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NESTING ECOLOGY OF THE ENDANGERED CHILEAN WOODSTAR (*EULIDIA YARRELLII*)

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Abstract · The Chilean Woodstar (*Eulidia yarrellii*) is a critically endangered hummingbird of the Atacama desert in northern Chile, with a population estimate of around 320 individuals in 2017. To generate useful information for the design of population-recovery actions, we conducted a study of the nesting ecology of the species between 2006 and 2008. Our specific goals were to provide a quantitative description of the species breeding habitat, to describe the basic breeding biology of the species, and to assess the current levels of nesting success. Most of our work was conducted in the valleys of Azapa and Vitor, two of the three last valleys where the species is known to persist. Although we recorded some juveniles in Azapa, we only observed the species nesting in one site in Chaca (Vitor valley), in a small (1.4 ha) olive grove where 13–20 simultaneous nests were found during the studied breeding seasons. Nesting occurs in September–October, and its timing is apparently synchronized with the flowering of chañar (*Geoffroea decorticans*). The species has a particularly long breeding period with an average of 48 days (17 d for the egg stage, 31 d for the nestling stage). The Mayfield index of nest success ranged from 21–44%. The probability of nest failure was significantly higher closer to the feeding areas. The implications of our results for a habitat restoration program are discussed, particularly the different requirements of females and males.

Resumen · Ecología reproductiva del Picaflor de Arica (*Eulidia yarrellii*), una especie amenazada
El Picaflor de Arica (*Eulidia yarrellii*) es un colibrí críticamente amenazado del desierto de Atacama en el norte de Chile, con una población estimada en el año 2017 de alrededor 320 individuos. Para generar información útil para el diseño de acciones de recuperación de la especie, entre 2006 y 2008 realizamos un estudio sobre la ecología de nidificación de la especie. Los objetivos específicos fueron proporcionar una descripción cuantitativa del hábitat de nidificación, describir la biología reproductiva y evaluar el éxito de nidada de la especie. La mayor parte de nuestro trabajo se realizó en los valles de Azapa y Vitor, dos de los tres últimos valles donde aún persiste la especie. Aunque hemos registrado algunos juveniles en Azapa, sólo observamos nidificación de la especie en un sitio en Chaca (valle Vitor), en un pequeño olivar (1,4 ha) donde se encontraron 13–20 nidos simultáneos para las temporadas de nidificaciones estudiadas. El período reproductivo ocurre en septiembre-octubre, está aparentemente sincronizado con el florecimiento del chañar (*Geoffroea decorticans*). La especie tiene un período de cría particularmente largo con un promedio de 48 días (17 días de incubación, 31 días los polluelos permanecen en el nido). El índice de Mayfield de éxito de las nidadas varió entre 21 y 44%. La probabilidad de fracaso del nido fue significativamente mayor más cerca de las áreas de alimentación. Se discuten las implicaciones de nuestros resultados para un programa de restauración de hábitat para la especie, particularmente las diferencias entre los requerimientos de los machos y las hembras.

Key words: Atacama desert · Breeding habitat · Chile · Endangered species · Hummingbirds · Nesting site · Nest success

INTRODUCTION

In the course of six decades, the Chilean Woodstar (*Eulidia yarrellii*) went from apparently being the most common hummingbird in the desert valleys of northern Chile to being the rarest, and is officially considered a critically endangered species (Estades et al. 2007, BirdLife International 2017). Previously, it was reported from Perú as well (Parker 1982) but more recently has been considered officially extinct in this country (Cruz 2006), making it effectively a Chilean endemic.

Since the first population estimate in 2003 (1539 individuals), the woodstar population has been reduced to approximately 70% with an estimate of around 320 individuals remaining in 2017 (AvesChile 2017). The apparent causes that led the population to its current status include the accelerated transformation of the last remaining natural habitats into agriculture, the intensive use of pesticides, and the potential competition with the Peruvian Sheartail (*Thaumastura cora*), a similar-sized hummingbird that spontaneously invaded the region in the 1970's (Estades et al. 2007).

Although the above mentioned threat factors may be evident, it is unclear what are the specific mechanisms causing the observed population decline. Because one of the most important potential limiting factors for the growth of bird populations is

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reproduction (Newton 1998), in 2006 we began to study the species' breeding ecology. Previous information on the topic was mostly anecdotal and clearly insufficient as a tool for decision-making. These data suggested that the species builds its nests mostly in olive trees, and that the bulk of the reproduction takes place during the Austral spring (authors, pers. obs.).

Our main objectives were to provide a quantitative description of the species breeding habitat, to describe the basic breeding biology of the species, and to assess the current levels of nesting success as a starting point for the design of population-recovery actions.

METHODS

Study area. The study was carried out between 2006 and 2008 in the valleys of Azapa (18°34'S, 70°05'W) and Vitor (18°49'S, 70°09'W) in the region of Arica-Parinacota, northern Chile (Figure 1) where most of the remaining populations of the Chilean Woodstar are found (Estades et al. 2007). The study area is part of the Atacama desert, which is considered the driest place on earth, with some areas showing only traces of biological activity (Navarro-González et al. 2003). However, substantial precipitation in the high Andes (e.g., 242 mm in Putre, 3520 m a.s.l.; Santibañez 1981) allows water to flow to the Pacific Ocean through a few narrow, vegetated valleys. Because of a long history of human cultivation of these valleys, there is not a clear description of their original vegetation, but currently most of the areas that have some access to water are covered with salt tolerant crops, orchards (mainly olive trees), or riparian scrub (Estades et al. 2007).

Characterization of breeding habitat. During early September 2006 and based on our previous experience with the species, we sampled potentially suitable breeding areas in the valleys of Azapa and Vitor (Figure 1) with the intention of relating nest density with habitat characteristics (e.g., vegetation composition, tree density, management attributes, etc.).

All the selected sites included fruit groves of different species (mostly olives, citrus, guava, and mango), with varying types of management and landscape contexts. Within the sample, we deliberately included a site in the Vitor valley where we had previously found nests of the species (hereafter "Chaca", Figure 1). Additionally, we included a site in the lower part of the Lluta valley (Figure 1) composed solely of native scrub, and dominated by chañar (*Geoffroea decorticans*, Fabaceae), whose flowers are the main natural source of nectar for the species during spring (Estades et al. 2007).

At each site, we conducted a search of the species, and if we found at least one individual, we selected a 1.5–2 ha representative area where we (one group of 2–4 people) thoroughly searched for nests or other signs of reproductive activity. For this purpose, we focused on presence and behavior of females. Depending on the characteristics of the site, each search took between 0.5 to 1 hour.

By 8 September 2006, we had assessed a total of 14 sites in areas ranging from 5 to 1825 m a.s.l. in the mentioned valleys (Figure 1). However, because we only found evidence of reproduction in Chaca, we decided to concentrate our field work on the study of the breeding population there (18°49'S, 70°08'W, 390 m a.s.l.).

Breeding biology. In order to describe some aspects of the basic breeding biology of the species and to estimate levels of nesting success, we monitored breeding in Chaca during the springs of 2006 to 2008. During the three years of the study we made several visits to the area (2006 = 8, 2007 = 5, 2008 = 18) between September and October, which is the time when most of the reproductive activity takes place. In each visit, we systematically searched for nests in a small (1.4 ha) olive grove and an area of mixed fruit trees (0.6 ha). With less regularity we also searched for nests in the surrounding native scrub (yaro *Acacia macracantha*, Fabaceae; chilca *Pluchea chingoyo*, Asteracerae; and chañar). For each nest found, we recorded its status (in construction, with eggs, or with nestlings), height above the ground, and position in the tree and orchard. When we found abandoned eggs, we measured them with a caliper. We collected some old nests to investigate their composition.

In order to infer the existence of nesting habitat selection by females, we used a Chi-square test to contrast the number of nests per vegetation type with the availability (i.e., relative area) of such vegetation.

Estimation of nest success. We estimated nest-success rates following Mayfield (1975). This technique requires the determination of the most plausible date for events, such as hatching, nest failure, or fledgling departure. For that purpose, when nest status changed between visits (e.g., from eggs to nestlings, from nestlings to an empty nest), we assigned the critical date to the intermediate date between the two visits (Mayfield 1975). The following criteria were applied to observations of emptied nests. First, if the estimated time since hatching was less than 20 days we considered the nest as failed, as it was well under the estimated range for the nestling stage (see results). Second, as a conservative measure, if the time elapsed between the last record of an active nest with more than 20 days since hatching and the first observation of the emptied nest was more than a one week, we made no inference about the fate of the nest (i.e., failure or success). Finally, in order to calculate the length of incubation and nestling stages we only used nests for which we had a level of uncertainty of no more than 1 day.

In order to explore the effect of distance to food resources on nest success we compared the distance to the nearest flower patches of successful and failed nests with the help of a *t*-test. For this purpose we measured distances on a map of the site produced out of a Google Earth image and ground truthing.

RESULTS

Nesting habitat. As mentioned earlier, the fact that all nests were found in just one place (Chaca) prevented us from conducting a more quantitative analysis of the breeding habitat characteristics. Therefore, the following description is based on just one site plus information on a few additional, non-systematic records.

Out of a total of 76 recorded nests, most (65.9%) were located in olive trees and a few (9.1%) were found in mango trees. Only one nest was found in a native tree (*Salix*

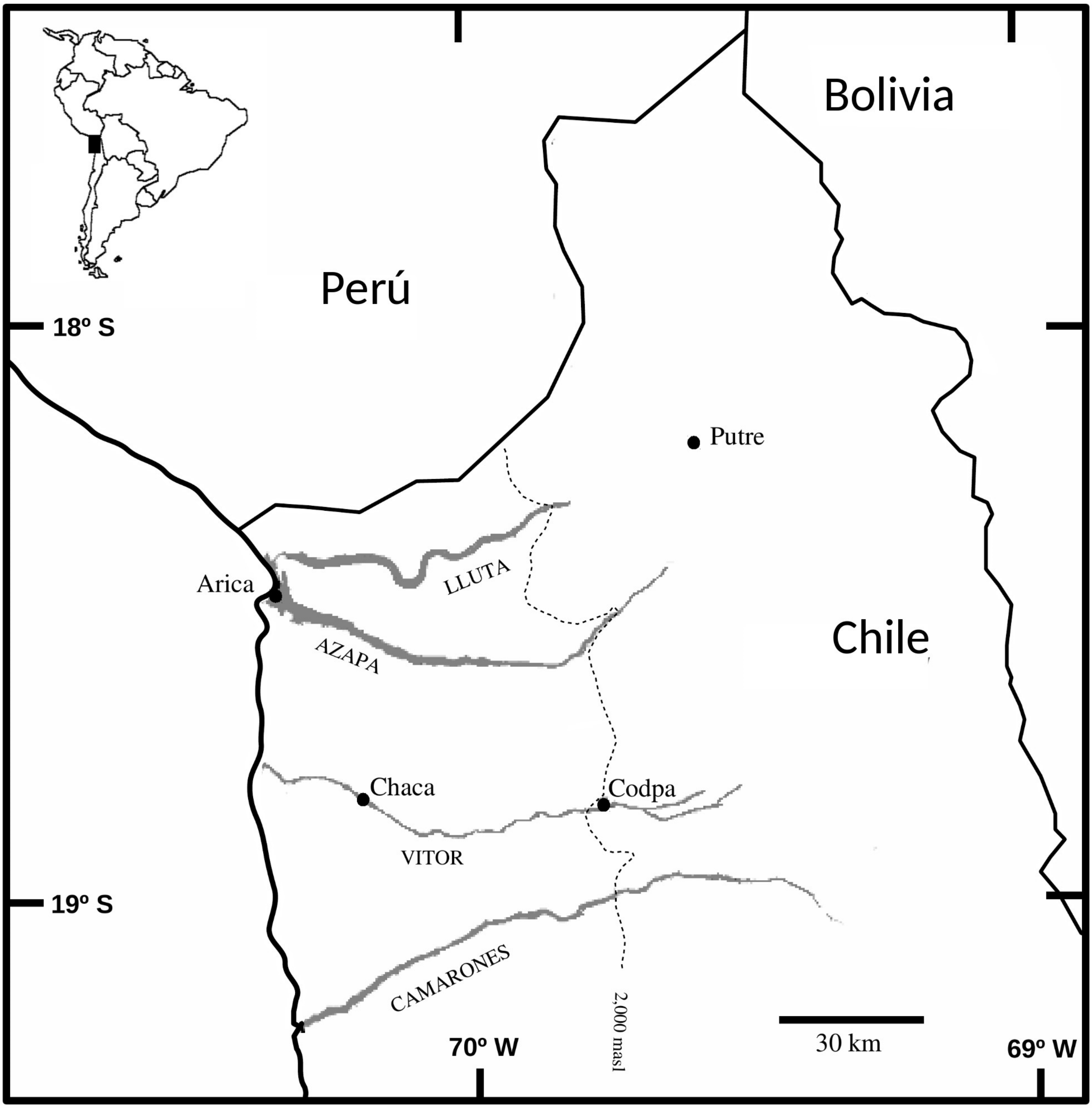

Figure 1. Map of the study area showing the main vegetated valleys of the Arica-Parinacota Region, northern Chile.

humboldtiana, Salicaceae, Codpa, Figure 1) and one in a native shrub (*Tessaria absinthioides*, Asteraceae, Chaca, Figure 1). More recently, we have recorded > 10 nests of the species in tamarugo (*Prosopis tamarugo*, Fabaceae) and pimiento (*Schinus areira*, Anacardiaceae) trees in the Camarones valley, and one in a Eucalyptus tree in Azapa (Figure 1). Almost all (> 90%) nests were attached to descending outer branches (Figure 2A). Average height above ground was 2.2 ± 0.9 m (mean ± SD, n = 64). A few nests (n < 5) were as low as 1.0 m above the ground.

The spatial location of 58 active nests observed during three years of study in Chaca is shown in Figure 3. We detected some spatial segregation between sexes, where male territories were aggregated in an apparent exploded lek (*sensu* Gilliard 1969) located in an area with high concentration of flowers (mostly chañar and citrus). Other nectar sources included some garden plants and a few Eucalyptus trees, but we did not observe male territories associated to these resources. The male territories surrounded the nesting area of no more than 2 ha of orchards. Territorial males continuously chased away other males and even females who visited the flower patches for feeding.

Considering that the olive grove represents approximately 70% of the area covered with fruit trees in the studied site, the aggregation of 51 (88%) of 58 nests in this type of vegetation suggests a positive selection by the species (χ^2 = 8.3, p = 0.004). On the other hand, the absence of nests in the citrus grove (10% area) indicates that woodstars may be avoiding these trees as a nesting site (χ^2 = 6.7, p = 0.01). The observation of up to three nests (two old and one active) in a

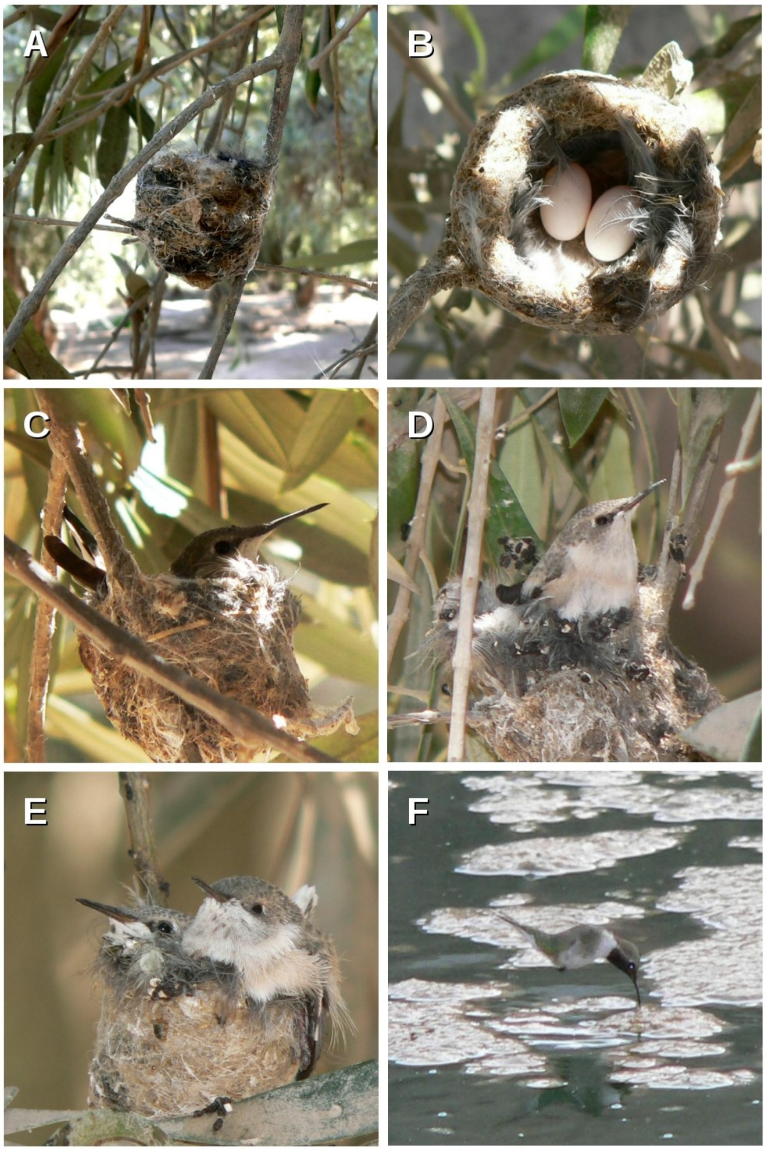

Figure 2. A) Typical position of a Chilean Woodstar (*Eulidia yarrellii*) nest in a hanging branch of an olive tree. B) Clutch of eggs. C) Female incubating. D) Nestling (approximately 35 days old) whose sibling apparently fell off the nest a week earlier. E) Nestlings (approximately 27 days old). F) Male Woodstar drinking in a water reservoir. All images are from the Chaca population (all photographs by C.F. Estades).

single tree and some records of nests built on top of an older one suggest that some individual females may select the same nesting site between seasons.

The number of active nests found in the olive grove in 2006, 2007, and 2008 was 18, 13, and 20, respectively (9.3–14.3 active nests/ha). In some cases, two simultaneously active nests were found at a few meters from each other (i.e., adjacent olive trees), but we did not observe any significant nest defense behavior among neighbor females, in contrast to the aggressive behavior displayed by males and females around the flowering trees that surround the olive grove.

Although in Azapa we did not find any nests of the species during this study, we recorded two "families" (i.e., one female plus two fledglings) feeding in *P. chingoyo* hedges, close to agricultural fields.

Breeding biology. Female woodstars build cup-shaped nests typical for many trochiline hummingbirds (Figure 2A–E). Average (mean ± SD, n = 11) dimensions were: height = 42.2 ± 6.6 mm, depth = 19.8 ± 2.6 mm, external diameter = 39.2 ± 2.9 mm, and internal diameter = 20.8 ± 1.8 mm. Main construction materials in Chaca were sheep wool, feathers, undetermined plant fibers, and spider webs. Eggs are white, very small (average dimensions 11.2 x 6.3 mm, n = 16) and laid invariably in clutches of two (Figure 2B).

We detected a few nests under construction during mid-August. However, because of their small size and the inconspicuous behavior of females, detectability of nests in this stage is apparently very low. For that reason, we did not try to calculate the duration of the nest building stage. By early September, most of the breeding activity had begun. The sequence of the nesting stages for the three years of study is shown in Figure 4. Although the quality of the data differs among years, it is clear that there was some interannual variation in the timing of the breeding activities, particularly an earlier start in 2008 (Figure 4).

Out of 58 nests recorded in Chaca we obtained a precise estimate of the duration of the incubation stage (Figure 2C) for only seven, yielding an average of 17.3 days (range 16–19 days). This period begins after the second egg is laid, which normally occurred two days after the first one. The length of

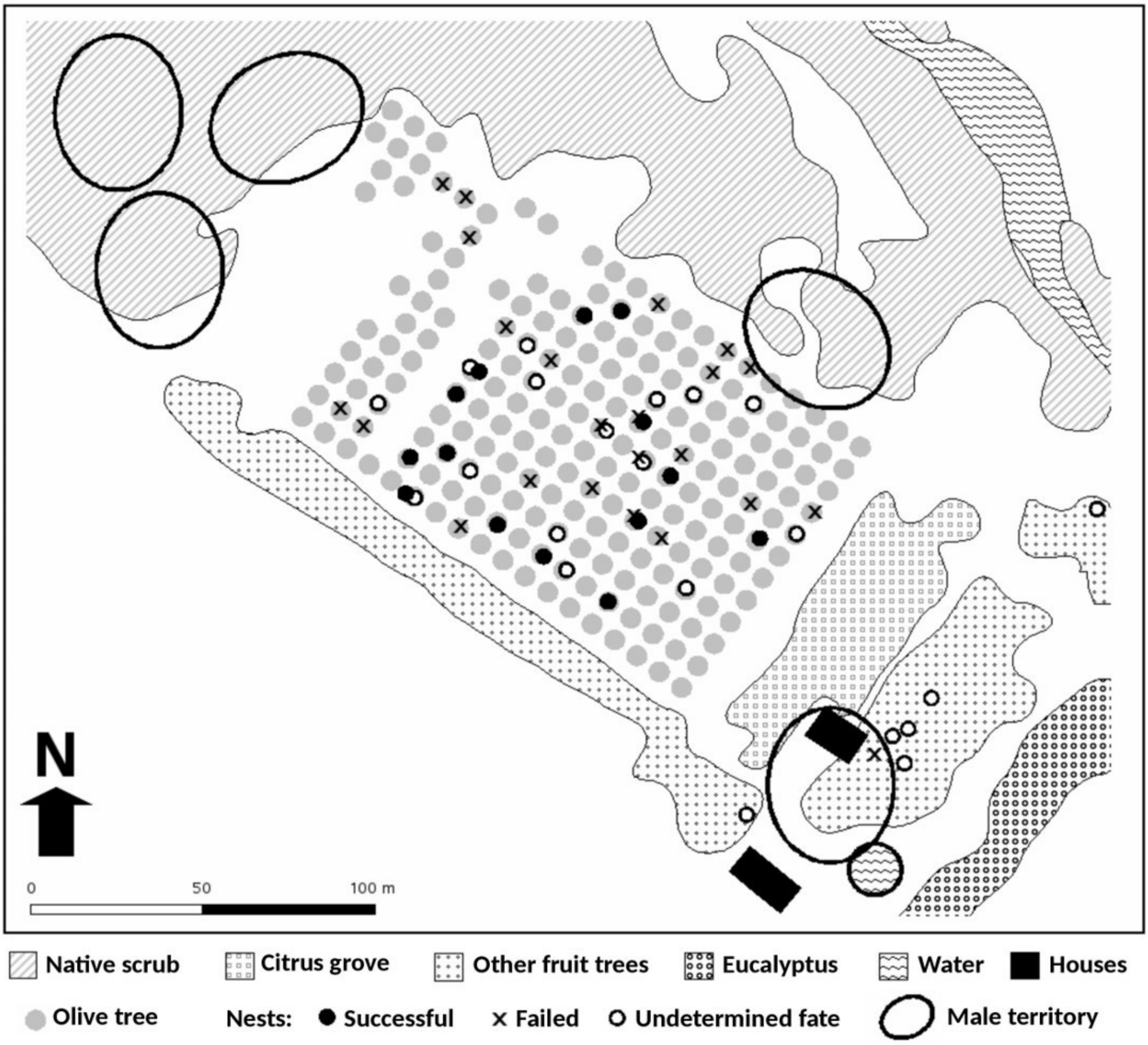

Figure 3. Relative location of Chilean Woodstar (*Eulidia yarrellii*) nests, vegetation types, and other habitat features in the Chaca study site.

the nestling period was calculated from eight nests, with an average duration of 31 days (range 27–35 days). The total time of the breeding cycle of a nest from incubation start to fledging took approximately 48 days (range 45–54 days).

Nest success. We could not calculate the Mayfield index during 2007 due to the low number of visits to the study area. The estimated rate of nest success in Chaca was 21% in 2006 (344 exposure days, 11 failed nests) and 44% in 2008 (529 exposure days, 9 failed nests).

For 16 nests, we recorded the following reasons of failure: four (25%) and three (19%) nests were abandoned (i.e., offspring were present in the nest but dead, and the mother was absent) during the egg and nestling stage, respectively. In five cases (31%), the complete nest disappeared, in two (13%) the nestlings disappeared, and in two other nests (13%) the eggs were lost.

Failed nests tended to be located closer to feeding areas (Figure 3). In fact, average distance to foraging sources (chañares or citrus trees) was significantly smaller (t = 2.2, p = 0.02, df = 36) for failed nests (average = 40.3 m, SE = 5.0 m, n = 14) than for the successful ones (average = 59.1 m, SE = 6.9 m, n = 24).

Although we estimated nest success for the nest as a unit, not all successful nests produced two fledglings. Four (11.1%) out of 36 non-failed nests had one unhatched egg, and in two (5.6%) cases one nestling apparently fell from the tiny nest (Figure 2D). The latter assumption was supported by the fact that during their last days in the nest, the two nestlings can barely stay together in such a small structure (Figure 2E).

During this study we found no direct evidence of second nesting attempts after a failure. Because we did not mark birds individually we cannot tell whether the few females that initiated their nests in late September or even October had already attempted to breed, or if that was their first time in the season.

DISCUSSION

Breeding habitat. Despite the fact that nest search is substantially easier in orchards and gardens than in dense thick-

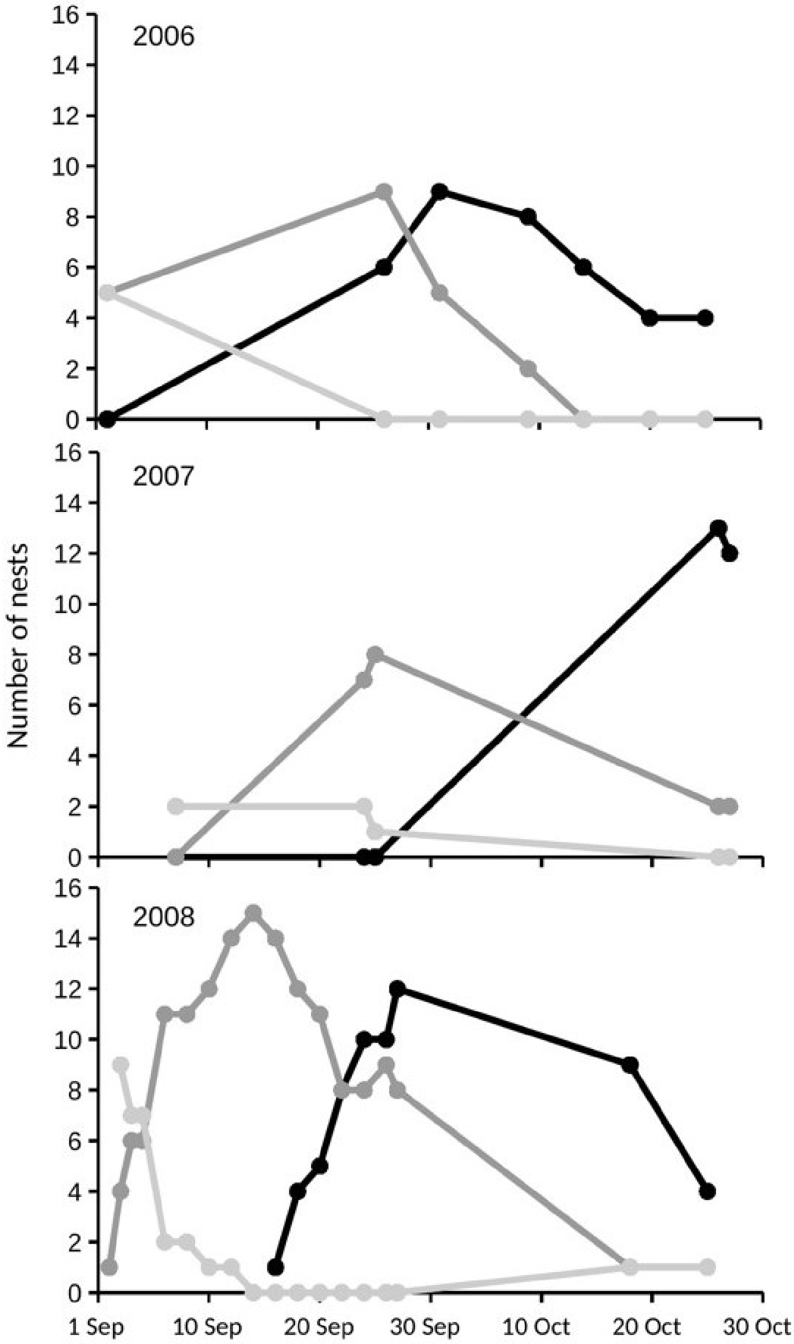

Figure 4. Number of Chilean Woodstar (*Eulidia yarrellii*) nests at different stages (i.e., building, light gray; with eggs, gray; and nestlings, black) recorded in Chaca, Vitor valley, Arica-Parinacota Region, northern Chile, between September and October of 2006–2008. Circles represent the individual dates in which data were collected.

et, after several seasons of work in the region we are confident that, although nesting in native vegetation may be underestimated, exotic trees as a breeding substrate for the Chilean Woodstar in the Azapa and Vitor valleys are certainly more important than native trees. This finding is in agreement with our observation of a positive association of bird-species diversity and olive groves in the study region (Estades et al. 2007). A potential explanation for these patterns is that olive trees might have replaced long lost native woodlands. Evidence for such a vegetation is scant, but the fact that a few scattered native trees do survive in some areas, and that some of these species (e.g., *Morella pavonis*, Myricaceae) may form small continuous woodlands in other areas (Luebert 2004) indicates that the potential for a past woodland-type vegetation existed. Interestingly, *M. pavonis* (officially classified as Vulnerable, Ministerio del Medio Ambiente 2008) has a size, shape, and foliage that strikingly resemble those of olive trees.

What is special about Chaca? The Chaca population was known to us years before this study, and its inclusion in our sample was deliberate and not the result of a random sampling. Although our data did not allow us to perform a formal analysis, we believe that a combination of certain attributes of this site might be responsible for the unusual concentration of nests in Chaca.

The most evident difference between Chaca and the other sites we visited during this study is the presence of a "pure" patch of breeding sites (olive grove), adjacent to a large patch of foraging resources (chañar and a small citrus grove). In no other site we observed this apparently favorable combination of vegetation types. The other areas had only nesting sites but no or very few flowers, or just (chañar) flowers and no nesting sites, or a close mix of both (i.e., interspersed olive and citrus trees). Although we initially thought that the latter would provide a good nesting habitat for the species, our observations in Chaca suggest that female Woodstars could be avoiding nesting sites that are very close to flowering patches that might attract a large number of birds. Baltosser (1996) showed that female hummingbirds were distracted by the presence of several other species of birds, leaving the nest and, therefore, reducing the time dedicated to incubation.

Although it was not formally abandoned, the olive grove where we observed nesting had a minimal management during the previous years. The trees were old and their crowns had grown wider than what is probably advisable for olive production, as neighboring trees were practically touching each other. However, despite the lack of pruning the foliage was less dense than that of many other orchards that we visited, likely favoring air circulation and an easy access of females to their nests.

Another important factor associated to the lack of management is that no pesticides had been used in the orchard for years. Additionally, the fact that there were no nearby crops in the area clearly minimizes the exposure of hummingbirds to toxic substances. The use of high-pressure water to remove mold from trees is a normal activity in some olive groves (Chávez-Lazo et al. 2008), posing an obvious risk for nests. However, to our knowledge the latter technique has not been used in the Chaca site for years.

Water is very important for hummingbirds, and many species build their nests near streams (Skutch 1958, Hayes et al. 2000, Greeney et al. 2006) and bathe, drink (Figure 2F), and forage for arthropods (crucial for nestling development) along water courses (Wagner 1946, Stiles 1995). Although in Chaca there is a river, it is normally dry during the breeding season. The main source of water for hummingbirds in this site is a small reservoir used for irrigation (Figure 3). However, this reservoir was inside the territory of a male that actively chased away most females (likely the unreceptive ones). Only during the biweekly watering of the orchard, water is available for the females who take advantage of the short flooding for bathing (Lühr pers. comm.).

The scarcity of water in the system is apparently reflected in the fact that the diet of woodstar nestlings is based mostly on insects of the orders *Hymenoptera*, *Homoptera*, and *Coleoptera* (Estades et al. 2007), while in many hummingbird species the most frequent insects in their diet belong to water-related groups, such as *Ephemeroptera* and *Diptera* (Baltosser 1989, Greeney et al. 2006).

Breeding biology and nesting success. The breeding of the Chilean Woodstar is apparently synchronized with the flowering of chañar, a legume tree that flowers intensively during September-October and produces nectar rich in sugar (Eynard & Galetto 2002, Lühr 2011). During the same period, citrus trees are also in flower, constituting the second-most important nectar source for the species in the study area (Lühr 2011).

Compared to other hummingbirds, the estimated parameters indicate that the Chilean Woodstar has a very long nesting cycle. Although incubation time (17.3 days) falls within the normal range for this family (15–20 days; Skutch 1931, 1964; Fraga 1984, Thomas 1994, Marín 2001, Winkler et al. 2015), the nestling stage (average 31 days) is longer than that reported for most species (18–30 days; Skutch 1931, 1951, 1961; Brown 1992, Thomas 1994, Marín 2001, Greeney et al. 2006, Fierro-Calderón & Martin 2007). A potential problem of a long nesting cycle is a higher exposure to agents causing nest failure. However, although our estimates of nest success seem low (21–44%), they fall within the range of nest success estimated by Baltosser (1983) for different species of hummingbirds in the southern United States (14.6–59.4%).

The duration of the breeding cycle, combined with the short flowering season of the main nectar producing plants in Chaca, suggests that opportunities for a second brood are limited (Lazzoni 2014). We observed a few nests that were initiated in October but we were not able to follow their development beyond that month. We had initially suspected that the species might have another breeding period during the fall, because of the existence of a second flowering period during the Austral summer (authors' observations). However, more thorough observations in Azapa and Vitor (Lazzoni 2014) have failed to support this hypothesis, thus confirming the existence of just a single breeding season from mid-August to November.

Predation is usually an important cause of nest loss in hummingbirds (Baltosser 1986). Although we did not witness predation events, our data suggest that in up to 56% of the failures an "external" agent might have been involved. We have no information regarding potential predators but they might include some passerine birds (Baltosser 1986). At least two species known to prey on bird nests (Menezes & Marini 2017) are present in the area: Shiny Cowbird (*Molothrus bonariensis*) and Southern House Wren (*Troglodytes musculus*). Due to the position of woodstar nests in the tree, access by non-volant predators (e.g., rats) is probably restricted. The South American elegant racer (*Pseudalsophis elegans*), a snake, is present in the area, but it is very rare and we have never observed it climbing a shrub or tree.

Although the two persons that work in the orchard are well aware of the presence of woodstars and are very careful, sometimes the movement of people with ladders and other equipment may, inadvertently, cause destruction or abandonment of some nests. Also, we cannot rule out the accidental tipping of nests by individuals of the very abundant Pacific Dove (*Zenaida meloda*) that nest in the same trees as woodstars. Finally, the effect of weather on nest failure is probably negligible, as strong winds are relatively rare and there is virtually no rainfall in the region.

Implications for habitat restoration. Although the generalization of our results is difficult because most of them come from one site, our observations suggest that, if appropriate breeding conditions are offered, the species may have the potential to produce a reasonable number of recruits per season. In the first place, these conditions involve the apparent key combination of suitable nesting sites with nearby foraging resources and a minimal exposure to disturbance, and a site that can accommodate a lek of males. Some recent evidence indicates that leks need not to be in the vicinity of a nesting site but can be located several hundred meters apart (Lazzoni 2014). Second, breeding habitat may be based on already available exotic vegetation, although a long-term habitat restoration program should probably focus on the use of native plant species in order to minimize the risks posed to the species by agricultural activities. However, the restoration of lek sites may represent a bigger challenge, because the high fidelity that males show to these "traditional" places may limit their ability to use newly established sites (Lazzoni 2014).

More recent studies on this species (Lazzoni 2014, AvesChile 2017) suggest that the Chilean Woodstar is more sensitive to habitat changes than the other hummingbirds species present in this region, including its direct competitor, the Peruvian Sheartail, and the larger, more common Oasis Hummingbird (*Rhodopis vesper*). The information presented in this study should provide some keys to the recovery of this critically endangered species.

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