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Avian nesting and roosting on glaciers at high elevation, Cordillera Vilcanota, Peru

Spencer P. Hardy,[1,4]* Douglas R. Hardy,[2] and Koky Castañeda Gil[3]

ABSTRACT—Other than penguins, only one bird species—the White-winged Diuca Finch (*Idiopsar speculifera*)—is known to nest directly on ice. Here we provide new details on this unique behavior, as well as the first description of a White-fronted Ground-Tyrant (*Muscisaxicola albifrons*) nest, from the Quelccaya Ice Cap, in the Cordillera Vilcanota of Peru. Since 2005, >50 old White-winged Diuca Finch nests have been found. The first 2 active nests were found in April 2014; 9 were found in April 2016, 1 of which was filmed for 10 d during the 2016 nestling period. Video of the nest revealed infrequent feedings (>1 h between visits), slow nestling development (estimated 20–30 d), and feeding via regurgitation. The first and only active White-fronted Ground-Tyrant nest was found in October 2014, beneath the glacier in the same area. Three other unoccupied White-fronted Ground-Tyrant nests and an eggshell have been found since, all on glacier ice. At Quelccaya, we also observed multiple species roosting in crevasses or voids (caves) beneath the glacier, at elevations between 5,200 m and 5,500 m, including both White-winged Diuca Finch and White-fronted Ground-Tyrant, as well as Plumbeous Sierra Finch (*Phrygilus unicolor*), Rufous-bellied Seedsnipe (*Attagis gayi*), and Gray-breasted Seedsnipe (*Thinocorus orbignyianus*). These nesting and roosting behaviors are all likely adaptations to the harsh environment, as the glacier provides a microclimate protected from precipitation, wind, daily mean temperatures below freezing, and strong solar irradiance (including UV-B and UV-A). Indeed, the global range of White-winged Diuca Finch coincides relatively closely with the distribution of Andean glaciers, and because no nests are known to have been found away from ice, this species may be a glacier obligate. Given the number of individuals observed and diversity of species associated with, and possibly dependent on, the ice, ongoing loss of tropical glaciers may have a direct, negative effect on High Andean biodiversity. *Received 30 August 2017. Accepted 20 August 2018.*

Key words: Andes, glaciers, high-elevation, *Idiopsar speculifera*, *Muscisaxicola albifrons*, nesting, roosting.

Nidos y dormideros de aves en glaciares de alta elevación, Cordillera Vilcanota, Perú

RESUMEN (Spanish)—Además de los pingüinos, solo una especie de ave —el pinzón *Idiopsar speculifera*— se conoce por anidar directamente en el hielo. Aquí proveemos nuevos detalles de este comportamiento único, así como la primera descripción de un nido del mosquero *Muscisaxicola albifrons* del glaciar Quelccaya en la Cordillera Vilcanota de Perú. Desde 2005, hemos encontrado más de 50 nidos usados de *I. speculifera*. Los primeros dos nidos activos en abril de 2014 y nueve en abril de 2016, uno de los cuales fue filmado por 10 d durante el periodo de polluelos en el nido de ese mismo año. El video del nido revela episodios de alimentación poco frecuentes (>1 h entre visitas), lento desarrollo de los polluelos (estimado en 20–30 d) y alimentación por la vía de la regurgitación. El primer y único nido de *M. albifrons* fue encontrado en octubre de 2014, debajo del glaciar en esa misma área. Desde entonces, hemos encontrado otros tres nidos desocupados y un cascarón de huevo, todos en el hielo del glaciar. En Quelccaya también observamos múltiples especies en dormideros en grietas o cuevas debajo del glaciar, a elevaciones entre 5,200 y 5,500 m, incluyendo a *I. speculifera*, *M. albifrons*, así como el pinzón *Phrygilus unicolor*, y las agachonas *Attagis gayi* y *Thinocorus orbignyianus*. Todos estos comportamientos de anidación y dormideros son muy posiblemente adaptaciones al ambiente inhóspito, dado que el glaciar provee un microclima protegido de la precipitación, viento, temperaturas medias diarias por debajo del punto de congelación y una fuerte radiación solar (incluyendo UV-B y UV-A). Así, la distribución global de *I. speculifera* coincide con relativa cercanía con la distribución de los glaciares andinos, y dado que no se han encontrado nidos lejos del hielo, ésta podría ser una especie obligada del glaciar. Dado el número de individuos observados, y la diversidad de especies asociadas con y posiblemente dependientes del hielo, la pérdida progresiva de glaciares tropicales podría tener un efecto negativo directo en la biodiversidad de los altos Andes.

Palabras clave: alta elevación, Andes, anidación, dormideros, glaciares, *Idiopsar speculifera*, *Muscisaxicola albifrons*.

The Andes are among the highest and most biodiverse mountain ranges on the planet, yet as is the case for much of South America, the biology of many bird species breeding in this region remains poorly documented. Given their high elevation and tropical location, parts of the Andes represent an extreme environment with unique pressures on the local avifauna. One Andean subrange in southeastern Peru, the Cordillera Vilcanota, holds global elevation records for potatoes, angiosperms, orchids, amphibians, pelecypods, and lizards (Seimon et al. 2017). Within this mountain range is the Quelccaya Ice Cap, the largest tropical glacier on Earth (13.9°S, 70.8°W). Since the mid-1970s, the Quelccaya area has seen considerable research in glacial geology (e.g., Mercer et al. 1975, Arnao 1998, Stroup et al.

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[1] Department of Biology, Middlebury College, Middlebury, VT, USA

[2] Geosciences Department, University of Massachusetts, Amherst, MA, USA

[3] Mountain Guide (AGMP, UIAGM), Vicencio Expeditions, Huaraz, Peru

[4] Current address: Norwich, VT, USA

* Corresponding author: spencerphillipshardy@gmail.com

2015), paleoclimatology (e.g., Thompson et al. 1985), and modern climate (e.g., Hastenrath 1997).

In conjunction with ice-core drilling at Quelccaya (Thompson et al. 2013), a long-term climate and snow accumulation monitoring project was initiated in 2003 (Hardy 2008, Hurley et al. 2015). In the mid-2000s, fieldwork associated with this climate research at the summit revealed evidence of White-winged Diuca Finch (*Idiopsar speculifera*) nesting at 5,300 m on the ice cap (Hardy and Hardy 2008), rendering this species one of the highest-nesting passerines in the world, and the only non-penguin known to regularly nest on ice.

Breeding at this extreme elevation presents numerous unique physiological challenges to birds, including low air density and oxygen pressure (with both thermal and mechanical effects; Scott 2011), increased rate of water loss from eggs (Rahn and Ar 1974), low air temperature with extreme diurnal fluctuations (Martin and Wiebe 2004), intense incoming solar UV irradiance (Piazena 1996), and an extended wet season with year-around snowfall possible (Hurley et al. 2015). Despite these challenges, at least 60 species of birds representing 18 families are known from the Quelccaya area (SPH, pers. obs.).

Our primary objective was to provide the first detailed description of White-winged Diuca Finch breeding biology, a species currently undergoing taxonomic reevaluation (Remsen 2016). We also investigated possible explanations for the close association between this species and the glacier. In addition, we here provide the first evidence of glacier nesting by White-fronted Ground-Tyrant (*Muscisaxicola albifrons*), along with observations on several other species that may have independently evolved or learned similar associations with the glacier. The information we provide is based on 10 yr of glacier nest observations during the nonbreeding season, and 2 yr of breeding-season observations. Our observations contribute to the study of avian adaptation to elevation, and high-elevation tropical ecology.

Methods

Study area

The Cordillera Vilcanota is a glacierized range at the eastern edge of the Altiplano (Arnao 1998). With abundant Late Holocene moraines (Kelly et al. 2012), melting glaciers maintain numerous lakes and extensive bofedales (wetlands or *Distichia* peatlands) throughout the range, especially at elevations >4,500 m. These lakes and bofedales support locally high species richness and abundance (Doyle et al. 2003, Gibbons et al. 2016).

Quelccaya Ice Cap (QIC) is the largest glacier in the range and within the global tropics, currently encompassing ~40 km^2 (Albert et al. 2014). The ice cap's central summit area is a relatively flat dome at 5,680 m, with radial flow to outlet glaciers (e.g., Qori Kalis; Fig. 1). Excluding these outlet glaciers, the main ice cap spans a relatively small elevation range of ~300–400 m between the summit and the ice margin.

This study was concentrated on Quelccaya's western side to the south of Qori Kalis (Fig. 1), emphasizing the glacier edge (margin) and terrain deglacierized within decades to centuries (Supplemental Fig. S1 and S2). In conjunction with our funded mission of climate and glacier research on the ice cap, this study was conducted from camps near the glacier margin (Fig. 1) beginning in 2003, with observations every year since.

Nest and roost observations

Our nest searches and observations at QIC became increasingly systematic and thorough beginning in 2006. Annual surveys of 2–6 km along the ice margin (Fig. 1) recorded all nests, concentrations of old nest material, and any evidence of White-winged Diuca Finch predation (e.g., wing fragments, feather concentrations). Typically, observations also included photographs and GPS locations. Prior to April 2014, all visits to the field area were made during June–August (i.e., austral winter); at this time most nests appeared not to be in situ, having fallen from the steep ice margin to the ground below (e.g., Supplemental Fig. S3).

Avian observations in April and October 2014 were likewise ancillary to our funded fieldwork. However, discovery of active nests led to further investigation, which motivated an expedition to obtain film documentation of White-winged Diuca Finch nesting on glaciers. In April 2016 we were accompanied to QIC by a crew from the BBC Natural History Unit (Supplemental Reference). Expedition timing was determined only by the observation of 2 active nests in April 2014, a considerable gamble even without the 1.4 °C

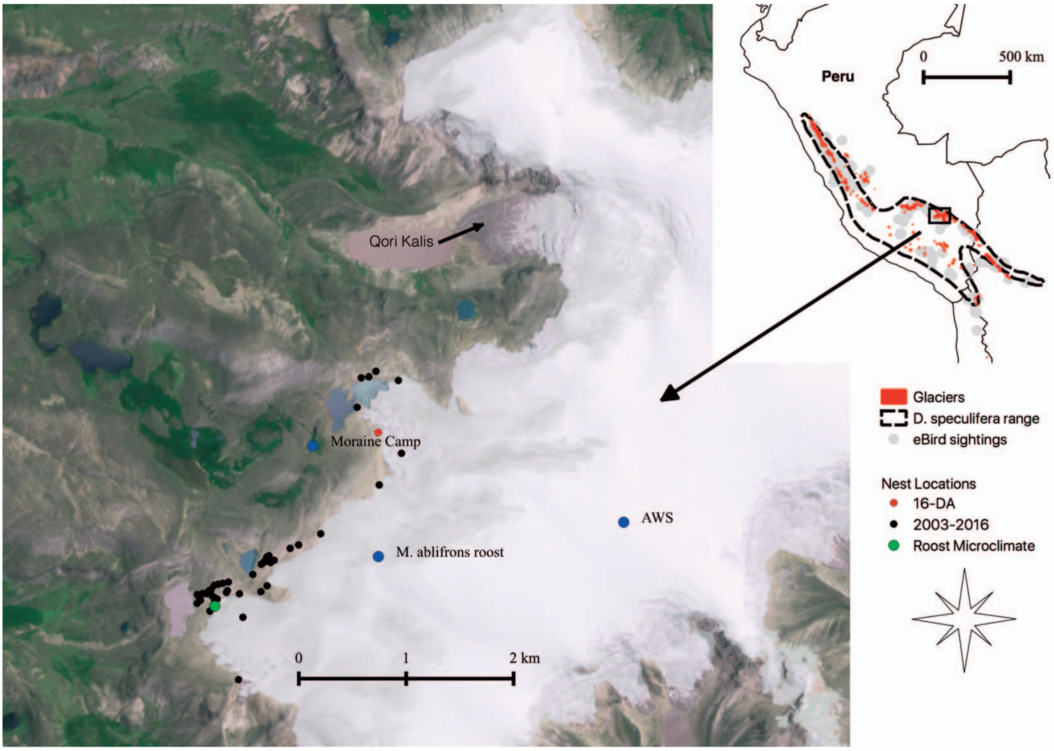

Figure 1. Quelccaya Ice Cap study site, within the Cordillera Vilcanota. All observed locations of White-winged Diuca Finch nests are shown with black dots. The active nest filmed in 2016 (16-DA) is shown in red. The global range of White-winged Diuca Finch is shown in the inset (Schulenberg et al. 2007, Hardy 2010), along with an estimated distribution based on all eBird records (Sullivan et al. 2009) with traveling distances of <50 km as of April 2016. Background image is a composite of ASTER and Sentinal-2 imagery acquired in 2016.

anomalous warmth of January–March 2016 associated with the 2015–2016 El Niño event (DRH unpubl. data, relative to 2007–2015). After locating a suitable, active nest, a remotely controlled camera was installed to observe nestlings.

An active nest discovered 21 April 2016, designated nest 16-DA, was selected for possible filming with a remotely operated camera. Although not visible from the ground, it was located by following adults flying onto the glacier, briefly disappearing into the cavity, and seen exiting with a fecal sac. The opening to nest 16-DA was ~40 m above the ground on a near-vertical, 60 m ice cliff facing approximately west (Supplemental Fig. S4).

The camera at nest 16-DA ("nestcam") was remotely operated, including zooming and panning, from a camouflaged tent near the glacier (Supplemental Fig. S4). A monitor provided a real-time view of activity at the nest. The nestcam was maintained and operated from 23 April to 3 May for ~8 h/d, during daylight hours. When the camera was first installed, the adults seemed hesitant to enter the nest. Accordingly, after one parent fed, the camera was removed and the nest site was undisturbed for a full day. When the camera was reinstalled on 25 April, the parents were not significantly bothered and continued to feed normally. Because of the high rate of ice-wall ablation, the camera had to be repositioned each morning, which was always done between feeding bouts. When the camera was being monitored, the clock time was recorded as parents entered or left the vicinity of the nest. By the end of the observation period (3 May), nest 16-DA was nearly exposed and beginning to tip, as the margin melted back. At least 7.5 h of edited nestcam video was recorded over 10 d, depicting all aspects of activity at the nest. Complementing this footage were day-long observations near the site by 2–8 people.

In addition to nest surveys since 2004, we also opportunistically noted and/or photographed avian behavior while working or camping near the glacier margin. During the late afternoon, pre-roost movements of White-winged Diuca Finch were consistently observed near the glacier margin, moving onto the ice. On 2 occasions, in July 2011 and April 2016, concerted efforts were made to document and quantify this White-winged Diuca Finch pre-roost behavior. Three locations (1 in 2011, 2 in 2016) were visited on 1 night each, starting in the late afternoon before roost movement had begun, and continuing until birds stopped appearing and/or it became too dark to see. Exact counts were only attempted in 2016 by 1 observer.

Nest and roost observations of other species were made incidentally; adult birds carrying food, fledglings demonstrating begging behavior, and assembly of birds near or on the glacier at dusk were noted and/or photographed.

Climate and microclimate measurements

A comprehensive, automated weather station (AWS) was installed at the ice cap summit in August 2003 (Fig. 1), with the objective to help develop a better understanding of ice core records recovered from the site in 1983 and 2003 (Hardy 2008). Measurements made at the AWS include wind speed and direction, air temperature and relative humidity, shortwave and longwave radiation, snow accumulation and ablation, and barometric pressure. Near-annual service of the station is necessary to raise the tower and accommodate a net annual snow accumulation of ~2.2 m, as depicted by Hardy (2011; also see Supplemental Fig. S5). Additional details about Quelccaya climate are available in Hurley et al. (2015, 2016) and Yarleque et al. (2016).

Microclimate measurements were made during brief field investigations in 2011. To compare thermal effects of roosting within vs. off the glacier, we placed temperature/light dataloggers (HOBO model UA-002-64; Onset Computer Corporation, Bourne, MA, USA) in potential and known roosting locations near the glacier margin (Fig. 1). Roosts were found by searching crevasses and other openings for evidence of birds (i.e., feathers, droppings). Additionally, a sensor was placed at ground level among rocks within 100 m of the ice margin to simulate a potential non-glacier roost location. Sensors were placed on a piece of fleece, preventing direct contact with the ice or ground.

Adjacent to the glacier margin (~25 m) a similar temperature logger (HOBO model H08-031-08; Onset Computer Corporation) with a full multi-plate radiation shield (model 41003; RM Young Company, Traverse City, MI, USA) was used to record ambient air temperature at a height ~1.5 m above the ground. Temperatures were recorded every 10 min in 2011 over 108 continuous hours. Data were processed with R 3.2.3 (R Core Team 2015).

Results

To provide a context for the environmental conditions to which White-winged Diuca Finch and other species have adapted at QIC, we first present a climate overview and results of an initial microclimate investigation. The QIC climate record from a location halfway through the atmosphere (515 hPa at AWS) provides a unique perspective on the nesting and roosting of passerine species that are among the highest-nesting species known.

Climate

At 14° south latitude near the eastern edge of the Altiplano, the Cordillera Vilcanota climate is characterized by a pronounced seasonality in humidity and precipitation, with less temperature seasonality than mid-latitude mountain ranges. A core wet season during the Southern Hemisphere summer (Dec–Feb) is associated with the highest annual cloud cover and humidity, as measured by incoming longwave radiation (Fig. 2). This wet season is responsible for about half of the QIC summit's snowfall (Hurley et al. 2015). Nonetheless, snow occurs throughout the year (Fig. 2) and often extends to lower elevations during the austral winter dry-season months. The seasonality of air temperature is much less than that for precipitation, with an austral summer mean of –3.3 °C and mean during austral winter of –5.1 °C (see annual cycle shown in Fig. 2). Wind speeds (Fig. 2) are highest during July, averaging 5.0 m/s,

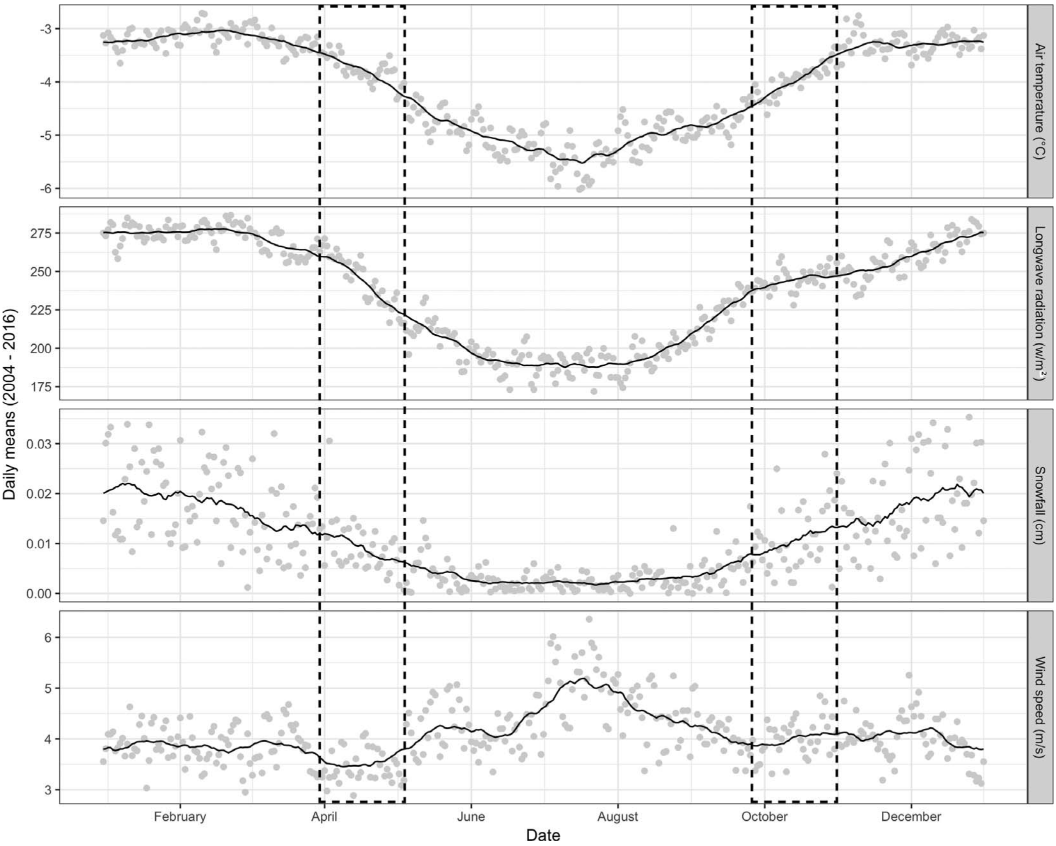

Figure 2. Seasonal climate at the summit of Quelccaya Ice Cap (~400 m above nest 16-DA). The black lines are 29-day moving averages of mean daily values for each variable (gray dots) during 2004–2016. Daily values were averaged across 7–13 yr depending on the available data. The dashed boxes indicate the likely nesting period for White-winged Diuca Finch (Apr) and White-fronted Ground-Tyrant (Oct). See text for discussion.

and most frequently from the northwest during winter, in contrast to the summer wet season when the wind is most frequently from the east, averaging 3.8 m/s.

In our study area near the glacier margin, some aspects of climate differ from those at the summit (Fig. 2), 300–400 m higher in elevation. Although we do not have a long-term record from the nest area, our years of subjective observations indicate that extrapolation over the horizontal distance of only ~2.4 km is justified. Incoming solar and downward longwave radiation—the most important energy terms—are likely similar at the sites. Snowfall differences are not known, although we have measured a strong gradient in net snow accumulation; the summit averages ~2 m of net accumulation annually, whereas net ablation is measured every year at the glacier margin. Based on on-site observations and analysis of satellite imagery (DRH, unpubl. data), snow accumulation on the landscape surrounding QIC rarely persists longer than days to weeks, especially outside the austral winter months. Air temperature in the nest area is likely to be ~2 °C higher, based on our finding of an average free-air temperature lapse rate of 5.4 °C/km (Bradley et al. 2009). Thus, an extrapolated mean air temperature of –1.1 °C during the wet season likely accounts for the lack of seasonal snow accumulation. Lastly, observed wind speeds in the nest area are lower than over the expansive summit area; katabatic winds have not been observed, and are unlikely because of the minor elevation difference and lack of topographic channeling.

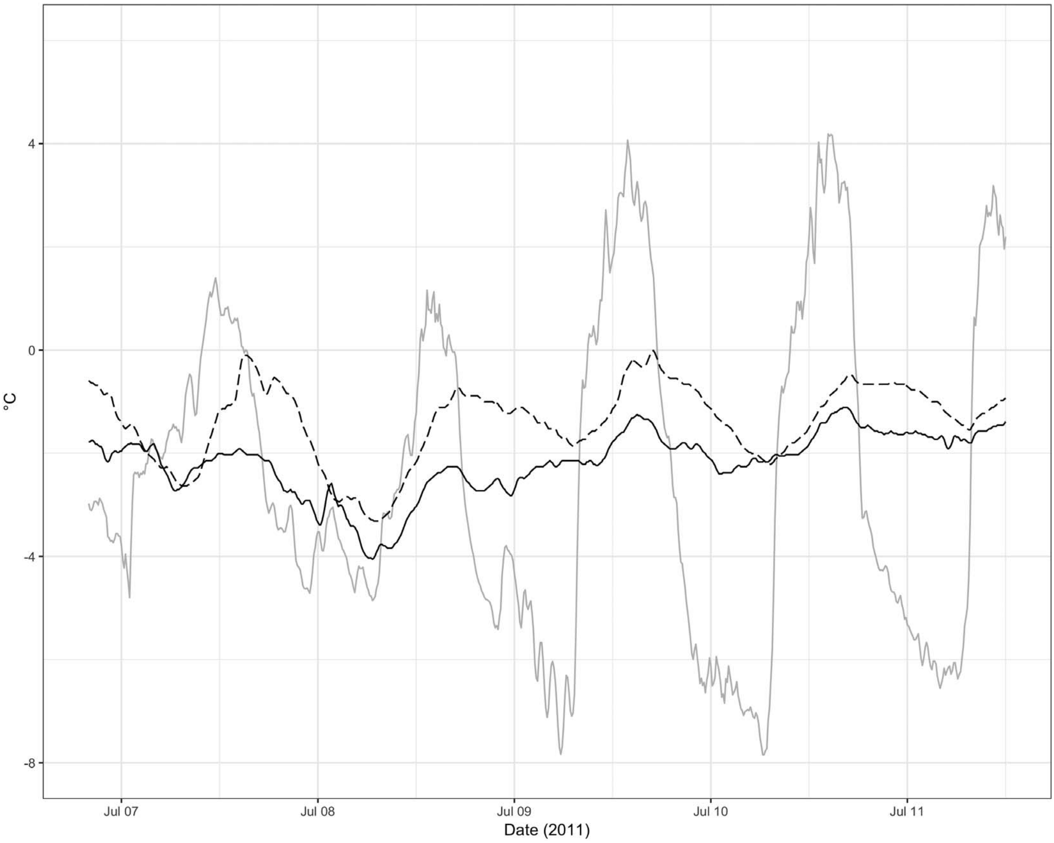

Figure 3. Daily temperature fluctuations during early July 2011 at the glacier margin. Air temperature at 1.5 m height adjacent to the glacier (gray) fluctuated up to 12 °C per day, while temperatures within an ice cavity (black line) and rock cavity (dashed line) were more stable. Values shown are 30 min moving averages.

Microclimate

The microclimate we investigated at Quelccaya reveals differences between the open environment in the margin area (at ~1.5 m above ground level) and that within an ice cavity or beneath the glacier, particularly at night—with considerably smaller diurnal temperature fluctuations in glacier cavities (Fig. 3). The magnitude of fluctuations varied from day to day, yet the glacier roost location had warmer nights than the surrounding air during the brief period of our microclimate measurements. This nocturnal thermal benefit of glacier roosts varied from ~1 °C to >5 °C. Two nights of similar short-term measurements in 2009 had similar results to those in 2011 (Fig. 3) but are also not directly comparable because of radiation shield differences. Finally, a sensor placed in a hypothetical alternative roost site among rocks in 2011 (~100 m from the glacier margin) also revealed a pattern of diurnal temperature fluctuation. Our microclimate measurements (Fig. 3) were only able to address the direct thermal effects of the glacier cavities, but we note that ice cavities likely also provide wind and longwave energy loss protection, as well as from precipitation.

Nesting

White-winged Diuca Finch—By 2008 we recognized that austral winter was not the breeding season for White-winged Diuca Finch. Although fresh-looking nests were found at ground level beside the ice margin, and sometimes in situ on the glacier, no other breeding evidence had been observed. Indeed, based on our understanding of Quelccaya-area climate, we hypothesized in Hardy and Hardy (2008) that Quelccaya glacier nesting

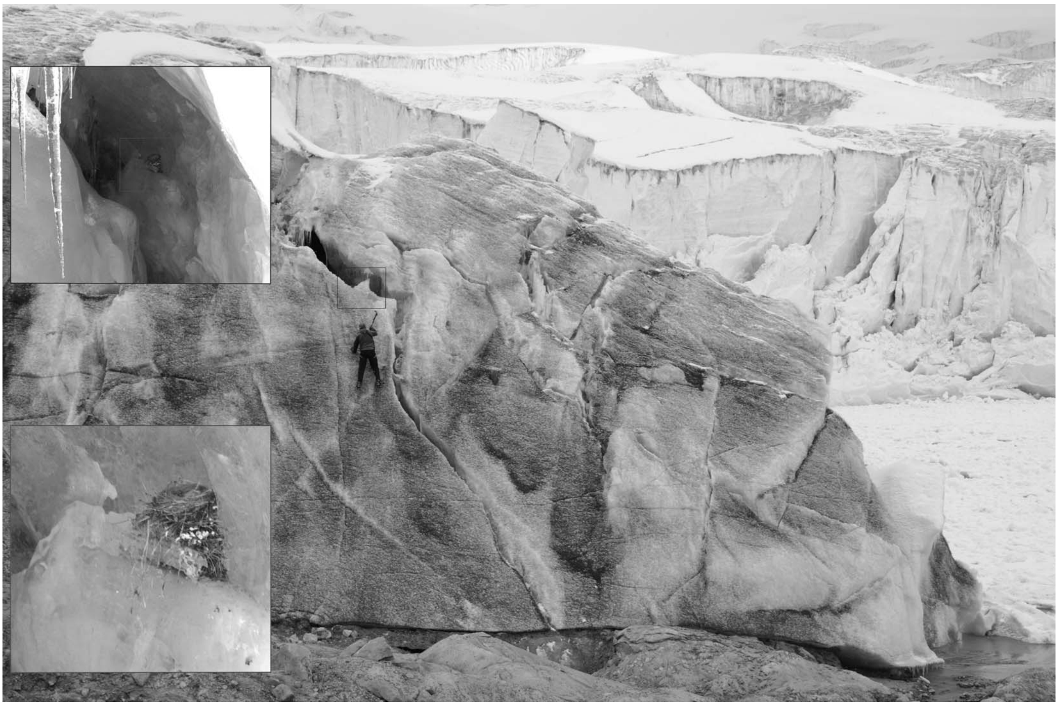

Figure 4. Active White-winged Diuca Finch nest, April 2014. This location is typical of many of the nests we found, virtually inaccessible without ice-climbing equipment or wings. Note the ascending observer, for scale. See Supplemental Fig. S10 for color version.

most likely occurs as the wet season concludes in April.

Fieldwork to sample snow accumulation in April 2014 provided an opportunity to test this breeding-season hypothesis. Ascending from 4,800 m to the glacier margin, we observed considerable avian activity in the bofedales, more-abundant insects, and decidedly warmer, more-humid conditions than seen during winter trips.

On 26 April 2014 we made what we believe to be the first observations of an active White-winged Diuca Finch nest, at the ice margin just above our camp (Fig. 1, Supplemental Fig. S1). We were alerted when adult birds acted agitated by our presence. Our next 2 d were spent working at the summit; in this interim, observations included hummingbirds (unidentified species) in camp (5,200 m) and at the summit (5,680 m), and a pair of White-winged Diuca Finch eating *Trichocera* sp. on the glacier at 5,520 m.

The first active nest we found was built at the near-vertical glacier margin ~1 m back into a narrow vertical crack, probably an old crevasse; the nest was ~5 m above the rocks below and barely visible from ground level. One nestling was observed and photographed in the nest. During several periods of observation, we consistently observed 2 adults sequentially feeding the chick. Departure of adults with a fecal sac was also observed and photographed.

A second active White-winged Diuca Finch nest was located and observed on 29 April 2014, ~300 m farther north along the same ice margin and across the proglacial lake. The nest was also built in a narrow vertical crack, adjacent to a section of margin actively calving into the lake (Fig. 4). The ice margin here was inclined at ~60°, inaccessible by 4-legged predators from either below or above. We estimate the nest height at ~11 m above the base, situated 2–3 m inside the crack on a ledge offering excellent protection from predation and heat loss. Two nestlings were observed, being fed by 2 adults.

Castañeda Gil (2015) provides an initial report of the 2 active nests found in 2014. Photographs and text supplementing the results above are available in Hardy (2015a, 2015b) and in our supplemental materials (Supplemental Fig. S6 and S7).

The 2016 filming project began 18 April at QIC with searches for active nests (Supplemental Reference). Within 4 d, 7 fresh (i.e., 2016) nest sites were located, and observation of pairs flying together up the glacier suggested at least twice this many in the area. In general, these nest sites varied in location from the ice margin to ~1,000 m up the glacier; most were considerably farther up from the margin than post-breeding-season observations in prior years suggested. All observed 2016 nests were recessed into ice features, such that they were not readily visible from the ground (e.g., Fig. 4, Supplemental Fig. S4). Indeed, of the 6 active nests located, only 2 were visited by researchers because access required ice-climbing equipment and experience. For example, one nest was ≥3 m below a relatively horizontal glacier surface in a narrow, contorted, and deep crevasse—barely visible even from within. Most nests were built inside generalized ice cavities, defined here as holes or voids unrelated to active glacier flow dynamics, inconspicuous and well protected.

All observed nests—active, in situ and no longer occupied, and fallen due to ablation—were similar in structure, composition, and size as described in Hardy and Hardy (2008).

The only 2 fresh 2016 nests accessible without climbing the ice were recently abandoned. Both were on the glacier within a few meters of the margin. One contained a broken egg and an intact egg, while the other had at least one crushed egg and feathers of a depredated adult.

Two chicks were alive in nest 16-DA on 23 April, with the foot of a dead sibling clearly visible. The middle rectrices on the surviving chicks had just emerged from the sheath, the outer rectrices were less than one-third grown, and most secondaries and primaries were between one-third and two-thirds grown. Some down remained on the head, back, and wing coverts. Experts with experience handling mid-latitude mountain songbirds independently estimated the age of the White-winged Diuca Finch nestlings at 8–12 d from photographs. This fits with North American species shown in Jongsomjit et al. (2007); however, the White-winged Diuca Finch nestlings appeared visually similar to Plumbeous Sierra Finch (*Phrygilus unicolor*) nestlings from 4,500 m in Ecuador that were estimated to be roughly 20 d old (M. Read, unpubl. data). When our observations ended 10 d later, both chicks were mobile and had left the nest for periods of multiple hours in the previous 48 h; however, as we departed, both were back in the nest and being fed by the adults. The likely age at fledging—defined as first departure from the nest—was thus around 20–30 d.

During the 9 d of video monitoring, the time between feedings was observed and recorded for 46 feeding bouts (mean = 67 min, SD = 11 min; $n = 46$). Video was recorded of 54 visits, and on all occasions, both parents came to the nest area to feed at the same time, and never with visible food. Most visits resulted in multiple regurgitation events per parent (mean = 4.0, SD = 3.0; $n = 54$), with an individual parent feeding both chicks 59% of the time ($n = 54$).

On multiple occasions, only 1 arriving parent would feed, and at least once, a parent removed a fecal sac and left without feeding the chicks. Overall, fecal sacs were removed 96% of the time when video of the parent leaving was available ($n = 54$). At ~1730 h local time (5 min before sunset) on 26 April, a parent made 5 visits in quick succession, each time removing a fecal sac without feeding.

The juvenile plumage of the White-winged Diuca Finch chicks was similar to that of the adults, with slightly less white on the primaries, throat, and below the eye. In our final video footage, the chicks' eyes were black (vs. red in adults) and their bills were stubbier. Once the tail is fully grown, field identification of hatch-year birds at a distance may be difficult.

All nests where the full contents were visible had clutches of either 2 or 3. The first in situ, abandoned nest found in June 2008 had 2 eggs (Hardy and Hardy 2008). One of the nests found in 2014 had 2 chicks; the other had at least 1 chick. In 2016 one abandoned nest had 2 eggs, a depredated nest had 1 or 2, and nest 16-DA had 3 hatched with 2 surviving nestlings. In addition, 2 adults with 3 fledglings were observed from 19 April to at least 22 April. All observed eggs were a light blue, with dark speckles.

White-fronted Ground-Tyrant—An active White-fronted Ground-Tyrant nest was discovered on 13 October 2014 at 5,200 m, beneath the ice at

Figure 5. Glacier nest site of both White-fronted Ground-Tyrant and White-winged Diuca Finch, found in July 2017 at 5,330 m. Approximate position of White-fronted Ground-Tyrant nest—built directly on glacier ice—is indicated by the left-hand arrow in the upper image, with detail provided in middle and lower images. Right-hand arrow of upper image marks White-winged Diuca Finch nest location; note person for scale. Two of 3 nearly identical White-fronted Ground-Tyrant nests found previously were also directly on glacier ice. Fecal pellets are within the ellipse (middle), and a shell fragment is visible in the lower image. See Supplemental Fig. S11 for color version.

a near-vertical margin. It was built inside a thin horizontal subglacier cavity, on top of a large boulder ~2 m back from the margin. Because the space was so narrow, and only the nest edge was visible from ground level, our best perspective was obtained by holding a camera overhead; images from 17 October revealed the presence of 2 young nestlings (Supplemental Fig. S8). This nest was initially located when the nestlings were heard calling to a parent arriving with food. Photographs of the adults reveal the food source to repeatedly include one or more large arthropods carried in their bill. Feeding duration was just a few seconds and was sometimes accompanied by fecal sac removal; adults often flew out of sight ($\geq$100 m) before releasing the fecal sac. We did not ascertain the time interval between feedings.

Although the structure and composition of this first White-fronted Ground-Tyrant nest found at QIC could not be observed in detail, we visited the same site in June 2015, April 2016, and July 2017—now fully exposed by recession of the ice margin—and found what we strongly suspect to be the residual nest material. This nest was distinctly different from that of White-winged Diuca Finch nests, containing small, dark root fibers and large quantities of mammal hair, likely vicuña (*Vicugna vicugna*); examination of $\geq$30 White-winged Diuca Finch nests has not revealed root fibers, and sparse quantities of hair have rarely been found.

Three additional nests have been found at QIC, closely resembling that at the 2014 White-fronted Ground-Tyrant nest site, all built directly on glacier ice (e.g., Fig. 5). Their volume was similar to that of a White-winged Diuca Finch nest, yet they were compositionally different, as described earlier. One was found on the ice in June 2015 near our microclimate and roost site (Fig. 1), an area less-commonly used by White-winged Diuca Finch in recent years. Another was found in April 2016, inside an ice cavity and within several meters of a recently abandoned White-winged Diuca Finch nest. These inactive, suspected White-fronted Ground-Tyrant nests were close to the ice margin and within a few meters of the ground. A third nest, found in July 2017, was the least accessible (Fig. 5). During all fieldwork in the area, White-fronted Ground-Tyrant has been present in bofedales near camp (Fig. 1) and on rocks at the glacier margin.

Timing of nesting

Prior to 2016 fieldwork, our only information on White-winged Diuca Finch nest timing was from the 2 nest observations in 2014; during 26–29 April, both had young in the early nestling stage. During our active study period in 2016 (22 Apr to

3 May), most adult White-winged Diuca Finch were observed flying in pairs toward and away from likely nest sites, suggesting most pairs were in the process of feeding young. This timing is consistent with 2014 observations, despite higher temperatures and less precipitation associated with the 2015–2016 El Niño event (DRH, unpubl. data). However, we also observed considerable variation in this timing. For example, on 21 April one adult was seen repeatedly taking nest material from an old nest and carrying it to a likely nest site within a large, actively calving, inaccessible ice cavity; if successful, young from this nest might not have fledged until the end of May. This nest was possibly a second attempt, given the presence of failed nests and relative synchrony of other nest activity we observed. With one other exception, adults at all the active nests we located in 2016 were in the process of feeding young, which may in part be an artifact of differing detection probabilities. Yet fledglings were observed on 21 April; thus at least one pair may have started nesting in early to mid-March. Any breeding activities continuing into late June or July are unlikely because this has been the timing of most of our fieldwork, when observed nests have all been empty and starting to degrade.

The timing of White-fronted Ground-Tyrant nesting is less-well known, but the active nest in October 2014 and the 3 degraded glacier nests found subsequently suggest breeding is most probable after the dry season, yet prior to the wet season onset, which typically begins in November.

Active nests of other species not associated with the glacier were found in April (Ash-breasted Sierra Finch [*Phrygilus plebejus*] at ~4,860 m; Bright-rumped Yellow-Finch [*Sicalis uropygialis*] at ~4,770 m) and in June (Variable Hawk [*Geranoaetus polyosoma*] at ~4,770 m; Bright-rumped Yellow-Finch at ~4,420 m).

Roosting

As a result of the high elevation and low latitude of our study site, birds in the area experience extreme diurnal temperature fluctuations (Fig. 3) with nearly equal length days and nights, and with nighttime low temperatures often well below freezing. Although determining roosting sites is difficult due to darkness, our observations suggest that several species utilize the glacier for roosting.

White-winged Diuca Finch—We have observed pre-roosting behavior in the late afternoon since 2007, consisting of evening gatherings at the glacier margin. Direct evidence of roosting in glacier cavities (e.g., birds, fecal pellets, feathers) has been found repeatedly. For example, on 19 April 2016, 101 White-winged Diuca Finch were observed flying toward the glacier between 1710 h and 1740 h local time, which was after the last White-winged Diuca Finch were seen making the 2-way trips, presumably to feed young. Our stationary observation site was but one location along the glacier margin, with groups of 2–10 individuals passing overhead. Favorable roost sites seem to draw individuals from considerable distance (cf. Niethammer 1953), as densities during the day are much lower than those observed just before dusk. Other areas of the margin (with fewer crevasses and ice cavities) receive less pre-roost traffic, suggesting that areas of pre-roost concentration are relatively localized, based on the abundance of such suitable roost locations. A given area is likely to remain favorable for multiple years, although within the past decade, recent changes in the margin morphology at one nearby location—because of recession and ablation—have changed a previously active-roost area into a gradual slope with few protective roosts.

White-fronted Ground-Tyrant—Individuals of this species were seen nearly every day during fieldwork, often at or near the ice margin (5,200–5,300 m) where few others species are regularly seen during the day. White-fronted Ground-Tyrants are also occasionally seen flying toward the glacier just before dusk. Our most definitive observation of this species going to roost was shortly before dusk on 10 July 2011; 2 birds were perched on the ice at a crevasse entrance at 5,480 m (Fig. 1), 500 m from the margin (KCG, pers. obs.). A third individual was flushed when the crevasse was approached for photos, and a snow ledge within the crevasse was later observed to contain droppings from previous nights (DRH, pers. obs.).

Plumbeous Sierra Finch—Although not as common in the area as other finches, this species was found in the rocks above the Moraine Camp (Fig. 1), where vegetation and passerines are sparse. During the day, we found it foraging as high as 5,150 m. The most interesting observation, however, occurred just before dusk at $\geq$5,200 m.

While watching White-winged Diuca Finch gather around the ice margin, at least 2 Plumbeous Sierra Finch were seen and photographed on and around the glacier margin. One, and maybe more individuals, appeared to enter ice cracks in a behavior similar to White-winged Diuca Finch; given the time of day, this event strongly suggests Plumbeous Sierra Finch is also roosting within the ice at QIC, supporting observations of Niethammer (1953, 1956) in Bolivia.

Rufous-bellied and Gray-breasted seedsnipe—Nearly every day in the field area at ~5,200 m, during different months over multiple years, seedsnipe have been heard flying toward the glacier shortly before dusk (typically 15–20 min after sunset) and flying downhill just before dawn (typically 30–45 min prior to sunrise). Most visual observations have occurred at or slightly before dusk, an artifact of our own diurnal cycle (i.e., usually in tents at dawn). Based on size, limited impressions of color, and recorded calls, both species of seedsnipe (Rufous-bellied Seedsnipe [*Attagis gayi*] and Gray-breasted Seedsnipe [*Thinocorus orbignyianus*]) present at the location were involved, often in pairs. Many of these birds were flying high above camp and headed toward the margin of the glacier ~100–200 m upslope, indicating they are roosting above 5,200 m and close to, if not on or under, the ice; depredated remains of a Rufous-bellied Seedsnipe were found beneath the ice margin in August 2018 (Supplemental Fig. S9). Areas with concentrated, cylindrical bird droppings >1 cm long, along with footprints, have been found on numerous occasions up to 5,400 m, both consistent with seedsnipe. Most often they are found on rocks near or at the margin, but on one occasion in April 2016, droppings were found directly on the ice >100 m above the margin. In the Cordillera Central, KCG once flushed a small group of unidentified seedsnipe from a glacier at ~0500 h which, given the lack of light at that hour, is strongly suggestive of nocturnal roosting.

Discussion

This study provides new breeding biology observations of 2 high-elevation Andean species which, despite being locally common, are almost entirely unstudied because of their inhospitable habitat. Our observations occurred above the upper elevations included in previous gradient studies and represent one extreme of avian adaptation to unique environments. Although neither of the 2 species studied is currently listed as threatened or endangered, their critical nesting habitat in glaciers of the Central Andean Wet Puna ecoregion is already feeling the effects of climate change, and these species may be vulnerable in a warmer Andes without glaciers. While there are no other known glacier-nesting species with which to compare our results, we discuss the literature examining how elevation affects aspects of avian biology.

Few observations exist for other species nesting above 5,000 m, perhaps partially because the environmental conditions are also difficult for human observers. The highest elevation nesting record we are aware of belongs to the Alpine Clough (*Pyrrhocorax graculus*), at 6,500 m (Rahn and Ar 1974). Our observations at QIC, those of Scott (2011), and the global compilation of Quintero and Jetz (2018) indicate that numerous taxonomic groups from hummingbirds to caracaras to Wallcreepers (*Tichodroma muraria*) reside above 5,000 m and may indeed nest this high.

The upper-elevation limits of distribution and roosting are probably more dependent on suitable habitat than any physiological limit. At least in our study area, complete ice cover exists above ~5,400 m. In the Andes, the published elevation record for a songbird may belong to White-fronted Ground-Tyrant, which occurs up to 5,600 m according to Fjeldså and Krabbe (1990), consistent with our 5,500 m roost observation.

Glacier nesting by White-winged Diuca Finch

The taxonomic classification of White-winged Diuca Finch was recently changed from *Diuca speculifera* by the South American Classification Committee (SACC) based on agreement that it does not belong in the genus *Diuca* (Burns et al. 2016, Remsen 2016). The sierra finches (*Phrygilus* spp.), which White-winged Diuca Finch is at least superficially similar to and shares habitats with, build large grassy nests on a variety of substrates, from shrubs (M. Read, pers. comm.), to cracks in rocky cliffs (Salvador 2015), to an old coffee can hanging from a fence (SPH, pers. obs.). The large, grassy nests and blue spotted eggs of *Phrygilus* are similar to those of White-winged Diuca Finch, which may be further evidence for a closer taxonomic relationship. Elsewhere in the Andes, Plumbeous Sierra Finch (M. Read, unpubl. data) and Red-backed Sierra Finch (*Idiopsar dorsalis*; Stevens and England 2016) have been documented feeding young via regurgitation.

Our roosting observations are in accordance with observations by Niethammer (1953), who described ~100 individuals—and a single Plumbeous Sierra Finch—gradually gathering at dusk and disappearing into a crevasse at 5,200 m on the no-longer-present Chacaltaya Glacier in Bolivia. Likewise, Johnson (1967: p. 368) reported P.R. Parker's observation of a nest "in an ice cave" at 5,300 m on the same glacier.

Aside from Hardy and Hardy (2008), only a single, secondhand White-winged Diuca Finch nest description exists in the literature (Johnson 1967; Chile–Bolivia border). However, we have received reports and photographs of nests on glaciers elsewhere in the Cordillera Vilcanota that closely fit the description for White-winged Diuca Finch (C.A. Chutas and D.M. Romero, pers. comm.). More specifically, an abandoned nest was found in 2008 on a glacier ~15 km from our study area (C. Braun, unpubl. data). Dozens of probable White-winged Diuca Finch nests have been observed in recent years at the margins of glacier Osjollo Ananta by K. Reider (pers. comm.), ~30 km northwest of our study area, and one was photographed nearby shortly after melting off Puca Glacier (Reider 2013). In the Cordillera Blanca of Ancash Department (~800 km northwest of study area), old nests have been observed at the margin of Pastoruri Glacier and on the wall of a crevasse (KCG, pers. obs.).

Globally, the range of White-winged Diuca Finch closely coincides with Andean glaciers (Fig. 1 inset), which could indicate that the species is an obligate glacier-nester. As described earlier, all known nests have been associated with glaciers; however, no systematic nest-searching efforts have occurred throughout the range, and we cannot yet determine whether the species nests exclusively on glaciers.

In addition to living in remote, challenging environments, the behavior of breeding White-winged Diuca Finch makes locating nests during the breeding season difficult. Adults carry food internally and nearly always arrive via long flights from feeding grounds, probably out of sight from the nest. Incoming pairs were often detected by their calls as they approached the glacier at significant altitude. Following a pair from their feeding grounds to the nest location would be almost certainly impossible. Only by positioning ourselves near likely breeding areas were we able to locate active nests, and even then it was a tedious process because parents would only feed once per hour, and in most cases observing multiple visits was necessary before we knew the exact location of a nest.

The long flights and significant time intervals between feedings suggest that the glacier offers an important resource that is not available closer to the preferred feeding grounds. Two possible explanations are that the glacier offers some form of protection from predators and/or from the environment. Potential predators observed in the area include culpeo or Andean fox (*Lycalopex culpaeus*), Andean cat (*Leopardus jacobita*), and Mountain Caracara (*Phalcoboenus megalopterus*). Evidence for predation of adults has been noted at roosting sites, depredated nests, and on the glacier; it seems that predators have cued in on nesting and roosting White-winged Diuca Finch as a food resource. On one occasion in April 2016, a young caracara was observed for several minutes flying low across a section of the glacier with several White-winged Diuca Finch nests but few, if any, other food sources. In addition, feces and tracks of a small cat and/or fox were found inside a subglacier ice cavity where White-winged Diuca Finch or White-fronted Ground-Tyrant would be the only likely prey item. Conversely, many of the active nests we found in 2016 would be completely inaccessible to any mammal or large bird.

In addition to avoiding predation, White-winged Diuca Finch and other avian species at Quelccaya must contend with an environment that can be very harsh, with low temperatures, frequent snow, and strong solar radiation. The High Andes experience some of the strongest solar UV-B and UV-A irradiance anywhere on earth (Piazena 1996, Cabrol et al. 2014), which in combination with highly reflective snow and ice could create dangerous conditions for developing birds. Naturally occurring levels of ultraviolet light have been shown to be detrimental to plants (Bader et al. 2007), amphibians (Blaustein et al. 1995, Anzalone et al. 1998), mammals (Weihs et al. 2012), and trout (Bullock and Coutts 1985). In birds, developing embryos are sensitive to UV-B, and eggshell color plays a role in moderating their exposure, with blue-green eggs thought to offer more protection than white eggs (Lahti 2008, Maurer et al. 2015). In addition to blue eggshells, ice surrounding a nest may offer protection from solar radiation to White-winged Diuca Finch embryos. All of the active nests we examined closely received little, if any, direct sunlight—especially early in the nesting period before substantial melt occurred.

Being surrounded by ice provides protection from other environmental hazards, including precipitation, wind, and temperature extremes. Our nest 16-DA and others were sheltered from falling snow, even with strong wind. Accumulating snowfall is common during early April, when the young are hatching; snowstorms in other high-elevation environments can lead to significant nest mortality, as demonstrated by Hendricks and Norment (1992) with American Pipits (*Anthus rubescens*) in Wyoming. Within the Quelccaya area, which is largely devoid of woody vegetation nest sites (Supplemental Fig. S1 and S2), we found passerine nests in several well-protected locations other than the glacier: abandoned flicker burrows (Bright-rumped Yellow-Finch), cracks in cliffs (Bright-rumped Yellow-Finch, passerine sp.), overhanging banks (Ash-breasted Sierra Finch), and abandoned houses (passerine sp.)—but never in the open or directly on the ground. Several of the other common species in the area (miners, earthcreepers, and flickers) presumably nest underground in burrows.

Numerous North American passerines and hummingbirds have adapted to breeding at low temperature by increasing the density of nest material and/or choosing microclimates protected from wind or radiational heat exchange (Skowron and Kern 1980). Glaciers, and probably other well-protected nesting locations, provide a stable thermal environment. Cavities within the glacier experience less diurnal temperature fluctuation and are warmer at night than either the ambient air or surfaces exposed to the sky (Fig. 3).

Unfortunately, we were not in the field long enough to establish timing of the full breeding cycle, but all indications point to White-winged Diuca Finch being an extremely slow breeder. Although we have minimal information on the nest-building or incubation periods, the large nest and low ambient temperatures suggest longer than average periods for both. In addition, the long distance between nests and foraging areas probably increases the length of off-bouts, which reduces egg temperature and increases the incubation period (Martin et al. 2018). Variation in nestling development rates is also tied to environmental conditions (Remeŝ and Martin 2002), with higher-elevation populations generally having slower development rates (Badyaev and Ghalambor 2001).

We did observe one individual repeatedly taking material from an old nest and flying to a likely new nest location. Nest material reuse makes energetic sense, given that the woody vegetation and tall grass is scarce in the rocky zone surrounding the glacier (Supplemental Fig. S1–S3). A long, energy-intensive breeding process fits with previous work on breeding biology along elevation gradients; high-elevation species generally have a slower life history strategy, with lower fecundity but higher juvenile survivorship than their lower-elevation relatives (Badyaev and Ghalambor 2001, Bears et al. 2009, Boyle et al. 2016). In a meta-analysis, Badyaev and Ghalambor (2001) showed that in phylogenetically similar species pairs, the higher-elevation species had smaller clutches and longer periods of nest building, incubation, nestling development, and post-fledgling care. Also, males of higher-elevation species were more likely to help in the feeding process.

Glacier nesting by White-fronted Ground-Tyrant

The benefits of glacier nesting by White-fronted Ground-Tyrant are probably similar to those of White-winged Diuca Finch, so much of the above discussion applies to this species as well. Within *Muscisaxicola*, 30% of the species (including White-fronted Ground-Tyrant) had no information published on clutch size, egg measurements, incubation, or nesting period as of 2012 (Heming et al. 2013). Of the species with documented nest descriptions, nests have been found in animal burrows, rock crevices, among rock scree, on cliffs, and on the open ground. To our knowledge, nests of the White-fronted Ground-Tyrants have never been formally described, although 2 different juveniles were collected in January (1935 and

1959) in the La Paz district of Bolivia (Chesser 1996).

Our October 2014 observation of what we believe to be the first documented White-fronted Ground-Tyrant nest is also the first record of a passerine other than White-winged Diuca Finch nesting in association with a glacier. The flexibility in nest location and preference for cliffs by other *Muscisaxicola* suggest this behavior is not entirely unexpected because nesting on a subglacier rock offers similar thermal and predatory protection. Furthermore, the 3 nests we found directly on ice match the structure and composition of the observed White-fronted Ground-Tyrant nest, even though 6–9 months had elapsed—with substantial ice melt—between the suspected nesting period (Oct) and when we found them (Apr, Jun, Jul). Curiously, the October 2014 active nest was the first White-fronted Ground-Tyrant nest found at QIC; despite distinct differences from White-winged Diuca Finch nests, no traces of old White-fronted Ground-Tyrant nests were previously noted or photographed during systematic nest surveys along the ice margin since 2005.

Timing of nesting at Quelccaya

Without nest records, the breeding period of many high-elevation species is not known, and it likely varies by species and with differences in regional climate. For example, in the highlands of northern Ecuador (3,800–4,230 m), many passerines, including close relatives of species that also occur in the Cordillera Vilcanota, nest primarily between September and November, but with nesting behavior also observed in May, July, August, and December (Greeney et al. 2011), while the breeding period for White-throated Sierra Finch (*Idiopsar erythronotus*) is suspected to be March–May (Fjeldså and Krabbe 1990). Prior to 2014, we had only visited the Quelccaya region during the core, cold dry-season months of June and July, an unlikely time for breeding. Given the number and duration of visits during this period, we are confident that White-winged Diuca Finch does not regularly breed during the dry season. White-fronted Ground-Tyrant nesting is probably limited to the beginning of the wet season because old nests have primarily been found in April; if fresh nests were present in June we would likely have found them. A few species (e.g., Bright-rumped Yellow-Finch, Variable Hawk) have been found nesting in June, although at slightly lower elevations—and in the case of Bright-rumped Yellow-Finch, in a sheltered environment (i.e., old flicker burrow).

Both White-winged Diuca Finch and White-fronted Ground-Tyrant nest during transitions between the dry and wet seasons. April and October share many climatic similarities, with conditions most suitable for breeding (Fig. 2). The core wet season (Nov–Mar) is the warmest period, with relatively low wind speeds and prevalent clouds, but more-frequent snowfall is likely to briefly cover food resources. During the dry season, other variables make conditions unsuitable for raising young (e.g., higher wind speed, lower temperatures, more solar radiation, and potentially longer-duration snow cover).

Glacier roosting

The benefits of roosting in a glacier may be similar to those of nesting in a glacier: protection from predators and the elements. We observed evidence of predation in glacier roosts but cannot quantify the relative danger, having no basis on which to compare predation rates with those of species roosting elsewhere. Likewise, although our preliminary data show a thermal benefit of several degrees to glacier roosting, and that radiative heat loss from exposed surfaces is considerable (DRH, pers. obs.), we cannot quantify the full thermal consequences of roosting away from the glacier.

The adaptive benefits for roosting, and the important factors in determining roost location, have been the subject of considerable research, especially in recent decades (Beauchamp 1999). No solid consensus has emerged regarding the benefit that roosting in cavities or in groups provides. Because White-winged Diuca Finch feed primarily in pairs, or less often in small groups, we suspect little if any information sharing is happening as a result of the pre-roost gathering or communal roosting. Numerous studies (e.g., Kendeigh 1961, Mainwaring 2011) have shown considerable thermal benefits for individuals roosting in cavities, although the source of the thermal benefit varies. Kendeigh (1961) found that the insulating properties of an enclosed space enabled a single House Sparrow (*Passer domesticus*) to increase the temperature of its nest box by up to 6 °C. Paclík and Weidinger (2007) showed that birds select tree cavities for maximum nighttime thermal benefit and gained the most benefit when cavities buffered nest microclimate against large fluctuations in daily ambient temperature. In addition, roosts can provide shelter from wind, which can cause substantial energy loss. In the United Kingdom, wind speed was the best predictor of White-throated Dipper (*Cinclus cinclus*) numbers at a communal roost completely protected from the wind (Shaw 1979), and in Indiana, USA, at about 250 m a.s.l., Webb and Rogers (1988) calculated an 11% difference in metabolic power as the result of Dark-eyed Juncos (*Junco hyemalis*) being sheltered from wind. The same study found only a 0.2 °C direct thermal benefit and a 3% difference in metabolic power from reduced longwave radiation escape within the dense row of cedars (*Juniperus virginiana*) being used as a roost. Outgoing longwave radiation emission increases with decreasing atmosphere (due to lower air density), strongly suggesting that high-elevation species like White-winged Diuca Finch lose more energy via longwave radiation than do birds at low elevations.

Many questions remain concerning the roosting behavior we observed. For example, we have yet to determine whether White-winged Diuca Finch and White-fronted Ground-Tyrant roost in small groups, pairs, as individuals, or a combination of these. The role of glaciers as roosting locations for Plumbeous Sierra Finch, Rufous-bellied Seedsnipe, and Gray-breasted Seedsnipe is still a mystery, and little recent information is available about the roosting behavior of other species in this high-elevation region, including those not associated with glaciers.

At 3,400 m in southern Peru—nearly 2,000 m lower in elevation than QIC—Pearson (1953) reported cave roosting by a goose, a hillstar, a falcon, an owl, a spinetail, 3 species of ground-tyrant, a shrike-tyrant, and a sierra finch. He also suggested that many of the other species found in this region use burrows for roosting. As with glacier cavities, both caves and tunnels likely provide similar thermal and wind protection but perhaps with differing levels of safety from predators. In our study area, Andean Flickers (*Colaptes rupicola*) seem to be the main constructor of tunnels, many of which are used by other species (e.g., Bright-rumped Yellow-Finch). While flickers are abundant up to ~4,900 m, our highest observation at ~5,150 m is higher than the previously known upper elevation for this species (Fjeldså and Krabbe 1990, Schulenberg et al. 2007). Suitable substrates for burrow excavations (e.g., stream cut banks) are rare in the Quelccaya landscape above 5,000 m, and thus such tunnels may not be an option for roosting or nesting near the glacier. No caves are known from the field area, which is composed of glacial drift underlain by ignimbrite bedrock (Stroup et al. 2015).

Climate change and glacier nesting

A 15 yr study of amphibians in a valley near QIC has documented both the retreat of glaciers and the associated shift in wetland communities from the cushion plant *Distichia* to tussock grass (Seimon et al. 2017). Such environmental changes have direct implications for White-winged Diuca Finch and many of the other species found in this region. Particularly during the dry season, bofedales are primarily glacier fed (Tomko and Cullen 2017), and water availability plays a crucial role for bird communities in the puna region (Tellería et al. 2006, Quenta et al. 2016). The QIC will likely be present for much or all of this century (e.g., Albert et al. 2014), but the glacier is changing increasingly rapidly, with potentially negative consequences for White-winged Diuca Finch, White-fronted Ground-Tyrant, and other species that rely on the glacier for roosting and nesting. In the past decade, our observations and photographs demonstrate that many sections of the margin are thinning, with fewer steep cliffs and features associated with glacier flow (e.g., crevasses). Subjectively, in our immediate study area, the highest density of White-winged Diuca Finch nesting and roosting has seemingly shifted to a tongue of ice with an actively calving face and more-numerous crevasses. The margin has also been retreating at a GPS-measured rate of ~11 m/yr since 2008 (DRH, unpubl. data), requiring a gradual increase in average nesting elevation for White-winged Diuca Finch and White-fronted Ground-Tyrant. Whether nesting at higher elevations will affect fecundity is unclear, but glacier retreat presents several other potential challenges. Rapid melting of the glacier may directly endanger individual nests built close to vertical margins. Nearly a meter of retreat is possible during the month or more required for nesting, which could expose or dislodge active nests; DA-16 was tipping and exposed to direct sunlight by the time the chicks were close to fledging.

Related to this issue, the retreat of the margin is increasing the distance to foraging locations because primary succession is occurring more slowly than recession (Schmidt et al. 2008). Although anurans have quickly colonized pools exposed by deglaciation since the 1960s (Seimon et al. 2007), White-winged Diuca Finch rely upon a complex bofedal ecosystem for food and nest material. These habitats will not expand upward at the same rate as glacier retreat, and they may become less extensive as the timing and amount of runoff changes in response to glacier recession.

Assuming glaciers are indeed a critical, range-wide element of White-winged Diuca Finch ecology, the direct effect of climate change may be realized sooner elsewhere than at Quelccaya because the smallest and most vulnerable glaciers have already begun to disappear (e.g., Ramírez et al. 2001). For example, the Chacaltaya Glacier disappeared by 2010 (Rabatel et al. 2013), and the only recent eBird report from the area did not include White-winged Diuca Finch (Brooks 2008), which was once locally abundant there (Niethammer 1953, 1956).

A pan-Andean effort to locate and document White-winged Diuca Finch nesting sites, either associated with glaciers or not, will be critical to assessing this species' long-term population viability. In the absence of systematic nest searching, refining distribution maps of White-winged Diuca Finch should help resolve whether this species can persist in the forthcoming era of an Andes without ice.

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