The Scientific Naturalist

Ecology, 101(4), 2020, e02947

Macroinvertebrates on glaciers: a key resource for terrestrial food webs?

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Manuscript received 19 September 2019; accepted 11 November 2019. Corresponding Editor: John Pastor.

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Citation: Hotaling, S., P. H. Wimberger, J. L. Kelley, and H. E. Watts. 2019. Macroinvertebrates on glaciers: a key resource for terrestrial food webs? Ecology 101(4):e02947. 10.1002/ecy.2947

Key words: climate change; cross-boundary subsidy; cryosphere; glacier biology; glacier subsidy; Gray-crowned Rosy Finch; ice worm; Mesenchytraeus solifugus*; mountain ecology; trophic ecology.*

Glaciers around the world support diverse, thriving ecosystems (Rosvold 2016, Hotaling et al. 2017a). Though dominated by microbial life, glaciers also provide key habitat for larger macroinvertebrates (Hotaling et al. 2019) and vertebrates (Rosvold 2016). However, the ecology of larger organisms on glaciers, including trophic connections among them, remains largely unknown. This knowledge gap is particularly pressing in light of the rapid, ongoing glacier recession occurring in mountain ecosystems (Roe et al. 2017). Throughout the late spring and early summer of 2019, we observed Gray-crowned Rosy Finches (*Leucosticte tephrocotis*, hereafter Rosy Finches) feeding upon glacier ice worms (*Mesenchytraeus solifugus*; hereafter "ice worms") on the Paradise Glacier of Mount Rainier, Washington, USA (Fig. 1a). These were not one-off observations; rather, every visit to the Paradise Glacier from mid-June to July (four visits), included an observation of at least one Rosy Finch feeding on ice worms (range = 1–8 Rosy Finches simultaneously feeding). Moreover, surveys on other glaciated peaks of the Pacific Northwest indicate this trophic connection is not unique to Mount Rainier (S. Hotaling and P. H. Wimberger, *personal observations*). Instead, Rosy Finches appear to feed on ice worms where the geographic ranges of the two species intersect. While breeding phenology of Rosy Finches nesting on Cascade Volcanoes remains unknown, high-elevation populations in the Sierra Nevada and Rocky Mountains lay and incubate their eggs from mid-June to July (Wheeler 1940, Johnson 1983), the same time period where our observations indicate that ice worm predation peaks in the Pacific Northwest (PNW). In this paper, we describe this phenomenon, bird predation of glacier ice worms, and discuss its ecological implications. We conclude by highlighting the potential for similar trophic connections to exist in ice-dominated ecosystems worldwide.

Ice worms are small, heavily pigmented annelids (~1–1.5 cm in length; Fig. 1b) that require permanent ice for survival and reproduction (Hotaling et al. 2019). On Mount Rainier, ice worms first appear on the glacier surface in late spring (e.g., early June) and can be observed daily until October (S. Hotaling, *unpublished data*). On a typical summer day, ice worms migrate vertically a few hours before sunset from within the glacier to the surface where they spend approximately four daylight hours, presumably to feed on microbiota in the glacier's sun-softened upper layer (Hotaling et al. 2017a). Through this behavior, ice worms diurnally cover coastal glaciers from central Oregon to southern Alaska at densities in excess of 100 worms/m^2 (Fig. 1b). Generally, their densities are consistent across the ice surface and on Mount Rainier, they appear most abundant within an ~1,000-m elevational band (~2,250–3,250 m), with the upper limit likely determined by lower temperatures (Dial et al. 2016). To date, only adult Rosy Finches have been observed feeding on ice worms, typically at a rate of ~0.5–1 pecks/s during peak availability (Fig. 1a; P. H. Wimberger, *personal observations*). However, at least five other bird species, in addition to Rosy Finches, also feed on ice worms: American Pipits (*Anthus rubescens*), Common Ravens (*Corvus corax*), Horned Larks (*Eremophila alpestris*), Semipalmated Plovers (*Charadrius semipalmatus*), and Snow Buntings (*Plectrophenax nivalis*; Goodman 1971; P. H. Wimberger, *personal observations*).

Alpine ecosystems are often harsh and resource-limited, with large swaths of glacier cover and limited snow-free area. Thus, with glacier ice dominating, there is clear potential for glacier-derived resource subsidies to be critical to adjacent terrestrial food webs. Cross-boundary subsidies, where resources are transferred between distinct habitat types (e.g., glacier ice and adjacent exposed ground), can positively influence the consumers that exploit them. For instance, aquatic subsidies to terrestrial consumers have been highlighted for an array of taxonomic groups, from invertebrates to birds (Epanchin et al. 2010). In mountain ecosystems, snow cover limits permanent residency for most organisms,

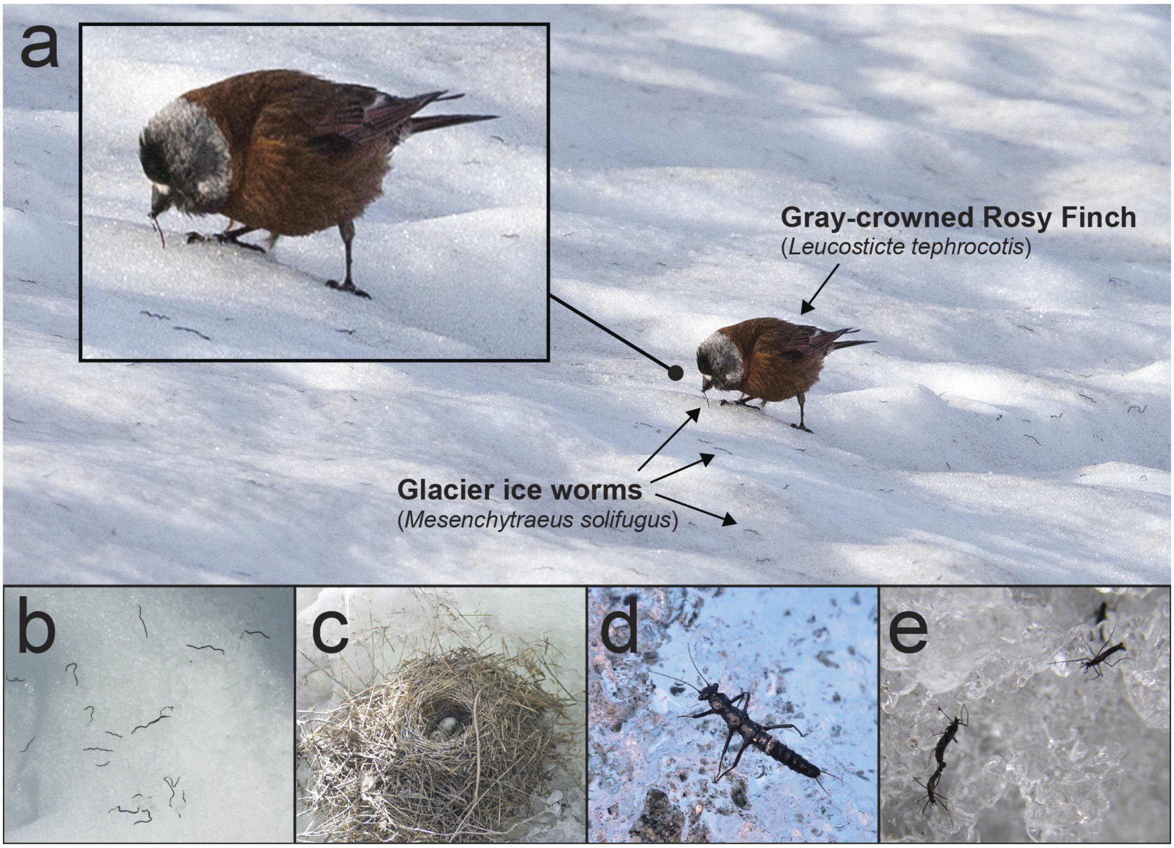

FIG. 1. (a) One of six Gray-crowned Rosy Finches (*Leucosticte tephrocotis*) simultaneously feeding on abundant (>100 worms/m^2) glacier ice worms (*Mesenchytraeus solifugus*) at ~2,500 m on the Paradise Glacier of Mount Rainier, Washington, USA. The photograph was taken near dusk on 17 June 2019. (b) Ice worms on the Paradise Glacier. (c) A White-winged Diuca Finch (*Idiopsar speculifer*) nest with eggs on the ice of the Quelccaya Ice Cap, Peru. (d) A nymph of the Patagonian dragon (*Andiperla willinki*), a glacier-obligate stonefly. (e) Adult glacier midges (*Diamesa kohshimi*) on the Yala Glacier, Nepal.
Photograph credits: (a) Scott Hotaling, (b) Rachael Mallon, (d) Doug Hardy, (d, e) Shiro Kohshima.

therefore species that can move across habitat boundaries easily (e.g., birds) may be especially likely to take advantage of glacier-derived resources. Rosy Finches nest high in the major mountain ranges of western North America, often near permanent snowfields and glaciers (Macdougall-Shackleton et al. 2000). On heavily glaciated peaks like Mount Rainier, Rosy Finches appear to initiate breeding when seasonal snow cover is near its peak (e.g., mid-June), snow-free foraging grounds are extremely limited, and foods typical of their diet (e.g., seeds, insects) are either scarce or would require long flights to lower elevations to access them. In the high Sierra, Rosy Finches rely heavily on aquatic subsidies (e.g., emerging mayflies) to feed their young (Epanchin et al. 2010). Our observations suggest a similar, close ecological coupling between Rosy Finches and ice worms. Indeed, ice worms present a regular, temporally stable, lipid- and protein-rich resource during what is almost certainly a key reproductive period for Rosy Finches in the region.

From a global perspective, predicted impacts of receding glaciers on hydrology, biodiversity, and geomorphology have been widely discussed (Hotaling et al. 2017b). However, the idea that glaciers may provide subsidies to terrestrial food webs has been overlooked despite the potential for these relationships to exist worldwide. For instance, in the Andes, the White-winged Diuca Finch (*Idiopsar speculifer*) nests directly on high-elevation glaciers (Fig. 1c) where predators (e.g., the Andean fox, *Lycalopex culpaeus*) venture onto glaciers to prey on both adults and eggs (Hardy et al. 2018). Predation by larger metazoans on glacier-obligate birds highlights the potential for vertebrate-to-vertebrate resource subsidies to exist in glaciated ecosystems. In addition to ice worms, other glacier-obligate macroinvertebrates that may subsidize higher trophic levels include another ice worm species, the Tibetan ice worm (*Sinenchytraeus glacialis*, Liang 1979); the "Patagonian Dragon" (*Andiperla willinki*; Fig. 1d), an ~2.5-cm stonefly inhabiting Patagonian glaciers (Vera et al. 2012); and two chironomid midges that inhabit glaciers in the Himalayas (*Diamesa kohshima*, Kohshima 1984; Fig. 1e) and New Zealand (*Zealandochlus latipalpis*, Boothroyd and Cranston 1999).

The potential for glaciers to provide resource subsidies (e.g., organic carbon) to downstream, aquatic ecosystems is well-known (Caraco et al. 2010). However, another direction of resource flux, glaciers subsidizing adjacent terrestrial food webs directly, is unexplored. In the case of alpine glaciers and Rosy Finches, it is possible that an abundant, consistent prey item like ice worms allows Rosy Finches to nest on the upper slopes of Mount Rainier and other stratovolcanoes, hundreds to thousands of meters above the permanent treeline. Moreover, nutrient limitations on mountain glaciers, including extremely low concentrations of phosphorous (Ren et al. 2019), likely translate to unique stoichiometry of ice worms and thereby their Rosy Finch consumers. Future studies exploring ecological stoichiometry in the mountain cryosphere, from primary producers (e.g., snow algae) to larger organisms (e.g., ice worms and birds), will yield key insights into nutrient fluxes in these ecosystems including the relative importance of macroinvertebrates to the diets of their consumers (Ren et al. 2019).

Ultimately, vertebrates (and other large-bodied organisms) deriving resource subsidies from macroinvertebrates living on glaciers raises many questions, ranging from nutrient fluxes in mountain ecosystems to impacts on vertebrate behavior. However, the magnitude of these relationships and their prevalence, both geographic and temporal, remain largely unknown. Thus, as glaciers recede around the world, there is a pressing need to better understand trophic connections between glacier-obligate macroinvertebrates and their consumers before these relationships are permanently altered or lost.

Acknowledgments

We acknowledge that our research was conducted on the traditional lands of the Cowlitz, Muckleshoot, Nisqually, Puyallup, Squaxin Island, and Yakama tribes. We thank the staff of Mount Rainier National Park for their logistical support. S.H. was supported by NSF awards #OPP-1906015 and #IOS-1557795.

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