FACTORS INFLUENCING SURVIVAL OF BLACK-CHINNED HUMMINGBIRD NESTS IN SOUTHWEST COLORADO

JOSEPH C. ORTEGA, Department of Biology, Fort Lewis College, 1000 Rim Drive, Durango, Colorado 81301; ortega_j@fortlewis.edu

CATHERINE P. ORTEGA, Durango, Colorado 81301

ABSTRACT: We estimated survival of Black-chinned Hummingbird (*Archilochus alexandri*) nests in southwest Colorado in 1998, 2001, and 2004 by means of models generated in program Mark. The best supported, and parsimonious, model suggested nest age (i.e., time since the nest was initiated) as the most important variable in indicating nest survival; daily survival rates of nests with eggs were lower than those of nests with nestlings. Substrate type was a second covariate that had some support in describing nest survival. Nests in Gambel oak (*Quercus gambelii*) or narrow-leaf cottonwood (*Populus angustifolia*) had greater daily survival rates than did those built in other substrates. No other ecological covariates were strongly supported in explaining nest survival. Of the 24 nests studied, 10 were successful, fledging an average of 1.7 (standard error 0.14) chicks.

Among the hummingbird species that regularly breed in the western and southwestern United States, the Black-chinned Hummingbird (*Archilochus alexandri*) has the widest breeding range. The largest breeding populations are in riparian habitats of southern New Mexico and Arizona (Baltosser and Russell 2020). According to the Breeding Bird Survey, the population trends in Colorado were negative from both 1966 to 2019 (–0.88 %/year, 95% confidence interval –2.57 to 0.66) and from 1993 to 2019 (–1.69 %/year, 95% confidence interval –3.59 to 0.23, Sauer et al. 2020). Because of the weakness of the supporting data (Sauer et al. 2020) and because the 95% confidence intervals straddle zero, however, these apparent trends might not be significant (Arnold 2010). In contrast, results of the two Colorado breeding bird atlases imply that the Black-chinned Hummingbird's breeding distribution in Colorado spread from 1987–1995 to 2007–2012 (Lyon 2016).

Stiles (1973), on the basis of 55 nests in southern California, and Baltosser (1978, 1983, 1986), on the basis of 157 nests in southwestern New Mexico and southeastern Arizona, were the first to report on the Black-chinned Hummingbird's apparent nest success. Using the logistic exposure method (Shaffer 2004), Smith et al. (2009) greatly increased knowledge of the Black-chinned Hummingbird's nest survival (not the same as apparent nest success) in a study of the effects of fire fuel reduction along the middle Rio Grande (n = 635 nests) in central New Mexico. Smith et al. (2014) also reported (n = 434 nests) on the effects of nonnative tamarix (*Tamarix ramosissima*) and Russian olive (*Elaeagnus angustifolia*) on nest survival along the Rio Grande in central New Mexico, comparing it to that along the Gila River (n = 137 nests) in southwest New Mexico, where native boxelder (*Acer negundo*) was the most common nest substrate. In southeast Arizona, Greeney et al. (2015) used the Mayfield method (Mayfield 1961, 1975, Johnson 1979) to determine the daily survival rate of 342 Black-chinned Hummingbird nests near Northern Goshawk (*Accipiter gentilis*) and Cooper's Hawk (*A. cooperii*) nests.

Previous research on the apparent success, daily survival rate, and survival of Black-chinned Hummingbird nests has taken place where the population density is high (Greeney and Wethington 2009, Smith et al. 2009, 2014, Greeney et al. 2015). In our study, we evaluated the Black-chinned Hummingbird's nest survival in southwestern Colorado where its population density is lower than described in previous studies. We examined various ecological factors (including nest substrate, substrate height, nest height, and nest age) that have been considered previously (see Baltosser 1986, Smith et al. 2009, 2014, Greeney et al. 2015) as well as other variables that could affect nest survival.

METHODS

Study Area

In 1998, 2001, and 2004, we studied the nesting of the Black-chinned Hummingbird at the San Juan Basin Research Center (then administered by Colorado State University). The site is located at 37° 14′ N, 108° 3′ W) in La Plata County, southwest Colorado. It covers 2541 ha at elevations ranging from 2312 to 2365 m (Ortega and Ortega 2003a, b, 2016). Along the La Plata River, riparian habitat extends from 5 to 200 m from the river and is dominated by narrow-leaf cottonwood (*Populus angustifolia*). River birch (*Betula fontinalis*) and thinleaf alder (*Alnus tenuifolia*) are also present. The upland habitat is dominated by Gambel oak (*Quercus gambelii*) with scattered ponderosa pines (*Pinus ponderosa*), junipers (*Juniperus* spp.), and quaking aspens (*Populus tremuloides*). Because of grazing by up to 3.3 head of cattle per hectare, the understory is low, but various forage grasses are present (Ortega and Ortega 2003a, 2016).

Data Collection

We followed nests of Black-chinned Hummingbirds to assess their outcomes. We typically visited nests every 2 or 3 days, viewing them directly or by use of an adjustable mirror attached to an extendable pole (Ortega and Ortega 2016) and noting whether they contained eggs or chicks. We considered a nest successful if we observed fledging or fledglings nearby, or, if the nest was empty at the time we expected fledging (the species' nestling period is about 21 days [Baltosser and Russell 2020]), it did not show any obvious signs of predation (the nest was not pulled over, destroyed, or disheveled). In addition, if a nest was stretched and soiled with fecal material, we inferred the chicks had fledged successfully (Smith et al. 2009, Ortega and Ortega 2016). We estimated the height of the nest and its substrate by using a 2-m pole as a guide (Ortega and Ortega 2003a).

Statistical Analyses

Commonly, nest success has been quantified as apparent nest success or by the Mayfield method (Mayfield 1961, 1975, Dinsmore et al. 2002, Dinsmore and Dinsmore 2007, Rotella 2023). Apparent nest success is calculated by taking the total number of nests from which a chick successfully fledged and dividing this number by the total number of nests found. However, this method usually overestimates the percentage of successful nests since it does

not account for those nests that had already failed prior to being discovered (Mayfield 1961, 1975, Dinsmore et al. 2002, Dinsmore and Dinsmore 2007, Rotella 2023), and unsuccessful and successful nests may not be found at the same rate (Rotella 2023). Understanding this problem, Mayfield (1961, 1975) suggested the use of both the number of nests that failed while they were being followed and the number of exposure days—the number of days that a nest was exposed (and followed) to possible predation—allowing for the calculation of both the daily mortality rate and hence the daily probability of survival (Mayfield 1961, 1975, Dinsmore et al. 2002, Dinsmore and Dinsmore 2007, Rotella 2023). The Mayfield method, however, implies that daily survival rate is constant through the nesting cycle, and it does not allow for the easy analysis of covariates that could be important in potentially explaining nest survival and nest success (Dinsmore et al. 2002, Dinsmore and Dinsmore 2007, Rotella 2023). Therefore, several other methods for analyzing nest survival and success have been developed (Dinsmore et al. 2002, Shaffer 2004, Dinsmore and Dinsmore 2007, Johnson 2007, Rotella 2023), and one of these methods is the program Mark, which allows one to assess the importance of multiple covariates on nest survival and how a nest's daily survival rate might vary through time (Dinsmore et al. 2002, Dinsmore and Dinsmore 2007, Rotella 2023).

Therefore, we estimated nest survival with this program. We initially evaluated 10 *a priori* candidate models (Table 1), nine of which combined a constant daily survival rate with a potentially important ecological variable. The other was based on a constant daily survival rate only, and this model is the same as the maximum-likelihood method for calculating nest success by

Table 1 Summary Statistics for 12 *a Priori* Candidate Models and One Exploratory Model Generated in Program Mark to Describe Survival of 24 Nests of the Black-chinned Hummingbird at the San Juan Basin Research Center, Hesperus, Colorado, in 1998, 2001, and 2004

Model	ΔAIC_c[a]	AIC_c weight	K[b]	Deviance
Nest age	0.000	0.220	2	96.074
Nest age + substrate	0.041	0.215	4	92.047
Constant DSR[c] + substrate	1.003	0.133	3	95.048
Constant DSR + nest height	2.235	0.072	2	98.309
Constant DSR + precipitation	2.383	0.067	2	98.456
Constant DSR + year	2.622	0.059	2	98.696
Constant DSR + snowfall	2.799	0.054	2	98.873
Constant DSR	3.220	0.044	1	101.313
Constant DSR + grazing intensity	3.427	0.040	3	97.471
Constant DSR + substrate height	3.997	0.030	2	100.070
Constant DSR + habitat	4.339	0.025	2	100.413
Varying DSR	4.416	0.024	2	100.489
Constant DSR + ratio of nest height to substrate height	5.008	0.018	2	101.081

[a]Difference from 100.102, the value of AIC_c (Akaike's information criterion corrected for small sample sizes) for the most strongly supported model.

[b]Number of parameters.

[c]DSR, daily survival rate.

the Mayfield method (Mayfield 1961, 1975, Rotella 2023). We then considered two additional models, one that allowed the daily survival rate to vary over the breeding season and one that examined whether a nest's age affected its daily survival rate. Specifically, evaluation of a model with nest age can suggest whether a nest's daily survival rate varies through time (for example, if it differs at the incubation or nestling stages). To evaluate the covariate of nest age, we needed to know the date that the first egg was laid. We did this by identifying when an egg was newly laid, by using the median of a range of dates within which laying of the first egg was contained, or by back-dating to when the first egg was laid based on when eggs hatched and/or when chicks fledged. For back-dating, we estimated on the basis of a 2-day egg-laying period, a 13-day incubation period starting with laying of the second egg (incubation takes 12–14 days), and a 21-day nestling period (Baltosser and Russell 2020). Therefore, the entire nesting attempt could last about 35 days.

The environmental covariates that we initially considered were habitat (riparian versus Gambel oak-dominated upland), substrate (Gambel oak, narrow-leaf cottonwood, or other), and grazing intensity (none, low, or moderate to high; Ortega and Ortega 2016). We also evaluated the potential importance of nest height (m), substrate height (m), and ratio of nest height to substrate height. Because soil moisture might affect production of flowers and of insects that forage on newly growing vegetation, we included the covariates of winter snowfall (cm) during the preceding October through April and precipitation (cm) from May through August in a breeding season. We obtained data for winter snowfall prior to a breeding season and total precipitation during a breeding season from Colorado State University's Colorado Climate Center at Fort Lewis (http://www.climate.colostate.edu/data_access_new.html). We also included the possible effect of year as a covariate.

Using an information-theoretic approach, we compared the candidate models by means of Akaike's information criterion corrected for small sample sizes (AIC_c; Burnham and Anderson 2002). Under this method, the model with the smallest AIC_c value is the most parsimonious, or best supported, model at explaining nest survival according to the inclusion, or not, of various possible covariates (Burnham and Anderson 2002). It is to this best-supported model that all other models are compared, the difference being ΔAIC_c. Models with $\Delta AIC_c \leq 2$ are also considered to have some support (Burnham and Anderson 2002). In addition, the AIC_c weight, compared to that of other models (Table 1), can also be used to gauge a model's support (Rotella 2023): if one takes the value of a model with a larger weight and divides by the value of a model with a smaller weight, one obtains another estimate of the two models' relative support.

RESULTS

We followed the outcome of 24 Black-chinned Hummingbird nests. The first Black-chinned Hummingbird egg appeared in a nest on 18 May (2004), and the latest nest was initiated on 29 June (2001). Fourteen of 24 (58%) nests failed, all because of depredation; therefore, apparent nest success was 42%. We found nine nests (37.5%) in Gambel oak-dominated uplands and 15 (62.5%) in riparian habitat. Black-chinned Hummingbirds placed ten (42%)

nests in Gambel oaks, 11 (46%) nests in narrow-leaf cottonwoods, and three (12.5%) nests in another substrate. The 17 chicks observed or determined to have fledged had an average age when last observed in the nest of 20.3 ± 0.39 days (± 1 standard error). An average of 1.7 ± 0.14 chicks fledged from successful nests.

Of our 12 *a priori* candidate models, one with daily survival rate allowed to vary with nest age was the best supported (Table 1). According to this model, within any nesting attempt, the daily survival rate increased from the beginning of incubation through the end of the nestling period. This model suggested that, for example, the daily survival rate of a nest initiated on 11 June (the mean date of nest initiation in our study), was 0.952 (standard error 0.014) on the seventh day of incubation (midway through the 13-day incubation period). But by the eleventh day of the nestling period (midway through the 21-day nestling period), the rate had increased to 0.983 (± 0.008). These values imply a nest's overall chance of survival as 0.179 (0.952^{35}) on the seventh day of incubation but of 0.549 (0.983^{35}) on the eleventh day of the nestling period.

The only other model in the initial set with some support ($\Delta AIC_c \leq 2$) was one with a constant daily survival rate plus the covariate of substrate. In this model, the daily survival rates of nests in Gambel oak (0.971 ± 0.012) or narrow-leaf cottonwood (0.976 ± 0.011) were the same but survival of those few nests on other substrates was lower (0.820 ± 0.096). Because of the potential importance of substrate, we devised one exploratory model combining substrate with nest age (Table 1). This model had almost the same support as our best-supported model (Table 1). The fourth best-supported model suggested that nest survival increased with nest height, but because the lower (–0.080) and upper (0.796) 95% confidence intervals included zero, this parameter was not likely useful in explaining nest survival (Arnold 2010).

Of the other models that we examined (Table 1), neither snowfall in the previous winter (from October through April) nor precipitation during the breeding season (from May through August) demonstrated strong support explaining nest survival. In addition, we found no support for the possibility that a nest's daily survival rate varies through the breeding season.

DISCUSSION

We found nest age was important in determining the daily survival rate of a Black-chinned Hummingbird nest. Of 14 nests lost to predators, 12 were depredated during incubation whereas in only two were nestlings depredated. In the Santa Monica Mountains of southern California, Stiles (1973) found a low apparent nest success of 31.9% for Anna's Hummingbird. Baltosser (1986: table 3) indicated that for the Black-chinned Hummingbird, "nesting success" during the incubation and nestling periods was complicated but that over three study areas in southwest New Mexico and southeast Arizona nesting success averaged only 34.0%. In their study of the effects of fire-fuel reduction along the middle Rio Grande, Smith et al. (2009) found several ecological variables affecting survival of Black-chinned Hummingbird nests, and that survival varied substantially from year to year, from 31% to 73%—their best model included an interaction between nest height and substrate along with a

year effect. In another study, Smith et al. (2014) estimated nest survival along the middle Rio Grande at 52% but that along the Gila River in southwest New Mexico at only 23%. Smith et al. (2009, 2014) estimated nest survival on the basis of a 38-day nesting period, which would lower the survival rates projected in our study. In the Chiricahua Mountains of southeast Arizona, Greeney et al. (2015) reported enhanced success of Black-chinned Hummingbirds nesting ≤300 m from Northern Goshawk or Cooper's Hawk nests. Near an *Accipiter* nest, the predicted success of a Black-chinned Hummingbird nest was 31.2%, but away from an *Accipiter* nest, predicted success was only 6.2% (these authors also based their calculations on a 38-day nesting period).

Our second- and third-most supported models both implied some importance of substrate to nest survival (Table 1). Smith et al. (2009) found an interaction between substrate and nest height where the daily survival rate of nests in both Russian olives and Rio Grande cottonwoods (*Populus deltoides*) was lower than that of nests in *Tamarix*. Daily survival rate decreased with increasing nest height in both Russian olives and Rio Grande cottonwoods. Smith et al. (2014) also found daily survival rate decreasing with increasing nest height in Russian olives and in Rio Grande cottonwoods, as it did along the Gila River for nests in boxelder, the most common substrate in that area. Baltosser (1986) and Baltosser and Russell (2020) also reported that the chance of failure was greater for higher nests, and predation was the major cause of this failure. In all of these previous studies, birds were observed or implicated as predators of at least Black-chinned Hummingbird eggs. These observed or suggested avian predators included the Mexican Jay (*Aphelocoma wollweberi*), Summer Tanager (*Piranga rubra*), Hooded Oriole (*Icterus cucullatus*), and Bullock's Oriole (*I. bullockii*). In addition, Greater Roadrunners (*Geococcyx californianus*) have been observed capturing Black-chinned Hummingbird nestlings in New Mexico (Elliston and Baltosser 1995, Baltosser and Russell 2020). At our study site, other potential avian predators include the Steller's Jay (*Cyanocitta stelleri*), Woodhouse's Scrub-Jay (*A. woodhouseii*), and Black-billed Magpie (*Pica hudsonia*)—which we have observed depredating nests of the Red-winged Blackbird (*Agelaius phoeniceus*). Bullock's Orioles were also numerous. In addition, potential small-to-medium-sized mammalian predators include the western deer mouse (*Peromyscus sonoriensis*), chipmunks (*Neotamias* spp.), long-tailed weasel (*Neogale frenata*), and rock squirrel (*Otospermophilus variegatus*)—which we have observed depredating nests of the American Robin (*Turdus migratorius*) (Ortega and Ortega 2003b, 2016).

One means of understanding how nest success, or nest survival, affects a population is to consider the number of young a female successfully fledges within a breeding season (Ricklefs and Bloom 1977, Baltosser 1986): clutch size × breeding success × rate of nest initiation (Ricklefs and Bloom 1977:87, Baltosser 1986:356). While the complete clutch in the Black-chinned Hummingbird is invariably two eggs (Baltosser and Russell 2020), and our data allow an estimate of breeding success (i.e., nest survival), since the females we studied were not marked, we cannot estimate the rate of nest initiation, so we cannot estimate the number of young fledged by a female during a breeding season.

With nest success in some areas as low as 6.2% (Greeney et al. 2015) and

9.0% (Greeney and Wethington 2009), source populations must be feeding these sink populations. At least one population with high nest success has been identified in northwest New Mexico where apparent nest success was 86.5% ($n = 37$ nests with known outcomes, C. Ortega and C. Francis, unpubl. data). At that location, Black-chinned Hummingbirds nested close to noisy compressors for gas wells, and the high noise level appeared to deter predators (Francis et al. 2009). Other differences that might have had an effect on nest success include lower density of hummingbirds toward the northern side of their range and habitat. The dominant trees at the study site in northwest New Mexico were native piñon pine (*Pinus edulis*) and Utah juniper (*J. osteosperma*), whereas the study areas farther south were wooded with different native and non-native tree species. We recognize that with our comparatively small size of our Colorado sample ($n = 24$ nests), the results of our study should be considered tentative. However, to the best of our knowledge, no other studies have addressed survival of Black-chinned Hummingbird nests in southwest Colorado, in habitats dominated by Gambel oak and narrow-leaf cottonwood, and under different grazing regimes. To improve understanding of the Black-chinned Hummingbird's population dynamics, the number of nests studied should be increased, and further studies should focus on latitudinal differences in the variables that most affect seasonal nest success, which requires determining the number of nests attempted per season by banded females.

ACKNOWLEDGMENTS

We appreciate the help of our field assistants including Susan Allerton, John Arnett, Florence Bliss, Jessica Cable, Samuel Henna, Heather Lyon, Ann Maurer, Peter Nylander, Arik Skromme, Carly Thornton, Joseph Vagneur, and Michael Vivalda. This research was funded by grants from the National Geographic Society, the National Fish and Wildlife Foundation, and the Colorado Wetlands Program to Catherine P. Ortega. Also, Catherine P. Ortega and John Arnett were supported by a Colorado Alliance for Minority Participation Grant (administered by the National Science Foundation). David Schafer and Douglas Zalesky allowed us access to the San Juan Basin Research Center (administered by Colorado State University at the time of this research). The manuscript also benefited from the review of Matthew Baumann and two anonymous reviewers.

LITERATURE CITED

Arnold, T. W. 2010. Uninformative parameters and model selection using Akaike's information criterion. J. Wildlife Mgmt. 74:1175–1178.

Baltosser, W. H. 1978. Ecological relationships among hummingbirds in southwestern New Mexico and southeastern Arizona. Master's thesis, New Mexico State Univ., Las Cruces.

Baltosser, W. H. 1983. Nesting ecology of sympatric hummingbirds in Guadalupe Canyon. Ph.D. dissertation, New Mexico State Univ., Las Cruces.

Baltosser, W. H. 1986. Nesting success and productivity of hummingbirds in southwestern New Mexico and southeastern Arizona. Wilson Bull. 98:353–367.

Baltosser, W. H., and Russell, S. M. 2020. Black-chinned Hummingbird (*Archilochus alexandri*), *in* Birds of the World (A. F. Poole and F. B. Gill, eds.). Cornell Lab of Ornithol., Ithaca, NY; doi.org/10.1273/bow.bkchum.01.

Burnham, K. P., and Anderson, D. R. 2002. Model Selection and Multimodel Inference: A Practical Information-Theoretic Approach, 2nd ed. Springer-Verlag, New York.

Dinsmore, S. J., and Dinsmore, J. J. 2007. Modeling avian nest survival in program Mark. Studies Avian Biol. 34:73–83.
Dinsmore, S. J., White, G. C., and Knopf, F. L. 2002. Advanced techniques for modeling avian nest survival. Ecology 83:3476–3488.
Elliston, E. P., and Baltosser, W. H. 1995. Sex ratios and bill growth in nestling Black-chinned Hummingbirds. W. Birds 26:76–81.
Francis, C. D., Ortega, C. P., and Cruz, A. 2009. Noise pollution changes avian communities and species interactions. Current Biol. 19:1415–1419.
Greeney, H. F., and Wethington, S. M. 2009. Proximity to active *Accipiter* nests reduces nest predation of Black-chinned Hummingbirds. Wilson J. Ornithol. 121:809–812.
Greeney, H. F., Meneses, M. R., Hamilton, C. E., Lichter-Marck, E., Mannan, R. W., Snyder, N., Snyder, H., Wethington, S. M., and Dyer, L. A. 2015. Trait-mediated trophic cascade creates enemy-free space for nesting hummingbirds. Sci. Adv. 1:e1500310.
Johnson, D. H. 1979. Estimating nest success: The Mayfield method and an alternative. Auk 96:651–661.
Johnson, D. H. 2007. Estimating nest success: A guide to the methods. Studies Avian Biol. 34:65–72.
Lyon, E. 2016. Black-chinned Hummingbird (*Archilochus alexandri*), in The Second Colorado Breeding Bird Atlas II (L. E. Wickersham, ed.), pp. 282–283. Colo. Breeding Bird Atlas Partnership and Colo. Dept. of Parks and Wildl., Denver.
Mayfield, H. 1961. Nesting success calculated from exposure. Wilson Bull. 73:255–261
Mayfield, H. 1975. Suggestions for calculating nest success. Wilson Bull. 87:456–466.
Ortega, C. P., and Ortega, J. C. 2003a. Brown-headed Cowbird (*Molothrus ater*) parasitism of Warbling Vireos (*Vireo gilvus*) in southwest Colorado. Auk 120:759–764.
Ortega, C. P., and Ortega, J. C. 2003b. Comparison of Black-headed Grosbeaks nesting in riparian and Gambel oak pastures in southwestern Colorado. Southwest. Nat. 48:383–388.
Ortega, J. C., and Ortega, C. P. 2016. Contributing variables to nest survival, and the breeding biology, of the Western Wood-Pewee (*Contopus sordidulus*) in southwestern Colorado. Southwest. Nat. 61:312–320.
Ricklefs, R. E., and Bloom, G. 1977. Components of avian breeding productivity. Auk 94:86–96.
Rotella, J. 2023. Nest survival models, in Program Mark: A Gentle Introduction (E. G. Cooch and G. C. White, eds.), 22nd ed., pp. 17-1–17-19. Colo. State University, Fort Collins, CO; http://www.phidot.org/software/mark/docs/book/pdf/chap17.pdf.
Sauer, J. R., Link, W. A., and Hines, J. E. 2020. The North American Breeding Bird Survey analysis result. U. S. Geological Survey data release; https://doi.org/10.5066/P96A7675.
Shaffer, T. L. 2004. A unified approach to analyzing nest success. Auk 121:526–540.
Smith, D. M., Finch, D. M., and Hawksworth, D. L. 2009. Black-chinned Hummingbird nest-site selection and nest survival in response to fuel reduction in a southwestern riparian forest. Condor 111:641–652.
Smith, D. M., Finch, D. M., and Stoleson, S. H. 2014. Nest-location and nest-survival of Black-chinned Hummingbirds in New Mexico: A comparison between rivers with differing levels of regulation and invasion of nonnative plants. Southwest. Nat. 59:193–198.
Stiles, F. G. 1973. Food supply and the annual cycle of the Anna Hummingbird. Univ. Calif. Publ. Zool. 97:1–109.

Accepted 5 November 2023
Associate editor: Matthew J. Baumann