



## *Sturnira hondurensis* (Chiroptera: Phyllostomidae)

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**Abstract:** The Honduran yellow-shouldered bat (*Sturnira hondurensis* Goodwin, 1940) is a medium-sized Stenodermatinae with a vestigial uropatagium and no tail; it typically has reddish or yellowish patches on the shoulders. It is found in temperate habitats from Mexico to northern Nicaragua, and it is one of 24 described species of the genus *Sturnira*. *S. hondurensis* is considered a common species and is listed as “Least Concern” (LC) by the International Union for Conservation of Nature and Natural Resources. Nevertheless, it primarily depends on the preservation of native and continuous forest, so maintaining the connectivity of vegetation patches and the availability of food in modified landscapes are strategies for the preservation of *S. hondurensis* and the ecosystem services that it provides.

**Key words:** bat, Central America, frugivore, Honduran yellow-shouldered bat, Mexico

**Resumen:** El murciélago hondureño de charreteras amarillas (*Sturnira hondurensis* Goodwin, 1940) es un estenodermatino de tamaño mediano sin cola, con uropatagio vestigial, y que usualmente presenta manchas rojizas o amarillentas sobre los hombros. Se distribuye en ambientes templados desde México hasta el norte de Nicaragua, y es una de las 24 especies descritas en el género *Sturnira*. *S. hondurensis* se considera una especie común de “preocupación menor” por la Unión Internacional para la Conservación de la Naturaleza y los Recursos Naturales. Sin embargo, este murciélago depende de la conservación de los bosques nativos y continuos, por lo que la conectividad entre parches de vegetación, y la disponibilidad de alimento en paisajes modificados, representan estrategias para la preservación de *S. hondurensis* y los servicios ecosistémicos que provee.

**Palabras clave:** América Central, frugívoro, México, murciélago, murciélago hondureño de charreteras amarillas

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### *Sturnira hondurensis* Goodwin, 1940

#### Honduran Yellow-shouldered Bat

*Sturnira hondurensis* Goodwin, 1940:1. Type locality “La Cruze Grande [= La Cruz Grande], near San Jose; elevation about 3000 feet; Department La Paz, Honduras” (see “Nomenclatural Notes”).

*Sturnira ludovici*: Hershkovitz, 1949:441. Name combination (see “Nomenclatural Notes”).

*Sturnira oporaphilum*: de la Torre, 1961:113. Name combination.  
*Sturnira ludovici occidentalis* Jones and Phillips, 1964:477. Type locality “Plumas, 2500 feet elevation, Sinaloa,” Mexico.



**Fig. 1.**—An adult female *Sturnira hondurensis* from Ahuatepec, Zongolica municipality, Veracruz, Mexico, November 2015. Photograph by Alfredo Andrés Gutiérrez-González used with permission.

*Sturnira ludovici ludovici*: Jones and Phillips, 1964:477. Name combination.

*Sturnira ludovici hondurensis*: Koopman, 1994:86. Name combination.

*Sturnira hondurensis hondurensis*: Ramírez-Pulido et al., 2014:13. First use of current name combination.

*Sturnira hondurensis occidentalis*: Ramírez-Pulido et al., 2014:13. First use of current name combination.

*Sturnira hondurensis ludovici*: Téllez-Girón, 2014:737. Name combination.

**CONTEXT AND CONTENT.** Order Chiroptera, suborder Yangochiroptera, family Phyllostomidae, subfamily Stenodermatinae, tribe Sturnirini, genus *Sturnira*. *S. hondurensis* is one of 24 described species (Velazco and Patterson 2019). The following two subspecies are currently recognized (Ramírez-Pulido et al. 2014):

*S. h. hondurensis* Goodwin, 1940:1. See above.

*S. h. occidentalis* Jones and Phillips, 1964:477. See above.

**NOMENCLATURAL NOTES.** In our examination of the type specimen of *Sturnira hondurensis* we noticed that the spelling of the type locality on the original specimen tag was “La Cruz Grande” as opposed to “La Cruze Grande” as it appears in Goodwin (1940). *Sturnira hondurensis* was described in 1940 by Goodwin as a smaller species of *Sturnira*, distinct from *S. ludovici*, because the lower incisors were deeply bilobed instead of simple, as seen in *S. ludovici*. Nevertheless, *S. hondurensis* was synonymized to *S. ludovici* by Hershkovitz (1949), because he noted that some specimens of Colombian *S. ludovici* with bilobate lower incisors wear down these teeth and thus lose this characteristic with age. Nevertheless, subsequent molecular and morphological reviews of the genus *Sturnira* have supported recognizing *S. hondurensis* as an independent Mesoamerican species (Judica 2000; Velazco and Patterson 2013).

*Sturnira* comes from the Latin *sturnirus* or *sturnus* (starling), possibly in reference to the “H. M. S. Starling,” an escort vessel on which the type specimen of the genus was collected. The specific epithet *hondurensis* was coined to indicate that the type specimen is from Honduras (Gannon et al. 1989; Sánchez-Hernández et al. 2016).

One common name of *S. hondurensis* is highland yellow-shouldered bat (Téllez-Girón 2014; Álvarez-Castañeda and Gonzalez-Ruiz 2018); however, it is the same common name currently used for *S. ludovici* (Burgin et al. 2018). *S. hondurensis* has also been called Honduran yellow-shouldered bat (Sánchez-Hernández et al. 2016), and in Spanish murciélago de charreteras (Álvarez-Castañeda and Gonzalez-Ruiz 2018).

## DIAGNOSIS

For positive identification purposes, *Sturnira hondurensis* (Figs. 1 and 2) needs to be compared with other species of the



**Fig. 2.**—An adult male *Sturnira hondurensis* from Santuario de Bosque de Niebla, Area Natural Protegida Francisco Javier Clavijero, Xalapa municipality, Veracruz, Mexico, February 2007. Photograph by Antonio Guillén Servent used with permission.

genus, especially species that are more closely related, or with which it can be sympatric (*S. parvidens*). *S. hondurensis* has four well-developed lower incisors, whereas *S. bidens* (bidentate yellow-shouldered bat) and *S. nana* (lesser yellow-shouldered bat) have only two functional inferior incisors (Molinari and Soriano 1987). In *S. hondurensis* the metaconoid and entoconoid in m1–2 are poorly defined, whereas in many other species of *Sturnira* (*S. angeli* [Dominica yellow-shouldered bat], *S. arata-thomasi* [Arata-Thomas yellow-shouldered bat], *S. bakeri* [Baker’s yellow-shouldered bat], *S. giannae* [Gianna’s yellow-shouldered bat], *S. lilium* [little yellow-shouldered bat], *S. luisi* [Luisi’s yellow-shouldered bat], *S. cf. mistratensis* [Mistratoan yellow-shouldered bat], *S. parvidens* [little yellow-shouldered Mesoamerican bat], *S. paulsoni* [Paulson’s yellow-shouldered bat], *S. perla* [Perla yellow-shouldered bat], and *S. tildae* [Tilda’s yellow-shouldered bat]), they are well separated by a deep notch (Judica 2000).

*Sturnira hondurensis* can be easily distinguished from *S. magna* (greater yellow-shouldered bat) by its smaller size. The forearm and greatest skull lengths of *S. hondurensis* are 38.58–46.9 mm and 21.7–25.6 mm, respectively, whereas those of *S. magna* are 56.3–59.6 mm and 27.9–29.1 mm (de la Torre 1966). The fourth metacarpal is shorter than the third metacarpal in *S. hondurensis*, whereas they are of similar length in *S. adrianae* (Adriana's yellow-shouldered bat—Molinari et al. 2017). The basisphenoid pits are deep and divided by a high septum in *S. hondurensis*, whereas they are shallow and divided by a low midline septum in *S. burtonlimi* (Burton's yellow-shouldered bat), *S. ludovici* (highland yellow-shouldered bat), *S. mordax* (Talamancan yellow-shouldered bat), and *S. oporaphilum* (Tschudi's yellow-shouldered bat—Velazco and Patterson 2014). The sphenorbital fissure is subcircular in *S. hondurensis*, whereas it is oval in *S. adrianae*, *S. ludovici*, and *S. parvidens* (Velazco and Patterson 2014; Molinari et al. 2017). The proximal end of the stylohyoid is narrow in *S. hondurensis*, whereas it is expanded in *S. burtonlimi*, *S. ludovici*, *S. oporaphilum*, and *S. parvidens* (Velazco and Patterson 2014). The palate of *S. hondurensis* is depressed but it is flat in *S. bogotensis* (Bogota yellow-shouldered bat) and *S. erythromos* (hairy yellow-shouldered bat—Pacheco and Patterson 1991). In *S. hondurensis* all teeth are close together, but in *S. koopmanhilli* (Choco yellow-shouldered bat) there are diastemas among premolars and molars (McCarthy et al. 2006). The upper central incisors in *S. hondurensis* have a single cusp, in contrast, they are bilobed in *S. adrianae*, *S. ludovici*, *S. mordax*, *S. oporaphilum*, and *S. parvidens* (Velazco and Patterson 2014; Molinari et al. 2017). *S. hondurensis* lacks the small distal cusp on P3 that is present in *S. burtonlimi* and *S. oporaphilum* (Velazco and Patterson 2014). The direction of the premetacrista of M1 is oblique to the upper alveolar plane in *S. hondurensis*, whereas it is perpendicular in *S. burtonlimi*. One labial cusp is present on M3 in *S. hondurensis*, whereas there are two in *S. parvidens* (Velazco and Patterson 2014). The lower incisors are bilobed in *S. hondurensis* but they are trilobed in *S. parvidens* and *S. cf. soriano* (Soriano's yellow-shouldered bat—Sánchez-Hernández et al. 2005; Velazco and Patterson 2014). The lower canines are not laterally divergent in *S. hondurensis*, whereas they are laterally divergent with shafts slanted outward in *S. burtonlimi*, *S. ludovici*, and *S. parvidens* (Velazco and Patterson 2014).

Average measurements (external and cranial) were smaller for *Sturnira h. occidentalis* than *S. h. hondurensis*. Also *S. h. occidentalis* is paler (both ventrally and dorsally) than *S. h. hondurensis* and it has a relatively broader skull with a shorter and more abruptly elevated rostrum (Fig. 3; Jones and Phillips 1964).

## GENERAL CHARACTERS

*Sturnira hondurensis* is a medium-sized stenodermatine bat. As in other stenodermatines, the eyes are large and have eyelashes (de la Torre 1961). The ears are sharp-pointed, and the tragus is long, falcate, curved, and tapers to a point. A large

antitragus forms a thickened horizontal ledge at the base of the ear. Two glandular ridges originate laterally to the anterior base of the noseleaf and continue dorsally to the level of the eyes. The nares are directed anteriorly, and are located at the basal part of the well-developed triangular noseleaf. The upper lip is simple and has small and variable warty growths. The lower lip has wart-like cutaneous pads that occur as a semicircular row of small pads surrounding a large central pad (Fig. 1; Goodwin 1940; de la Torre 1961; Sánchez-Hernández et al. 2016).

The propatagium originates medially at the level of the shoulder. The plagiopatagium extends laterally down to the ankles and is sparsely covered with short hairs. The fourth metacarpal is shorter than the third. There is a vestigial uropatagium, and the trailing edge of the uropatagium is furred with long hairs (7.0–9.0 mm); there is no tail and the calcar is short (de la Torre 1961; Velazco and Patterson 2014).

Fur color ranges from dark gray to dark brown, and the venter is paler than dorsum. Young are paler than adults, and most individuals, especially adult males, have reddish or yellowish patches on the shoulders. Dorsal (between the shoulders) and ventral pelage is long (7.0–10 mm). The proximal portion of the forearm, the dorsal surfaces of the femur, tibia, feet, and digits of the feet are densely covered with long hairs (Fig. 2; Téllez-Girón 2014; Velazco and Patterson 2014; Sánchez-Hernández et al. 2016).

Ranges of external measurements (mm or g) in *S. h. hondurensis* from eastern Mexico, Guatemala, El Salvador, Honduras, and Nicaragua (Goodwin 1940; Lukens and Davis 1957; de la Torre 1961; Jones et al. 1971; Swanepoel and Genoways 1979; Velazco and Patterson 2014), and *S. h. occidentalis* from Colima, Jalisco, and Sinaloa (Mexico—Jones and Phillips 1964; Sánchez-Hernández et al. 2002, 2016), respectively, were: head–body length, 65.0–77.0 and 52.0–77.0; length of hind foot, 12.0–15.0 and 11.0–16.0; ear length, 12.9–19.0 and 12.0–19.0; forearm length, 43.0–46.9 and 38.58–44.93; and weight, 26.8 and 12.0–22.5. Ranges of cranial measurements (mm) in *S. h. hondurensis* and *S. h. occidentalis*, from previous references in addition to those from the Mexican states of Durango and Jalisco (*S. h. occidentalis*—Jones and Phillips 1964) were: greatest length of skull, 21.8–25.6 and 21.7–24.23; condyle–canine length, 20.1–22.2 and 19.0–20.79; zygomatic breadth, 12.5–14.2 and 12.49–14.3; mastoid breadth, 11.5–12.4 and 10.8–12.48; braincase breadth, 10.1–10.6 and 9.58–10.70; length of maxillary tooththrow, 6.3–7.2 and 5.8–7.36; length of mandibular tooththrow, 7.2–8.0 and 6.7–8.17; and interorbital width, 6.0–6.3 and 5.3–7.71 (Fig. 3). In *S. hondurensis* from Oaxaca, Mexico it has been suggested that males average slightly larger than females (Swanepoel and Genoways 1979).

## DISTRIBUTION

After *Sturnira hondurensis* was recognized as an independent species (Judica 2000; Velazco and Patterson 2013),





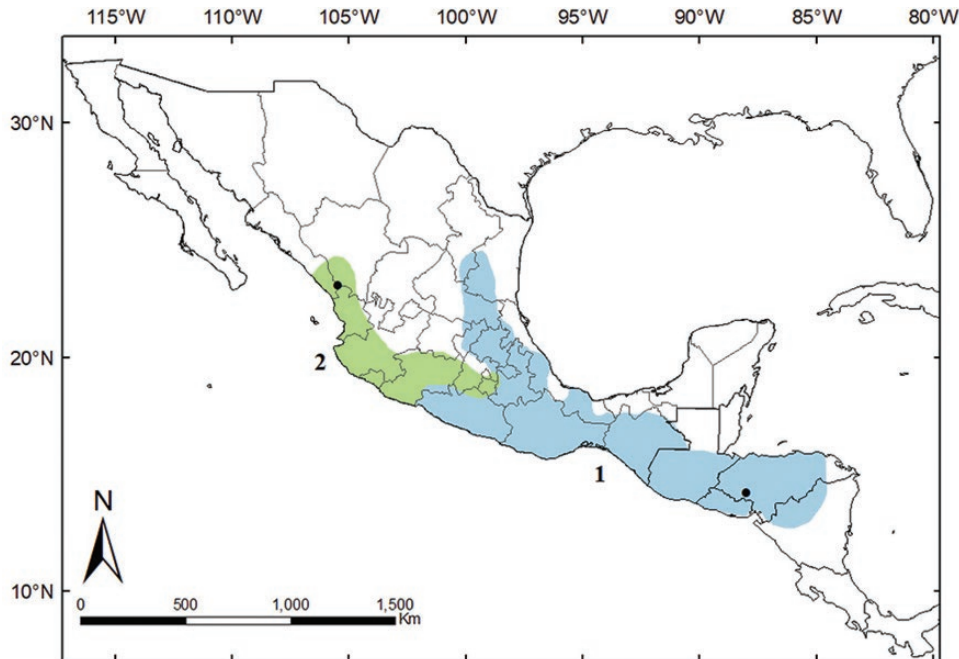
**Fig. 3.**—Dorsal, ventral, and lateral views of skulls and lateral view of mandibles of two adult males of *Sturnira hondurensis*. Left, *Sturnira hondurensis occidentalis* (MZFC-M [Museo de Zoología, Facultad de Ciencias – UNAM] 14980) from La Noria, Tepic municipality, Nayarit, Mexico. Greatest length of skull, excluding incisor is 21.79 mm. Right, *Sturnira hondurensis hondurensis* (MZFC-M 10015) from 1.3 km al NNW de Chiquihuites, Unión Juárez municipality, Chiapas, Mexico. Greatest length of skull, excluding incisor is 23.49 mm. Photograph by Sara Carolina Lucero-Verdugo used with permission.

there was no consensus concerning its southern geographic boundary (Télez-Girón 2014; Sánchez-Hernández et al. 2016; Torres-Morales 2019); however, a phylogeographic analysis of *S. hondurensis* populations confirmed that the southern boundary is located in northern Nicaragua (Hernández-Canchola 2018). *S. h. hondurensis* occurs on mountain ranges in eastern Mexico, from Nuevo León and Tamaulipas southward to northern Nicaragua. On the other hand, *S. h. occidentalis* occurs in western and central Mexico. Jones and Phillips (1964) described this subspecies from western Mexico, occurring from southern Sinaloa and Durango to Jalisco (Sierra Madre Oriental), but analyses with mitochondrial DNA showed that *S. h. occidentalis* occurs as far east as the state of Estado de Mexico, through the eastern and central portions of the Trans-Volcanic Belt (Fig. 4; Hernández-Canchola 2018). *S. hondurensis* has been found from sea level up to 2,900 m (Lavariega et al. 2012; Molinari et al. 2017;

Verde Arregoitia et al. 2018). No fossils of *S. hondurensis* are known.

### FORM AND FUNCTION

The skull of *Sturnira hondurensis* is relatively long and narrow, and the braincase is moderately high with a moderately well-developed sagittal crest (Goodwin 1940). The rostrum is slender, the basisphenoid pits are deep and divided by a high septum, the sphenorbital fissure is subcircular, the anterior process of the glenoid fossa is well developed, and the proximal end of the stylohyoid is narrow (Velazco and Patterson 2014). The brain of *S. hondurensis* closely resembles that of *S. parvidens*. It has deep and extremely smooth cerebral hemispheres. The pseudocentral sulci and sulci anterior to the pseudocentral sulci



**Fig. 4.**—Geographic distribution of *Sturnira hondurensis*. Subspecies: 1, *S. h. hondurensis* (blue shading); 2, *S. h. occidentalis* (green shading); distribution according to [Hernández-Canchola \(2018\)](#). Black dots indicate the type locality of each subspecies.

are poorly developed compared to other stenodermatine bats. The pseudotemporal lobes are angular and project ventrally. The inferior colliculi are completely covered, and the cerebellum is simple and has a medial crest ([McDaniel 1973](#)). [Phillips et al. \(1977\)](#) described in detail the gross anatomy and histology of the parotid, submandibular, and sublingual glands. The parotid gland is large and is posterior to the masseter, on the midline of the throat. It is a compound acinar gland that is densely packed with elongate secretory acini comprised of typical serous cells, and is characterized by an extensive system of ducts. Stenson's duct arises from the anterior edge of the parotid to the oral cavity at the level of the posterior side of the canines. The submandibular gland is large and triangular, filling the cervical fossa. It is a compound tubuloacinar gland with large and densely packed secretory acini. The duct system of the submandibular is relatively simple; Wharton's duct arises from the center of the inferior surfaces and is joined to the main duct from the sublingual gland, and together they open near the first lower premolar. The sublingual gland is moderately sized, triangular, and soft. It is unilobular but has numerous fine subdivisions that can be seen clearly. The sublingual gland is a compound tubuloacinar gland comprised of mucous cells with a relatively simple duct system ([Phillips et al. 1977](#)).

The dental formula is  $i\ 2/2, c\ 1/1, p\ 2/2, m\ 3/3$ , total = 32 ([Télez-Girón 2014](#)). I1 is unicuspidate and larger than I2 ([Jones and Phillips 1964](#)). The direction of the premetacrista of M1 is oblique to the upper alveolar plane, and there is one labial cusp in M3 ([Velazco and Patterson 2014](#)). P3–4 and M1 occur in straight, slightly diverging lines, but M2–3 are at an inward-directed angle. The lower incisors are deeply bilobate, though

these teeth wear with the age as in other member of the genus *Sturnira* ([Goodwin 1940](#); [Hershkovitz 1949](#)). The lower canines are not laterally divergent ([Velazco and Patterson 2014](#)). The paraconid and metaconid of m1–2 are poorly defined and the entoconid suppressed, with no division between them and the metaconid ([Hershkovitz 1949](#)). The coronal portion of the dentin in the teeth of *S. hondurensis* is characterized by distinct, highly arborized dentinal tubes that follow a general S-shaped path from the pulpal chamber to the dentino–enamel junction. The pulpal cavity is filled with a complex soft tissue that is continuous with the periapical tissue through the apical foramen of the roots. In *S. hondurensis*, the pulp is most often healthy and odontoblastic cells are essentially normal. Nonetheless, extensive hyperemia (dilation of capillaries) is commonly found in *S. hondurensis*. This condition has been shown to be either transitory or an indication of early pulpitis ([Phillips et al. 1977](#)).

*Sturnira hondurensis* has a simple stomach with a well-developed, elongated and tapered cardiac vestibule ([Rouk 1973](#); [Forman et al. 1979](#)). The fundic cecum is saccular and thin-walled, forming a spacious chamber with an apex ([Forman et al. 1979](#)). The pyloric valve is vestigial ([Rouk 1973](#)). The gastroesophageal junction lies well superior to the gastroduodenal junction ([Forman et al. 1979](#)), and the latter is clearly marked by a decreased thickness of the muscularis ([Rouk 1973](#)). The corpovestibular and vestibulocecal junctions are marked by distinct sulci that anastomose near the midregion of the stomach ([Rouk 1973](#)). The tunica muscularis is bilaminar, and the tunica submucosa forms the rugae, which in general are longitudinally oriented; there are numerous branches forming transverse secondary folds, but there are not many elastic fibers ([Rouk 1973](#)). In

the tunica mucosa, cardiac glands surround the gastroesophageal junction (Rouk 1973; Forman et al. 1979), and they are weakly reactive or nonreactive to procedures intended to demonstrate the presence of acid mucopolysaccharides (Forman et al. 1979). Oxyntic glands occupy the cardiac vestibule, the cardiac cecum, and a portion of the corpus (Rouk 1973). In the basal one-third of these glands, there are numerous alpha chief cells and only a few mucous gland cells (Rouk 1973). As oxyntic glands disappear, transitional glands (mainly mucous cell glands) become increasingly apparent (Rouk 1973). There are cells within the bases of the pyloric glands which are histologically identical to the submucosal glands of Brunner located in the uppermost duodenum (Forman et al. 1979). The morphology of the stomach of *S. hondurensis* resembles that of *S. parvidens*, though there are some differences between the two species. In *S. hondurensis*, the stomach is more robust, the pyloric tube is shorter, the pyloric sphincter is only a short projection on the lesser curvature, the musculature of the terminal portion is relatively thinner, and mucous neck cells in the lower portion of the fundic glands are more abundant (Forman 1973). *S. hondurensis* has a mean gut area of 4.34 cm<sup>2</sup> (Saldaña-Vázquez et al. 2015).

The hairs of *S. hondurensis* do not have a medulla, and the scales are coronal and unequally hastate (Baca-Ibarra and Sánchez-Cordero 2004). In Hidalgo (Mexico), one of 16 individuals of *S. hondurensis* showed partial leucism in both wings (García-Morales et al. 2012b). In the same Mexican state, another individual of *S. hondurensis* had a white spot extending from above the left eye to the mouth (Sánchez-Hernández et al. 2012). In both of the previous mentioned cases, the individuals were pregnant females, supporting the idea that chromatic disorders are not detrimental for bats (Lucati and López-Baucells 2017; Hernández-Canchola et al. 2019). In Nicaragua, the stable-hydrogen isotope ( $\delta D$ ) in claws was  $-78.8\%$  and in hair was  $-80.7\%$ , similar values were reported in other frugivorous bats from the same region (Fraser et al. 2010).

In Oaxaca (Mexico) the wing aspect ratio [wing span in m<sup>2</sup>/wing area in m<sup>2</sup>] of *S. hondurensis* was 11.11, and the relative wing loading [(mass in g) (gravitational acceleration in m/s<sup>2</sup>)/wing area in m<sup>2</sup>] was 5.97 (García-García et al. 2014).

## ONTOGENY AND REPRODUCTION

Pregnant females were found in January–February (Mexico: Guerrero), March (El Salvador: Santa Ana; Mexico: Puebla), April (El Salvador: Santa Ana; Mexico: Jalisco), May (El Salvador: Santa Ana), June (El Salvador: Santa Ana; Mexico: Guerrero, Jalisco), July (El Salvador: Santa Ana; Mexico: Jalisco), August (El Salvador: Santa Ana; Mexico: Chiapas, Puebla), September–October (El Salvador: Santa Ana), November (Mexico: Jalisco), and December (Mexico: Guerrero). In all cases, females had a single embryo (Jones and Phillips 1964; Villa-R 1966; Watkins et al. 1972; Hellebuyck

et al. 1985; Iñiguez-Dávalos 2005; Jiménez-Salmerón 2008; Cabrera-Garrido 2016; Morales-Rivas 2016).

As in most bats, there are two axillary mammary glands (de la Torre 1961). Lactating females were found in March (Mexico: Puebla), April (El Salvador: Santa Ana; Mexico: Colima, Guerrero, Jalisco), May–June (El Salvador: Santa Ana; Mexico: Jalisco), July (El Salvador: Santa Ana; Mexico: Colima, Guerrero, Jalisco), August (El Salvador: Santa Ana; Mexico: Colima, Jalisco, Puebla), September (El Salvador: Santa Ana; Mexico: Jalisco), October (Mexico: Jalisco, Puebla), November (El Salvador: Santa Ana), December (Guatemala—de la Torre 1961; Baker and Phillips 1965; Watkins et al. 1972; Hellebuyck et al. 1985; Sánchez-Hernández et al. 2002; Iñiguez-Dávalos 2005; Jiménez-Salmerón 2008; Cabrera-Garrido 2016; Morales-Rivas 2016). Post-lactating females were reported during April (El Salvador: Santa Ana; Mexico: Guerrero), May (El Salvador: Santa Ana), June (El Salvador: Santa Ana; Mexico: Guerrero, Jalisco), July (El Salvador: Santa Ana; Mexico: Guerrero), August–September (El Salvador: Santa Ana—Iñiguez-Dávalos 2005; Jiménez-Salmerón 2008; Morales-Rivas 2016). One juvenile was recorded in August (Mexico: Colima), and sub-adults during August (Mexico: Colima) and December (Guatemala—de la Torre 1961; Sánchez-Hernández et al. 2002).

Males with scrotal testes were reported in January (Mexico: Colima, Guerrero), February (Mexico: Guerrero), March (Guatemala; Mexico: Puebla), April (Mexico: Guerrero, Jalisco), May–June (Mexico: Jalisco), July (Mexico: Guerrero), September (Mexico: Guerrero, Jalisco), October (El Salvador: Santa Ana), November (Mexico: Guerrero), and December (Mexico: Colima, Guerrero—de la Torre 1961; Villa-R 1966; Sánchez-Hernández et al. 2002; Iñiguez-Dávalos 2005; Jiménez-Salmerón 2008; Cabrera-Garrido 2016; Morales-Rivas 2016).

In the Mexican state of Guerrero a bimodal, polyestrous reproductive pattern has been suggested (Jiménez-Salmerón 2008), but a continuous, polyestrous reproductive pattern interrupted by periods of inactivity was suggested in El Salvador, possibly due to severe climate during autumn and winter (Morales-Rivas 2016). On the other hand, in western Mexico the maximum frequency of pregnant and lactating females and juveniles of *S. hondurensis* is observed between May and July, coinciding with the greatest seasonal abundance of the primary fruit (*Solanum nigricans*) consumed locally by *S. hondurensis* (Iñiguez-Dávalos 2005).

## ECOLOGY

**Population characteristics.**—Although a 1:1 sex ratio has been reported for juvenile *Sturnira hondurensis* (Iñiguez-Dávalos 2005), adult females tend to be more numerous than adult males (Saldaña-Vázquez et al. 2010): the latter constitute the 27–33% of the adults in populations of the species (Iñiguez-Dávalos 2005; Jiménez-Salmerón 2008; Morales-Rivas 2016). It has been suggested that male *S. hondurensis* decrease their local population density by migrating seasonally, or using marginal habitats, to avoid competing with females, thus allowing



them to forage in areas where fruit is more abundant and to ensure reproductive success (Iñiguez-Dávalos 2005; Saldaña-Vázquez et al. 2010, 2013).

*Sturnira hondurensis* is highly sensitive to habitat degradation and fragmentation: it is more abundant in conserved and continuous forests than in artificial plant communities, such as shade-grown coffee plantations, and smaller forest fragments, which it uses as stepping stones to travel among larger forest patches (Saldaña-Vázquez et al. 2010, 2013; Castro-Luna and Galindo-González 2012; García-García and Santos-Moreno 2014; García-García et al. 2014; Ávila-Gómez et al. 2015). The abundance of *S. hondurensis* is positively related to the density of understory chiropterophilic plants (Saldaña-Vázquez et al. 2010; Castro-Luna and Galindo-González 2012). Although where it occurs, *S. hondurensis* is a permanent resident, its abundance changes throughout the year. In eastern Mexico, it was relatively more abundant between November and May (Hidalgo and San Luis Potosí—García-Morales et al. 2014, 2016), and in Guerrero, it was less abundant between June and September–December (Jimenez-Salmerón 2008). In western Mexico, *S. hondurensis* is most abundant between May and July, when most reproductive activity takes place (Iñiguez-Dávalos 2005).

*Sturnira hondurensis* is a dominant bat species in tropical montane cloud forests and shade-grown coffee plantations in Mexico (Hernández-Montero et al. 2011; García-Estrada et al. 2012). In contrast, it is relatively rare in Nicaragua, where it is confined to the highlands of the central north (Jones et al. 1971; Medina-Fitoria and Saldaña-Tapia 2012).

**Space use.**—*Sturnira hondurensis* is more abundant in higher-elevation environments (Lukens and Davis 1957; Hellebuyck et al. 1985; Sánchez-Hernández et al. 2016), including tropical montane cloud forest, pine–oak and coniferous forests, and temperate riparian vegetation. It has been collected in scrub vegetation, and is also common in the transitional zones between temperate and tropical forests (Jones and Phillips 1964; Watkins et al. 1972; Cornejo-Latorre et al. 2011; Cortés-Delgado and Sosa 2014; Rodríguez-Macedo et al. 2014; Téllez-Girón 2014). *S. hondurensis* has been collected in mist nets in very humid environments, mostly bordered by dense vegetation, streams or bodies of water, canyons, orchards, and coffee crops (Jones and Phillips 1964; Watkins et al. 1972; Cortés-Delgado and Sosa 2014; Téllez-Girón 2014; Sánchez-Hernández et al. 2016).

Environmental analyses in Colima (Mexico) showed that *S. hondurensis* is most often found in places with the following mean parameters: annual precipitation = 1,047.4 mm, precipitation in the coldest quarter = 42.2 mm, precipitation in the driest quarter = 11.6 mm, precipitation in the wettest quarter = 720 mm, annual temperature = 23.4°C, temperature in coldest month = 12.9°C, temperature in warmest month = 32.5°C, annual temperature range = 19.6°C, temperature in the coldest quarter = 21.2°C, temperature in the warmest quarter = 25°C, temperature in the driest quarter = 22.2°C, temperature in the wettest quarter = 24.4°C, diurnal temperature

range = 13.6°C, and isothermality = 69.2% (Sánchez-Hernández et al. 2016). Whereas in Michoacán (Mexico), *S. hondurensis* inhabits temperate forests with mean annual temperatures of 14–20°C and precipitation of 800–1,200 mm (Wang et al. 2003). Climatic niches of Chiapan–Central American versus eastern Mexican populations are similar, but they are different between Chiapan–Central American versus western Mexican populations (Hernández-Canchola 2018).

*Sturnira hondurensis* mainly roosts in hollows located 1.3–8.0 m above ground level in old, live trees. These trees have a height of 9.0–25.0 m, a breast-high diameter of 25.0–149.1 cm, and are surrounded by other large trees often containing more hollows. In Veracruz (Mexico) *S. hondurensis* uses the following trees as roosts: *Enterolobium cyclocarpum* (Fabaceae), *Liquidambar styraciflua* (Altingiaceae), *Quercus sartorii* (Fagaceae), and *Trema micrantha* (Cannabaceae). Other trees that are less frequently used as roosts are *Alchornea latifolia* (Euphorbiaceae), *Annona cherimola* (Annonaceae), *Cinnamomum effusum* (Lauraceae), *Ficus crocata* (Moraceae), *Inga jinicuil*, *Inga paterno*, *Inga* aff. *spuria*, and *Schizolobium parahyba* (Fabaceae). The majority of the roosts occur in shade-grown coffee plantations and in tropical montane cloud forest, but some occur in trees surrounded by pastures (Cortés-Delgado and Sosa 2014). It appears that *S. hondurensis* does not use caves as day roosts because there are reports of the species roosting near caves, but no reports of individuals roosting inside of those caves (León-Paniagua and Romo-Vázquez 1993; Divoll and Buck 2013).

Information on movement patterns in *S. hondurensis* is sparse. In Honduran populations of *S. hondurensis*, the isotopes in hair keratin were utilized to track elevational movements; however, isotope levels did not differ significantly between populations at different elevations ( $-96.2\% \pm 10.0$  SD at 1,202 m, and  $-95.0\% \pm 7.4$  SD at 1,546 m), indicating that the elevational gradient may be too small or that variation in hair keratin isotopes among individuals is too large to reflect elevational movements of less than 400 m (Erzberger et al. 2011). In a census that lasted for more than 2 years in Veracruz (Mexico), only one of the 36 marked individuals of *S. hondurensis* was recaptured; it was found 580 m away from the original place of capture (Estrada et al. 1993).

The home range of *S. hondurensis* varies widely (mean = 56.7, range = 3.93–311.30 ha). The mean distance (m  $\pm$  SE) from the daytime roost to the foraging area is  $822.71 \pm 383.4$  in coffee plantations, and  $590.78 \pm 161$  in forests. The maximum distance traveled is  $1,466.73 \pm 340$  in coffee plantations, and  $776.82 \pm 141.4$  in forest (Cortés-Delgado and Sosa 2014). *S. hondurensis* seems to move more in disturbed areas than in natural forests. This idea is reinforced by the strong relationship between the abundance of *S. hondurensis* and the understory food items. Because *S. hondurensis* depends on understory for food provision, if this resource is scarce, bats need to forage more (Saldaña-Vázquez et al. 2010; Cortés-Delgado and Sosa 2014). Indeed, it has been reported that *S. hondurensis* moves little

outside continuous forest (García-García et al. 2014), and that it mainly forages in the understory and canopy (Saldaña-Vázquez et al. 2010), in primary vegetation, secondary vegetation, coffee plantations, and complex agrosystems (Galindo-González 2004; García-Estrada et al. 2006; García-Morales et al. 2016).

In Mexico (Veracruz), *S. hondurensis* leaves its roosts about 30 min after sundown (Cortés-Delgado and Sosa 2014). In Mexico (Guerrero), the peak of maximum activity is observed at 2100–2300 h (Jiménez-Salmerón 2008), whereas in El Salvador (Santa Ana) it is observed 2 h after sunset (Morales-Rivas 2016). In Mexico (Tamaulipas), *S. hondurensis* forages at the same time as *S. parvidens* (Arriaga-Flores et al. 2012).

**Diet.**—Based on the identification of seeds found in fecal samples of *Sturnira hondurensis* and *S. parvidens*, the value of the diet similarity index was 0.705 (García-Morales et al. 2012a). Nevertheless, the diversity of the diet (Shannon index = 3.20 versus 3.91) and the ratio of assimilated to ingested sugar (0.46 versus 0.65) were both lower in *S. hondurensis* than in *S. parvidens* (its congener and in some places sympatric species—Saldaña-Vázquez et al. 2015). The diet of *S. hondurensis* is mainly based on fruits with high concentration of carbohydrates and proteins; low-quality fruits are typically avoided by *S. hondurensis* (Saldaña-Vázquez and Schondube 2013).

*Sturnira hondurensis* finds its food mainly by smell; the size, grouping, and position of the fruits apparently do not affect its choice (Iñiguez-Dávalos 2005). *S. hondurensis* has a relatively ample dietary niche, and mainly feeds on fruit of plants of early successional stages (Hernández-Conrique et al. 1997; García-Estrada et al. 2012). Fruit of the families Solanaceae and Piperaceae comprise the bulk of the diet of *S. hondurensis*. In El Salvador (Santa Ana), it eats fruits of *Hedyosmum mexicanum*, *Peperomia*, *Piper*, *Saurauia*, *Solanum*, and *Urera* (Morales-Rivas 2016). Most of the information on the diet of *S. hondurensis* comes from Mexico. In Chiapas, it eats the fruits of *Cecropia obtusifolia*, *Drymaria*, *Ficus aurea*, *Ficus pertusa*, *Ficus* (unidentified species), *Garcinia intermedia*, *H. mexicanum*, *Juanulloa mexicana*, *Peperomia*, *Piper auritum*, *Piper pseudolindenii*, *Saurauia madrensis*, *Solanum chrysotrichum*, and *S. diphyllum* (García-Estrada et al. 2012). In Guerrero, it eats the fruit of *S. aligerum*, *S. nigricans*, and seems to eat (remains found in pelage) or ingest (remains found in stomach and feces) the pollen of *Alnus*, *Chiranthodendron pentadactylon*, *Cordia gerascanthus*, *Operculina*, *Pinus* (Jiménez-Salmerón 2008). In Hidalgo, it eats the fruit of *Coussapoa purpusii*, *Ficus*, *Markea*, *Physalis*, *Piper amalago*, *P. hispidum*, *Solanum diphyllum*, *S. rudepannum*, and *Trema micrantha* (García-Morales et al. 2016). In Jalisco, it eats the fruit of *Conostegia volcanalis*, *Epiphyllum anguliguer*, *Ficus obtusifolia*, *Solanum aphyodendron*, *S. nigricans*, and *Solanum* (unidentified species—Iñiguez-Dávalos 2005). In Puebla, it eats the fruit of *F. obtusifolia*, *Manilkara zapota*, and *Sideroxylon palmeri*, and some insects of the orders Hymenoptera and Diptera (Herrera and López 2017). In San Luis Potosí, it eats the fruit of *Ficus cotinifolia*, *Maclura*

*tinctoria*, *Muntingia calabura*, *Piper hispidum*, *P. yzabalanum*, *S. diphyllum*, and *S. erianthum* (García-Morales et al. 2012a). In Veracruz, it eats the fruit of *C. obtusifolia*, *Ficus*, *H. mexicanum*, *Lycianthes geminifolia*, *Miconia glaberrima*, *P. auritum*, *P. hispidum*, *P. lapathifolium*, *Piper* (unidentified species), *Solanum acerifolium*, *S. aphyodendron*, *S. chrysotrichum*, *S. pseudocapsicum*, *S. schlechtendalianum*, *Solanum* (unidentified species), *T. micrantha*, and *Vismia mexicana* (Cortés-Delgado and Sosa 2014; Hernández-Montero et al. 2015).

The seeds of *Solanum nigricans* that passed through the digestive tract of *S. hondurensis* germinated 2 days before seeds taken directly from the fruit. In the case of *S. aphyodendron*, only the seeds that were ingested germinated (Iñiguez-Dávalos 2005). *S. hondurensis* is considered a legitimate disperser of plants of the genus *Solanum* (Hernández-Montero et al. 2011), and the main bat disperser of plants in early stages of successional vegetation in both natural and disturbed cloud forests (Hernández-Montero et al. 2011; García-Estrada et al. 2012).

*Sturnira hondurensis* has been kept in captivity for up to 3 months, while being fed with bananas, guavas, mandarins, melons, papayas, watermelons, and nutritional supplements (Iñiguez-Dávalos 2005; Saldaña-Vázquez and Schondube 2013). In captivity, it has also been fed with capuli cherries (*Prunus serotina*), peaches (*Prunus persica*), Mexican hawthorns (*Crataegus mexicana*), and some plants of the family Moraceae (*Trophis*—Sánchez-Hernández et al. 2016).

*Sturnira hondurensis* needs a variety of sources of nitrogen and carbohydrates for proper nutrition (Iñiguez-Dávalos 2005). In captivity, individuals lost weight when fed only fruit of *Solanum nigricum*, despite this being the experimental fruit with the highest concentration of carbohydrates and proteins. When fed on less nutritious fruit (either *Conostegia volcanis* or *S. aphyodendron*), individuals died (Iñiguez-Dávalos 2005). In an investigation of digestive capacity in *S. hondurensis*, it was found that its digestive capacity was not compatible with compensatory feeding and thus *S. hondurensis* changes its food intake and feeding behavior when its food has different percentages of nutrients (Saldaña-Vázquez and Schondube 2013). Additionally, there is a positive relationship between the time invested in feeding and the energy obtained (Iñiguez-Dávalos 2005).

**Diseases and parasites.**—*Sturnira hondurensis* is ectoparasitized by the streblid bat flies *Aspidoptera delatorrei*, *Aspidoptera falcate*, *Megistopoda proxima*, *Megistopoda theodori*, *Metelasmus pseudopterus*, *Trichobius brennani*, and *Trichobius joblingi* (Whitaker and Morales-Malacara 2005; Dick 2013; Tlapaya-Romero et al. 2015; Cuxim-Koyoc et al. 2016; Ramírez-Martínez et al. 2016). The streblid bat fly *Paratrachobius longicrus* is considered suspect (Dick 2013), whereas *Paratrachobius sanchezi* is an accidental record (Colín-Martínez et al. 2018).

The mites found on *S. hondurensis* are *Macronyssoides kochi*, *Parichoronyssus euthystrernum* (Mesostigmata: Macronyssidae); *Periglischrus ojustii* (Mesostigmata: Spinturnicidae); *Paralabidocarpus tonatiae* (Sarcoptiformes:



Chirodiscidae); *Chirnyssoides brasiliensis* (Sarcoptiformes: Sarcoptidae); *Eudusbabekia lepidoseta* (Trombidiformes: Myobiidae); *Microtrombicula sturnirae*, *Parasecia bulbocalcar*, and *Parasecia soucouyanti* (Trombidiformes: Trombiculidae—Morales-Malacara 1998; Whitaker and Morales-Malacara 2005; Colín-Martínez et al. 2018). The mites *M. kochi* (Mesostigmata: Macronyssidae), *Eudusbabekia viguerasi* (Trombidiformes: Myobiidae), and *Radfordiella desmodi* (Mesostigmata: Macronyssidae) have been reported as ectoparasites of *S. hondurensis*; however, the first two were considered as accidental records, and the third appears to be an erroneous record caused by a mistake during field collection, because this mite is mainly found on *Desmodus rotundus* (common vampire bat—Morales-Malacara 1998; Colín-Martínez et al. 2018).

In Mexico, *S. hondurensis* is recorded as a host of *Trypanosoma cruzi* (Rengifo-Correa et al. 2017). Likewise, in Tabasco (Mexico), *S. hondurensis* was considered an incidental host of *Leishmania (L.) mexicana* (Berzunza-Cruz et al. 2015), though it is possible that the bat specimen analyzed was misidentified, because *S. hondurensis* had not been previously collected in that tropical Mexican state (Téllez-Girón 2014).

**Interspecific interactions.**—*Sturnira hondurensis* has been collected in the same mist nets with other bat species, including Molossidae: *Tadarida brasiliensis* (Mexican free-tailed bat); Mormoopidae: *Pteronotus davyii* (Davy's naked-back bat), *P. parnellii* (Parnell's common mustached bat); Phyllostomidae: *Anoura geoffroyi* (Geoffroy's tailless bat), *Artibeus aztecus* (Aztec fruit-eating bat), *A. jamaicensis* (Jamaican fruit-eating bat), *A. lituratus* (great fruit-eating bat), *A. toltecus* (Toltec fruit-eating bat), *Carollia perspicillata* (Seba's short-tailed bat), *C. sowelli* (Sowell's short-tailed bat), *Centurio senex* (wrinkled-faced bat), *Chiroderma salvini* (Salvin's big-eyed bat), common vampire bat, *Glossophaga commissarisi* (Commissaris's long-tongued bat), *G. soricina* (Pallas's long-tongued bat), *Hylonycteris underwoodi* (Underwood's long-tongued bat), *Leptonycteris nivalis* (greater long-nosed bat), *Sturnira parvidens*; Vespertilionidae: *Eptesicus fuscus* (big brown bat), *Lasiurus borealis* (eastern red bat), *Myotis keaysi* (southern hairy-legged myotis), *M. velifer* (cave myotis), and *Rhogeessa gracilis* (slender yellow bat—Jones and Phillips 1964; Watkins et al. 1972; León-Paniagua and Romo-Vázquez 1993; Iñiguez-Dávalos 2005; Divoll and Buck 2013).

## BEHAVIOR

In captivity, it took 3–10 min for *Sturnira hondurensis* to consume the fruit of *Solanum nigricans*. The whole pulp, most of the seeds, and part of the pericarp were eaten. Feces (3–5 separate pellets) containing 75% of the seeds were produced 9–45 min after the meal. In the case of *Solanum aphyodendron*, *S. hondurensis* made an opening in the skin of the fruit through which it consumed the pulp and seeds in 2–5 min. The bats defecated 1–3 times, producing feces

containing 83% of the seeds 5–23 min after the meal. In the case of *Conostegia volcanis*, only one-half of the fruit was eaten, including the pulp, the pericarp, and some seeds. This process required 45 s to 3 min. *S. hondurensis* defecated 2–4 times, expelling about 500 seeds after 5–15 min (Iñiguez-Dávalos 2005).

## GENETICS

*Sturnira hondurensis* has a diploid number (2n) of 30 chromosomes and a fundamental number (FN) of 56. This karyotype is identical to that of *S. parvidens* (Baker 1967; Hsu et al. 1968), and possibly identical to that of other species of the genus *Sturnira* (Gannon et al. 1989). The X chromosome is large and subtelocentric and the Y chromosome is small and submetacentric. Its autosomal chromosomes (counted in pairs) are: seven metacentric, three submetacentric, and four subtelocentric (Baker 1967). Through fluorescent in situ hybridization, it was detected that only two medium subtelocentric chromosomes possess ribosomal genes (rDNA—Baker et al. 1992).

There is a review of the genus *Sturnira* based on mitochondrial cytochrome-*b* gene and morphological data, which concluded that *S. hondurensis* is an independent species from *S. ludovici* (Judica 2000). Additionally, sequences of the mitochondrial cytochrome-*c* oxidase subunit 1 (COI) were used to analyze the geographically and genetically distinct groups within *S. ludovici* (sensu lato). This research indicated that samples from El Salvador and Guatemala could represent a distinct lineage from Panamanian samples (Clare et al. 2011).

Based on three mitochondrial (cytochrome-*b*, hypervariable region HVRI section in D-loop, and ND2) and two nuclear (RAG1 and RAG2) loci, Velazco and Patterson (2013) concluded that the Mesoamerican “*S. ludovici*” represented two species, one of them *S. hondurensis*, and the other, found in Costa Rica and Panama, an undescribed species subsequently named as *S. burtonlimi* (Velazco and Patterson 2013, 2014). *S. hondurensis* is closely related to *S. burtonlimi*, *S. adrianae* (from Venezuela and Colombia), *S. ludovici* (from Colombia and Ecuador), and *S. oporaphilum* (from Ecuador, Peru, Bolivia, and Argentina—Judica 2000; Velazco and Patterson 2013, 2014; Molinari et al. 2017). Additionally, Judica (2000) observed genetic differentiation within the eastern populations of *S. hondurensis*, and he suggested that the involved clades may represent undescribed species or subspecies.

A phylogeographic analyses of *S. hondurensis*, using mitochondrial and nuclear loci (cytochrome-*b*, hypervariable region HVRI section in D-loop, and RAG1), showed intraspecific genetic variation produced by Pleistocene climatic oscillations and complex Mesoamerican topography. Three genetic groups were detected: western Mexico, central Mexico, and eastern Mexico—Central America. However, subtle environmental differences, morphological, and geometric morphometric data showed that only western Mexican populations are slightly different from other *S. hondurensis* populations (Hernández-Canchola 2018).

## CONSERVATION

In Mexico (Veracruz), the bioaccumulation of persistent organochlorine compounds (OCPs) was measured in riparian forests. The average concentrations (wet weight) of these pesticides in *Sturnira hondurensis* were:  $\Sigma$ DDT (p,p'-DDE, p,p'-DDD, p,p'-DDT), 6.86  $\mu\text{g/g}$ ;  $\Sigma$ HCH ( $\alpha$ -,  $\beta$ -,  $\gamma$ -,  $\delta$ -HCH), 28.22  $\mu\text{g/g}$ ;  $\Sigma$ heptachlor (heptachlor, heptachlor epoxide), 2.62  $\mu\text{g/g}$ ;  $\Sigma$ endosulfan (endosulfan I and II, endosulfan sulphate), 4.60  $\mu\text{g/g}$ ;  $\Sigma$ chlordan (metoxichlor,  $\alpha$ -chlordan), 3.24  $\mu\text{g/g}$ ; and  $\Sigma$ drines (aldrin, dieldrin, endrin, aldehyde, endrin cetone), 14.23  $\mu\text{g/g}$ . The sex of the bat and the season measured affect the concentrations of some of the pesticides examined in the study, and higher amounts of OCPs were found in transformed landscapes. Whereas most OCPs concentrations were below the level of detection, some individuals showed elevated concentrations of prohibited pesticides. These results suggested that *S. hondurensis* could play a useful role as bioindicator of contaminant pesticides at the community level (Valdespino and Sosa 2017). Also, *S. hondurensis* is less abundant in modified and natural areas in which pesticides, herbicides, and fertilizers are used (García-Estrada et al. 2006).

*Sturnira hondurensis* is considered a common species and is not assigned to any category of conservation risk (Téllez-Girón 2014); it is listed as “Least Concern” (LC) by the International Union for Conservation of Nature and Natural Resources (Solari 2017). Nevertheless, *S. hondurensis* is very sensitive to habitat fragmentation (García-García and Santos-Moreno 2014; García-García et al. 2014), and it mainly depends on conserved and continuous forest (Saldaña-Vázquez et al. 2010, 2013; Castro-Luna and Galindo-González 2012). The conservation of *S. hondurensis* requires the connectivity among large patches of natural vegetation. It is recommended that farmers allow understory vegetation to remain in their crops, or in the surrounding areas. These management practices are recommended because *S. hondurensis* is important for the regeneration of vegetation in both conserved and modified landscapes (Iñiguez-Dávalos 2005; Saldaña-Vázquez et al. 2010, 2013; García-Estrada et al. 2012; García-Morales et al. 2012a; Cortés-Delgado and Sosa 2014).

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