

**HMN's COORDINATED TREND MONITORING PROGRAM**  
STANDARDIZED PROJECT PROPOSAL TO BBL FOR NETWORK COLLABORATORS  
By Susan Wethington and Kira Monroe

While monitoring needs of hummingbird populations are similar to other animal populations, techniques used to effectively monitor them must consider their evolutionary history, specialized ecology, and constrained physiology. The need to use specialized techniques, coupled with the necessary additional training, has left a large data gap for hummingbird populations. The Hummingbird Monitoring Network (HMN), founded in 2002 with 501(C)(3) nonprofit status by 2004, began because hummingbird conservation had limited focus from the conservation world; population trend data for hummingbirds were lacking; and other bird monitoring programs did not effectively sample hummingbird populations. Its primary objectives include 1. Maintaining long-term monitoring sites that represent the region's hummingbird diversity across each species range; 2. Collecting detailed demographic information on hummingbird populations so trends in their populations, distribution and abundance, and movement patterns can be detected; and 3. Training individuals interested in working with HMN and/or whose work would benefit from hummingbird banding.

HMN's coordinated trend monitoring program is a systematic banding program with constant effort, robust design protocol that is stratified by geographic factors such as elevation, longitude, and latitude and vegetation type. Its sampling and experimental design is based upon the MAPS (Monitoring Avian Productivity and Survivorship) program but modified to include field techniques that account for hummingbirds' unique ecology, anatomy, and physiology. HMN's program has generated data with large sample sizes and high recapture rates that allow using Capture Mark Recapture models to estimate survivorship and other demographic estimates. It also provides information about which areas support a high diversity and abundance of hummingbirds, which areas are important breeding sites, the timing of hummingbird occurrence, and their seasonal movement patterns.

To meet HMN's primary objectives requires collaboration of banders across the ranges of hummingbird species monitored. Ideally, sites in each region will be identified that sample populations of all breeding species in the area as well as key migration stopover sites. These sites would be distributed so that each geographic factor and vegetation type is represented. With the submission of this standardized protocol for collaborating partners, HMN is positioned to expand its program to more fully monitor species across their range and identify emerging threats and conservation issues.

**NEW BANDER / SITE PROPOSAL**

Information in this section will be provided by the bander who is requesting permits to manage and run monitoring sites for HMN

- What characteristics of your site would make it an asset to the Network?
- Why is joining the Network important to you or your organization?
- Please describe your site's hummingbird population, physical characteristics, and the surrounding area.
- Will your site be included in outreach and environmental education opportunities?

# STANDARDIZED PROJECT PROPOSAL FOR BBL

## INTRODUCTION AND JUSTIFICATION

Cuckoos, penguins, herons, shorebirds, raptors, owls, parrots, and many more bird lineages are more closely related to passerines than are hummingbirds (Hackett et al. 2008). Hummingbirds' small size, physiological constraints, pollinator lifestyle, high-pitched vocalizations, and unique flight abilities (Stiles 1981, Brown and Bowers 1985, Rosero 2003, Schuchmann 1999, Temeles and Kress 2003, Gegear and Burns 2007) are just some of the traits that make them different. These physical characteristics, ecological adaptations, and evolutionary history make their pollinator lifestyle unique—so much so that survey techniques used to understand population trends of other birds are generally ineffective for hummingbirds.

In a report to the USFS Western Hummingbird Partnership (Wethington 2013), the following monitoring programs were assessed to determine the adequacy of current monitoring programs for hummingbirds.: MAPS (Monitoring Avian Productivity and Survivorship), MOSI (Monitoreo de Sobrevivencia Invernal), MAWS (Monitoring Overwinter Survival), BBS (Breeding Bird Survey), BBC (Breeding Bird Census), CBC (Christmas Bird Count), eBird, GBBC (Great Backyard Bird Count), CMMN (Canadian Migration Monitoring Network), Cornell's FeederWatch, and HMN (Hummingbird Monitoring Network) Of the Capture Mark Recapture programs evaluated, only HMN's program generate data with large sample sizes and high recapture rates that allow using CMR models to estimate survivorship and other demographic estimates.

However, MAPS's standardized sampling design has generated data that has been effective for answering questions about population trends in passerines and near-passerines (See Institute for Bird Populations Website). Because monitoring needs of hummingbird populations are similar to other animal populations, HMN adopted elements of the MAPS sampling design but added capture and banding techniques that have been developed specifically for hummingbirds' specialized ecology and physiology.

Finally, trend data for most hummingbird species are insufficient or non-existent. Existing long-term population trend data are considered adequate for only 4 of the 16 species that regularly breed in the USA and Canada (Rich et al. 2004, Berlanga et al. 2010). To maintain thriving hummingbird populations, it is important to understand (1) trends in hummingbird distribution, abundance, and movement patterns; (2) population dynamics, such as survivorship, productivity, and other demographic factors; (3) the effects of broader resource changes on hummingbirds; and (4) emerging threats or problem.

## ABOUT HMN

The Hummingbird Monitoring Network (HMN), founded in 2002 with 501(C)(3) nonprofit status by 2004, began because hummingbird conservation had limited focus from the conservation world and population trend data for hummingbirds were lacking. It started as a science-based, project-driven organization dedicated to maintaining hummingbird diversity and abundance throughout the Americas. It is a unique organization that combines collaborative research, community involvement and training,

with a view to understanding and appreciating the importance of hummingbirds and their conservation in a changing world.

HMN's original objectives are to: maintain long-term monitoring sites that represent the region's hummingbird diversity across each species range; collect detailed demographic information on hummingbird populations so trends in their populations can be detected; encourage and support research projects that promote hummingbird conservation; support efforts that preserve and restore hummingbird habitats; educate by disseminating information about hummingbirds to land managers, the scientific community, and the general public; train individuals interested in working with HMN and/or whose work would benefit from hummingbird banding; and use the resulting information to improve hummingbird conservation.

To address the lack of trend/status data, HMN began a coordinated trend monitoring program, mainly with volunteers who trained as citizen scientists. Now, it partners with federal and state agencies, nonprofit organizations, universities, citizen scientists, and volunteers. It is a systematic banding program stratified by geographic factors such as elevation, longitude, latitude, and vegetation type. Its sampling and experimental design is based upon techniques which has been effective for answering questions about population trends; however capture, banding techniques, and tools have been developed and employed specifically for hummingbirds' specialized ecology and constrained physiology.

With these modifications, HMN's program has generated data with large sample sizes and high recapture rates that allow using Capture Mark Recapture models to estimate survivorship and other demographic estimates. It also provides information about which areas support a high diversity and abundance of hummingbirds, which areas are important breeding sites, the timing of hummingbird occurrence, and their seasonal movement patterns.

In addition to the monitoring program, HMN has collaborated on numerous research projects, developed hummingbird field techniques, helped found Borderlands Restoration L3C to restore landscapes and engage communities along the Mexico/USA border, initiated an after school employment program for high school students, and developed an internship program for Latin American college students and young professionals to learn hummingbird field techniques.

## STUDY AREA

HMN began with sites in California and Arizona and has expanded to sites across western USA, British Columbia, and one site in Mexico. Between 15 and 30 sites have been active in any one year. Currently active sites are in British Columbia, Montana, Idaho, Utah, Colorado, New Mexico, and Arizona. To meet the goal of maintaining long-term monitoring sites that represent a region's diversity, additional sites are required to determine population trends for each species that occur in the USA and Canada. HMN's protocol effectively gather population level data for hummingbird species where feeders have become a part of their ecology. Hence, this program can expand throughout the USA and Canada.

## METHODS

HMN's coordinated trend monitoring program is a systematic banding program with constant effort, robust design protocol that is stratified by geographic factors such as elevation, longitude, and latitude

and vegetation type. Its sampling and experimental design is based upon the MAPS (Monitoring Avian Productivity and Survivorship) program run by the Institute of Bird Populations but modified to include field techniques that are defined based upon hummingbird ecology and physiology. Program partners include federal and state agencies (e.g. NPS, USFS, DOD, BLM, AZSP), nonprofit organizations (e.g. Rocky Pt Bird Observatory, Intermountain Bird Observatory, AMNH Southwestern Research Station, MPG Ranch) universities (e.g. Colorado State University, UNAM, University of Arizona), and individuals who work as volunteers or citizen scientists. For a list of current partners, please visit (HMNs WEBSITE- ADD LINK)

### HMN'S MONITORING PROTOCOL

1. Five feeders are maintained at each study site while hummingbirds occur there.
2. Hummingbirds are trapped and banded once every two weeks. Banders have all required permits from governmental agencies and local land managers.
3. Trapping and banding begins within one half-hour of sunrise and continues for five hours. For northern latitude sites, the monitoring start time may be delayed based upon local conditions. For example, the start of monitoring is scheduled so that it starts about the same time as the nearby hummingbird nectar plants begin to produce nectar. Monitoring should still last 5 hours.
4. Temperature may also cause delay in the start of monitoring. If the temperature is below 32°F or 0°C, the session is delayed until it is above freezing. For temperatures below 38°F or 3°C, the bander will use discretion as to when to start. If few birds are present or the team has a heater or warm place to hold the birds, the session can start normally with increased emphasis on bird safety. If the start of monitoring is delayed, monitoring should still last 5 hours.
5. When conditions, such as a short rainfall events, windy conditions, or bees dominating the feeders, cause interruption, the monitoring session may be stopped. If these conditions are temporary and last less than 30 minutes, please extend the monitoring session so the total time of active monitoring is 5 hours. If the conditions last longer than 30 minutes, the bander may choose to end the monitoring early and describe these events in the session report.
6. We use two Hall traps that each covers one feeder. The remaining three feeders are taken down and are not accessible to hummingbirds during the five-hour banding period.
7. One to three people operate the traps. They are responsible for removing birds from the traps, placing them into holding bags, opening the trap before taking the birds to the banding table. While a trapper takes a bird to the table, the other trapper(s) should watch both traps. While putting birds on the holding carousel, trappers should observe the bird to ensure its well-being and notify the bander if anything is of concern. This check will help improve bird safety. During slow periods and there is only one trapper, people at the banding table should help bring birds to the table. The highest priority for trap operation is to ensure that the traps are observed throughout the 5-hour period and that the time at the traps is minimized. Trappers are also responsible for taking trap data (See bullet 8). No other information is taken at the trap.
8. At the banding table, birds are processed in chronological order and are held no longer than 30 minutes. The bander determines how many birds that he/she can safely band within 30 minutes. When this number is reached, the bander requests the trappers to stop trapping and records the time

of the request. When the bander is ready to accept more birds, he/she informs the trappers to start catching birds and again records the time.

9. While the trapper is not actively catching birds, he/she records the number of birds that enter the perimeter of the trap. When bird numbers are high, counting the number of birds that either enter or leave the trap provides a better estimate than trying to keep track of which birds have not been counted while feeding. The trapper records all birds that escape when actively trapping. When bird numbers are low, the trapper also records the number of birds that approach the trap but do not enter. The trapper should watch a bird as long as it is near either trap. If a bird approaches one or both traps, does not enter any, and then leaves, the trapper will mark this bird as one trap checker. This data are used to estimate abundance of hummingbirds.
10. The bander bands, observes all the required identification traits, measures the hummingbirds, collect ecological data such as molt, fat, breeding condition, pollen information, and additional information such as feather collection needed to support additional research efforts.
11. The recorder records the data on a data sheet. He/she is responsible for ensuring that all measurements and required traits are accurately recorded; records the start and stop trapping times when visits at traps are counted; and manages the recapture list so that banded birds are not processed multiple times on a banding morning.
12. Once the bird is placed on the scale and the weight recorded, the bird is fed and released. During slow times (i.e. few birds), the recorder can do this job. But when there are large numbers of birds, an additional person to feed and release birds is helpful.
13. In public areas, another helper (who could also be the feeder) may present information to the public and ensure that the public does not impede the banding process. Many visitors will want to help. We allow them to release birds by holding their hand palm up and fingers straight. The feeder can then place the bird on the hand. Sometimes the bird will perch on the hand for a while, but often they fly off immediately.
14. HMN's goal is to have no injured or dead birds. Occasionally, it happens. If an injury or death occurs, everyone involved in the capture of the bird should discuss the incident. Each should re-evaluate their actions and determine if they could change something to prevent the injury. If so, these changes should be reported to the coordinator and integrated into the protocol. If death occurred, the specimen should be frozen and then donated to the nearest institution that maintains a bird collection.
15. At the end of each monitoring session, sub-permitted banders submit a session summary report along with the banding, trap, and other meta-data. Master Banders who are collaborating with HMN will submit a session summary report after each session but can submit their data annually.

## STATISTICAL ANALYSIS

Using the statistical computing program R (v. 3.4.0, R Core Team 2017), we are developing a library of R scripts that can summarize data collected from HMN sites. These scripts are generalized so that sets of locations and years of monitoring can be chosen per hummingbird species and sex. Specifically, information about the following topics are included: summary statistics of hummingbird population at each site, survival and recapture probability estimates, inter-site movement, recapture rates for site

fidelity estimates, breeding and migration timing, measurements, molt, abnormalities and stress, and pollen information.

To estimate annual apparent survival and recapture probabilities and hence provide initial population trend data, we use the R package RMark (v. 2.2.2, Laake 2013) to construct Cormack-Jolly-Seber (CJS) models (Cormack 1964, Jolly 1965, Seber 1965, Lebreton et al. 1992) in program MARK (v. 8.1, White and Burnham 1999). Because hummingbirds will readily move to find resources, there is potential for inclusion of a large proportion of “transient” individuals in the capture-recapture sample and thus decrease estimates of apparent survival (Saracco et al. 2010, Morrison et al. 2016). Therefore, we use a modified CJS model that accounts for transients by determining if each individual was observed on separate occasions during their first year of capture (resident bird) or not (unknown or transient bird; Pradel et al. 1997, Hines et al. 2003, Saracco et al. 2010). In subsequent years, individuals that were recaptured (resident, transient, or unknown) are considered as residents. Per research question, we consider a set of a priori models and evaluate models using Akaike’s Information Criterion (Burnham and Anderson 2002)

#### PUBLISHED LITERATURE USING HMN DATA

All papers listed below have used information gathered at HMN’s trend monitoring sites This section includes literature published peer-reviewed scientific papers and papers presented at scientific conferences.

1. Graham, C. H., S. R. Supp, D. R. Powers, P. Beck, M. C. W. Lim, A. Shankar, T. Cormier, S. Goetz and S. M. Wethington (2016). "Winter conditions influence biological responses of migrating hummingbirds." *Ecosphere* 7(10): 18. 219(22): 3518-3531.
2. Godoy L.A., L. S. Dalbeck, L. A. Tell, L. W. Woods, R. R. Colwell, B. Robinson, S. M. Wethington, A. Moresco, P. R. Woolcock, and H. B. Ernest<sup>1</sup>, (2013) Characterization Of Avian Poxvirus In Anna’s Hummingbird (*Calypte Anna*) In California, USA. *Journal of Wildlife Diseases*, Vol. 49, No. 4, October 2013: 978-985.
3. Licona-Vera Y, Ornelas J.F., Wethington, S.M. and Bryan K.B. (2018) Pleistocene range expansions promote divergence with gene flow between migratory and sedentary populations of *Calothorax* hummingbirds. *Biological Journal of the Linnean Society*, 124:645–667.
4. Malpica, A. and J. F. Ornelas (2014). "Postglacial northward expansion and genetic differentiation between migratory and sedentary populations of the broad-tailed hummingbird (*Selasphorus platycercus*)." *Molecular Ecology* 23(2): 435-452.
5. McCaffrey, R.E. and S. M. Wethington. 2008. How the presence of feeders affects the use of local floral resources by hummingbirds: a case study from southern Arizona. *Condor* 110(4):786–791.
6. Moran, J.A., L.I. Wassenaar, J.C. Finlay, C. Hutcheson, L.A. Isaac, S.M. Wethington. (2013). An exploration of migratory connectivity of the Rufous Hummingbird (*Selasphorus rufus*), using feather deuterium. *J. Ornith* (DOI 10.1007/s10336-012-0906-3)

7. Rodriguez-Gomez, F., C. Gutierrez-Rodriguez and J. F. Ornelas (2013). "Genetic, phenotypic and ecological divergence with gene flow at the Isthmus of Tehuantepec: the case of the azure-crowned hummingbird (*Amazilia cyanocephala*)." *Journal of Biogeography* 40(7): 1360-1373.
8. Rogers L.A., Wethington S.M., and Monroe K. (2016). One Size Does Not Fit All: How Band Size Affects Recapture and Survival Rates of Hummingbirds. Western Bird Banding Association Annual Meeting. Point Reyes Station, CA
9. Rousseau, J. S., J. D. Alexander and M. G. Betts. 2020. Using continental-scale bird banding data to estimate demographic migratory patterns for Rufous Hummingbird (*Selasphorus rufus*). *Avian Conservation and Ecology* 15 (2):2. [online] URL: <http://www.ace-eco.org/vol15/iss2/art2/>
10. Wethington S.M., Monroe K., Goetz S., and Graham C.H. 2016. Migration strategies and environmental factors influence annual survivorship in western USA hummingbirds. Oral Presentation. Program and Abstracts of Presented Papers and Posters: North American Ornithological Conference. Washington D.C.
11. Wethington S.M. 2013. An evaluation of monitoring data for hummingbirds, Submitted to the USFS Western Hummingbird Partnership
12. Wethington S. M., C. Carrothers, D. L. Craig. 2010. Western Hummingbird Partnership Action Plan. See: [http://www.hummonnet.org/pdf/201006whp\\_actionplan.pdf](http://www.hummonnet.org/pdf/201006whp_actionplan.pdf)
13. Wethington S.M., West G.C., Carlson B.A. 2006. Estimating abundance so trends in hummingbird populations can be detected. Book of Abstracts, 4th North American Ornithological Conference: Wings without Borders. Veracruz, Mexico.
14. Wethington, S. M. (2006). Hummingbird migration: Identifying potential route boundaries and abiotic factors affecting abundance of migrants. Book of Abstracts, 4th North American Ornithological Conference: Wings without Borders. Veracruz, Mexico.
15. Wethington, S.M.; West G.C., and Carlson B.A., 2005. Hummingbird conservation: Discovering diversity patterns in southwest USA. In *Connecting mountain islands and desert seas: biodiversity and management of the Madrean Archipelago II*. Compiled by G. J. Gottfried, B.S. Gebow, L.G. Eskew, and C.B. Edminster. 2004 May 11-15; Tucson, AZ. pp 162-168. Proceedings RMRS-P-36. Fort Collins, CO: U.S. Department of Agriculture, Forest Service, Rocky Mountain Research Station.
16. Wethington, S. M., S. M. Russell, and G. C. West. 2004. Timing of hummingbird migration in southeastern Arizona: Implications for their conservation. In Ralph, C. J. and T. D. Rich [eds.], *Bird Conservation Implementation and Integration in the Americas: Proceedings of the Third International Partners In Flight Conference*. 2002 March 20-24; Asilomar, California; Volume 1: pp 646-651. Gen. Tech. Rep. PSW-GTR-191. Albany, CA. Pacific Southwest Research Station, Forest Service, U.S. Department of Agriculture.
17. Wethington S.M. and Russell, S. M. 2003. The Seasonal Distribution and Abundance of Hummingbirds in Oak Woodland and Riparian Communities. *Condor* 105(3): 484-495.
18. Wethington, S.M., West G.C., and Carlson B.A., 2003. Hummingbird conservation: Discovering diversity patterns in southwestern USA. Program and Abstracts of Presented Papers and posters. Cooper Ornithological Society 75th Annual Meeting.
19. Wethington, S. M., G.C. West, B. A. Carlson, N.L. Newfield, and S.J. Peters. 2002. Longevity records for North American Hummingbirds. *N.Am. Bird Bander*. 27(4):131-133

20. Wethington, S. M., G.C. West, and B. A. Carlson. 2002. Studying hummingbird migration and monitoring their productivity and survivorship. *N.Am. Bird Bander*. 27(3):109.
21. Wethington, S. M., and S. M. Russell. 2001. A snapshot of hummingbird migration in southeastern Arizona. *North American Bird Bander* 26:157-160.
22. Zamudio-Beltrán, L.E. and B.E. Hernández-Baños. 2015. A multilocus analysis provides evidence for more than one species within *Eugenes fulgens* (Aves: Trochilidae). *Molecular Phylogenetics and Evolution* 90 (2015) 80–84.
23. Luz E Zamudio-Beltrán, Juan Francisco Ornelas, Andreia Malpica, Blanca E Hernández-Baños, Genetic and morphological differentiation among populations of the Rivoli's Hummingbird (*Eugenes fulgens*) species complex (Aves: Trochilidae), *The Auk*, , ukaa032, <https://doi.org/10.1093/auk/ukaa032>

#### CITED LITERATURE

1. Berlanga, H., J. A. Kennedy, T. D. Rich, M. C. Arizmendi, C. J. Beardmore, P. J. Blancher, G. S. Butcher, A. R. Couturier, A. A. Dayer, D. W. Demarest, W. E. Easton, M. Gustafson, E. Iñigo-Elias, E. A. Krebs, A. O. Panjabi, V. Rodriguez Contreras, K. V. Rosenberg, J. M. Ruth, E. Santana Castellón, R. Ma. Vidal, T. C. Will. 2010. Saving Our Shared Birds: Partners in Flight Tri-National Vision for Landbird Conservation. Cornell Lab of Ornithology: Ithaca, NY.
2. Brown, J. H. & M. A. Bowers. 1985. Community organization in hummingbirds: relationships between morphology and ecology. *The Auk* 102: 251-269.
3. Burnham, K. P., and D. R. Anderson. 2002. *Model Selection and Multimodel Inference: A Practical Information-Theoretic Approach*, second edition. Springer-Verlag, New York, NY, USA.
4. Cormack, R. M. 1964. Estimates of survival from the sighting of marked animals. *Biometrika* 51: 429–438.
5. Gegeer, R. J. and J. C. Burns. 2007. The birds, the bees, and the virtual flowers: can pollinator behavior drive ecological speciation in flowering plants? *American Naturalist* 170:551-566.
6. Hackett, S. J., R. T. Kimball, S. Reddy, R. C. K. Bowie, E. L. Braun, M. J. Braun, J. L. Chojnowski, W. A. Cox, K.-L. Han, J. Harshman, C. J. Huddleston, B. D. Marks, K. J. Miglia, W. S. Moore, F. H. Sheldon, D. W. Steadman, C. C. Witt and T. Yuri (2008). "A phylogenomic study of birds reveals their evolutionary history." *Science* 320: 1763-1768.
7. Hines, J. E., W. L. Kendall, J. D. Nichols, and F. R. Thompson III. 2003. On the use of the robust design with transient capture-recapture models. *The Auk* 120: 1151–1158.
8. Jolly, G. M. 1965. Explicit estimates from capture-recapture data with both death and immigration-stochastic models. *Biometrika* 52: 225–247.
9. Laake, J. L. 2013. RMark: An R interface for analysis of capture-recapture data with MARK. AFSC Processed Report 2013-01, 25 p. Alaska Fish. Sci. Cent., NOAA, Natl. Mar. Fish. Serv., 7600 Sand Point Way NE, Seattle WA 98115.
10. Lebreton, J., K. P. Burnham, J. Clobert, and D. R. Anderson. 1992. Modeling survival and testing biological hypotheses using marked animals: A unified approach with case studies. *Ecological Monographs* 62(1): 67–118.

11. Memmott, J., P. G. Craze, N. M. Waser, and M. V. Price. 2007. Global warming and the disruption of plant-pollinator interactions. *Ecology Letters* 10:710-717.
12. Morrison, C. A., R. A. Robinson, J. A. Clark, and J. A. Gill. 2016. Causes and consequences of spatial variation in sex ratios in a declining bird species. *Journal of Animal Ecology* 85: 1298–1306.
13. Rich T D, Beardmore C J, Berlanga H, Blancher P J, Bradstreet M S W, Butcher G S, Demarest D, Dunn E H, Hunter W C, Iñigo-Elias E, Kennedy J A, Martell A, Panjabi A, Pashley D N, Rosenberg KV, Rustay C, Wendt S and Will T. 2004. Partners In Flight North American Landbird Conservation Plan. Cornell Lab of Ornithology, Ithaca, NY.
14. Rosero, L. 2003. Interações planta/beija-flor em três comunidades vegetais da parte sul do Parque Nacional Natural Chiribiquete, Amazonas (Colombia). Tese apresentada ao instituto de Biología da Universidade Estadual de Campinas, como parte dos requisitos para obtenção do título de Doutor em Ciências Biológicas. Campinas, Brazil.
15. Schuchmann K.L. 1999. Family Trochilidae (Hummingbirds). In: Del Hoyo J., Elliot A., Sargatal J.. (Eds). *Handbook of the birds of the world. Vol. 5 Barn-owls to Hummingbirds.* Birdlife International. Lynx Editions, Barcelona, pp:468-680.
16. Stiles F. G. 1981. Geographical aspects of bird-flower co-evolution, with particular reference to Central America. *Ann. Missouri Bot. Gard.* 68: 323-351.
17. Temeles, E. J. and W. J. Kress. 2003. Adaptation in a plant-hummingbird association. *Science* 300:630-633.
18. Pradel, R., J. E. Hines, J. Lebreton, and J. D. Nichols. 1997. Capture-recapture survival models taking account of transients. *Biometrics* 53(1): 60–72.
19. R Core Team. 2017. R: A Language and Environment for Statistical Computing, version 3.4.0. R Foundation for Statistical Computing, Vienna, Austria. <https://www.R-project.org/>
20. Saracco, J. F., J. A. Royle, D. F. DeSante, and B. Gardner. 2010. Modeling spatial variation in avian survival and residency probabilities. 91(7): 1885–1891.
21. Seber, G. A. F. 1965. A note on the multiple recapture census. *Biometrika* 52: 249–259.
24. White, G. C., and K. P. Burnham. 1999. Program MARK: Survival estimation from populations of marked animals. *Bird Study* 46 (Supplement): 120 – 139.