds drop further, back to 2 cm d-1 while

271   the azimuths turn another 10-15 degrees further west. Over the final 28-day measurement

272 period, the azimuths remain stable, while speeds continued to fall. This decrease in speed is
273 apparent in the decline of the upper quartile of speeds, despite our not making sufficient new
274 measurements to influence the median speed.

275   Our fine-scale movement and ablation data allowed us to compare glacier moss ball
276 speeds and azimuths with potential drivers of their motion. We find that more rapid moss ball
277 speeds are associated with more rapid ablation; an ordinary least squares model between
278 ablation rate and speed indicates that, on average, for every 1 cm of surface ablation, the
279 glacier moss balls move horizontally 0.34 cm (Fig. 3b). However, the relationship between
280 ablation rate and speed is relatively weak (R^2 = 0.40). It should also be noted that during the
281 course of our study, participants in a program hosted by the Wrangell Mountains Center,
282 McCarthy, Alaska, visually confirmed the posited primary movement method described by
283 Porter et al. (2008), when a glacier moss ball was observed rolling off its elevated pedestal and
284 inverting in the process.

285   The directions of moss ball motion, however, are more puzzling. The southern and
286 western directions of moss ball movement are clearly distinct from both the prevailing, katabatic
287 wind direction as inferred from the dust plume (towards the southeast) or the downhill direction
288 of the gently sloping ice surface (towards the east-northeast; Fig. 3a). The herd-like change in
289 travel direction, from an initially southerly direction to a southwesterly direction late during our
290 measurement period, could potentially be explained by a shift in the dominant direction of
291 incoming solar radiation. If, during the latter portion of July and August, 2009, the afternoons
292 were sunnier than the mornings, then we would expect faster ice surface lowering on the
293 southwest side of moss balls than on their northeast sides, and the moss balls would be more
294 likely to roll off their ice pedestals towards the southwest, as observed. However, our analysis of
295 solar radiation measurements revealed no such asymmetry (Fig. S1). While some days
296 experience more solar radiation before or after noon, there was no pattern consistent with
297 morning clouds and afternoon sun. We do not expect preferential melting on the southwest
298 sides of moss balls during the latter portion of July and early portion of August, 2009. Identical
299 analysis using data from a boreal forest weather station site 20 km SE of our study site (RAWS
300 site: May Creek, AK) revealed a very similar pattern of solar radiation to the Gates Glacier site,
301 and the same lack of asymmetry in daily solar radiation timing. Thus, with the available data, we
302 cannot explain the direction of moss ball motion.

303

304 *Persistence*

305   We initially tagged 30 glacier moss balls in 2009. We subsequently recaptured 18 moss

306   balls each in 2010, 2011, and 2012 (although this was not the same 18 moss balls each year).

307   Recapture rates for individual moss balls were highly variable with some never seen again after

308   the first year (n = 8) and others detected every year (n = 13). The best-fit survival model

309   included differing apparent survival (ϕ) among years, but with constant detection probability (p;

310   Model 2; Table 1). This model received 58% of AICc weight, compared to 26% for the null

311   model (Model 1), and less than 10% for the other models (Models 3 & 4; Table 1). The average

312   annual rate of apparent survival, ϕ, based on the null model, was 0.86 [95% confidence interval

313   (CI) = 0.75-0.93], and the average detection rate was 0.84 (95% CI = 0.70-0.92). When

314   parameterized by year, the annual apparent survival rate ranged from 0.74 in 2009-2010 to 1.0

315   in 2011-2012 with a particularly large 95% CI for 2010-2011 (Table 2; Fig. 4).

316   Our detection rate estimates may underestimate actual glacier moss ball survival for

317   several reasons. First, at least four glacier moss balls lost their marking bracelet after the first

318   year because we found the marking bracelet on the ice, separate from a moss ball. Second,

319   another moss ball partially obscured its bracelet by growing to cover the beads, but we were

320   able to detect a single bead and then delicately "excavate" the bracelet. Since we did not

321   destructively search glacier moss balls that did not have an obvious bracelet, it is possible that

322   additional instances of lost marking bracelets or growth to cover beads may have impacted our

323   detection. Third, between 2009 and 2010, two tagged moss balls fell inside of a shallow

324   crevasse within the study area. The two crevasse-bound glacier moss balls persisted, and likely

325   continued to photosynthesize and grow to some capacity for the remainder of the study. We

326   continued to check crevasses in the study area carefully, but some moss balls could have fallen

327   into deeper crevasses, or into shallow crevasses in a way that obscured their markings, and

328   therefore persisted without detection.

329   Our estimate of average life expectancy for a mature moss ball varied depending on

330   whether the lowest overall or mean annual survival rate were used. If using the lowest annual

331   survival rate (0.74), average life expectancy was 3.3 years (95% CI = 1.67-7.18). However, we

332   expect this life expectancy to be biased low to some extent, because we were only able to

333   estimate apparent survival (e.g., some insecure tags fell off moss balls that likely still persisted).

334   If using the mean annual apparent survival rate across the entire study (0.86), average life

335   expectancy rose to 6.63 years (95% CI = 3.48-13.78). This estimate may be biased high

336   because we did not tag any new moss balls in years 2 and 3 (2010 and 2011), but simply re-

337   captured existing (and therefore high survival probability) glacier moss balls. When thinking of

338   lifespan, it is relevant to note that we also observed a glacier moss ball split roughly in half

339   during the course of the study along its intermediate axis. The moss ball had become elongated

340   and essentially pulled apart. This mechanism may contribute to keeping glacier moss balls

341   ovular and represent a mode of moss ball genesis.

342

343   **Discussion:**

344   Glacier moss balls are intriguing components of glacier ecosystems that integrate

345   physical (e.g., debris cover) and ecological (e.g., invertebrate colonization) factors into a unique

346   habitat type. Previous research has revealed a great deal about glacier moss ball biology (e.g.,

347   their invertebrate colonizers, Coulson and Midgley 2012) yet their movement and longevity has

348   remained unexplored. It has been speculated that glacier moss ball movement patterns likely

349   follow the general downward slope of the glacier (Porter et al. 2008) and that they represent an

350   ephemeral habitat type on glaciers, a factor that may limit colonization by specific invertebrate

351   taxa (e.g., a lack of spiders; Coulson and Midgley 2012). Our results did not align with these

352   predictions of movement and persistence.

353

354   *Movement*

355   Even on the gently-sloped Root Glacier, glacier moss balls move relatively quickly (~2.5

356   cm d^{-1}) in similar directions and at similar speeds. Herd-like moss ball movements did not,

357   however, follow the downward slope of the glacier, the dominant wind direction, nor the

358   dominant direction of incoming solar radiation (Figs. 3, S1). Thus, we are left with a puzzling

359   question: why do the azimuths of glacier moss balls appear to shift simultaneously throughout

360   the summer season, resulting in the moss ball "herd" synchronously changing directions (Fig.

361   3a)? Moss balls began the season moving generally south and slowly transitioned towards the

362   west. Given their movement independence from the dominant wind direction and downhill

363   direction of the glacier, we speculated that shifts in patterns of solar radiation drive this pattern.

364   Perhaps the weather transitioned from clear mid-day skies during late June and early July

365   (associated with the most rapid motion and southerly azimuths), to a different weather pattern in

366   late July of morning clouds and afternoon sun. Such a change could drive enhanced ablation on

367   the west sides of moss balls, and therefore preferential westward movement. However, we

368   found no evidence for diurnal solar radiation asymmetry during the study period (Fig. S1).

369   The relative contributions of downslope gravity versus another factor (e.g., solar

370   radiation) almost certainly depend on glacier steepness. Porter et al. (2008) posited a

371   considerable effect of gravity on glacier moss ball movement for a relatively steep (9.6°)

372   Icelandic glacier which contrasts with our much flatter Root Glacier study area (~3°). Still,

373 regardless of steepness, differential melt patterns create pedestals that moss balls rest upon

374 and, eventually, enough ice melts below the moss ball causing it to fall and flip (Porter et al.

375 2008). Assuming glacier moss balls are, on average, ~10 cm in their intermediate axis, and their

376 only means of movement is melt-induced flipping driven by pedestal emergence at the rate of 6-

377 9 cm d^{-1}, their rates of movement would imply each glacier moss ball flips every ~2-4 days.

378 However, we cannot rule out alternative modes of glacier moss ball movement. Many glacier

379 moss balls have one side that is flattened and commonly faces down, while a more rounded,

380 vegetated side faces skyward (Shacklette 1966). Given this orientation, an alternative scenario

381 is that glacier moss balls also move by basal sliding over the wet glacier surface below.

382

383 *Persistence*

384   Glacier moss balls persist across multiple years as stable ecological units. On average,

385 86% of the mature glacier moss balls included in this study survived annually which translates to

386 a lifespan of more than 6 years. Thus, with high rates of survival across multiple years, and

387 relatively high detection rates, we consider glacier moss balls to be long-lived, rather than

388 ephemeral, glacier features. Unlike living individual organisms which can senesce as they age

389 (e.g., Loison et al. 1999), moss ball survival rates are unlikely to decline with time in the

390 traditional sense, nor should they exhibit density dependent survival (e.g., Festa-Bianchet et al.

391 2003). However, unlike traditional systems, factors that control disaggregation are likely the key

392 process underlying moss ball longevity. The temporal stability of moss balls means they could

393 exist for long enough to develop complex biotic communities (e.g., Coulson and Midgley 2012).

394 However, the degree to which geographic location (e.g., distance to a glacier margin), and not

395 persistence, influences invertebrate colonization remains to be tested.

396   The limited scope of our mark-recapture data collection precludes us from drawing

397 conclusions about the inter-annual drivers of moss ball apparent survival. However, we can

398 highlight factors that may influence it. First, it is possible that glacier moss balls moved more

399 frequently out of the study area in one year versus others, perhaps due to exceptionally clear

400 skies (and thus higher rates of glacier ablation). Second, we observed a number of fragmented

401 moss balls. Fragmentation may be a normal part of moss ball growth trajectories, too frequent

402 or intense freeze thaw cycles, or an as yet unknown factor. If glacier moss balls did survive

403 within our study area, they had an 84% probability of being detected in a given year. This

404 indicates that our bracelet and colored beads marking scheme was effective. However, for

405 future studies, more robust marks should be considered (e.g., passive integrated transponder,

406 PIT; Castro-Santos et al. 1996).

407

Genesis, growth, and disaggregation

408
409   Our results allow us to add new speculation about patterns of glacier moss ball growth
410   as well as additional evidence for previous hypotheses regarding their genesis and
411   disaggregation (e.g., Heusser 1972; Perez 1991). In terms of growth, our documentation of
412   glacier moss balls rolling over a fine-grained, wet, sedimentary substrate is consistent with
413   growth through adherence of sediment to an existing moss ball. We observed "dirty" moss on
414   some glacier moss balls in our study area. As the moss itself grows, this adhered sediment may
415   become integrated within the fibrous material, increasing the size of the glacier moss ball. Field
416   observation of moss growth over and around our identification bracelets indicates that several
417   millimeters of growth can occur within years. However, the observation that most bracelets were
418   not engulfed by sediment accumulation and moss growth during our four-year study period
419   suggests either generally slow growth or an upper limit on moss ball size.

420   Understanding year-to-year moss ball growth, however, does not explain moss ball
421   genesis, nor disaggregation. It is well-established that fibrous moss provides the skeletal
422   structure that allows moss balls to be cohesive, ovoid structures. A source of moss spores is
423   therefore essential to moss ball genesis (in our study, putatively, the Donoho nunatak). The
424   question, then, is how glacier moss balls begin to grow in the first place, and on what substrate.
425   Eythórsson (1951) suggested that a "stone kernel" at their centers is key. However, later
426   investigations (e.g., Shacklette 1966; Coulson and Midgley 2012) found mixed results that
427   largely reflected a consensus that there is no general rule about rock cores at the center of
428   glacier moss balls. Our exploratory testing of moss balls also indicated that some, but not all,
429   moss balls contained a ~1-cm gravel "kernel" at their centers. Potentially, these kernels, with
430   adhered fine-grained sediment, provide a growth substrate for initially wind-deposited moss
431   spores. In our study area, the co-occurrence of moss balls within an unusually extensive, fine-
432   grained "plume" of sediment cover (Fig. 1b) aligns with a similar observation by Heusser (1972)
433   for the Gilkey Glacier in southeastern Alaska, USA. The origin of this fine-grained sediment is
434   unknown, but in satellite imagery (Fig. 1b), it appears to originate from the ice itself and may be
435   a volcanic ash layer being carried down from the high, volcanic, Wrangell Mountain peaks.

436   We identified few glacier moss balls greater than ~15 cm on their long axis. Generally,
437   moss balls appear to rarely exceed ~10 cm except for rare cases in Alaska where they have
438   been reported up to 18 cm (Benninghoff 1955; Heusser 1972). Why glacier moss balls in Alaska
439   appear to grow larger than elsewhere in the world remains an open question but, regardless of
440   location, there appears to be some size limiting process within the moss ball lifecycle.

441 Shacklette (1966) suggested that the tensile strength of moss stems may be key. Exceeding

442 this tensile limit may occur when the moss ball major axis grows too great relative to the

443 intermediate axis. For instance, when a moss ball becomes too elongated, subtle variations in

444 ice surface topography may lead the two ends of a moss ball to move in different directions and

445 tear in the middle. During our study, we observed a splitting of a long, linear moss ball. While

446 this process applies an upper-limit to moss ball size it also circles back to inform questions

447 regarding the presence of a rock kernel. If the upper size limit is reached and a moss ball splits,

448 only one of the two remaining moss balls involved in this "cloning" process will retain the gravel

449 kernel. This may explain why a number of moss balls do not appear to have any coarse-grained

450 rock at their cores. However, it is worth noting that in the case of Coulson and Midgley (2012),

451 none of the moss balls in the study had a rock core. Therefore, glacier moss balls can almost

452 certainly form without a "seed" rock.

453

454 **Conclusions**

455   In this study, we extended previous research on glacier moss balls to quantify their

456 movement and persistence on an Alaskan glacier. We showed that glacier moss balls move

457 relatively quickly, at a rate of centimeters per day, in herd-like fashion. However, we could not

458 explain the direction of moss ball movement by only considering the physical surface of the

459 glacier (i.e., the downslope direction), the intensity of glacier ice ablation, and patterns of solar

460 radiation. Thus, it appears a still unknown external force influences glacier moss ball movement

461 on the Root Glacier. We also showed that mature moss balls are long-lived, with an average life

462 expectancy of more than 6 years. The potential for glacier moss balls to act as relatively stable,

463 long-term ecological units highlight their potential to act as key biotic habitat. Coulson and

464 Midgley (2012) previously described invertebrate colonization of glacier moss balls and

465 suggested that a lack of Enchytraeidae and Aranea may be the result of the ephemerality of

466 moss balls in glacier habitats. Our results contrast this idea. Instead, we postulate that selective

467 invertebrate colonization of glacier moss balls depends instead on their locations and frequent

468 movements or, as Coulson and Midgley (2012) noted, the variable dispersal capacities of

469 colonizers. Given the importance of microbial diversity to carbon cycling (Anesio et al. 2009),

470 ecosystem function (Anesio et al. 2017; Hotaling et al. 2017a,b), and even albedo (Ganey et al.

471 2017), future efforts to understand the microbial ecology of glacier moss balls will further

472 illuminate their ecological role in glacier ecosystems. Like cryoconite, the granular, darkly

473 pigmented dust on glacier surfaces that drive hotspots of microbial activity (Cook et al. 2016),

474 glacier moss balls may have similar value at the ecosystem scale.

475

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480

Compliance with Ethical Standards:

The authors declare no conflicts of interest.

483

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Table legends:

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).

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.

Figure captions:

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.

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 2σ 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).

Fig. 4. Estimates of apparent moss ball survival (ϕ; dark circles) with 95% confidence intervals (thin dark lines) from model 2, the best-fit model, which included a year effect on ϕ. 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.

17

606 **Tables**
607
608 Table 1
609

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

610
611 Table 2
612

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)

613