Hummingbird foraging preferences during extreme heat events

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Abstract

Climate change is projected to increase mean temperatures as well as the frequency and intensity of extreme heat events. These changes are anticipated to alter the behavior of animals as they seek to thermoregulate in extreme heat. An important area of research is understanding how mutualistic interactions between animals and plants, such as pollination, will be affected by the cascading effects of extreme heat on animal foraging behavior. In this study, we used an experimental and observational approach to quantify the effects of extreme heat on hummingbird foraging preferences for nectar sources in shady versus sunny microsites. We also quantified pollen deposition using artificial stigmas at these sites to quantify any cascading effects on plant reproduction. We hypothesized that hummingbirds would respond to extreme heat by preferentially foraging in shady microsites. We found little support for this hypothesis, instead finding that hummingbirds preferred to forage in sunny microsites regardless of ambient temperature. We found that in sunny microsites on hot days pollen deposition was slightly higher than in all other microsite and ambient temperature interactions, though it was only near-significant.

Introduction

The continuation of pollination services to plants in a warming climate is critical to sustaining plant biodiversity and ecosystem function. A meta-analysis of plant dependence on vertebrate pollinators found that when birds were excluded from pollinating, fruit or seed production was reduced by 46% (Ratto et al. 2018). Changes in pollinator behavior can have cascading effects on plant populations (Anderson et al. 2011), as pollinator visitation rates have a positive effect on pollen receipt (Engel & Irwin 2003). An estimated 87.5% of flowering plant species rely on animal pollination (Ollerton et al. 2011). While some research has investigated the effects of higher ambient temperatures on insect pollinators such as bumblebees, vertebrate pollinators have received relatively little attention. Hummingbirds (Aves: Trochilidae) are a critical group of vertebrate pollinators in the western hemisphere, and visit over 1300 species of plants from 100 different families in the Americas (del Coro Arizmendi & Rodríguez-Flores, 2012).

Hummingbirds are highly reliant on daily nectar from plant mutualists due to their high metabolic rates (Cronk & Ojeda, 2008; González-Gómez et al., 2011; Shankar et al. 2019), though they do also eat insects as a source of amino acids that are absent from nectar (Russell 1996; Battey 2019). Hummingbirds have a low energy storage capacity and high fixed metabolic costs, and thus are sensitive to daily fluctuations in metabolic costs and energy availability (González-Gómez et al., 2011; Shankar et al., 2019; Shankar et al., 2020). Hummingbirds of some species decrease certain activities, like territorial defense behavior, past a threshold temperature of 19.9@C (González-Gómez et al. 2011). This type of behavioral thermoregulation may also affect hummingbird foraging behavior, with the potential for cascading effects on plant reproduction.

On extremely hot days, some birds will alter their movement ecology to preferentially spend time in the shade, or they may spend more time engaging in heat dissipating behaviors such as panting or spreading their wings. These behavioral shifts may come at an opportunity cost. For example, male Southern yellow-billed hornbills foraging on hot days panted more frequently and spent more time in thermal refugia, resulting in decreased foraging success and body mass losses (van de Ven et al. 2019). Du Plessis et al. (2012) found

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that the foraging effort of Southern pied babblers was not affected by ambient temperature, but foraging efficiency was negatively affected. Powers et al. (2017) found that hummingbirds use passive cooling from heat dissipating areas around the eyes, shoulders, and feet when a thermal gradient exists between their bodies and the ambient temperature. However, passive cooling is only effective if ambient temperature is below hummingbird body surface temperature, and thus behavioral thermoregulation may be necessary during heat waves.

In this study, we test the hypothesis that Anna's hummingbirds (*Calypte anna*) would preferentially forage at experimental feeders in shady microsites versus sunny microsites on extremely hot days (> 35@C) when compared to normal days over the summer in California. We also test for differences in pollen deposition on artificial stigmas at feeders between sunny and shady microsites on extremely hot days compared to normal days. We hypothesized that pollen deposition would be greater at shady versus sunny microsites on extremely hot days as compared to normal days.

Materials and Methods

Field site – This study took place in a semi-natural environment on the California State University East Bay (CSUEB) campus in Hayward, California in the U.S. (Fig. 1). The study site consists of a mix of parking lots, buildings, paved walkways, and ornamental landscaping. The climate in the region is Mediterranean, with cool, mild winters and hot, dry summers, and the heat and dryness generally extend well into November. In the City of Hayward over the period 1991-2020, the summer average temperature was 18.9 @C, summer high temperature was 23.9 @C, and summer minimum temperature was 13.8 @C. The study took place from June – November 2021, during the hottest time of the year. Hot days were categorized as when the maximum temperature in the sun was greater than or equal to 35 @C. This temperature was selected because previous research shows that the thermal gradient driving passive heat dissipation in 5 species of North American hummingbirds disappears between 36 and 40 @C (Powers et al. 2017).

Feeder Trials – Glass feeders with five feeding ports and perches (Perky Pet, Inc.) containing a 30% sucrose solution were placed under a tent canopy 10' x 10' x 8' in size. The sunny microsite treatment had the frame of the canopy, but not the shade cloth. The shady treatment had the shade cloth on. Treatments were placed 10 m apart in an open lawn to present foraging hummingbirds with a choice between the two microhabitats, and treatments were shuffled in position randomly during each session to avoid any spatial bias. Feeders were observed between 12:30 pm and 5:30 pm to capture the hottest part of the day, and each observation session averaged 135 min (min = 111 min, max = 213 min, SD = 22 min). To track temperature in each microsite, iButton temperature sensors and dataloggers (Maxim Integrated, Inc.) were attached to the feeders using modeling clay. For each session the following environmental data were recorded: weather, observation start and end times, the number of people that walked within 25 m of the feeders during the observations (low: < 10, moderate: 10-20, and high: >20), and the estimated number of open floral inflorescences within 25 m of the feeders. We quantified hummingbird preference by number of visits, defined as any time a bird entered the area under the canopy, foraging visits, defined as any time a hummingbird inserted its bill into the feeder, and visit duration, defined as the amount of time the bird spent in the canopy area.

Pollen deposition – We measured pollen deposition during feeder trials by placing artificial stigmas above the flowers on the feeding ports of the hummingbird feeders. Artificial stigmas were made by placing a 1 cm x 1 cm x 1 cm cube of fuchsin-stained pollen collecting gelatin (Kearns & Inouye 1993) inside a metal gemstone setting and attaching it to a length of wire 5 mm in length to simulate the stigma length and position of California fuchsia (*Epilobium canum*), a locally abundant hummingbird-pollinated California native plant. At the end of a feeder trial, artificial stigmas were collected and mounted on glass slides for analysis. Slides were observed at a magnification of 100x using a digital microscope, and any pollen grains present were photographed. Pollen grains deposited per feeder trial were counted manually in slide photos using the program ImageJ (Rasband 2021).

Semi-natural behavioral observations – In order to provide context to our feeder experiments, we also conducted observations of free-foraging birds in the campus landscape on extremely hot and average days to

determine if they preferred shady microsites to sunny microsites on extremely hot versus average days. Birds were observed at 8 different locations on the CSUEB campus (Fig. 1) that had blooming flowers and shady and sunny microsites. Each location was observed for 45 minutes between 12:30 and 5:30 pm. During sessions, we used scan sampling to record the behavior and microsite (sunny vs shady) of every visible hummingbird within a 25 m radius at 5 minute intervals. The following behavior categories were recorded: perching, preening, gaping, vocalizing, aggression, and foraging (fly-catching or nectaring) (Table 1). If a bird exhibited a combination of simultaneous behaviors, all simultaneously occurring behaviors were recorded (for example, perching and vocalizing). If a bird exhibited multiple sequential behaviors, only the behavior(s) that occurred at first sighting were recorded. During each session, the following environmental variables were recorded: weather, observation start and end times, the number of people that walked within 25 m of the feeders during the observations (low: < 10, moderate: 10-20, and high: >20), and the estimated number of open floral inflorescences within 25 m of the location.

Data Analysis – Feeder sessions and semi-natural observations were categorized as hot or average based on whether the maximum temperature in the sun exceeded 35 @C. All statistical analyses were conducted in the software program R (R Core Team 2022). The effect of temperature on number of visits, visits per hour, and visit duration to each category of microsite was analyzed using general linear mixed models (GLMM) using the R package "lme4" (Bates et al. 2015). For feeder trials, candidate GLMMs were constructed with the total number of visits, average number of visits per hour (rounded to the nearest integer), or visit duration as response variables. Microsite and temperature were included as interacting fixed effects, and separate models were constructed using categorical (hot/average) versus maximum temperature in the sun as the temperature term. Julian date, session ID, and human presence were included as random effects. Session duration varied slightly between trials, so it was included as an offset term in all models. Total number of visits and visitation rate (visits/hr) were modeled using a Poisson distribution. Visit duration data was heavily skewed to the right, and thus was centered and scaled by standard deviation before modeling (Bolker et al. 2009, Schielzeth 2010, Meehan et al. 2020). Initial data exploration showed the pollen count data was overdispersed, so an observation-level random effect was added to all pollen deposition models to correct for overdispersion. Model selection was done for each test (response of total visits, visit rate, or visit duration and fixed effect of categorical or continuous temperature) by constructing models with every possible combination of fixed and random effects. The package 'MuMIn' was then used to select the best model (Bartoń 2022). Candidate models were checked for normal distribution of residuals based on Q-Q and Shapiro-Wilk tests. Models were selected by the second order Akaike Information Criterion (AICc) (Bolker et al. 2009). Post-hoc pairwise comparison for significant interaction terms was conducted using the package 'emmeans' with Bonferroni corrections (Lenth 2022).

For semi-natural observations, we constructed GLMMs with a Poisson distribution using the cumulative number of foraging visits to a flower as the response variable, the interaction of microsite (whether individual was observed visiting a flower in the shade or the sun) and ambient temperature (categorical or maximum temperature in the sun, as in feeder trial models) as the fixed effect, and a unique session ID, Julian date, human presence (using same scale as in feeder trials), location, and floral abundance as random effects. Observation session duration was included as an offset term. Model selection, quality control, and post-hoc pairwise comparisons were conducted following the same process as in feeder trial models.

Results

Feeder Trials – We conducted a total of 30 feeder trials, during which we recorded 529 foraging visits by Anna's hummingbirds; 34% (N = 164) of all visits were in the shady microsite, while 69% (N = 365) were in the sunny microsite. Sessions were approximately balanced between hot (N = 14) and average (N = 16) ambient temperatures.

The best model for cumulative number of visits included the interaction of microsite and maximum sun temperature as fixed effects, session ID as the random effect, and an offset term for session duration (Fig. 2; Table 2a, Table S1). We found a significant effect of microsite, but not for ambient temperature or the interaction of ambient temperature and microsite. Sunny microsites had a significantly higher number of

visits than shady microsites regardless of ambient temperature (Coef = 1.50, z = 2.83, P < 0.01). A model with the same random effects but with temperature as a categorical variable found a similar result (Table 2b; Table S1), with sunny microsites receiving significantly more visits than shady microsites regardless of ambient temperature (Coef = 0.82, z = 4.85, P < 0.001).

When considering visitation rate as the dependent variable, the average visitation rate (visits/hour) was 2.67 ± 1.65 (SD) in shade and 5.75 ± 3.00 (SD) in sun during hot sessions, and 2.02 ± 1.08 (SD) in shade and 4.91 ± 2.07 (SD) in sun during average sessions. The best model for visitation rate included the interaction of microsite and maximum sun temperature as the fixed effect, session ID as a random effect, and session duration as an offset term (Fig. 3, Table 3a, Table S2). The only significant fixed effect was microsite, with sunny microsites receiving significantly more visits than shady microsites regardless of ambient temperature (Coef = 1.76, z = 2.17, P < 0.05). An identical model with temperature as a categorical variable was the second best model during model selection, and had a similar result, with sunny microsites receiving significantly higher visitation rates regardless of temperature category (Table 3b, Table S2; Coef = 0.96, z = 3.68, P < 0.001).

When considering visit duration during feeder trials, the average visit duration in the shade was 41.41 s ± 25.34 (SD) and 52.85 s ± 12.79 (SD) in the sun during hot days. The average visit duration in the shade was 28.81 s ± 18.23 (SD) and 45.61 s ± 14.93 (SD) in the sun during average days. The best model for the average visit duration included the interaction of microsite and categorical temperature as fixed effects, Julian day as a random effect, and session duration as an offset term (Fig. 4, Table 4, Table S3). No other models had a ΔAICc < 2. The final model found a significant effect of both temperature category and microsite, with higher visit duration on hot days (Coef = 0.50, t-value = 1.48, P < 0.05) and lower visit duration in the shade than in the sun (Coef = -0.67, t-value = -2.22, P < 0.01).

Semi-natural behavioral observations – We conducted a total of 20 sessions across 8 locations on the CSUEB campus; of these, 8 were categorized as hot days, and 12 were categorized as average. Session duration averaged 47 min ± 1.85 (SD), for a total of approximately 17 hrs of observations. Hummingbird time budgets were apparently different on hot and average days (Fig. 5) with greater incidences of foraging, aggressive interactions, and flying on hot days as compared to average days. Birds spent less time perching, vocalizing, and preening on hot days. Hummingbirds also apparently used microsites differently (Fig. 6). Birds spent more time foraging, flying, and in aggressive interactions in sunny microsites, and more time perching, preening, and vocalizing in shady microsites. Birds were observed feeding at different flowering ornamental plants during sessions (Table S4), of which Mexican sage (Lamiaceae, *Salvia leucantha*) and strawberry tree (Ericaceae,*Arbutus unedo*) were the most visited.

The best model for the cumulative number of nectaring observations per session included the interaction of microsite and categorical temperature (hot vs. average) as the fixed effect and session ID and floral abundance as random effects (Fig. 7, Table 5, Table S5). The interaction term was significant (Coef = 1.15, z-value = 2.87, P < 0.01), and post-hoc tests revealed that this was driven by differences in microsite use on hot days, where hot days had more foraging in the sun than in the shade (Ratio = 0.44, z-ratio = -2.97, P < 0.05), a pattern which differed from their preferences on normal temperature days (Table S6).

Pollen deposition – When considering pollen deposition during the feeder trials, the average number of pollen grains deposited in the shade was 81.29 ± 157.80 (SD) and 593.02 ± 950.29 (SD) in the sun during hot days. The average number of pollen grains deposited in the shade was 404.63 ± 747.27 (SD) and 275.38 ± 747.27 in the sun during average days. The average pollen load (total pollen grains deposited/total visits) in the shade was 14.90 ± 26.02 (SD) and 58.68 ± 109.22 (SD) in the sun during hot days. The average pollen load in the shade was 80.37 ± 170.30 (SD) and 20.03 ± 29.25 (SD) in the sun during average days. The best model for average pollen deposition included the interaction of microsite and categorical temperature as fixed effects, Julian day and observation effect as random effects, and session duration as an offset term (Table 6, Table S6). We found the interaction term was very close to significant (Coef = 1.52, z-value = 1.94, P = .05), but neither microsite nor categorical temperature was significant individually. On hot days the sunny microsite received much more pollen than the shady microsite, though the confidence interval is

considerably wider for the sunny microsite than the shady microsite (Fig. 8).

Discussion

The hypothesis that *C. anna* will forage preferentially in shady microsites on hot days was not supported by the feeder trials or semi-natural behavioral observations. In our feeder trials, hummingbirds visited feeders in sunny microsites with more frequency regardless of ambient temperature, and also stayed at the sunny feeder for longer periods of time. There was a trend towards higher pollen deposition at the sunny feeder on hot days than all other combinations of microsite and ambient temperature; however, it was only near-significant. In the semi-natural behavioral observations a similar trend emerged, as hummingbirds were more likely to be observed foraging on flowers in the sun than in the shade. In the semi-natural observations, this apparent preference for sunny foraging microsites was amplified by ambient temperature, with birds showing a stronger preference for sunny microsites on extremely hot days than on average days. However, there were some apparent differences in how hummingbirds spent their time between different behaviors on extremely hot days. The most frequently observed behavior in the sunny microsites during hot day sessions was foraging (44%, Fig. 5A), while the most frequently observed behavior in the sunny microsite during average sessions was aggression (29%; Fig. 6B). Perching was the most common behavior in shady microsites during both hot and average temperature days (Fig. 5, Fig. 6), likely due to the inherent presence of perching sticks in shade. It may be that extremely hot ambient temperatures have some effect on the overall time budget of hummingbirds, but that this does not change their foraging microsite preferences due to the ways in which they detect food sources.

Previous research on microsite occupancy in other avian taxa has found that birds will preferentially forage in the shade during hot periods (Cunningham et al. 2015, Lee et al. 2017, Abdu et al 2018, van de Ven et al. 2019). In many taxa, birds will forage in the shade above certain operative temperatures even when there is a fitness cost to doing so (Cunningham et al. 2015, van de Ven et al. 2019). In hummingbirds, there is evidence for context-dependent and contrasting responses to ambient temperature. In territorial hummingbirds like *C. anna* , increased thermoregulatory costs can lead to either decreased foraging activity to minimize energy loss, or conversely, increased foraging activity to maximize energy gain (Powers et al. 2017, Shankar et al. 2019). In our study, it is possible that the increased thermoregulatory costs of high temperatures could be driving increased foraging, in combination with a preference for sunny microsites. The preference for sunny microsites may be based on the reliance of hummingbirds on visual cues for detecting both nectar sources and threats from predators (though cover could also hide them from predators). There is some evidence that birds may feel less ability to leave an artificially shady microsite because of shade cloth, leading to more vigilance and lower preference for these sites (Abdu et al. 2018). Hummingbird dependence on visual cues to locate flowers is well established, and flowers in the sun may look different to them than flowers in the shade due to their ability to see ultraviolet light (Stoddard et al. 2022).

Hummingbirds do not typically drink water because their water needs are generally met through the nectar in their diet (Russell 1996, Nicolson & Fleming 2003), which is usually somewhat dilute in ornithophilous flowers (Nicolson & Fleming 2003). However, cooling through evaporative water loss is an important physiological thermoregulation mechanism for hummingbirds. At an average temperature of 24 @C, over 30% of a hummingbird's required daily water volume is lost through evaporation, while at 40 @C this can be up to 50% (Russell 1996). Gaping behavior allows birds to use evaporative cooling on hot days, and results in additional water loss. It is possible that hummingbirds need to forage for nectar more on hot days to keep up with their water needs. This increased demand for nectar sources on extremely hot days, combined with a preference for the visual stimuli presented by flowers in the sun, could explain the patterns we observed.

Our results demonstrate that contrary to our hypothesis, flowers in sunny microsites may experience increased pollen deposition on extremely hot days due to increased frequency and duration of hummingbird visits to flowers in sunny microsites on hot days. Similar to the trend observed in the semi-natural observations, the apparent preference for foraging in sunny microsites was amplified on hot days, with the sunny microsite receiving much more pollen than the shady site on hot days or either site on average days. Plants in sunny microsites may actually see increased hummingbird pollination services both during extreme heat events

and in the future under a warming climate regime. Pollen deposition was lowest in the shady microsite on hot days, suggesting that hummingbird-pollinated plants in shady microsites may be more likely to experience pollen limitation during extreme heat events. Pollinator behavior has major implications for plant conservation, particularly in plants that are specialists for hummingbirds and may not receive supplemental visits from invertebrate pollinators or other vertebrate pollinators.

It is thus not surprising that pollen deposition followed similar trends to visitation rate and visit duration, with sunny microsites on hot days receiving higher visitation and longer visit durations, and thus slightly higher pollen deposition. It is interesting that pollen deposition varied so much in sunny microsites on hot days; this is likely due to the fact that not all visitors had pollen already on their bodies when they visited the feeder. Thus, because there is a preference for sunny microsites on hot days, we see that there is greater variation in pollen deposition, as more birds are visiting overall.

Future studies should control for individual hummingbirds by using color markings to distinguish between individuals. Morgan et al. (2014) found evidence of individual foraging preferences in wild rufous hummingbirds (*Selasphorus rufus*). In addition, the sex and age of hummingbirds may affect their foraging decisions, as male, female, and juvenile hummingbirds in California have distinct diets (Hazlehurst et al. 2021). Another important factor that could have affected our results is aggressive territorial behavior, as being chased away from a feeder could artificially shorten visit duration or cause hesitancy to return. Previous research suggests that frequency of aggression declines at both low and high temperatures due to increased thermoregulatory costs (González-Gómez et al. 2011). Future studies should also consider foraging behavior over the entire daytime period rather than just focusing on the hottest part of the day. It is possible that hummingbirds shift as much of their foraging behavior as possible to early morning to avoid afternoon heat, and thus there may be additional factors that could influence pollen deposition patterns on hot and average days. However, there is mixed evidence for this strategy in hummingbirds, perhaps due to their need to feed frequently throughout the day, unlike in many other avian taxa. Powers et al. (2017) found only one of five hummingbird species studied became inactive during hot periods when it lacked a thermal gradient for passive cooling, and overall temporal patterns of foraging activity seem to vary by hummingbird species, time of year, and location (Russell 1996).

If *C. anna* foraging increases on hot days, especially in sunny microsites, then plants in sunny microsites could actually be more likely to be pollinated in the future under a warming climate. While this study was conducted in a semi-natural environment that consisted primarily of cultivated plants, future studies should consider pollination in more natural environments, as patterns of preference and pollen deposition may differ in those habitats. This is especially relevant considering the potential effects of heat stress and increased evaporation during periods of extremely high temperatures on floral trait expression (Carroll et al. 2001).

References

Abdu, S., McKechnie, A. E., Lee, A. T. K., & Cunningham, S. J. (2018). Can

providing shade at water points help Kalahari birds beat the heat? *Journal of Arid Environments*, *152*, 21-27.

Anderson, S.H., Kelly, D., Ladley, J.J., Molloy, S., & Terry, J. (2011). Cascading

effects of bird functional extinction reduce pollination and plant density. *Science*, *331*, 1068-1071.

Bartoń, K. (2022). MuMIn: Multi-Model Inference. R package version 1.46.0.

Bates, D., Maechler, M., Bolker, B., & Walker, S. (2015). Fitting Linear Mixed-Effect

Models Using lme4. *Journal of Statistical Software* 67, 1-48.

Battey, C.J. (2019). Ecological release of the Anna's hummingbird during a

northern range expansion. *The American Naturalist*, *194* (3), 306-315.

Bolker, B. M., Brooks, M. E., Clark, C. J., Geagne, S. W., Poulsen, J. R., Stevens, M. H.

H., & White, J. S. S. (2009). Generalized linear mixed models: a practical guide for ecology and evolution. *Trends in Ecology and Evolution, 24*(3), 127-135.

Carroll, A. B., Pallardy, S. G., & Galen, C. (2001) Drought stress, plant water

status, and floral trait expression in fireweed, *Epilobium angustifolium*(Onagraceae). *American Journal of Botany 88*(3), 438-446.

Cronk, Q., & Ojeda, I. (2008). Bird-pollinated flowers in an evolutionary and

molecular context. *Journal of Experimental Botany, 59*(4), 715-727. doi:10.1093/jxb/ern009.

Cunningham, S. J., Martin, R. O., & Hockey, P. A. R. (2015). Can behaviour buffer

the impacts of climate change on an arid-zone bird? *Ostrich,86*(2), 119- 126. doi:10.2989/00306525.2015.1016469

Del Coro Arizmendi, M., Rodríguez-Flores, C. I. (2012). How many plant species

do hummingbirds visit? *Ornitologia Neotropical, 23*, 71-75.

Du Plessis, K. L., Martin, R. O., Hockey, P. A. R., Cunningham, S. J., & Ridley, A. R.

(2012). The costs of keeping cool in a warming world: implications of high temperatures for foraging, thermo-regulation and body condition of an aridzone bird. *Global Change Biology, 18*, 3063-3070. doi:10.1111/j.1365-2486.2012.02778.x

Engel, E. C., & Irwin, R. E. (2003). Linking pollinator visitation rate and pollen

receipt. *American Journal of Botany, 90*(11), 1612-1618.

Hazlehurst, J. A., Rankin, D. T., Clark, C. J., McFrederick, Q. S., & Wilson-Rankin, E. E.

(2021). Macroecological patterns of resource use in resident and migratory hummingbirds. *Basic and Applied Ecology, 51*, 71-82.

Kearns, C. A., & Inouye, D. W. (1993). Techniques for pollination biologists. University

Press of Colorado.

Lee, A. T. K., Wright, D., & Barnard, P. (2017). Hot bird drinking patterns: drivers of

water visitation in a fynbos bird community. *African Journal of Ecology 55*, 541-553.

Lenth, R. V. (2022). emmeans: Estimated Marginal Means, aka Least-Squares

Means. R package version 1.7.4-1.*https://github.com/rvlenth/emmeans*

Meehan, T. D., Dale, K., Lebaron, G. S., Rowden, J., Michel, N. L., Wilsey, C. B., &

Langham, G. M. (2020). Interacting with hummingbirds at home: Associations with supplemental feeding, plant diversity, plant origin, and landscape setting. *Landscape and Urban Planning 197.https://doi.org/10.1016/j.landurbplan.2020.103774*

Morgan, K. V., Hurly, T. A., & Healy, S. D. (2014). Individual differences in decision

making by foraging hummingbirds. *Behavioural Processes,109*, 195-200.

Nicolson, S. W., & Fleming, P. A. (2003). Nectar as food for birds: the

physiological consequences of drinking dilute sugar solutions.*PlantSystematics and Evolution 238*(1/4), 139-153.*https://www.jstor.org/stable/23644984*

Ollerton, J., Winfree, R., & Tarrant, S. (2011). How many flowering plants are

pollinated by animals? *Oikos, 120*, 321–326. doi:10.1111/j.1600- 0706.2010.18644.x

Powers, D., Langland, K., Wethington, S., Powers, S., Graham, C., & Tobalske, B.

(2017). Hovering in the heat: Effects of environmental temperature on heat regulation in foraging hummingbirds. *Royal Society Open Science, 4(*12*)*. 171056. doi:10.1098/rsos.171056

Ratto, F., Simmons, B. I., Spake, R., Zamora-Gutierrez, V., MacDonald, M. A.,

Merriman, J. C., Tremlett, C. J., Poppy, G. M., Peh, K. S. H., & Dicks, L. V. (2018). Global importance of vertebrate pollinators for plant reproductive success: a meta-analysis. *Frontiers in Ecology and the Environment,16(2)*, 82-90. doi:10.1002/fee.1763

Russell, S.M. (1996). Anna's hummingbird (*Calypte anna*). In A.F. Poole, ed. *The*

Birds of North America. Cornell Lab of Ornithology, Ithaca, NY.

Shankar, A., Powers, D. R., Davalos, L. M., & Graham, C. H. (2020). The allometry of

daily energy expenditure in hummingbirds: An energy budget approach.*Journal of Animal Ecology, 89*(5), 1254-1261.*https://doi.org/10.1111/1365-2656.13185*

Shankar, A., Graham, C. H., Canepa, J. R., Wethington, S. M., & Powers D. R.

(2019). Hummingbirds budget energy flexibly in response to changing resources. *Functional Ecology, 33*(20), 1904–1916.*https://doi.org/10.1111/1365-2435.13404*

Stoddard, M. C., Eyster, H. N., Hogan, B. G., Morris, D. H., Soucy, E. R., & Inouye,

D. W. (2020). Wild hummingbirds discriminate nonspectral colors.*Proceedings of the National Academy of Sciences of the United States ofAmerica, 117*(26), 15112–15122.*https://doi.org/10.1073/pnas.1919377117*

Van de Ven, T. M. F. N., McKechnie, A. E., & Cunningham, S. J. (2019). The costs of

keeping cool: behavioural trade-offs between foraging and thermoregulation are associated with significant mass losses in an arid zone bird. *Oecologia, 191*, 205-215. https://doi.org/10.1007/s00442-019-04486-x.

Figures and Tables

Figure 1. Locations of feeder trials and semi-natural observations on the California State University East Bay (CSUEB) campus in Hayward, California.
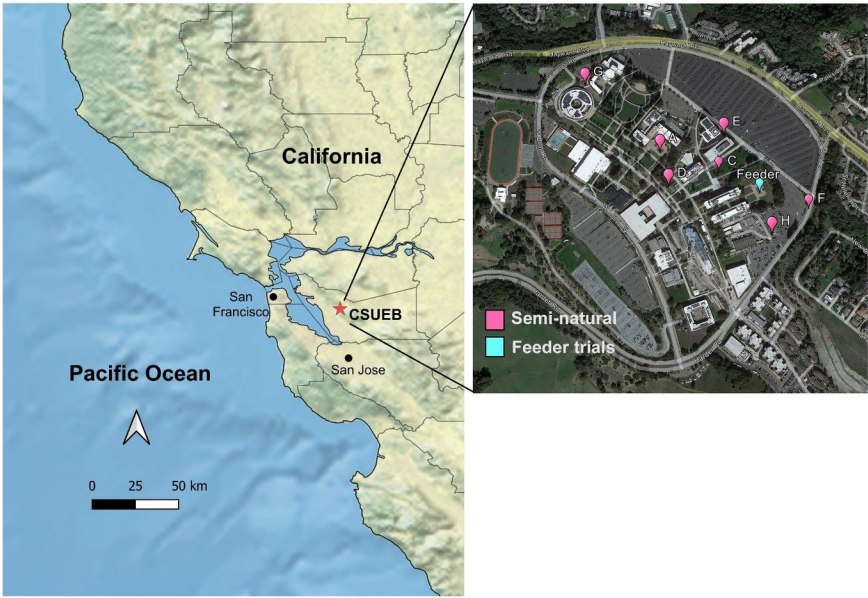
Figure 2. Effects plot showing significant positive effect of sunny microsite on the cumulative number of visits by Anna's hummingbirds during feeder trials.
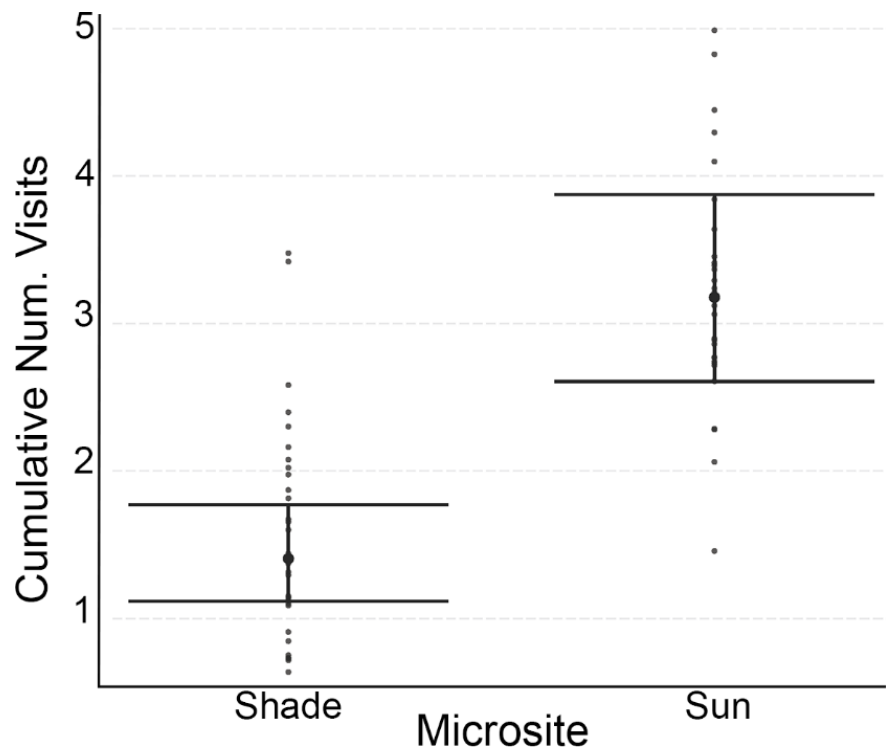

Figure 3 . Effects plot showing significant positive effect of sunny microsite on the visitation rate by Anna's hummingbirds during feeder trials.
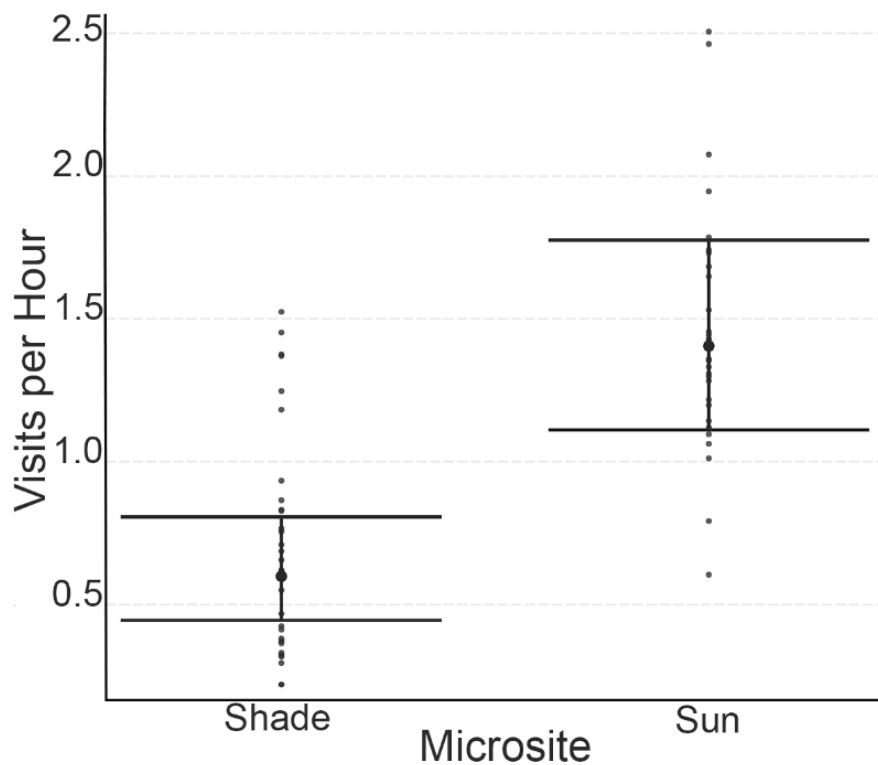
Figure 4. Categorical interaction plot showing significant positive interaction of microsite and ambient temperature on visit duration (scaled by standard deviation) in sunny microsites on hot days from feeder trials.
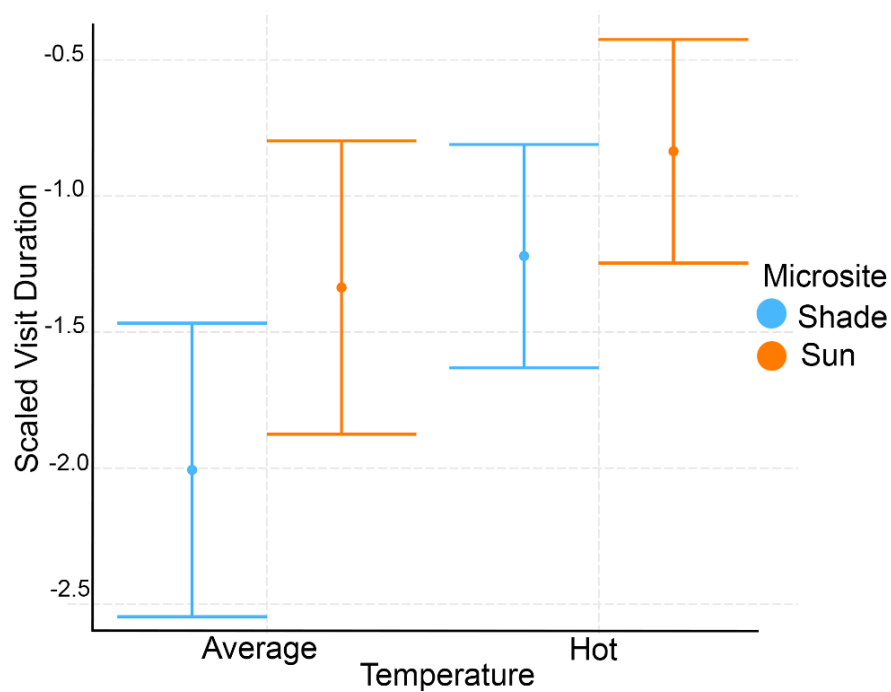
Figure 5. Time budgets of hummingbirds in sunny microsites based on average percent of observations falling into each behavior category per session on **A)** hot and **B)** average days.
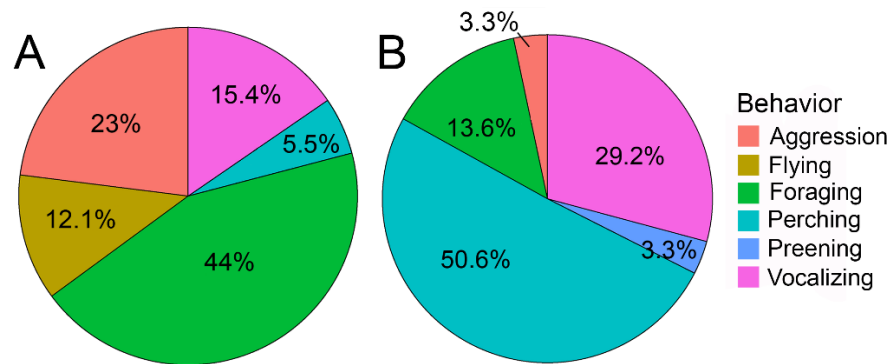

Figure 6. Time budgets of hummingbirds based on average percent of observations falling into each behavior category per session in **A)** sunny and **B)** shady microsites.
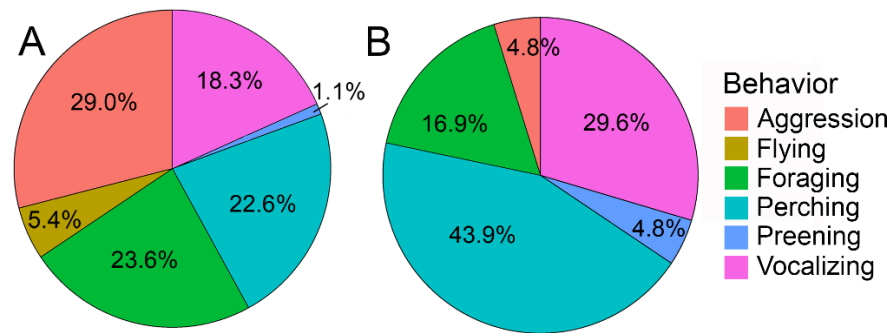

Figure 7. Categorical interaction plot for cumulative number of visits by Anna's hummingbirds during semi-natural observations from best model.
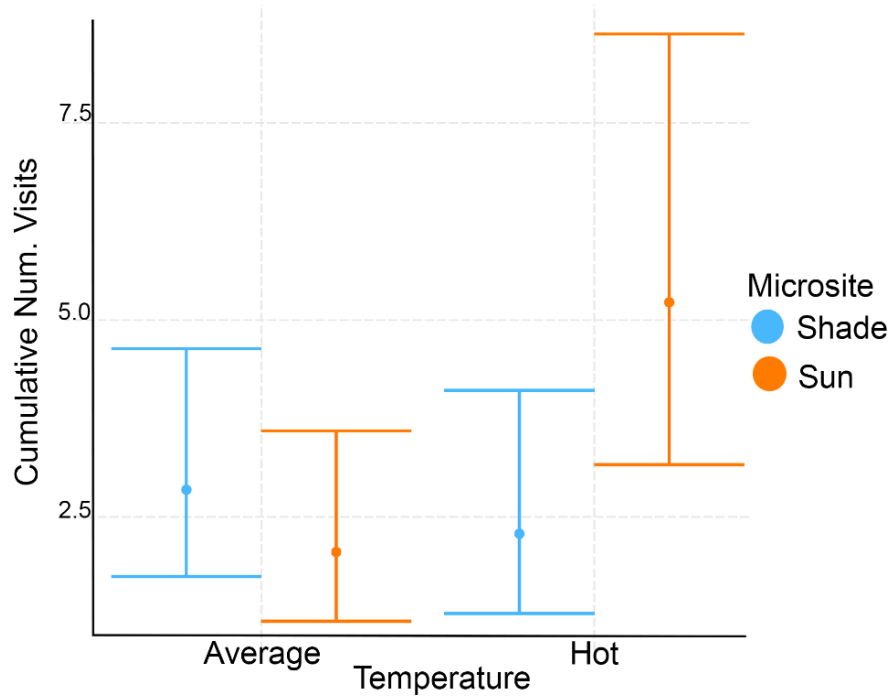
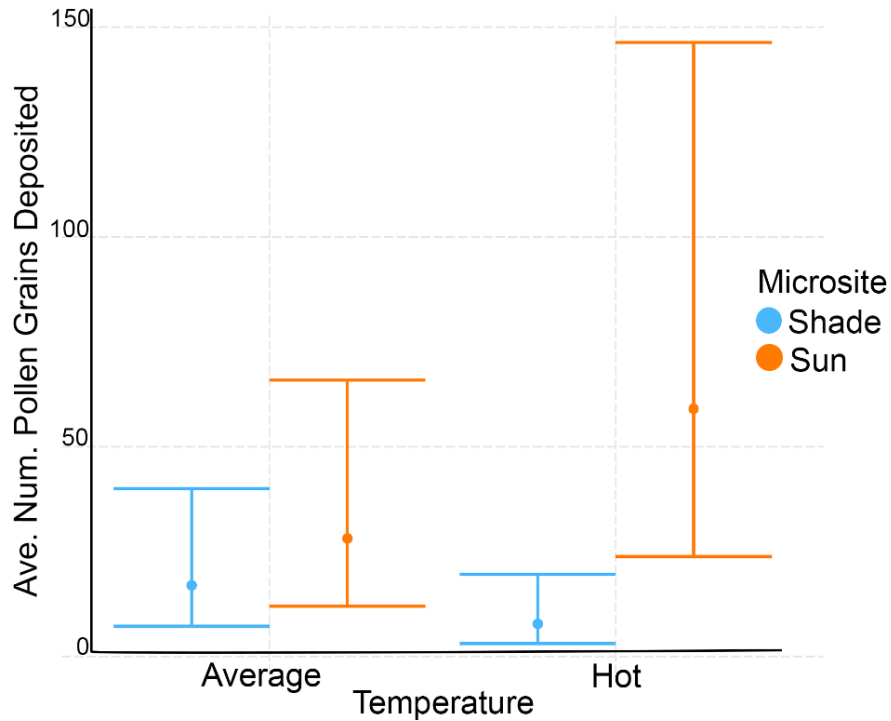**Figure 8.** Categorical interaction plot for pollen deposition during feeder trials from best model.

Table 1. Descriptions of behaviors recorded during semi-natural observation sessions

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Behavior	Description
Perching	Sitting on a perch
Foraging - nectar	Making physical contact with a flower
Foraging - insect	Fly catching or gleaning arthropods
Preening	Moving own feathers with bill or foot
Vocalizing	Making a vocalization of any kind
Aggression	Chasing or directed physical contact with another bird
Gaping	Bill hanging open in panting behavior

Table 2. Final model for cumulative number of foraging visits in feeder trials with **(A)** temperature as the maximum temperature in the sun during the session and **(B)** temperature as a categorical variable where "hot" is categorized as a maximum sun temperature > 35@C.

A. Model: num. visits ~ microsite*max_sun_temp + (1|session_id) + offset(session_duration)	A. Model: nu
Variable	**Coefficient**
(Intercept)	-1.2
Microsite (sun)	**1.5**
Max. sun temp (@C)	0.02
Microsite (sun)*Max. sun temp	-0.02
P < 0.05, ** P < 0.01, *** P < 0.001	* P < 0.05, **
B. Model: num. visits ~ microsite*temp_cat + (1|session_id) + offset(session_duration)	**B. Model: nu**
Variable	**Coefficient**
(Intercept)	**-0.74**
Microsite (sun)	**0.82**
Temp category (hot)	0.14
Microsite (sun)*Temp category (hot)	-0.02
P < 0.05, ** P < 0.01, *** P < 0.001	* P < 0.05, **

Table 3. Final model for visitation rate (visits/hr) in feeder trials with **(A)** temperature as the maximum temperature in the sun during the session and **(B)** temperature as a categorical variable where "hot" is categorized as a maximum sun temperature > 35@C.

A. Model: visit rate ~ microsite*max_sun_temp + (1|session_id) + offset(session_duration)	A. Model: visit
Variable	**Coefficient**
(Intercept)	**-2.19**
Microsite (sun)	**1.76**
Max. sun temp (@C)	0.02
Microsite (sun)*Max. sun temp	-0.03
P < 0.05, ** P < 0.01, *** P < 0.001	* P < 0.05, ** P
B. Model: visit rate ~ microsite*temp_cat + (1|session_id) + offset(session_duration)	**B. Model: visit**
Variable	**Coefficient**
(Intercept)	**-1.66**
Microsite (sun)	**0.96**
Temp category (hot)	0.25
Microsite (sun)*Temp category (hot)	-0.18
P < 0.05, ** P < 0.01, *** P < 0.001	* P < 0.05, ** P

Table 4 . Final model for visit duration in feeder trials with temperature as a categorical variable where "hot" is categorized as a maximum sun temperature > 35@C.

Model: visit duration ~ microsite*temp_cat + (1|session_id) + offset(session_duration)	Model: visit durati
Variable	**Coefficient**
(Intercept)	**-2.34**
Microsite (shade)	**-0.67**
Temp category (hot)	0.5
Microsite (shade)*Temp category (hot)	0.29
P < 0.05, ** P < 0.01, *** P < 0.001	* P < 0.05, ** P < 0.

Table 5. Final model from semi-natural observations for total visits (total number of birds observed foraging per session per microsite), with temperature as a categorical variable where "hot" is categorized as a maximum sun temperature > 35@C.

Model: semi-natural observations total visits ~ microsite*temp_cat + (1|session_id) + offset(session_duratio
Variable
(Intercept)
Microsite (sun)
Temp category (hot)
Microsite (sun)*Temp category (hot)
P < 0.05, ** P < 0.01, *** P < 0.001

Table 6. Final model for pollen deposition on the false stigmas during feeder trials with temperature as a categorical variable where "hot" is categorized as a maximum sun temperature > 35@C.

Model: pollen count ~ microsite*temp_cat + (1\|julian_day) + (1\|obs_effect) + offset(session_-duration)

Variable	Coefficient	SE
(Intercept)	**1.83**	**0.43**
Microsite (sun)	0.51	0.54
Temp category (hot)	-0.78	0.63
Microsite (sun)*Temp category (hot)	1.52	0.78
P < 0.05, ** P < 0.01, *** P < 0.001	* P < 0.05, ** P < 0.01, *** P < 0.001	* P < 0.05, ** P < 0.01, *** P < 0.001

Shady Microsite

Sunny Microsite

Heat Wave >30°C

Average Temp

Visitation rate

Visit duration

Near-significant effect on pollen deposition