Estimation of bat colony size even with low recapture rates: an example based on the Cormack-Jolly-Seber model in Oaxaca, México

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ABSTRACT. Introduction: Group or colony size is an important variable that is related to biological, ecological, and conservation aspects of bats. However, estimating the size of each colony or group in roosts used by more than one species is particularly difficult, especially when recapture rates are very low (< 10 %). **Objective:** Estimate the colony size of 14 species of bats: one emballonurid, one natalid, four mormoopids, seven phyllostomids, and one vespertilionid, which roosted throughout one year (July 2016 to June 2017) in a mine and two caves -Cerro Huatulco and El Apanguito- in the Sierra Sur and Costa of the state of Oaxaca. **Methods:** We constructed capture-recapture histories per species and roost, and for species for which we obtained recaptures that represented at least 10 % of the captures, we used the probabilistic Cormack-Jolly-Seber model. In the case of species with no recaptures or with a recapture proportion lower than 10 %, we estimated the number of individuals per roost by applying the same proportion between the number of captured specimens and the estimated number for species with recaptures greater than 10 % and that they belonged to the same family or trophic guild. **Results:** The total estimated number of bats in the three studied roosts was 20 105. The highest colony size estimates were for the mormoopids *Pteronotus fulvus* and *P. mesoamericanus* from El Apanguito and *P. fulvus* from Cerro Huatulco, with 6 609, 4 092 and 2 212 individuals, respectively. **Conclusions:** The methodology used in this study allowed estimating the colony size for all registered species, even though only for 21.42 % the recapture rates were greater than 10 %. Therefore, we consider that this methodology represents a viable alternative to estimate colony size in other roosts. This information, together with the high species richness and importance for reproductive processes, allow us to propose these sites as Bat Protection and Conservation Areas in Mexico.

Key words: abundance; capture-recapture; cave; chiropterans; Cormack-Jolly-Seber; mine.

Bat populations play a vital role in natural ecosystems and have a significant positive economic impact, particularly insectivore bat populations in the control of agricultural pests (Cleveland et al., 2006). Colony size is an important variable to understand the biology and ecology of organisms that live in groups. It is also important for the implementation of effective conservation actions for these organisms and can also provide useful ecological information, such as the amount of dispersed seeds, dynamic of the community, and foraging patterns (Hristov, Betke, Theriault, Bagchi, & Kunz, 2010). However, estimating colony size in the field is difficult and has been both a logistical and technological

challenge, particularly for endangered, rare, and cryptic species (Kunz & Anthony, 1996; Kunz, 2003; McCracken, 2003; Kunz, Betke, Hristov, & Vonhof, 2009). This is mainly due to the biological characteristics of bats, such as their small size, high vagility, and their strictly nocturnal lifestyle, although it is also a result of the methodologies employed. For example, estimations of colony size using thermal imaging are highly costly (Hristov, Betke, & Kunz, 2007) and visual counts and photographic estimations can be prone to bias (O'Farrell & Gannon, 1999). Capture-mark-recapture (CMR) methods, which consist in marking individuals in a first capture session and then recording the proportion of marked individuals in subsequent recapture sessions, have been demonstrated to be an efficient tool for the estimation of bat colony size (Puechmaille & Petit, 2007). Although to date there are no studies in which the population size of ecologically similar and taxonomically related sympatric bat species is compared, it is to be expected that when subjected to the same environmental conditions they will show similar population sizes, and therefore similar probabilities of capture. The empirical data, at least in the Mexican tropics, do not show a clear pattern in this sense, since some studies show a tendency for species of the same genus to show similar abundances (e. g., Navarro & Leon-Paniagua, 1995; Ramírez-Lucho, Coates, & González-Christen, 2017), while in others there is a clear predominance in the number of captures of a species (e. g. Moreno & Halfter, 2001; Mendoza, Horváth, Ruiz, Escalona, & Navarrete, 2017).

Given the low abundance of roosts that contain colonies of thousands of bats worldwide (Furey & Racey, 2016), it is necessary to carry out estimations of colony size that will help to obtain a better perspective of the dynamics of bat populations across time. In this sense, caves stand out due to their capacity to maintain thousands or millions of individuals (Arita, 1993; Trajano & Giménez, 1998), although they are also relatively more vulnerable systems compared to other roosting sites (Elliott, 2000; Hamilton-Smith & Eberhard,

2000) and are currently subject to threats (guano mining, unsupervised tourist visits, vandalism, and alteration and loss of surrounding vegetation cover) that put bat populations at risk and could even lead to the extinction of species that depend on cave roosts (Mickleburgh, Hutson, & Racey, 2002; Medellín, 2003; Elliott, 2004; Gunn, 2004; McCracken, 2011; Medellín, Wiederholt, & López-Hoffman, 2017).

Considering the above, there is an urgent need to perform studies that provide information about the identity and abundance of species that occupy a given roosts, such as caves and mine tunnels, in order to determine which are the main populations and sites that exhibit higher vulnerability and conservation value (Kloepper et al., 2016). This is important because in most conservation plans and identification of areas in need of protection, the parameters that are taken into account are vegetation cover and forest fragmentation, while subterranean ecosystems (caves, mines, cracks) tend to be underrepresented or even ignored (Sugai, Ochoa-Quintero, Costa-Pereira, & Roque, 2015; Medellín et al., 2017).

The roosts evaluated in this study had not been previously explored, so there are no previous studies that indicated the high diversity of species that the three roosts harbor. However, the results of the diversity (richness and abundance) of the three refuges have been published recently (Hernández-Aguilar & Santos-Moreno, 2020a), so work will continue so that the three sites are considered important sites for bat populations from Mexico. Therefore, the objective of this study was to estimate the colony size of 14 bat species that were recorded throughout one year in a mine and two caves. In addition, we present a new method to estimate the colony size of species with low recapture rates (< 10 %).

MATHERIALS AND METHODS

Study site: The study was carried out in a mine tunnel (hereafter La Mina, 15º54'52'' N & 96º24'59'' W, and an altitude of 1 110 m.a.s.l), in the municipality of Pluma Hidalgo, and two
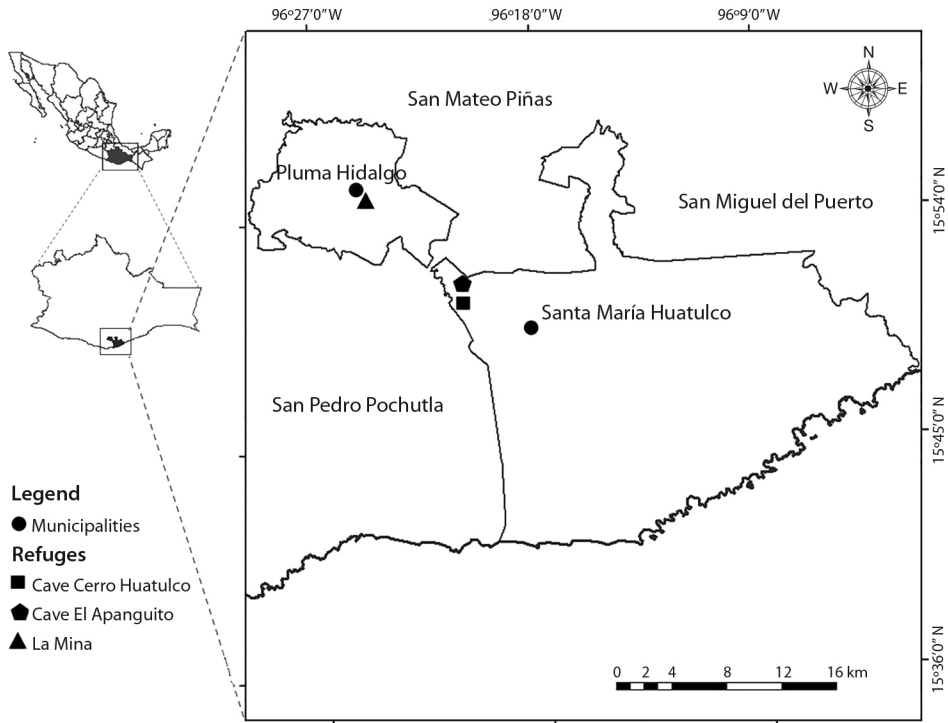
Fig. 1. Geographic location of the three roosts evaluated in the municipalities of Pluma Hidalgo and Santa María Huatulco, Oaxaca, Mexico.

caves in Santa María Huatulco: El Apanguito (15º51'58'' N & 96º21'13.2'' W, and an altitude of 695 m.a.s.l) and Cerro Huatulco (15º50'59'' N & 96º21'04.3'' W, and an altitude of 475 m.a.s.l), located in the state of Oaxaca, Mexico (Fig. 1). The entrances to La Mina are 3 m high and 2 m wide, for El Apanguito it is 1.20 x 1.5 m and at Cerro Huatulco it is 10 x 15 m. The Mine contains water for most of the year and only Cerro Huatulco has four chambers, the remaining two have only one chamber. A complete description of the roosting sites can be found in Hernández-Aguilar & Santos-Moreno (2020a; 2020b). The climate is hot subhumid with rainfall in the summer and the main vegetation in the zone is medium semi-evergreen forest with coffee plantations (Trejo, 2004; OEIDRUS, 2005).

Field work: We carried out monthly samplings from June 2016 to June 2017, with a duration of two nights per roost, including a dry season (October-April) and a rainy season (May-September). It was not possible to perform any sampling during the month of May 2017 due to adverse environmental conditions that made it impossible to access La Mina. Bats were captured with a G5 harp trap (Bat Conservation and Management, Inc., Carlisle, PA, EE. UU.), 1.5 m wide and 2 m high, that was placed at the entrance of the roosts from 18:00 to 00:00. All captured individuals were immediately placed in cloth bags and then processed. We identified the species and determined the sex and age category (juvenile or adult); according to the degree of the phalangeal epiphyses observed against the light of a headlamp (Handley, Wilson, & Gardner, 1991). Finally, we placed an aluminum ring (National Band and Tag Company, Newport, Kentucky, USA) on the forearm of each individual with a unique serial identification number depending on the size of the organism: category A (2.9 mm diameter) for species such as *Pteronotus*

fulvus and *Natalus mexicanus*; and category B (4 mm) for species such as *Artibeus toltecus, Carollia perspicillata, Glossophaga soricina, Pteronotus mesoamericanus,* and *Mormoops megalophylla.* Once all the information was recorded, we released the individuals in the place where they were captured. In the case of recaptured organisms, we obtained complementary data, such as time of recapture and if the ring caused any damage to the forearm. This study was carried out with a Scientific Collection License for wildlife teaching granted by the Ministry of Environment and Natural Resources (SEMARNAT-20/ks-0112/10/16).

Data analysis: We constructed capture-recapture histories of individuals grouped by species and roost. In the case of species with recaptures that represented at least 10 % of total captures, we applied a Cormack-Jolly-Seber model was applied, which includes four assumptions: 1) each animal marked in time (i) has the same probability of being recaptured (p_i); 2) each animal marked in the population at time (i) has the same probability of surviving time ($i + 1$); 3) the marks do not fall off or are erased, they are detectable, and 4) the information collection process is relative to the interval of each time elapsed between time (i) and time ($i + 1$). This model includes two parameters: capture probability (p) and apparent survival probability (ϕ). Each parameter can be constant (p o ϕ) or vary across time (p_t or ϕ_t), which results in four possible candidate models for each species and roost. The final model for each species and roost was selected based on the Akaike Information Criterion for small samples (AICc, Burnham & Anderson, 2002). Estimations were performed in Mark version 8.2 (White & Burnham, 1999). Once the final model was selected, we estimated the value or values of p (when the final model included this parameter as constant or varying across time, respectively) and used them to estimate monthly population sizes (N) as the ratio of the number of captured individuals (n) and the capture probability (p): N= n/p (Lindenmayer, Lacy, & Viggers, 1998). In order to apply the

Cormack-Jolly-Seber model to species with no recaptures or a recapture proportion lower than 10 % of the captures, we estimated the number of individuals per roost by applying the same proportion between the number of captured specimens and the estimated number for the recorded species that belonged to the same family or to the same trophic guild. For the phyllostomid bat species *Artibeus jamaicensis*, *A. toltecus*, *A. watsoni, Desmodus rotundus*, *Glossophaga soricina*, *Sturnira hondurensis,* and *Carollia perspicillata* from El Apanguito and Cerro Huatulco, the estimated number was obtained by applying the same proportion between the number of captured specimens and the estimated number for *Carollia perspicillata* from La Mina, whose capture probability had a narrower confidence interval than that of *A. toltecus* in the same roost. In the case of the mormoopid species *Pteronotus fulvus*, *P. mesoamericanus,* and *P. psilotis*, values were calculated with the proportion observed for insectivorous bat *Mormoops megalophylla* in El Apanguito, which was the only species of this family for which we obtained enough data to estimate capture probabilities. Moreover, this species shares ecological similarities with other species of the same family and can form large colonies, as those observed in the genus *Pteronotus*. Given that we did not record *M. megalophylla* in El Apanguito during the months of May, June, and July and could not estimate the proportion between the number of captured individuals and the number estimated with the Cormack-Jolly-Seber model, we considered the mean value of the proportions of the months when the species was recorded (from September to April). In the case of *Balantiopterix plicata* (Emballonuridae), *Natalus mexicanus* (Natalidae), and *Myotis pilosatibialis* (Vespertilionidae), which did not have recapture proportions higher than 10 % in any roost or an ecologically similar species, proportions were calculated in the same way as for mormoopids, which did not have recaptures or had recaptures lower than 10 % of total captures. The number of individuals per roost and month was calculated as the sum of the estimates of

each species present, while the total per roost was calculated conservatively as the sum of the maximum estimated number monthly of each species for each roost throughout the year. This restriction was applied because we do not know the number of individuals that remain in each refuge throughout the year and many individuals would be re-counted as much as 12 times if we the sum of all the monthly estimates of each species.

RESULTS

We captured, marked, and released 5 788 bats of 14 species, 10 genera, and five families: one emballonurid (*Balantiopterix plicata*), one natalid (*Natalus mexicanus*), four mormoopids (*Mormoops megalophylla*, *Pteronotus fulvus*, *P. mesoamericanus,* and *P. psilotis*), seven phyllostomids (*Artibeus jamaicensis*, *A. toltecus*, *A. watsoni*, *Carollia perspicillata*, *Desmodus rotundus*, *Glossophaga soricina,* and *Sturnira hondurensis*), and one vespertilionid (*Myotis pilosatibialis*). The most abundant species were *P. fulvus* and *P. mesoamericanus* with 41.01 and 32.34 % of the captures, respectively, and the least abundant species were *G. soricina* (3.11 %) and *A. toltecus* (1.31 %). We captured 570 individuals in La Mina, 4 306 in El Apanguito and 960 in Cerro Huatulco (Table 1).

The Cormack-Jolly-Seber model was applied only to the data of *A. toltecus* (16.92 % recaptures) and *Carollia perspicillata* (15.79 %), both in La Mina, and *Mormoops*

TABLE 1

Number of captured (first number) and estimated (second number) bats per month per roost for species or colonies to which we could not apply capture-recapture models (recapture proportions lower than 10 %)

	Month												Max
	Jul	Aug	Sep	Oct	Nov	Dec	Jan	Feb	Mar	Apr	May	Jun	
Roost	*Balantiopterix plicata*												
La Mina	0-0	0-0	0-0	0-0	0-0	0-0	0-0	0-0	0-0	0-0	0-0	0-0	0-0
CCH	1-13	0-0	0-0	0-0	0-0	0-0	0-0	0-0	0-0	0-0	0-0	0-0	1-13
CEA	0-0	0-0	0-0	0-0	0-0	0-0	0-0	0-0	0-0	0-0	0-0	0-0	0-0
Total	1-13	0-0	0-0	0-0	0-0	0-0	0-0	0-0	0-0	0-0	0-0	0-0	
	Natalus mexicanus												
La Mina	1-13	1-13	0-0	1-13	0-0	0-0	1-13	0-0	0-0	0-0	0-0	0-0	1-13
CCH	0-0	0-0	0-0	1-13	0-0	0-0	0-0	1-13	3-40	0-0	0-0	0-0	3-40
CEA	0-0	12-159	28-371	17-225	61-808	17-225	18-238	11-146	15-199	13-172	3-40	4-53	61-808
Total	1-13	13-172	28-371	19-251	61-808	17-225	19-251	12-159	18-239	13-172	3-40	4-53	
	Mormoops megalophylla												
La Mina	0-0	0-0	0-0	0-0	0-0	0-0	0-0	0-0	0-0	0-0	0-0	0-0	0-0
CCH	6-79	0-0	2-27	0-0	1-13	0-0	1-13	0-0	0-0	0-0	6-79	13-172	13-172
Total	6-79	0-0	2-27	0-0	1-13	0-0	1-13	0-0	0-0	0-0	6-79	13-172	
	Pteronotus fulvus												
La Mina	0-0	0-0	0-0	0-0	0-0	0-0	1-13	0-0	1-13	0-0	0-0	0-0	1-13
CCH	6-79	81-1 070	70-928	37-490	167-2 212	78-1 033	23-305	110-1 457	100-1 325	68-901	8-106	10-132	167-2212
CEA	0-0	2-26	151-2 001	65-861	138-1 828	190-2 516	177-2 345	499-6 609	311-4 119	38-504	27-358	11-146	499-6 609
Total	6-79	83-1 096	221-2 929	102-1 351	305-4 040	268-3 549	201-2 663	609-8 066	412-5 457	106-1 405	35-464	21-278	
	Pteronotus mesoamericanus												
La Mina	2-26	10-132	41-543	14-185	16-212	8-106	15-199	1-13	0-0	5-66	0-0	0-0	41-543
CCH	12-159	6-79	9-119	12-159	1-13	1-13	0-0	3-40	4-53	1-13	17-225	8-106	17-225
CEA	58-768	108-1 427	136-1 802	216-2 860	117-1 550	88-1 165	74-980	114-1 510	74-980	186-2 466	202-2 675	309-4 092	309-4 092
Total	72-953	124-1 638	186-2 464	242-3 204	134-1 775	97-1 284	89-1 179	118-1 563	78-1 033	192-2 545	219-2 900	317-4 198	

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TABLE 1 (Continued)

	Month												Max
	Jul	Aug	Sep	Oct	Nov	Dec	Jan	Feb	Mar	Apr	May	Jun	
	Pteronotus psilotis												
La Mina	0-0	0-0	0-0	0-0	0-0	0-0	0-0	0-0	0-0	0-0	0-0	0-0	0-0
CCH	2-26	0-0	0-0	0-0	0-0	0-0	0-0	0-0	0-0	0-0	0-0	0-0	2-26
CEA	0-0	0-0	0-0	0-0	0-0	0-0	0-0	0-0	0-0	0-0	0-0	0-0	0-0
Total	2-26	0-0	0-0	0-0	0-0	0-0	0-0	0-0	0-0	0-0	0-0	0-0	
	Desmodus rotundus												
La Mina	0-0	0-0	0-0	0-0	0-0	0-0	0-0	0-0	0-0	0-0	0-0	0-0	0-0
CCH	17-363	0-0	0-0	0-0	2.42	0-0	0-0	0-0	0-0	0-0	2.42	0-0	17-363
CEA	0-0	0-0	0-0	0-0	0-0	0-0	0-0	0-0	0-0	0-0	0-0	0-0	0-0
Total	17-363	0-0	0-0	0-0	2.42	0-0	0-0	0-0	0-0	0-0	2.42	0-0	
	Glossophaga soricina												
La Mina	0-0	0-0	11-235	10-214	27-576	6-128	7-149	11-234	19-406	39-833	0-0	0-0	39-833
CCH	2-43	4-85	0-0	2-42	33-704	0-0	0-0	0-0	0-0	0-0	11-235	0-0	33-704
CEA	0-0	0-0	0-0	0-0	0-0	0-0	0-0	0-0	0-0	0-0	0-0	0-0	0-0
Total	2-43	4-85	11-235	12-256	60-1 280	6-128	7-149	11-234	19-406	39-833	11-235	0-0	
	Carollia perspicillata												
CCH	0-0	1-21	0-0	0-0	0-0	0-0	0-0	0-0	0-0	0-0	0-0	0-0	1-21
CEA	0-0	0-0	0-0	0-0	0-0	0-0	0-0	0-0	0-0	0-0	0-0	0-0	0-0
Total	0-0	1-21	0-0	0-0	0-0	0-0	0-0	0-0	0-0	0-0	0-0	0-0	
	Artibeus jamaicensis												
La Mina	0-0	0-0	0-0	0-0	0-0	0-0	0-0	0-0	0-0	0-0	0-0	0-0	0-0
CCH	12-256	0-0	0-0	0-0	0-0	0-0	0-0	0-0	0-0	0-0	3-64	2-42	12-256
CEA	0-0	0-0	0-0	0-0	0-0	0-0	0-0	0-0	0-0	0-0	0-0	0-0	0-0
Total	12-256	0-0	0-0	0-0	0-0	0-0	0-0	0-0	0-0	0-0	3-64	2-42	
	Artibeus toltecus												
CCH	1-21	0-0	0-0	0-0	0-0	0-0	0-0	0-0	0-0	0-0	0-0	0-0	1-21
CEA	0-0	0-0	0-0	0-0	0-0	0-0	0-0	0-0	0-0	0-0	0-0	0-0	0-0
Total	1-21	0-0	0-0	0-0	0-0	0-0	0-0	0-0	0-0	0-0	0-0	0-0	
	Artibeus watsoni												
La Mina	0-0	2-43	0-0	0-0	3-64	0-0	0-0	1-21	1-21	0-0	0-0	0-0	3-64
CCH	0-0	0-0	0-0	0-0	0-0	0-0	0-0	0-0	0-0	0-0	0-0	0-0	0-0
CEA	0-0	0-0	0-0	0-0	0-0	0-0	0-0	0-0	0-0	0-0	0-0	0-0	0-0
Total	0-0	2-43	0-0	0-0	3-64	0-0	0-0	1-21	1-21	0-0	0-0	0-0	
	Sturnira hondurensis												
La Mina	2-43	1-21	2-43	0-0	1-21	0-0	0-0	0-0	0-0	0-0	0-0	1-21	2-43
CCH	0-0	0-0	0-0	0-0	0-0	0-0	0-0	0-0	0-0	0-0	1-21	0-0	1-21
CEA	0-0	0-0	0-0	0-0	0-0	0-0	0-0	0-0	0-0	0-0	0-0	0-0	0-0
Total	2-43	1-21	2-43	0-0	1-21	0-0	0-0	0-0	0-0	0-0	1-21	1-21	
	Myotis pilosatibialis												
La Mina	0-0	0-0	0-0	1-13	3-40	0-0	0-0	0-0	1-13	0-0	0 -0	1-13	3-40
CCH	0-0	0-0	0-0	0-0	0-0	0-0	0-0	0-0	0-0	0-0	0-0	0-0	0-0
CEA	0-0	0-0	0-0	0-0	0-0	0-0	0-0	0-0	0-0	0-0	0-0	0-0	0-0
Total	0-0	0-0	0-0	1-13	3-40	0-0	0-0	0-0	1-13	0-0	0-0	1-13	

Max=Maximum number of bats per roost per species throughout the entire sampling year. CCH: Cave Cerro Huatulco; CEA: Cave El Apanguito.

megalophylla in El Apanguito (13.17 %). For
C. perspicillata and *A. toltecus* in La Mina,
the final model was the one where both cap-
ture probability and apparent survival were
constant throughout the year (ϕp), whereas
for *Mormoops megalophylla* in El Apanguito,
apparent survival was also constant across the
whole sampling period, but capture probabili-
ties varied monthly (ϕp_t; Table 2). For the three
species, the best supported models presented
weights of 95.37, 99.21, and 98.77, respec-
tively. The capture probabilities estimated for
C. perspicillata and *A. toltecus* in La Mina and
M. megalophylla in El Apanguito were very
low, lower than 0.1. For *C. perspicillata* in La
Mina, we estimated a population size of 684
individuals throughout the year, with monthly

fluctuations between 107 (March) and 684
(September). For *A. toltecus,* we estimated 183
individuals, with a maximum abundance in
July (183 individuals) and a minimum abun-
dance in December and January (23 individu-
als in each month). For *M. megalophylla* in El
Apanguito, we estimated a total population size
of 2 106 individuals, with a maximum in March
(2 106 individuals) and a minimum in June and
July (0) (Table 3).

Even though we obtained recaptures of
four other species from the three roosts (*Glos-
sophaga soricina* in La Mina with 2.36 % of
recaptures, *Pteronotus mesoamericanus* in La
Mina and El Apanguito with 3.77 and 4.55 %,
respectively, *P. fulvus* in Cerro Huatulco with
0.39 % and in El Apanguito with 3.67 %, and

TABLE 2

Comparison of four candidate models and parameters of the final model (standard error of the estimation in parenthesis)
for the three bat species that had recapture proportions higher than 10 %

Candidate Model	AICc	ΔAICc	AICc Weights	Model Likelihood	Num. Par.	Deviance	Final model Parameter= Value (EE)
Carollia perspicillata La Mina							
ϕp	222.7785	0	0.9537	1	2	80.4352	ϕ=0.8585 (0.9500)
ϕp_t	228.8673	6.0888	0.0454	0.0476	11	66.9147	p=0.0467 (0.0899)
$\phi_t p$	236.7892	14.0107	0.0008	0.0009	11	74.8366	
$\phi_t p_t$	244.5441	21.7656	0.00002	0	19	63.1724	
Artibeus toltecus La Mina							
ϕp	97.0229	0	0.9921	1	2	42.6725	ϕ=0.7286 (0.8815)
ϕp_t	111.5070	14.4841	0.0007	0.0007	11	34.8584	p=0.0876 (0.2042)
$\phi_t p$	116.0200	18.9971	0.00007	0.0001	11	39.3715	
$\phi_t p_t$	127.5036	30.4807	0	0	19	24.4276	
Mormoops megalophylla El Apanguito							
ϕp_t	763.4193	0	0.9877	1	9	46.9828	ϕ=0.7818 (0.8784)
$\phi_t p_t$	772.9295	9.5102	0.0085	0.0086	15	44.099	$p_{September}$= 0 (0)
$\phi_t p$	774.5513	11.1320	0.0037	0.0038	9	58.1148	$p_{October}$=0 (0)
ϕp	785.3180	21.8987	0.00002	0	2	83.0995	$p_{November}$=0.0299 (0.1134)
							$p_{December}$=0.0679 (0.1230)
							$p_{January}$=0.1181 (0.1877)
							$p_{February}$=0.1218 (0.1932)
							p_{March}=0.0807 (0.1367)
							p_{April}=0.0212 (0.0487)

AICc = Akaike Information Criterion for small samples. ΔAICc = difference in AICc between the respective model and
the best candidate model. Num. Par. = Number of parameters. p = capture probability. Φ = apparent survival probability.

TABLE 3

Monthly number of captured (first number) and estimated bats with the probabilistic Cormack-Jolly-Seber model
(second number) in three roosts for the three species that had recapture proportions higher than 10 %

Month	*Carollia perspicillata*	*Artibeus toltecus*	*Mormoops megalophylla*
	La Mina	La Mina	El Apanguito
July	23 - 491	16 - 183	0 - 0
August	17 - 363	4 - 46	14 - 185
September	32 - 684	8 - 91	12 - 159
October	10 - 214	3 - 34	66 - 874
November	25 - 534	14 - 160	143 -1 894
December	8 - 171	2 - 23	99 - 1 311
January	10 - 214	2 - 23	133 - 1 762
February	20 - 427	3 - 34	155 - 2 053
March	5 - 107	15 - 171	159 - 2 106
April	19 - 406	4 - 46	35 - 464
May	0 - 0	0 - 0	0 - 0
June	7 - 150	5 - 57	0 - 0
Mean	15 - 313	6 - 72	68 - 901
Min	0 - 0	0 - 0	0 - 0
Max	32 - 684	16 - 183	159 - 2 106

Natalus mexicanus in El Apanguito with 1.52 % recaptures), the proportions with respect to the number of captures were lower than 10 %, and we were not able to apply the Cormack-Jolly-Seber model. There were no recaptures for the rest of the species, but we were able to obtain an estimation of colony size using the methodology described above. We did not observe any species that was consistently the most abundant in the three roosts. In El Apanguito, we obtained the highest estimations for *P. fulvus* in February (6 609 individuals), for *P. mesoamericanus* in June (4 092), and for *N. mexicanus* in November (808). In La Mina, the highest estimated number of individuals for *G. soricina* was observed in April (833 individuals), for *A. watsoni* in November (64 individuals)*,* for *S. hondurensis* in July and September (43 individuals), and for *M. pilosatibialis* in November (40 individuals), while in Cerro Huatulco, the highest estimations for *D. rotundus, A. jamaicensis, P. psilotis,* and *B. plicata* were obtained in July with 363, 256, 26, and 13 individuals, respectively (Table 1).

In the complex comprised of the three studied roosts, we estimated the presence of 20 105

bats, with 67.71 % in El Apanguito, 12.01 % in La Mina, and 20.26 % in Cerro Huatulco. Overall, we estimated a monthly mean value of 525.15 bats in La Mina, with a maximum in September (1 318) and a minimum in May (0). In Cerro Huatulco, the monthly mean was of 339.5 individuals, with a maximum (2 916) in November and a minimum (0) in September and October, December to February and April. In El Apanguito, the monthly mean was of 1 309 individuals, with a maximum (4 092) in June and a minimum (0) in July and May.

DISCUSSION

We obtained recapture rates higher than 10 % only for three bat species (*C. perspicillata* 15.79 %, *A. toltecus* 16.92 %, and *M. megalophylla* 13.17 %), and lower than 10 % for four species (*G. soricina* 2.36 %, *P. mesoamericanus* 5.51 %, *P. fulvus* 3.95 %, and 1.52 % for *N. mexicanus*); we did not record any recaptures for the other seven species. In the latter two cases, it was not possible to apply the Cormack-Jolly-Seber model or, if it was applied, the resulting estimations are not accurate. Thus,

the implementation of new methodologies is necessary to obtain estimations with extremely low recapture rates as occur with large colonies of bats. In our study, the two most abundant species (*P. fulvus* with 2 369 individuals and *P. mesoamericanus* with 1 868 individuals) had such low recapture rates (3.95 % and 5.51 %, respectively, perhaps because they occupy other alternative refuges, since we have identified three caves near El Apanguito and Cerro Huatulco) that it was not possible to directly apply the model. However, with the methodology implemented in this study and taking the proportion between the number of captures and the estimated colony size of *M. megalophylla,* it was possible to estimate the colony size of the mormoopids *P. fulvus* and *P. mesoamericanus*, obtaining thus the largest colony sizes in El Apanguito with 6 609 and 4 092 individuals, respectively.

The specific ecological characteristics of each species, such as roost fidelity, use of alternative roosts, flight patterns, the echolocation abilities to detect the net, and large colony sizes make it difficult to obtain high recapture rates, which makes it difficult to estimate their colony sizes (Lewis, 1995; Storz, Balasingh, Nathan, Emmanuel, & Kunz, 2000; Godoy et al., 2002; Chaverri & Kunz, 2006). The overall recapture percentage (average 6.1 %) were similar to those reported in other studies in México, North America (United States 40 %, Stevenson & Tuttle, 1981; Canada 14 %, Norquay, Martinez-Núñez, Dubois, Monson, & Willis, 2013), and South America (Brazil 0 %, Zortéa, Bastos, & Acioli, 2015; 1 %, McCracken, 2003; 27.4%, Trajano, 1996). In this sense, for bat species with recaptures lower than 10 %, we consider it appropriate to use the approach applied in the present study, where colony size was estimated by using the proportions of the observed number and the number estimated for species with recapture percentages higher than 10 % that are ecologically similar and share the same roost. Although this method has not been applied before in bat species, it is to be expected that when subjected to the same environmental conditions they will show similar population sizes and, therefore, similar capture probabilities. Although it should be noted that the precision of this method should be proven in subsequent studies.

The estimations of colony size obtained with the Cormack-Jolly-Seber capture-recapture model are reasonable for the three studied species (*M. megalophylla* with 2 106 individuals throughout the year in El Apanguito and *C. perspicillata* with 684 individuals and *A. toltecus* with 183 individuals in La Mina) if we consider that the estimated values are within the range known of colony size for these species. For example, *M. megalophylla* is cave-specialist species that can form colonies from less than 1 000 individuals (Torres-Flores, López-Wilchis, & Soto-Castruita, 2012) to up to 500 000 individuals (Bonaccorso, Arends, Genoud, Canton, & Morton, 1992; Iñiguez-Dávalos, 2005). In the cave system Cuevas del Silvino in Guatemala, the colony size of this species was estimated to be of approximately 44 200 individuals using video cameras (Cajas-Castillo, Echeverría, & Trujillo, 2015). In the case of *C. perspicillata* and *A. toltecus,* low population sizes have been reported throughout their distribution area in Mexico (Jalisco, Iñiguez-Dávalos, 1993; Stoner, 2002; Querétaro, Navarro & León-Paniagua, 1995; Oaxaca, García-García, & Santos-Moreno, 2008), which could be related to specific requirements of the roosts such as temperature, humidity, air flow, or light intensity, the diversity of other available roosts, and the availability of food, which could limit the presence of large populations (over 1 000 individuals according to Arita, 1993). *Artibeus toltecus*, together with *A. watsoni* and *S. hondurensis,* apart from roosting in caves, also form small colonies in tents constructed with leaves, holes in trees, tunnels, cracks in rocks, and abandoned constructions (Kunz & McCracken, 1996; McCracken & Wilkinson, 2000; Chaverri & Kunz, 2006). Other species with large colony sizes were *P. mesoamericanus* and *P. fulvus,* with colony size estimations of over 20 000 individuals throughout the year in El Apanguito. These are cave-specialist species that can form colonies

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of thousands of individuals (Bonaccorso et al., 1992; Arita, 1993; Ortega, 2005). Other studies that have carried out estimations for these species, through direct observations in Mexico (Torres-Flores et al., 2012) and video cameras in Guatemala (Cajas-Castillo et al., 2015), have reported colonies of over 6 000 individuals for *P. mesoamericanus* and up to 98 600 individuals for *P. fulvus* (Cajas-Castillo et al., 2015). In the case of *N. mexicanus,* we captured 199 individuals and estimated a colony size of 2 636 individuals in El Apanguito, 66 in Cerro Huatulco, and 52 in La Mina. This species has been observed to form colonies of up to 5 000 individuals, but it is generally found in colonies between 100 and 200 individuals (Torres-Flores & López-Wilchis, 2010). Finally, the estimated colony size of *G. soricina* was of 833 individuals in La Mina and 704 individuals in Cerro Huatulco. For this species, estimated colony sizes have been of less than 500 individuals in other caves in Mexico (Torres-Flores et al., 2012). Therefore, the estimates obtained in this study are higher than those estimated in other areas, so the precision and usefulness of this method should be tested in the future. We found considerable variation in the monthly estimations of the species recorded in all three roosts, which suggests that the composition of the colonies exhibits considerable dynamics (Hristov et al., 2010).

The total estimated number of bats in the three studied roosts was 20 105, with higher concentrations in El Apanguito (13 615 individuals) and Cerro Huatulco (4 074 individuals). These estimations, together with high species richness, reproduction processes, and occupation dynamics between these roosts (Hernández-Aguilar & Santos-Moreno, 2020a; Hernández-Aguilar & Santos-Moreno, 2020b), allow us to propose these sites as Bat Protection and Conservation Areas in Mexico. We also recommend continuing to monitor the bat populations of these sites and, if possible, implementing other methods to evaluate the accuracy of our estimations.

Some studies have demonstrated that the use of video cameras to record bats emerging from roosts (Escalona-Segura, Vargas-Contreras, & Sosa, 2002; Vargas-Contreras, Escalona-Segura, Arroyo, Rendon Von Osten, & Navarro, 2012; Cajas-Castillo et al., 2015) and the incorporation of acoustic recordings (Kloepper et al., 2016) could be techniques that may produce robust estimations of size of bat colonies. Thus, further studies using these techniques could complement our results or even improve estimates of the number of bats that use the roosts, as well as provide the tools that allow to establish priority criteria for the conservation of roosts and bats in the area.

Even though recent advances, such as digital photography and image analysis, in some cases allow estimating the number of individuals emerging from a roost (Corso, Woolley, & Lacher, 2010), they do not allow to determine the species identity and, thus, it is not possible to know the colony size of each species, except in cases where the roost includes only one species. This is the same limitation of passive acoustic methods (Kloepper et al., 2016), thermal detection systems (Otálora-Ardila et al., 2020), and thermal infrared imaging and computer vision analysis (Hristov et al., 2010). The Light Detection and Ranging (LiDAR) scanning system allows to estimate the number of individuals per species by scanning the roosts and visually recognizing and labelling the areas occupied by each species (Shazali et al., 2017); however, the cost of this system is currently too high for its generalized use. Very recently, genetic tag-recapture methods are expensive but seem to offer advantages over other more invasive methods, although it is only recommended for species that show high fidelity to the refuge and that do not form colonies of thousands or millions of individuals (Oyler-McCance et al., 2018). Therefore, we consider that the estimation method used in the present study provides a low-cost, and reasonably reliable option for the estimation of bat colony size, especially for roosts occupied by more than one species.

Ethical statement: authors declare that they all agree with this publication and made

significant contributions; that there is no conflict of interest of any kind; and that we followed all pertinent ethical and legal procedures and requirements. All financial sources are fully and clearly stated in the acknowledgements section. A signed document has been filed in the journal archives.

RESUMEN

Estimación del tamaño de colonia en murciélagos incluso con bajas tasas de recaptura: un ejemplo basado en el modelo Cormack-Jolly-Seber en Oaxaca, México. Introducción: El tamaño del grupo o colonia es una variable importante que está relacionada con los aspectos biológicos, ecológicos y de conservación de los murciélagos. Sin embargo, estimar el tamaño de cada colonia o grupo en refugios utilizados por más de una especie es particularmente difícil, especialmente cuando las tasas de recaptura son muy bajas (< 10 %). **Objetivo:** Estimar el tamaño de la colonia de 14 especies de murciélagos: un emballonúrido, un natálido, cuatro mormópidos, siete filostómidos y un vespertiliónido, que se refugiaron durante un año (Julio 2016 a Junio 2017) en una mina y dos cuevas -Cerro Huatulco y El Apanguito- en la Sierra Sur y Costa del estado de Oaxaca. **Métodos:** Construimos historias de captura-recaptura por especie y refugio, y para las especies que se obtuvieron recapturas que representaban al menos el 10 % de las capturas, utilizamos un modelo probabilístico de Cormack-Jolly-Seber para estimar el tamaño de sus colonias. En el caso de especies sin recapturas o con una proporción de recaptura inferior al 10 %, estimamos el número de individuos por refugio aplicando la misma proporción entre el número de individuos capturados y el número total estimado para las especies con recapturas mayores del 10 % y que pertenecieran a la misma familia o gremio trófico registradas con la mayor similitud ecológica y con suficientes recapturas para aplicar el modelo Cormack-Jolly-Seber. **Resultados:** El número total estimado de murciélagos en los tres refugios de estudio fue de 20 105. Las estimaciones de tamaño de colonia más altos fueron para los mormópidos *Pteronotus fulvus* y *P. mesoamericanus* de El Apanguito y *P. fulvus* en Cerro Huatulco, con 6 609, 4 092 and 2 212 individuos, respectivamente. **Conclusiones:** La metodología utilizada en este estudio permitió estimar el tamaño de la colonia para todas las especies registradas, a pesar de que solo para el 21.42 % las tasas de recaptura fueron superiores al 10 %. Por lo tanto, consideramos que esta metodología representa una alternativa viable para estimar el tamaño de colonia en otros refugios. Esta información, junto con los procesos de alta riqueza de especies y reproducción que tienen lugar en esta área, permiten proponer estos sitios como áreas de protección y conservación de murciélagos en México.

Palabras clave: abundancia; captura-recaptura; Cormack-Jolly-Seber; cueva; mina; quirópteros.

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