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Behavioral response to high temperatures in a desert grassland bird: use of shrubs as thermal refugia

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Abstract.—Birds inhabiting hot, arid ecosystems contend with trade-offs between heat dissipation and water conservation. As temperatures increase, passerines engage in various behaviors to reduce exposure to heat, solar radiation and insolation, and reradiation of heat from the ground. These responses to rising temperatures may result in subordination of reproductive urgency or nutrient acquisition to the need for thermoregulation. During studies on Arizona Grasshopper Sparrow (*Ammodramus savannarum ammolegus*) life history and ecology, we noted that these sparrows abandoned territoriality and foraging behaviors under certain circumstances in favor of cooler microsites. In this paper we document the extreme temperatures to which these and other ground-foraging and ground-nesting birds are exposed in southwestern desert grasslands, and we present evidence that *A. s. ammolegus* avoids exposure to extreme air and ground temperatures by using shrubs as thermal refugia. Our observations have implications for Arizona Grasshopper Sparrows and other desert grassland passerines in the southwestern United States, where the climate is projected to become hotter and drier. We provide some of the only behavioral data, and associated temperature data, associated with the use of thermal refugia by desert grassland birds. We encourage further studies that use more robust methods to supplement our observational data.

Resumen.—Las aves que habitan en ecosistemas cálidos y áridos enfrentan a compensaciones entre la disipación de calor y la conservación del agua. A medida que aumentan las temperaturas, los paseriformes participan en diversos comportamientos para reducir la exposición al calor, la radiación solar y la insolación, y la re-radiación de calor que proviene del suelo. Estas reacciones al aumento de las temperaturas pueden resultar en la subordinación de la urgencia reproductiva o la adquisición de nutrientes que necesitan para la termorregulación. Durante los estudios sobre el chingolo saltamontes de Arizona (*Ammodramus savannarum ammolegus*), observamos que estos gorriones abandonaron los comportamientos de territorialidad y de alimentación bajo ciertas circunstancias a favor de micrositios más fríos. En este informe de investigación documentamos las temperaturas extremas a las que éstas y otras aves que buscan comida y anidan en el suelo están expuestas en los pastizales del desierto del suroeste. De igual manera, presentamos evidencia de que el *A. s. ammolegus* evita la exposición a temperaturas extremas del aire y del suelo mediante el uso de arbustos como refugios. Nuestras observaciones tienen implicaciones para el chingolo saltamontes de Arizona y otros paseriformes de pastizal desérticos en el suroeste de los Estados Unidos, donde se prevé que el clima sea más cálido y seco. Proporcionamos algunos de los únicos datos de comportamiento, y datos de temperatura asociados, relacionados con el uso de refugios termales por el ave de pastizal desértico. Alentamos el fomento a más estudios que utilicen métodos más robustos para complementar nuestros datos de observación.

Birds inhabiting arid desert and grassland ecosystems in the southwestern United States contend with the trade-off between heat dissipation to prevent hyperthermia and water conservation to prevent dehydration (Williams and Tieleman 2001). As effective environmental temperature (T_e) increases while remaining less than body temperature (T_b), passerines engage in various behaviors to reduce exposure to high temperatures, solar radiation/insolation, and reradiation of heat from the ground—all sources of heat stress for birds. Passerines have the lowest heat tolerance among studied avian taxa (passerines, columbids, and galliforms; Smith et al. 2017), and smaller passerine species exhibit lower heat tolerance than larger species (McKechnie et al. 2017). When temperature increases and water is limited, survival may depend on redirecting behavior and physiology toward survival—an

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"emergency life history stage" per Wingfield et al. (1998).

Passerines, which rely solely on panting for evaporative heat loss (EHL) at high temperatures, are vulnerable to the warming of arid regions (Whitfield et al. 2015, McKechnie et al. 2017, Smith et al. 2017). They may be more vulnerable than other birds such as nightjars or doves, which use more efficient evaporative mechanisms such as gular flutter and cutaneous evaporation, respectively (Smith et al. 2015, McKechnie et al. 2016, O'Connor et al. 2017, Talbot et al. 2017). Passerine responses to higher temperatures and heat stress include reduced territorial advertisement (Santee and Bakken 1987); reduced foraging (Smit et al. 2013, Pattinson and Smit 2017, Funghi et al. 2019); reduced foraging efficiency and success (du Plessis et al. 2012, Cunningham et al. 2015); reduced body condition (i.e., reduced mass; du Plessis et al. 2012, Gardner et al. 2016, 2018); increased amount of time resting, perching, or using cooler, shaded microsites (Wolf et al. 1996, Williams 2001, Smit et al. 2013, Cunningham et al. 2015, Martin et al. 2015, Jacobs 2017, Pattinson and Smit 2017); and increased time dissipating heat (e.g., panting and wing-spreading; Wolf et al. 1996, Wolf and Walsberg 1996, Smit et al. 2013, 2016, Pattinson and Smit 2017, Funghi et al. 2019). Fitness effects of heat stress include reduced survival (Gardner et al. 2016), negative effects on nestling development and delayed fledging (Cunningham et al. 2013), and decreased daily nest survival (Conrey et al. 2016). In addition, ground-foraging passerines exhibited greater use of densely shaded sites as thermal refugia on hot days than arboreal foragers did (Martin et al. 2015).

Range-wide, the Grasshopper Sparrow (*Ammodramus savannarum*) is a species of conservation concern (NABCI 2014, Sauer et al. 2014, Ruth 2015, Rosenberg et al. 2016). The desert grasslands of southeastern Arizona, southwestern New Mexico, and northern Sonora, Mexico, are home to breeding populations of the Arizona Grasshopper Sparrow subspecies (*A. s. ammolegus*; Vickery 1996, Ruth 2008), which is of concern (USFWS 2008, NMDGF 2016) in a region predicted to experience extreme drought and warming under climate change scenarios. *Ammodramus savannarum ammolegus* is found in open bunchgrass with few shrubs or trees. These cryptic sparrows spend the majority of their time on the ground where they forage, nest, and conduct other maintenance behaviors (Ruth and Skagen 2017). In favorable conditions, they are rarely seen using the sparse shrubs in their territory, except when males use a shrub as a perch for territorial song and display (Ruth and Skagen 2017). Males vigorously defend their territories by chasing intraspecific interlopers, and outside of pair interactions and tending offspring, the species is quite solitary.

While foraging on the ground in relatively open desert grasslands, and when males perch on shrubs or tall grasses, *A. s. ammolegus* individuals are exposed to intense solar radiation, extreme temperatures at and just above ground level, and radiant heat from open ground, as has been documented in other desert species (Walsberg 2000). *Ammodramus savannarum ammolegus* exhibits several adaptations to mitigate the effects of the heat and aridity to which it is exposed: (1) it is smaller than subspecies farther north (Ruth 2017), possibly facilitating heat loss following Bergmann's rule (Ashton 2002); (2) mating pairs delay nest initiation until the arrival of monsoons in July and August (Corman and Wise-Gervais 2005, Ruth 2017, Ruth and Skagen 2018); (3) females construct domed nests beneath bunchgrass clumps with openings oriented to the north, away from solar radiation and prevailing winds (Long et al. 2009, Ruth 2017, Ruth and Skagen 2017); and (4) males limit their territorial song period to early morning, avoiding the heat of the day (J.M. Ruth personal observation). In addition, during our *A. s. ammolegus* life history and ecology studies, we noted that birds occasionally abandoned territoriality and foraging to perch in sparsely distributed shrubs. We present here data associated with this "birds in bushes" behavior. Our natural history observations supplement the growing base of physiological research on avian thermoregulation in arid systems, as cited above, which has largely been conducted in laboratories. Our study aimed to determine whether *A. s. ammolegus* individuals were using shrubs as thermal refugia in response to factors associated with temperature and solar radiation.

The desert grasslands in southeastern Arizona include semidesert grassland interspersed in a mosaic with plains grassland (Brown and Makings 2014). The main ecological driver is drought/precipitation (Askins et al. 2007). These data were collected in Santa Cruz County, Arizona, in the Davis Pasture, administered by the Bureau of Land Management (BLM) as part of the Las Cienegas National Conservation Area (NCA) (Davis Pasture: 1560 ha, 31.70° N, 110.60° W, elevation 1430 m), just east of Sonoita, Arizona. We worked on a randomly selected, open grassland portion of the study site of approximately 67 ha.

The climate experienced by *A. s. ammolegus* is dry, hot, and sunny (Askins et al. 2007). Long-term weather data from a similar site ~13 km away showed mean annual precipitation of 454 mm, with 55% of this precipitation occurring during the months of July through September, a mean daily summer temperature (summer = June–August) of 23.8 °C, and a mean daily summer maximum temperature of 31.6 °C (Audubon Research Ranch, based on NOAA 1981–2010 Normals; Arguez et al. 2012). Solar radiation/insolation is an important component of the conditions to which *A. s. ammolegus* individuals are exposed. Direct normal irradiance (DNI) is the amount of solar radiation received per unit area by a surface held perpendicular to the rays of the sun. The multiyear Physical Solar Model's DNI of 7.6 kWh/m^2 per day for Sonoita, Arizona, (Department of Energy, National Renewable Energy Lab's National Solar Radiation Database, https://maps.nrel.gov/nsrdb-viewer) is very similar to the DNI values for the Sonoran Desert. A portion of the solar radiation hitting an object (in this case either the sparrow or the ground) is absorbed, increasing its temperature. In the absence of site-specific DNI values, we used ground temperature as both a measure of the heat being reradiated from the ground and an index of the insolation to which the sparrows were exposed.

We began collecting data in 2007 to learn more about "birds in bushes" behavior. We identified 20–30 shrubs and monitored them in the summers of 2007 and 2011–2013 at varying times of day. We located shrubs along the dirt track that bisects Davis Pasture from the gate at Hwy. 82 to the gate at Lower Elgin Road. The number of shrubs monitored varied by year as individual shrubs disappeared or were added to increase sample size. We identified each shrub to species and measured dimensions (overall height and widest diameter) by using a telescoping pole marked at 10-cm intervals. We measured distance to the nearest shrub by using a rangefinder.

We approached the shrub and counted the number of birds that flushed out. Sparrows that flew from the shrub were already there; they did not flush into shrubs upon observer approach. In fact, this species generally does not flush into shrubs in response to approaching observers (or predators), but rather flies a short distance and drops back to the ground (Pulliam and Mills 1977, Vickery 1996, Ruth et al. 2014). We identified birds to species or, when that was not possible, to genus.

When we recorded bird observations, we also used the probe on an EXTECH hygrothermometer + infrared thermometer to record the following air temperature and relative humidity measures (2007; 2011–2012): (1) air temperature (not in direct sun) and relative humidity (not in direct sun)—both measured at chest height (approximately 1.2 m) in the shadow cast by the observer—and (2) air temperature in the shrub and relative humidity in the shrub—both measured within the shrub at about 10 cm off the ground. We used the EXTECH infrared thermometer with laser sensor to measure the following ground temperatures (2011–2013): (1) ground temperature in direct sun (on bare ground) and (2) ground temperature beneath the shrub.

Twenty-six (87%) of the 30 shrubs we monitored in 2011–2013 (Fig. 1) were velvet mesquite (*Prosopis velutina*); the others were elderberry (*Sambucus* spp.; *n* = 2), apricot (*Prunus armeniaca*; *n* = 1), and Arizona cypress (*Hesperocyparis arizonica*; *n* = 1). In 2011, the year with the most complete shrub measurement data set for the mesquite shrubs, mean dimension (SD; range) values were as follows: shrub height = 1.8 m (0.5 m; 0.8–2.7 m); width = 2.0 m (0.6 m; 0.9–3.1 m); and distance to the nearest shrub = 60.2 m (51.9 m; 15–228 m). See Supplementary Materials 1 and 2 for photos and dimensions of all monitored shrubs.

We measured air temperatures ranging between 21.5 °C and 44.8 °C (2007, 2011–2012). On 20 of the sampled days, air temperatures exceeded 35 °C. We measured ground temperatures in direct sun ranging between 14 °C and 84 °C (2011–2013). On 19 of the sampled days, ground temperatures exceeded 50 °C, indicating the extremes to which Grasshopper Sparrows were exposed.

Fig. 1. Example photographs of the sparsely distributed shrubs (clockwise from top left — Shrubs #4, #13, #14, and #19) monitored for sparrows on the Davis Pasture, BLM Las Cienegas National Conservation Area, Santa Cruz County, Arizona. Photographs were taken in July 2011 by Janet M. Ruth.

On multiple occasions, when air temperatures exceeded about 35 °C, we observed increasing numbers of Grasshopper Sparrows occupying isolated shrubs (Supplementary Material 3), apparently having suspended foraging and territorial advertisement and defense activities. Often in quick response to apparent changes in insolation and temperature (e.g., as cloud shadows moved across the landscape), these individuals left surrounding territories to perch in these shrubs. Birds initially flew into the tops of the shrubs, where they exhibited cooling behaviors such as lifting their wings away from their bodies and panting. They gradually worked their way down to perch in the shadow of a branch and eventually moved into the foliage-shaded areas of the shrub and the ground beneath. We recorded as many as 20 Grasshopper Sparrows flushing from a single shrub over the course of the study. We also regularly recorded Botteri's Sparrow (*Peucaea botterii*), Cassin's Sparrow (*P. cassinii*), and Eastern Meadowlark (*Sturnella magna lilianae*) using the same shrubs, although in smaller numbers. The Grasshopper Sparrows were also quite persistent in their use of a shrub. When observers approached a shrub and flushed sparrows from it, the birds flew in circles around the observer; as soon as the observer moved away from the shrub (by as little as 5–10 m), they returned to the shelter of the shrub.

On one occasion, when we approached a shrub to count flushed birds and record

TABLE 1. Numbers and behavior of Grasshopper Sparrows (GRSPs) recorded at Shrub #14 over 19 min during the afternoon of 16 July 2011. GRSP position in the shrub is described as low, middle, or high. See Fig. 1 for a photo of Shrub #14.

Time	Sun (S) or cloud shadow (CS)	No. of GRSPs in shrub	Observations	Temperature data
1:08:00 PM	CS	2	Observers approached shrub and flushed 2 GRSPs—1 high, 1 low	Air temp, 39.4 °C; ground temp in open, 48 °C; ground temp beneath shrub, 37 °C; difference in ground temperatures, 11 °C
1:09:00 PM	CS	0		
1:14:00 PM	S	0	Cloud and its shadow moved off; shrub and surrounding area exposed to full sun	
1:15:00 PM	S	3	3 GRSPs flew in—1 GRSP flew in low and hopped up to middle; 2 GRSPs flew in high	
1:16:00 PM	S	6	3 more GRSPs flew in high	
1:16:30 PM	S	8	2 more GRSPs flew in; all visible GRSPs perched in shadows of branches or leaves; those perched high were panting; those near the ground were not	
1:17:00 PM	S	11	3 more GRSPs entered—1 GRSP came in on the ground below the shrub; 2 flew in high; visible birds were panting	
1:18:00 PM	S	11	Visible GRSPs high in the shrub were panting and had their eyes closed; 1 GRSP dropped from a high perch to the ground and crawled in below the shrub	
1:20:00 PM	S	11	All but 3 GRSPs (1 high, 2 in middle) were low in the shrub and invisible	
1:23:00 PM	S	12	1 more GRSP flew in; all visible GRSPs in the middle of the shrub perched in the shade of a branch or leaves	
1:27:00 PM	S	16	Observers approached the shrub and flushed 16 GRSPs—4 from the middle, and 12 from low in the shrub (we obviously missed a few that flew or walked in from the back!)	Air temp, 42.4 °C; ground temp in open (full sun), 81 °C; ground temp beneath shrub, 40 °C; difference in ground temperatures, 41 °C

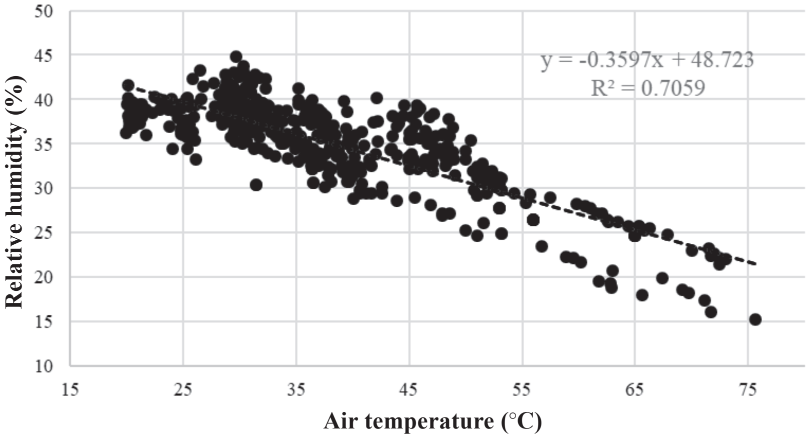

Fig. 2. Relative humidity outside the shrub (not in direct sun) versus air temperature outside the shrub (not in direct sun); $n = 521$.

temperatures, the shrub and surrounding area were in a cloud shadow (not experiencing direct sun). We then moved away from the shrub to observe from a distance with binoculars. We were able to document what happened over a short time period as the cloud moved off and the shrub and surrounding area were once more exposed to direct sunlight (Table 1). Within 3 minutes of sun exposure, there were 11 Grasshopper Sparrows in or beneath the shrub, and at 13 minutes after sun exposure, when observers approached the shrub, 16 individuals flushed out (see Table 1 for the time details). These 16 adults represented pairs from at least 8 territories.

We plotted associations among air temperature, ground temperature, relative humidity, and bird numbers. These observational data did not warrant more sophisticated statistical analyses but increased our understanding of the "birds in bushes" behavior. We excluded data for the apricot and Arizona cypress trees but retained data for the mulberry and mesquites because the structure of apricot and cypress were tree-like (single trunk and no foliage near the ground), whereas mesquites and mulberry exhibited a shrub-like form (with multiple stems and foliage at or near the ground). We were concerned that the birds would use shrubs and trees differently due to this structural difference, but we did not have a large enough sample of trees to test that possibility.

Air temperature in the shrub at 10 cm above ground level was directly proportional (slope = 1.00) to air temperature outside the shrub (not in direct sun) (Supplementary Material 4A); relative humidity in the shrub was also directly proportional (slope = 0.99) to relative humidity outside the shrub (Supplementary Material 4B). Relative humidity was inversely proportional to air temperature (Fig. 2; slope = −0.36). We know that absolute humidity can be important in thermoregulation—setting the gradient for evaporative cooling (Walsberg 2000)—and that evaporative water loss is less effective as relative humidity increases (Gerson et al. 2014). However, because of the close associations we found between air temperatures and relative humidity, in subsequent graphs we used air temperature (not in direct sun) to represent all measures of air temperature and relative humidity.

As the day progressed, all measures of temperature (air temperature not in direct sun, ground temperature in direct sun, and ground temperature beneath a shrub) increased initially and then declined or plateaued (Fig. 3). The most striking association between time of day and temperature was for ground temperature in direct sun, where the curve was steepest and reached strikingly high temperatures of 70–84 °C. In an associated pattern, as air temperature increased, ground temperature in direct sun increased exponentially, whereas ground temperature beneath shrubs increased at a much slower rate (Fig. 4). As a result, as air temperature increased, the difference between ground temperature beneath

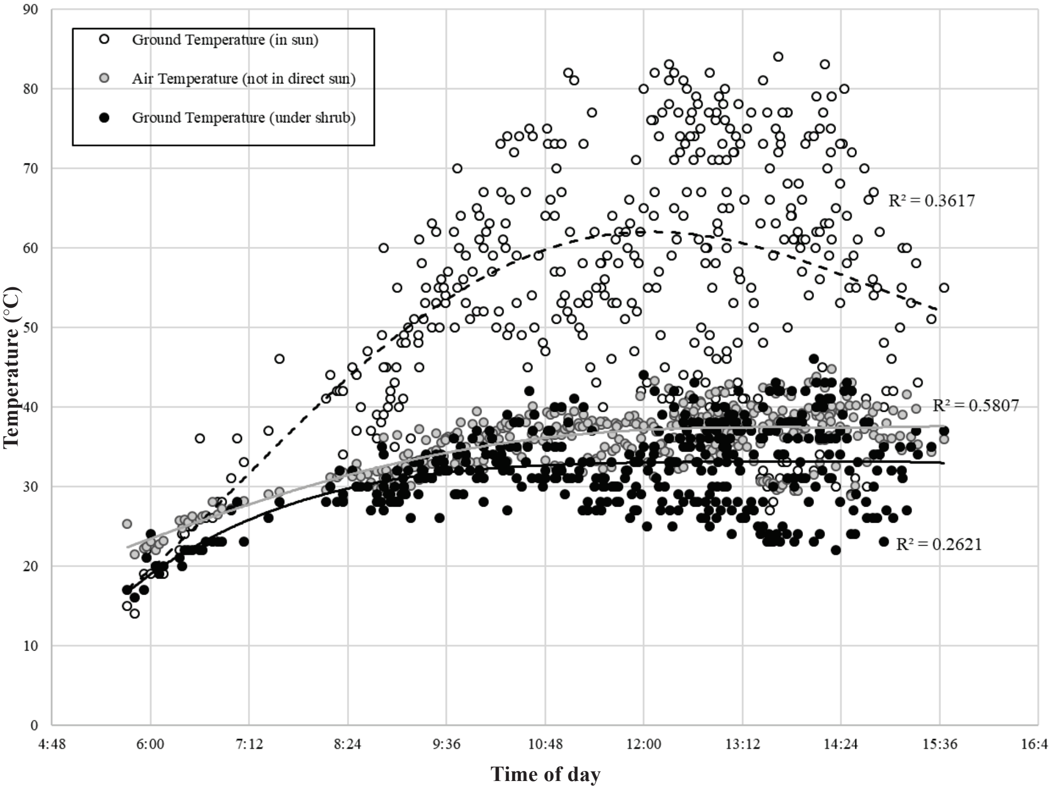

Fig. 3. Three measures of temperature (air temperature outside the shrub [not in direct sun], ground temperature beneath the shrub, and ground temperature in direct sun) versus time of day; $n = 399$.

a shrub and in direct sunlight increased, although the difference began to plateau at the highest air temperatures (Fig. 4).

Given the striking differences in ground temperature beneath shrubs compared to ground temperature in full sunlight as air temperature increased, we compared the numbers of Grasshopper Sparrows using shrubs with the difference between ground temperature in direct sun and beneath shrubs. The number of sparrows in shrubs was positively associated with the difference between ground temperature in direct sun and beneath shrubs (Fig. 5). All incidents of >5 sparrows flushed from a shrub occurred when that difference exceeded 15 °C.

In this paper we documented the extreme temperatures to which Arizona Grasshopper Sparrows were exposed in the summer and identified ways that this exposure influenced the birds' thermoregulatory behavior. Daytime temperatures (Figs. 3, 4) were similar to those in the Sonoran Desert (Walsberg 2000). We showed that as air and ground temperatures increased, sparrows (1) abandoned territories, (2) suspended advertisement, defense of territories, and foraging, and (3) sheltered in shrubs with other sparrows. These are unusual behaviors for a solitary, territorial species. Our observations are consistent with use of thermal refugia by small-bodied birds in the Sonoran (Wolf et al. 1996) and Karoo Deserts (Pattinson and Smit 2017), where selection of cooler microsites can have a profound effect on conditions to which birds are exposed.

Arizona Grasshopper Sparrows appear to be employing this "birds in bushes" behavior to minimize their exposure to high air temperatures, insolation, and heat radiated back from the ground when $T_e < T_b$. Use of thermal refugia is especially associated with times when the difference between ground temperature in direct sun and beneath shrubs is greatest. During the hottest times of day, ground temperatures in direct sun can reach 80 °C. Shade provided by shrub foliage and

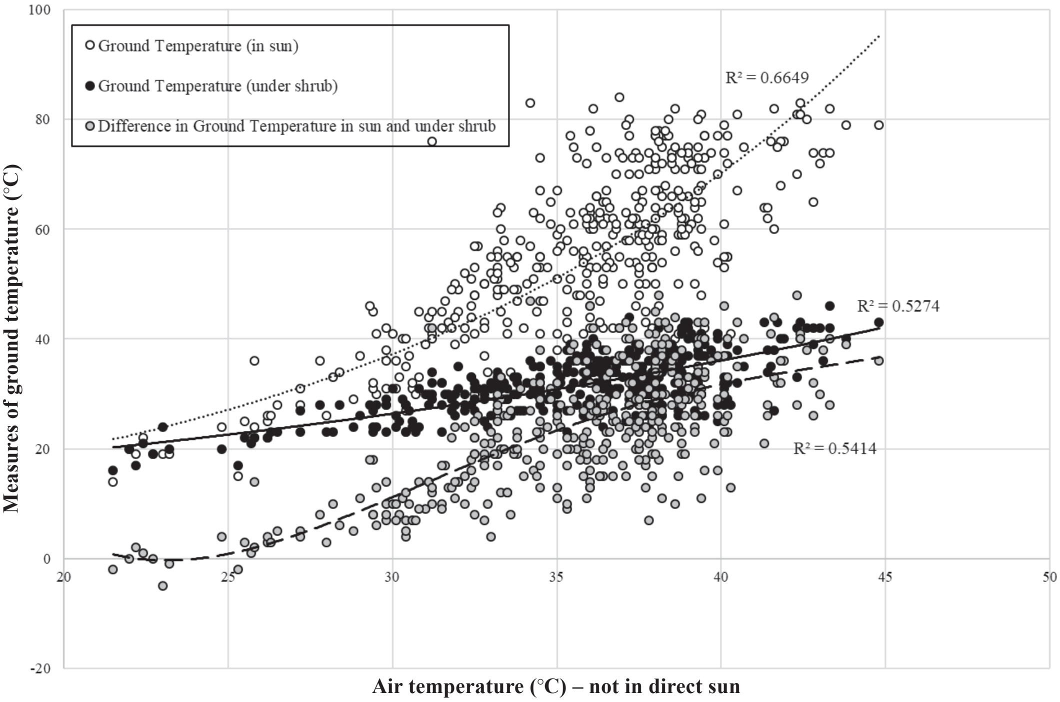

Fig. 4. Three measures of ground temperature (in direct sun, beneath the shrub, and the difference between ground temperature in direct sun and beneath the shrub) versus air temperature outside the shrub (not in direct sun); $n = 399$.

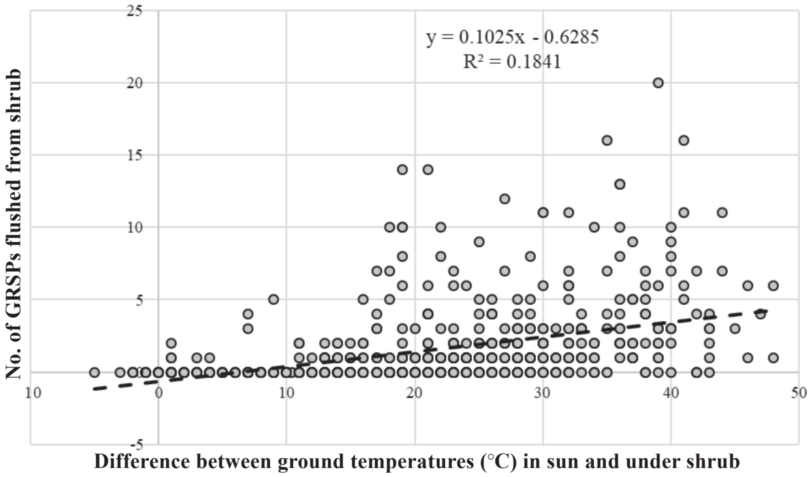

Fig. 5. Number of Grasshopper Sparrows (GRSPs) flushed from the shrub versus the difference between ground temperature in direct sun and beneath the shrub; $n = 605$.

branches, and the lower ground temperatures beneath them, provide sought-after thermal refugia. The shrub did not have to be very large or have dense foliage in order to provide a refugium (Fig. 1; Supplementary Materials 1 and 2). Such behaviors exhibit the species' hierarchy of needs, given that use of thermal refugia comes with tradeoffs and consequences to survival and reproductive success.

Our observations have implications for a warming climate and its impact on Arizona Grasshopper Sparrows. Small-bodied birds in arid ecosystems often survive near their physiological tolerances for heat and dehydration (Wolf and Walsberg 1996, Whitfield et al. 2015). Once $T_e > T_b$, the behavioral adaptations documented in this study will no longer be effective, and EHL will be the only avenue for heat dissipation (Calder and King 1974) to maintain T_b below lethal levels. The climate in the southwestern United States is projected to become hotter, and many models predict reduced rainfall, increased aridity, or changes in seasonality (Coe et al. 2012, Finch 2012, Bagne and Finch 2013). Increased frequency, intensity, duration, and spatial extent of droughts and heat waves are also predicted (Finch 2012, Garfin et al. 2013). If Arizona Grasshopper Sparrows are operating near the limits of their physiological tolerances, these climatic changes may lead to increases in mortality (McKechnie and Wolf 2010) and negative impacts on survival, even at temperatures below those associated with mortality (McKechnie et al. 2012, Cunningham et al. 2013, Gardner et al. 2016).

Our information provides some of the only behavioral data and associated temperature data that we are aware of regarding use of thermal refugia by desert grassland birds. We encourage further studies that use more robust field-based behavior and temperature data collection methods and analyses (e.g., Edwards et al. 2015, Martin et al. 2015, Smit et al. 2016, Pattinson and Smit 2017) to document how desert grassland birds are responding to thermoregulatory challenges.

SUPPLEMENTARY MATERIALS

Four online-only supplementary files accompany this article (https://scholarsarchive.byu.edu/wnan/vol80/iss2/15).

Supplementary Material 1. Photos of 28 shrubs monitored for sparrows on the Davis Pasture, BLM Las Cienegas National Conservation Area, Santa Cruz County, Arizona.

Supplementary Material 2. Species, dimensions, and distance to nearest shrub of the 28 shrubs monitored for sparrows on the Davis Pasture, BLM Las Cienegas National Conservation Area, Santa Cruz County, Arizona.

Supplementary Material 3. Photos of Arizona Grasshopper Sparrows using mesquite and elderberry as thermal refugia on hot days and exhibiting wing-spreading behavior for cooling.

Supplementary Material 4. ***A***, Air temperature in the shrub at 10 cm above ground level versus air temperature (not in direct sun); $n = 473$. ***B***, Relative humidity in the shrub at 10 cm above ground level versus relative humidity (ambient); $n = 521$.

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