Journal of Mammalogy, 101(1):61–79, 2020
DOI:10.1093/jmammal/gyz161

Body size and diet–related morphological variation of bats over the past 65 years in China

Xinke Yue, Alice C. Hughes, Kyle W. Tomlinson, Shangwen Xia, Song Li,* and Jin Chen*

CAS Key Laboratory of Tropical Forest Ecology, Xishuangbanna Tropical Botanical Garden, Chinese Academy of Sciences, Menglun, Yunnan 666303, China (XY, SX, JC)
University of Chinese Academy of Sciences, Beijing 100049, China (XY)
Centre for Integrative Conservation, Xishuangbanna Tropical Botanical Garden, Chinese Academy of Sciences, Menglun, Yunnan 666303, China (ACH, KWT)
Kunming Natural History Museum of Zoology, Kunming Institute of Zoology, Chinese Academy of Sciences, 32 Jiaochang Donglu, Kunming, Yunnan 650223, China (SL)

* *Correspondents: cj@xtbg.org.cn; lis@mail.kiz.ac.cn*

We examined both historical (1960s) and recent (2017) specimens of an insectivorous bat species (*Hipposideros armiger*) and a phytophagous bat (*Rousettus leschenaultii*) from the same latitudinal range to explore phenotypic responses to environmental change in China over the past 65 years. *Hipposideros armiger* exhibited significant increases in forearm length and three diet-related cranial traits, as well as carbon and nitrogen stable isotope composition, suggesting that modern *H. armige*r must travel farther for food and may now use different food resources. In contrast, *R. leschenaultii* showed no change in forearm length but displayed significant increases in diet-related cranial traits. This study provides evidence for differential responses to recent environmental changes in bat species with different diets. The changes in diet-related traits of the two species and the forearm length change on the insectivorous bats suggest that recent phenotypic changes may be adaptions to land-use changes rather than to climate change.

Key words: body size, climate change, diet-related cranial structure, isotope analysis, land-use change

Both climate and land-use changes may affect biodiversity patterns and processes (Pereira et al. 2012; Newbold et al. 2015; Scheffers et al. 2016). Studies quantifying the effects of these changes at the species level are geographically and taxonomically limited (Pacifici et al. 2015; Tilman et al. 2017). Fortunately, existing natural history collections constitute resources for comparisons of historical and modern specimens (Holmes et al. 2016). Recent studies using historical and modern specimens to assess changes over time have revealed both phenotypic and genetic alterations over short timescales. These alterations may have been caused by contemporary environmental changes (Rubidge et al. 2012; Walsh et al. 2016). Understanding the various components of how species respond to environmental change and how these components interact is essential to better assess the vulnerability of species and ecosystems, and to inform efforts to manage biodiversity and ecosystem services (Bonebrake et al. 2018; Titeux et al. 2018).

Bats are the second-most diverse order of extant mammals and are distributed across nearly all terrestrial biomes (Simmons 2005). They perform many important ecosystem services, including seed dispersal and pollination, and they consume large quantities of insects (Kunz et al. 2011). Because bats have low reproductive rates, long generation times, high trophic positions, and high metabolic rates (Jones and Rebelo 2013), they are highly susceptible to environmental change. Climate change may affect the distribution, physiology, habitat use, and roosting sites of bats. Unfortunately, we know little about the phenotypic responses of bats to climate change or related factors. Some studies have explored temporal trends in the morphological traits of bats (Yom-Tov and Geffen 2006; Snell-Rood and Wick 2013; Tomassini et al. 2014). These studies suggest that anthropogenic environmental changes have imposed selective pressures on bats that could lead to changes in bat morphology and behavior. More study is needed to elucidate the responses of bats to environmental changes (Jones and Rebelo 2013; Sherwin et al. 2013; Voigt and Kingston 2016).

Two principal hypotheses have been proposed to explain phenotypic responses under climate change: body size changes driven by increased need for heat dissipation (the selective pressures that are usually proposed to explain Bergmann's rule) and the resource rule (McNab 2010; Yom-Tov and Geffen 2011). Indeed, decreasing body size in response to climate warming has been observed in a number of homeothermic species (Millien et al. 2006; Sheridan and Bickford 2011). Although the mechanisms underlying different hypotheses have yet to be resolved, there have been few empirical tests, perhaps because there are insufficient long-term collections of the specimens necessary to perform such analyses (Boutin and Lane 2014; Teplitsky and Millien 2014).

In addition to body size, bat morphology may be sensitive to changes in habitat and prey availability, primarily caused by local anthropogenic disturbances (Taylor et al. 2012; Jung and Threlfall 2016). For example, wing morphology influences flight characteristics, which directly influence foraging fitness (Norberg and Rayner 1987; Furey and Racey 2016). Habitat fragmentation may force bats to travel further to forage and to move among distant fragments (Stoner et al. 2010; Fuentes-Montemayor et al. 2013). Increased distances among patches may select for reduced cost of transport and thus more efficient flight. This may result in selection for longer, thinner wings, which in turn could affect the individuals' abilities to acquire their preferred prey species (Norberg and Rayner 1987; Marinello and Bernard 2014).The response of wing morphology to selection may be linked to diet, with greater effects apparent for insectivorous rather than frugivorous bats because the life histories and activity patterns of insects are more sensitive and dependent on environmental conditions when compared to plants (Kingsolver et al. 2011; Dirzo et al. 2014; Sánchez-Bayo and Wyckhuys 2019).

Size and shape of the cranium are related to food resource use and may be subject to selection pressure (Evin et al. 2011). Variation in size and shape of cranial elements across bat species is consistent with a priori predictions based on functional demands of different diets (Santana et al. 2011, 2012). Cranial morphology varies not only among different diets but also within diet types (Freeman 1979; Dumont 1999; Santana et al. 2012). For example, *Chiroderma* (Phyllostomidae) has traits that are adaptations to a granivorous diet, including a higher anterior zygomatic arch, longer masseter moment arm, and larger masseter volume (Nogueira et al. 2009), while *Myotis* bats that feed on hard-shelled diet items have relatively narrow skulls and long tooth rows (Ghazali and Dzeverin 2013). Even within dietary groups, insectivorous bats that eat soft-shelled insects have long and delicate jaws, whereas those feed on hard-shelled insects have short and thick-jawed skulls (Freeman 1981).

Differences between sexes in morphology, physiology, and life-history traits may result in sex-specific responses to environmental change (Høye et al. 2009; Petry et al. 2016). Male dispersal and female philopatry may subject the sexes to different selective pressures (Flanders et al. 2009; Lin et al. 2014). Female reproduction may impose greater challenges than those experienced by males when exposed to climate change and other anthropogenic modifications (Ruedas et al. 1994; Cryan et al. 2000; Adams 2010). Moreover, this dimorphic response may be large in bats, because they have long gestation times and relatively high embryo weights (Sherwin et al. 2013).

Over the past 60 years, significant and regionally specific climate change has occurred across China: a warming trend and greater frequency of extreme weather, including extremely hot and cold days, have dominated this period (Fang et al. 2017). Annual precipitation has decreased (ca. 8.84 mm per decade) between 1961 and 2010, with large fluctuations among years (Wang et al. 2015). Increased risks of both drought and floods were recorded throughout China since 1960 (Liu et al. 2014b; Shao et al. 2015). In Yunnan Province, southwestern China, annual temperature increased significantly at a rate of 0.17°C per decade from 1961 to 2011 (Ren et al. 2017), which is slightly higher than the global mean (0.12°C per decade for the period 1951–2012—Stocker et al. 2013). Furthermore, since 1960, winter temperatures in Yunnan Province exhibited the most pronounced increases and highest risk of concurrent extreme flood and drought events (Shi and Chen 2018).

In addition to climate changes, China has seen substantial spatial and temporal changes in land-use from 1990 to 2010 (Liu et al. 2014a). Forest cover has decreased, urban areas have expanded, and habitat fragmentation has increased (Liu and Tian 2010; Deng et al. 2015; Ning et al. 2018). Forest cover in Yunnan Province decreased dramatically because of an exponential increase in rubber plantations in southern Yunnan, intensification of land-use change, and a history of poor water management over the last few decades (Zhang et al. 2012; Zomer et al. 2015).

A total of 134 bat species from seven families have been recorded in China, accounting for nearly 10% of the world's described bat species in just over 6% of the planet's land surface (Jiang et al. 2017; Burgin et al. 2018). One study of 17 bat species in China indicated that nearly half of these species exhibited changes at their northern distributional limit or at the center of their ranges during the past few decades (Wu 2016). This highlights the need to broaden our understanding of the influence of environmental change on bats.

The aim of this study is to explore phenotypic variation in bats as a function of its potential response to environmental change. We assess whether anthropogenic environmental changes, specifically climate and land-use changes, correlate with phenotypic responses in bats. We used traditional morphometric techniques to compare 310 museum specimens of two bat species, *Hipposideros armiger* (Hodgson, 1835) and *Rousettus leschenaultii* Desmarest, 1820, with those of 134 recently collected specimens. All specimens were from the same latitudinal range in China. We test four hypotheses. First, we predict larger body size in response to increased growth periods under climate change (Yom-Tov and Yom-Tov 2005; Yom-Tov et al. 2010). Second, because of recent landscape fragmentation in China (Liu and Tian 2010;Liu et al. 2014a; Song and Deng 2017), we predict that recently collected bats will have longer wings because habitat fragmentation imposes greater travel distances between foraging patches. Third, we predict that modern samples of bats will exhibit greater variation in diet as revealed by stable isotopes of carbon and nitrogen (Ben-David and Flaherty 2012a), and that these changes will be accompanied by variation in diet-related cranial traits. Fourth, because energetic costs are likely higher for females than males, we expect females to display greater change in all above-mentioned characters over time than males.

MATERIALS AND METHODS

Study species.—In this study, we examined one insectivorous and one phytophagous species, based on detailed sampling records and well-preserved specimens held in six museums in China: National Zoological Museum of China, Chinese Academy of Sciences (NZMC, CAS); Kunming Institute of Zoology, Chinese Academy of Sciences (KIZ, CAS); Northwest Institute of Plateau Biology, Chinese Academy of Sciences (NIPB, CAS); Shaanxi Institute of Zoology (SIZ); Guangdong Institute of Applied Biological Resources (GIABR); and China West Normal University (CWNU). A total of 310 specimens were examined: *Hipposideros armiger* (234 specimens) and *Rousettus leschenaultii* (76 specimens). Specimen data are provided in Appendix I. The geographic range of the historical samples covered most of China with the majority from the southeastern and southwestern regions (provinces of Hainan, Guangdong, and Yunnan; Fig. 1).

Hipposideros armiger is one of the largest species of the genus, typically roosts in caves, and feeds on insects in open spaces in woodlands and around trees (Bates and Harrison 1997). It is widely distributed in mainland of Southeast Asia (Bates et al. 2008).

Rousettus leschenaultii is the largest phytophagous bat in China of the family Pteropodidae. It typically roosts in colonies in caves, ranging from a few to several thousand individuals, in caves and old and ruined buildings and tunnels, and feeds on fruits and flowers (Bates and Harrison 1997). It occurs from Pakistan to Sumatra and Java, incongruously skipping Peninsular Malaysia (Bates and Harrison 1997; Bates and Helgen 2008).

Data collection.—Adult bats were collected and measured from across China. Two criteria were used to distinguish adults: 1) lack of metacarpal epiphyseal cartilages and 2) full closure of cranial sutures and, when stripped wing joint specimens were not available, full eruption of adult dentition (Handley et al. 1991). Due to historical specimens being dry, and wingspan and area not being available for examination, we used forearm length as a surrogate for both body size and foraging behavior in our study (Kunz 1974). Forearm length was measured using the right wing when possible. Greatest skull length (GSKL), length of the lower tooth row (LLTR) from the anterior margin of the incisors to the caudal terminus of the molars, and external width across the lateral margins of the lower molars (EWALM) were measured to describe diet-related cranial structures in both historical and modern specimens (Supplementary Data SD1; Yang et al. 2007). The mandibular symphysis is often not fused; as specimen dry, the mandible can thus become distorted. To determine if this was an issue in our mensural data, our modern cranial specimens were prepared and preserved at the Xishuangbanna Tropical Botanical Garden for 2 years, and then remeasured. Because the EWALM for modern samples of *H. armiger* ($t_{115} = -1.302$, $P = 0.1957$) and *R. leschenaultii* ($t_{77} = -0.755$, $P = 0.452$) did not change significantly, mandibular distortion is not likely to have influenced our results. All phenotypic characters were measured using a digital caliper (SF2000, Qualitot, 0.01 mm) and measured only by the senior author to ensure consistency. Measurements were repeated three times for each character, and the average value used in subsequent analyses.

Based on the distribution of historical specimens collected in the 1960's, we sampled bats from 18.73°N to 32.86°N to ensure consistency between the 1960's and modern datasets for each species (Fig. 1). Mist nets were used to capture insectivorous bats near their roosts and phytophagous bats in their foraging areas during April to September 2017 following guidelines of the American Society of Mammalogists (Sikes et al. 2016). A total of 134 individuals were captured in 2017. The cranium of newly captured specimens was removed and cleaned, and the GSKL, LLTR, and EWALM were measured. Including historical samples, a total of 444 individuals were used for wing forearm measurements and 385 for cranial measurements (Fig. 1; Appendix I).

Land-use type conversion.—We obtained the land cover dataset for China with a resolution of ca. 5 km from the National Earth System Science Data Sharing Infrastructure, National Science and Technology Infrastructure of China (http://www.geodata.cn; Li et al. 2017). We then extracted land cover data for our sampling sites using ArcGIS 10.0 and ArcMAP (ESRI 2011, Redlands, California). For each sampling site, we obtained land cover type for each decade from 1980 to 2010. We classified land cover at each site based on the nearest date to that of the sampling for the site. Because the earliest land cover data that we were able to obtain were for 1980, we classified land cover types for all historical sites based on this dataset. We classified land-use types into two groups: modified and open (farmland, prairie, and rice paddy) versus natural and closed (closed shrub forest, broad-leaved evergreen forests, broad-leaved evergreen forests, and deciduous broad-leaved forest) to explore whether the composition of land-use type has changed in the locations where the samples for the two bat species were collected (Li et al. 2017).

Stable isotope composition over time.—We analyzed stable carbon and nitrogen isotopes of wing membrane samples collected from KIZ, CAS, and from the newly collected 2017 individuals. Dietary differences were inferred for the modern and historical specimens for both *H. armiger* and *R. leschenaultii*. We obtained 34 samples from historical specimens of the two target species: 25 *H. armiger* were sampled from four populations, and nine *R. leschenaultii* were obtained from Mengla Co., Yunnan Province (Supplementary Data SD2). Because the turnover time of carbon in bats is 2–3 months (Voigt et al.

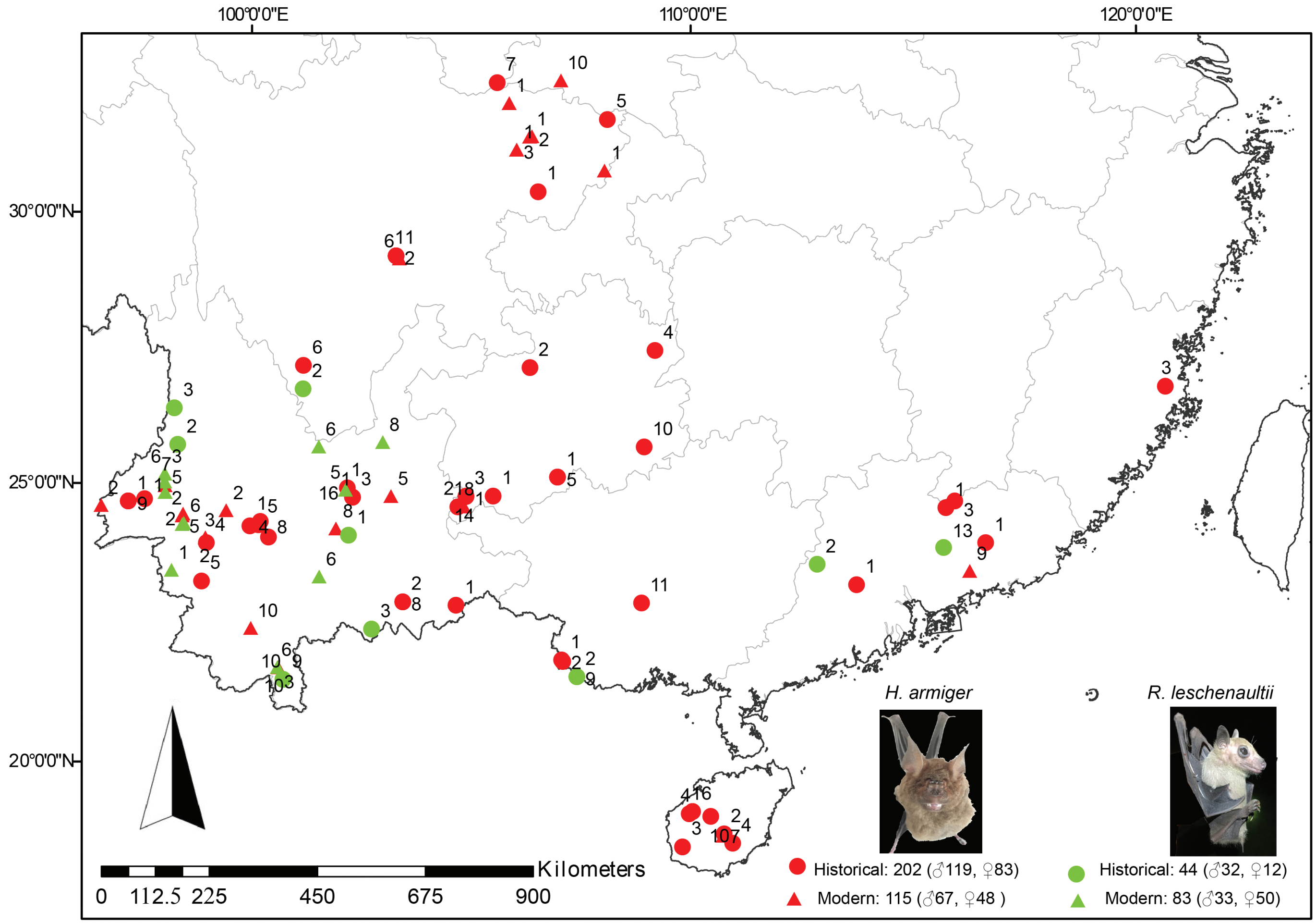

Fig. 1.—Map of collection sites for 444 bat specimens from two species. Species are color-coded, and the sample size is denoted on the upper right side for each site.

2003; Dalerum and Angerbjörn 2005), samples for the present day were collected from the same month as the historical specimens, and the sampled sites restricted to the same county. Tissue samples were collected by removing a small amount (~2 mm × 2 mm patch) of the wing membrane from each specimen. The wing membranes of newly collected bats were obtained after measurements were completed, air-dried, and preserved in sampling tubes for subsequent processing. Both historical and modern samples were preserved by air-drying, which has no substantial effect on $\delta^{15}N$ or $\delta^{13}C$ values (Barrow et al. 2008; Bessey and Vanderklift 2014). In total, 44 new samples from the two species were collected de novo. Thus, a total of 78 individuals were included for comparison of stable isotope composition (Supplementary Data SD2).

A mixture of methanol and chloroform was used to wash samples and remove contaminants (O'Connell et al. 2001). Samples were then air-dried for 24 h. Dried samples were ground into powder, and 1.4–1.7 mg was packaged into tin capsules. The stable isotope composition of the wing membrane was expressed as $\delta h\ X = (Rsample / Rstandard - 1) \times 1{,}000$, where X is the element of interest, h is the stable isotope with the higher mass number, and R is the ratio of the heavy to light isotope in the sample or standard (Dawson et al. 2002). The final values were expressed in parts per thousand (‰) and are denoted as $\delta^{13}C$ and $\delta^{15}N$ for the isotope compositions of C and N respectively. The standard for carbon was CO_2, and the standard used for nitrogen was N_2. The $\delta^{13}C$ and $\delta^{15}N$ values of samples were measured using a stable isotope ratio mass spectrometer (IsoPrime100; Isoprime, Stockport, UK) at the Central Laboratory of the Xishuangbanna Tropical Botanical Garden.

Statistical analyses.—With respect to morphological parameters, because collection dates were concentrated during the 1960s (with some specimens collected until 1970) and after 2000, we treated collection date as a categorical factor; specimens collected before 1970 were defined as historical and specimens collected after 2000 were defined as modern. Sex was treated as an indicator variable in our data analysis. All variables were normally distributed; we performed a factor analysis on the original data of forearm length and three diet-related cranial measurements with principal function in the "psych" package in R (Revelle 2019). Because all three cranial variables loaded positively on the first principal component (PC1), PC1 score was used as an estimate of allometric cranial size (Supplementary Data SD3 and SD4). We then used a generalized least squares model analysis to account for spatial autocorrelation between data points with the gls function in the "nlme" package in R (R Development Core Team 2017). This approach is efficient for handling spatial autocorrelation in comparison to other methods (Dormann et al. 2007; Bolker et al. 2009). The full model tested was: Y ~ sex*era*latitude + longitude + elevation. We modeled spatial correlation between data points using exponential decay on Euclidean distance. We began with the full model and conducted model selection by the stepwise exclusion of nonsignificant terms using likelihood ratio tests of nested models. Following model selection, we repeated the analysis for the best models using restricted maximum likelihood to estimate coefficient parameters.

For the stable isotope composition analysis, we used the oldest historical sampling date for each population as the reference date and calculated the time interval for each paired population. Then, the δ^{13}C values were corrected to account for deviation caused by the Suess effect, i.e., the decrease of δ^{13}C ratios because of atmospheric CO_2 by approximately −0.015‰ per year with increased fossil fuel combustion (Keeling 1979), and the corrected δ^{13}C values = measured values + (time × 0.015). Four populations were obtained for *H. armiger*. A linear mixed-effects regression model was used to examine the differences in stable isotope ratios in *H. armiger* using the “lme4” package in R (Bates et al. 2014). We included the sampling period (historical and modern) as fixed effect and sampling county as a random effect. One population was obtained for *R. leschenaultii*; an independent-sample *t*-test was used to compare δ^{13}C and δ^{15}N values between historical and modern samples to explore dietary differences over time. All statistical analyses were performed using R (R Development Core Team 2017).

RESULTS

Variations in forearm length.—Of the two species, only *H. armiger* showed a significant increase ($P = 0.008$) in the forearm length from historical ($X = 91.58$ mm) to modern individuals ($X = 93.08$ mm). The increasing trend was 1.64% during our study period when scaled by the historical mean of forearm length. The species also showed a significant positive correlation between forearm length and latitude for all specimens combined ($P < 0.001$), but not in modern specimens; and males were larger than females ($P < 0.001$; Fig. 2; Table 1). In addition, longitude was included and was statistically significant in the best candidate model ($P = 0.007$**). In *R. leschenaultii*, males are larger than females ($P = 0.002$), and only longitude and elevation were statistically significant ($P < 0.001$ and $P = 0.002$, respectively) in the best candidate model (Fig. 2; Table 1).

Variation in the PC1 score of three diet-related cranial structures.—In *H. armiger*, statistically significant increases were found in the PC1 scores between historical and modern specimens ($P < 0.001$). There was also a significant positive correlation in this species between PC1 score and latitude in all specimens combined ($P = 0.023$) and males were larger than females ($P = 0.022$). In addition, longitude was significant and present in the best candidate model ($P < 0.001$). In *R. leschenaultii*, PC1 scores increased significantly from historical to modern specimens ($P < 0.001$) and were significantly positively correlated with latitude for the data set containing all specimens ($P = 0.012$). Males were larger than females ($P = 0.002$). Longitude and interaction between latitude and era were significant ($P = 0.034$, $P < 0.001$, respectively) and present in the best candidate model (Fig. 3; Table 2).

Variation in stable isotope composition.—With respect to *H. armiger*, both δ^{13}C and δ^{15}N differed significantly between historical and modern specimens (Fig. 4; Table 3). For *R. leschenaultii*, δ^{13}C increased significantly over time ($t_{8.65} = -2.89$, $P = 0.02$*; Fig. 4), but no significant change was detected in δ^{15}N ($t_{5.63} = -0.54$, $P = 0.61$; Fig. 4).

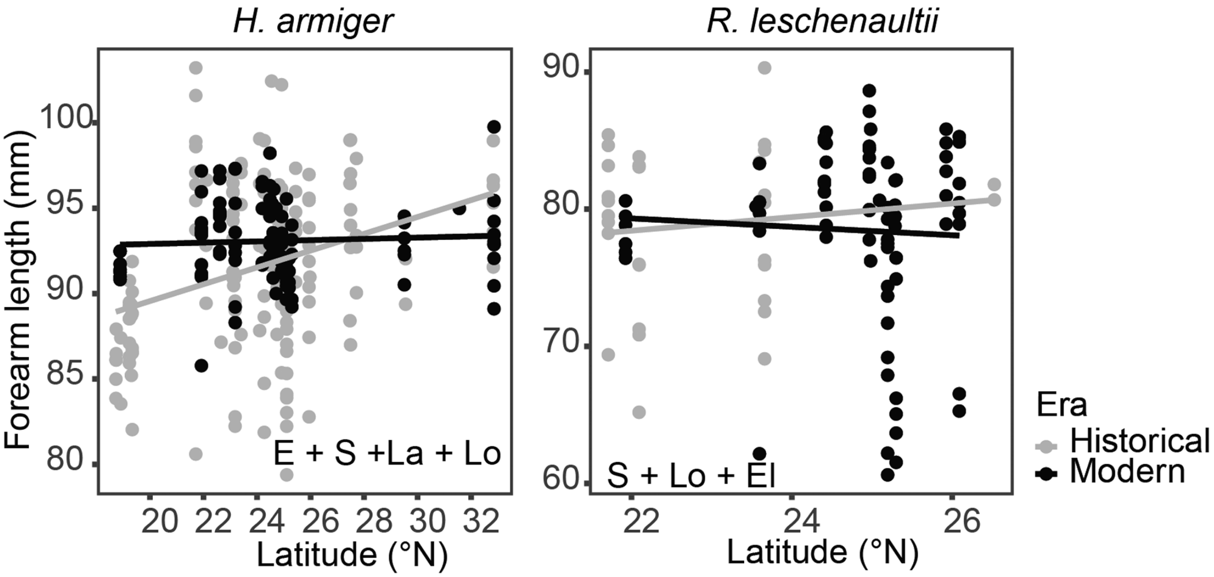

Fig. 2.—Temporal and latitudinal pattern of forearm length in two bat species. The statistically significant predictors that were included in the best models are indicated in the panels. Predictors included era (E), sex (S), latitude (La), longitude (Lo), and elevation (El). A significant increasing trend from historical to modern was found only for *H. armiger*.

Table 1.—The best models for the change in the forearm length of two bat species, as evaluated using generalized least squares. The values in the tables are the coefficient estimates, together with their level of significance. Probabilities for *t*-estimates were estimated using Satterthwaite approximation of denominator degrees of freedom. The significance levels are: *$P < 0.05$, **$P < 0.01$ and ***$P < 0.001$.

Species	Predictors	Estimate	*SE*	*t*	*P*	R^2
H. armiger (*N* = 317)	Intercept	98.886	5.383	18.37	< 0.001***	0.180
	Era modern	1.166	0.435	2.68	0.008**	
	Sex male	2.376	0.416	5.71	< 0.001***	
	Latitude	0.211	0.060	3.51	< 0.001***	
	Longitude	−0.132	0.048	−2.72	0.007**	
R. leschenaultii (*N* = 127)	Intercept	131.107	15.781	8.31	< 0.001***	0.172
	Sex male	3.828	1.210	3.16	0.002**	
	Elevation	−0.004	0.001	−3.20	0.002**	
	Longitude	−0.502	0.148	−3.39	< 0.001***	

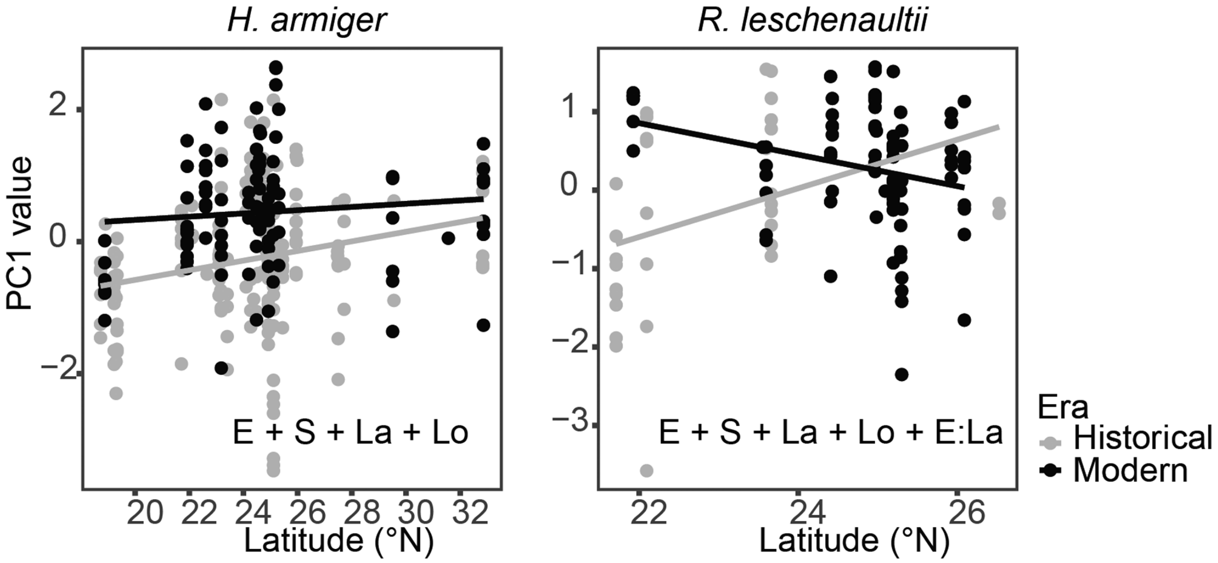

Fig. 3.—Temporal and latitudinal variation of PC1 scores for diet-related cranial measurements in two bat species. The statistically significant predictors included in the best models are indicated in each panel. Predictors included era (E), sex (S), latitude (La), and longitude (Lo), and E*La indicates the influence of interaction between era and latitude.

Variation in land-use type.—There was a higher proportion of modified and open land-use types present in the modern era (0.400 versus 0.183) within the sampling range of *H. armiger*. The ratio was relatively stable for *R. leschenaultii* (Fig. 5; Supplementary Data SD5).

DISCUSSION

We found that *H. armiger* exhibited an increase in forearm length and PC1 score for the three diet-related cranial dimensions, as well as differences in stable isotope ratios of carbon and nitrogen in wing membrane tissues. The phytophagous bat species, *R. leschenaultii*, displayed significant increases in PC1 scores for three diet-related cranial traits and in values of $\delta^{13}C$. As a whole, this study provides evidence for significant and consistent phenotypic variation in the two bat species in response to recent environmental changes; these phenotypic changes were more evidently associated with land-use changes than climate change.

Forearm length is the standard general index of body size in bats (Kunz 1974) and body size affects animal physiology and life-history attributes (Calder 1984). There is partial support for our first hypothesis of a significant body size increase for *H. armiger*. The resource rule hypothesis provides a partial explanation for the significant increase in forearm length in *H. armiger*. Previous studies have shown that bats exhibit fluctuating reproductive rhythms with climate change (Lučan et al. 2013; Linton and Macdonald 2018). It is therefore possible that *H. armiger* had an extended ontogenesis and growth period because of earlier parturition resulting in a longer forearm during our experimental period.

In contrast, Bergmann's rule predicts that selection imposed by warming will lead to a reduction in body size (Gardner et al. 2011). In this study, the significant positive correlation between body size and latitude in *H. armiger* was consistent with Bergmann's rule at the spatial scale, although the magnitude of the spatial elevational scales is a confounding factor. Notwithstanding, previous research has suggested that a warming climate may not necessarily result in selection for increased heat dissipation in bats (Tomassini et al. 2014), as most bats roost in caves, where temperature is moderated and only relatively weakly correlated with temperature of the

Table 2.—The best models for the change in the PC1 score of three diet-related cranial structure in two bat species, as evaluated using generalized least squares. The values in the tables are the coefficient estimates, together with their level of significance. Positive numbers indicate significant positive correlation with corresponding predictor and vice versa. Probabilities for t-estimates were estimated using Satterthwaite approximation of denominator degrees of freedom. The significance levels are as follows: $*P < 0.05$, $**P < 0.01$ and $***P < 0.001$.

Species	Predictors	Estimate	SE	t	P	R^2
H. armiger ($N = 276$)	Intercept	3.367	1.517	2.22	0.027*	0.197
	Era modern	0.630	0.116	5.45	< 0.001***	
	Sex male	0.260	0.113	2.30	0.022*	
	Latitude	0.040	0.018	2.29	0.023*	
	Longitude	−0.045	0.013	−3.39	< 0.001***	
R. leschenaultii ($N = 109$)	Intercept	−13.525	3.273	−4.13	< 0.001***	0.285
	Era modern	13.790	3.515	3.92	< 0.001***	
	Sex male	0.522	0.168	3.11	0.002**	
	Latitude	0.314	0.122	2.57	0.012*	
	Longitude	0.053	0.024	2.15	0.034*	
	Modern & latitude	−0.534	0.150	−3.57	< 0.001***	

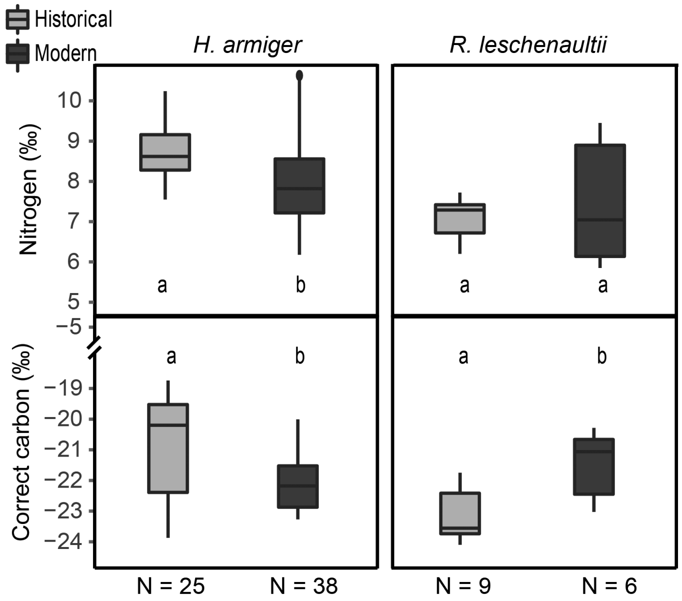

Fig. 4.—Boxplot of corrected δ^{13}C (‰) and δ^{15}N (‰) values of historical (1960) and modern (2017) specimens. Letters indicate statistically significant differences between variable means of historical and modern specimens based on t-tests of model coefficients (the same letter indicates no statistically significant difference).

external air (Park et al. 2000). Country-wide, average annual mean surface air temperature in China has been rising at a rate of 0.25°C per decade since the 1950's (Ren et al. 2017), which is trivial when compared to the range of temperature across their sampling range of 9.28–13.48°C for *R. leschenaultii* and *H. armiger*, respectively (Fick and Hijmans 2017). Hence, our results suggest that heat dissipation may not be critical for bats under contemporary climate warming regime in China. In contrast to birds, where body size and different annual cycles have been significantly influenced by climate change (Goodman et al. 2012; Tomotani et al. 2018), bats are less threatened by contemporary climate change. Even so, extremely high temperatures have been reported to lead to the death of large numbers of *Pteropus* sp. in Australia since 1994 (Welbergen et al. 2008). Such unpredictable extreme events pose greater challenges to bats than increased mean temperature. However, in the latter example, the two species of *Pteropus* are tree roosting bats found in exposed, relatively open and isolated trees, rather than the cave roosting species that we examined in this study.

Variation in wing traits such as forearm length is often considered an adaptation to foraging habitat (Marinello and Bernard 2014; Furey and Racey 2016). Only *H. armiger* showed a significant increase in forearm length, which supports our second hypothesis, given that we found significant differences between natural and modified habitat use over time in *H. armiger* but not *R. leschenaultii*. Wing morphology is correlated with foraging strategy and flight performance in bats (Furey and Racey 2016). Wing characters that allow for flexible foraging strategies confer an advantage and should be favored by selection under regimes of widespread anthropogenic habitat change (Lewis and Maslin 2015; Voigt and Kingston 2016). In China, human population growth, economic development, and improvement of transportation infrastructure are degrading and fragmenting landscapes (Liu and Tian 2010; Zhang et al. 2016). Further, the cave systems that provide roosting sites for many bat species are threatened because of the need for cement for infrastructure development (Tanalgo et al. 2018). The significant increase in forearm length of *H. armiger* may be a consequence of fragmentation of foraging habitat and a decrease in the prey base worldwide (Hallmann et al. 2017, Sánchez-Bayo and Wyckhuys 2019). This idea is supported by the land-use change analysis in which more open habitats were found in the modern sampling range than in the historical era. Land-use change may force modern *H. armiger* to travel further between fragments to forage. The absence of significant change in the forearm length of *R. leschenaultii* may reflect relatively less habitat change together with less effect to its food base, which is also supported by the land-use change analysis.

Food abundance and composition are fundamental factors influencing the activity of bats, particularly insectivorous bats (Wang et al. 2010). Climate warming can increase insect overwinter survival (Kiritani 2006) and fecundity (Miles et al. 1997). However, long-term records from many parts of

Table 3.—Linear mixed-effect model analysis of the variation in $\delta^{13}C$ and $\delta^{15}N$ between historical and modern *H. armiger* specimens. "Era" indicates the comparison between historic and modern specimens.

Parameters	Predictors	Estimate	*SE*	*d.f.*	*t*	*P*
$\delta^{13}C$	Intercept	−21.330	0.495	3.64	−41.00	< 0.001 ***
	Era modern	−0.769	0.239	58.75	−3.18	0.002**
$\delta^{15}N$	Intercept	8.765	0.283	6.23	30.94	< 0.001 ***
	Era modern	−0.707	0.261	60.83	−2.71	0.009 **

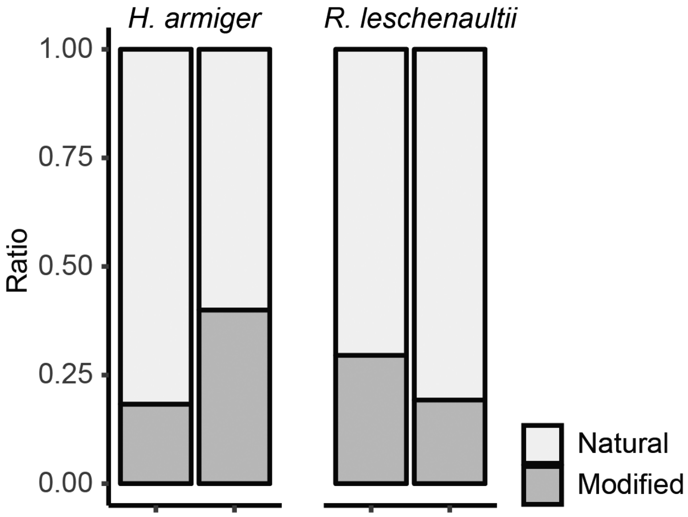

Fig. 5.—The temporal conversion pattern of land-use type over the past 60 years in two bat species. Ratio was calculated as the number of individuals divided by the total number of individuals in the sampling era.

the world indicate that the local abundance of Lepidoptera and many other invertebrates have decreased significantly over the past decades (Dirzo et al. 2014; Lister and Garcia 2018). In addition, continuing land-use changes will exacerbate fluctuations in food resources for many insects (Williams-Guillén et al. 2016). Unfortunately, studies of variation in insect populations over the past decades in China are lacking. The results of one study on *Pipistrellus kuhlii* in Italy suggests that this species increased tooth size to expand the bats' access to varied food resources. This change was considered an adaptive response to increased abundance of larger insects near street lamps (Tomassini et al. 2014). Both *H. armiger* and *R. leschenaultii* showed statistically significant increases in PC1 scores from the historical to the modern era, suggesting that the changes in cranial measurements might be a common adaptation to environmental change. In addition, the statistically significant interaction between era and latitude implies site-based specific land-use changes existed for *R. leschenaultii*, which in our study ranged from 21.71°N to 26.53°N latitude. The exponential increase in rubber plantations and other cash crops over the last few decades has resulted in a dramatic decrease in natural forest cover in the Yunnan Province (Zhang et al. 2012; Zomer et al. 2015). This is one possible explanation for the stronger variation in forearm length of bats in this latitudal range between the historical and modern era.

The differences we observed in stable isotope composition between historical and modern specimens support the hypothesis that food resources for bats have changed over time, especially for insectivorous bats. Tissue composition of stable isotopes of carbon and nitrogen is influenced by the foods they consume (Kelly 2000, Fry 2006) or by changes in the stable isotopes in the food itself. The different isotopic composition of wing punches from historical and modern specimens of *H. armiger* suggests that the food resources consumed have changed over time. In contrast to insects, the response of plants to climate change involves in situ accommodation through the adjustment of phenology or distributional range (Kelly and Goulden 2008). Only the isotopic composition of carbon showed significant differences between the historical and modern specimens in *R. leschenaultii*. Because water limitation and stomatal closure affect plant discrimination of heavy and light carbon during carbon assimilation, low levels of precipitation could lead to increased $\delta^{13}C$ ratios in C_3 plants (Fry 2006, Ben-David and Flaherty 2012a, 2012b). Thus, the change in isotopic carbon in *R. leschenaultii* could also be caused by water supply changes in this region over the past few decades (Shi and Chen 2018). Overall, the results indicate fewer changes in food composition over the past 65 years in *R. leschenaultii* than *H. armiger.* As noted above, it is possible that changing isotope ratios in the food of the bats could lead to changing isotope values in their tissues even if their diet remains constant. Although we used the same resampling sites, with time and tissue consistent between historical and modern eras, we cannot exclude this possibility. However, combined with the consistent variation in the PC1 score of the three diet-related cranial structures for the two species, we believe their food resource has changed over the past few decades. Thus, we hypothesize that bats have experienced pressure from both climate change and land-use change. These factors have in combination resulted in changes in food resources although the magnitude of these changes may vary among species. *Hipposideros armiger* appears to have experienced greater pressure, because all three cranial measurements showed consistent increases in this species, in addition to a significant increase in body size.

Temperature increases are projected to push many tropical mammal species beyond their thermoneutral zones this century (Khaliq et al. 2014). The absence of sample sites from Southeast Asia, the core of *R. leschenaultii*'s range, may have resulted in an underestimation of their response. However, despite admittedly insufficient sampling for phytophagous bats, significant changes were observed in the diet-related cranial structures and in the stable isotope ratios in our study. This suggests that diet-related structural changes may reflect general responses of bats to current environmental changes.

Because females nurture offspring during pregnancy and lactation, they face greater challenges than males when exposed to environmental changes. For example, the reproductive output of *Eptesicus fuscus* was influenced by drought conditions in Colorado from 1996 to 2008 (Adams 2010). The fact that significant interactions between era and sex were not found in our study implies that females did not suffer greater pressure than males, although the requirements of females still should drive choice of conservation efforts for bats in the future.

Anthropogenic environmental change has a significant effect on biodiversity at the global scale (McGill et al. 2015). Bats provide extensive ecosystem services; they can increase human well-being via pollination, seed dispersal, and pest control, and enhance agricultural yields (Kunz et al. 2011). While research on effects of environmental change on bats is limited (McCain and King 2014; MacLean and Beissinger 2017), our results indicate that variation in diet-related structures is evident both in insectivorous and frugivorous bats, suggesting this could be a common phenomenon for bats facing contemporary environmental change. Furthermore, it is necessary to determine if the combination of phenotypic plasticity and adaptive evolution will enable bats to respond to anthropogenic environmental changes and whether we can distinguish the influences of climate and land-use change (Yom-Tov and Geffen 2011). These questions deserve more attention (Merilä and Hendry 2014; Voigt and Kingston 2016). In this study, we present evidence for rapid morphological change in concert with environmental change over a small temporal gradient. Although changes were small, they were consistent and reflected the ability of the species to accommodate environmental change associated with both climatic and land-use changes.

Acknowledgments

We are grateful to the six museums that allowed access to the specimens and provided permission to conduct the measurements. We are grateful to Doyle McKey (University of Montpellier, France) and Richard T. Corlett's for generous help in revising earlier drafts of the manuscript. The study was financially supported by the Xishuangbanna Tropical Botanical Garden of the Chinese Academy of Sciences and the National Special Fund on Basic Research of Science and Technology of China (2014FY110100). This research was approved by the Committee on Biomedical Ethics at the Xishuangbanna Tropical Botanical Garden of the Chinese Academy of Sciences (approval number: XTBG-2017-001).

Supplementary Data

Supplementary data are available at *Journal of Mammalogy* online.

Supplementary Data SD1.—Phenotypic cranial variables measured. The photographed specimen is *R. leschenaultii*. The measured variables were as follows: greatest skull length (GSKL) (1–2), length of the lower tooth row (LLTR) (3–4), and external width across lower molars (EWALM) (5–6).

Supplementary Data SD2.—Map showing the distribution of 78 isotopic samples from *H. armiger* and *R. leschenaultii* in the two eras. Era is color-coded and sample size is noted at the upper right side for each site. The site with black edge indicates that both *H. armiger* and *R. leschenaultii* were sampled and the number in brackets represents sample size for the two species, respectively.

Supplementary Data SD3.—Standardized loadings based varimax rotation of the first two components from a factor analysis of forearm length and three diet-related cranial structures in the two bat species. The abbreviations for the three cranial parameters are: greatest skull length (GSKL), length of the lower tooth row (LLTR), and external width across lower molars (EWALM).

Supplementary Data SD4.—Diagram of factor analysis for forearm length and three diet-related cranial structures in the two bat species. The abbreviations for three measured cranial parameters are greatest skull length (GSKL), length of the lower tooth row (LLTR), and external width across lower molars (EWALM).

Supplementary Data SD5.—Variation of land-use type for two bat species. Values in the tables are the number of individuals captured in the corresponding land-use type. The modified group of land-use types include farmland, prairie, and paddy field and the natural group of land-use types includes closed shrub forest, broad-leaf evergreen forests, broad-leaf evergreen forests, and deciduous broad-leaf forest. The ratio was calculated as the number of modified divided by the total number within the era.

Literature Cited

Adams, R. A. 2010. Bat reproduction declines when conditions mimic climate change projections for western North America. Ecology 91:2437–2445.

Barrow, L. M., K. A. Bjorndal, and K. J. Reich. 2008. Effects of preservation method on stable carbon and nitrogen isotope values. Physiological and Biochemical Zoology 81:688–693.

Bates, D., M. Mächler, B. M. Bolker, and S. C. Walker. 2014. Fitting linear mixed-effects models using lme4. Journal of Statistics Software arXiv:1406:133–199.

Bates, P., Bumrungsri, S., Francis, C., and Csorba, G. 2008. Hipposideros armiger. The IUCN Red List of Threatened Species 2008: e.T10110A3162617. http://dx.doi.org/10.2305/IUCN.UK.2008.RLTS.T10110A3162617.en. Accessed 25 September 2019.

Bates, P., and D. Harrison. 1997. Bats of Indian Subcontinent. Harrison Zoological Museum Publications. Sevenoaks, United Kingdom.

Bates, P., and K. Helgen. 2008. Rousettus leschenaultii. The IUCN Red List of Threatened Species 2008:e.T19756A9011055. http://dx.doi.org/10.2305/IUCN.UK.2008.RLTS.T19756A9011055.en. Accessed 25 September 2019.

Ben-David, M., and E. A. Flaherty. 2012a. Stable isotopes in mammalian research: a beginner's guide. Journal of Mammalogy 93:312–328.

Ben-David, M., and E. A. Flaherty. 2012b. Theoretical and analytical advances in mammalian isotope ecology: an introduction. Journal of Mammalogy 93:309–311.

Bessey, C., and M. A. Vanderklift. 2014. Drying method has no substantial effect on δ(15)N or δ(13)C values of muscle tissue from teleost fishes. Rapid Communications in Mass Spectrometry 28:265–273.

Bolker, M. B., et al. 2009. Generalized linear mixed models: a practical guide for ecology and evolution. Trends in Ecology and Evolution 24:127–135.

Bonebrake, T. C., et al. 2018. Managing consequences of climate-driven species redistribution requires integration of ecology, conservation and social science. Biological Reviews of the Cambridge Philosophical Society 93:284–305.

Boutin, S., and J. E. Lane. 2014. Climate change and mammals: evolutionary versus plastic responses. Evolutionary Applications 7:29–41.

Burgin, C. J., J. P. Colella, P. L. Kahn, and N. S. Upham. 2018. How many species of mammals are there? Journal of Mammalogy 99:1–14.

Calder, W. A. 1984. Size, function and life history. Harvard University Press, Cambridge, Massachusetts.

Cryan, P. M., M. A. Bogan, and J. S. Altenbach. 2000. Effect of elevation on distribution of female bats in the Black Hills, South Dakota. Journal of Mammalogy 81:719–725.

Dalerum, F., and A. Angerbjörn. 2005. Resolving temporal variation in vertebrate diets using naturally occurring stable isotopes. Oecologia 144:647–658.

Dawson, T. E., S. Mambelli, A. H. Plamboeck, P. H. Templer, and K. P. Tu. 2002. Stable isotopes in plant ecology. Annual Review of Ecology and Systematics 33:507–559.

Deng, X., J. Huang, S. Rozelle, J. Zhang, and Z. Li. 2015. Impact of urbanization on cultivated land changes in China. Land Use Policy 45:1–7.

Dirzo, R., H. S. Young, M. Galetti, G. Ceballos, N. J. Isaac, and B. Collen. 2014. Defaunation in the Anthropocene. Science 345:401–406.

Dormann, C. F., et al. 2007. Methods to account for spatial autocorrelation in the analysis of species distributional data: a review. Ecography 30:609–628.

Dumont, E. R. 1999. The effect of food hardness on feeding behaviour in frugivorous bats (Phyllostomidae): an experimental study. Journal of Zoology 248:219–229.

ESRI. 2011. ArcView GIS. Ver. 9.3. Environmental System Research Institute, Inc. Redlands, California.

Evin, A., I. Horáček, and P. Hulva. 2011. Phenotypic diversification and island evolution of pipistrelle bats (*Pipistrellus pipistrellus* group) in the Mediterranean region inferred from geometric morphometrics and molecular phylogenetics. Journal of Biogeography 38:2091–2105.

Fang, S., et al. 2017. Change in temperature extremes and its correlation with mean temperature in mainland China from 1960 to 2015. International Journal of Climatology 37:3910–3918.

Fick, S. E., and R. J. Hijmans. 2017. WorldClim 2: new 1-km spatial resolution climate surfaces for global land areas. International Journal of Climatology 37:4302–4315.

Flanders, J., et al. 2009. Phylogeography of the greater horseshoe bat, *Rhinolophus ferrumequinum*: contrasting results from mitochondrial and microsatellite data. Molecular Ecology 18:306–318.

Freeman, P. W. 1979. Specialized insectivory: beetle-eating and moth-eating molossid bats. Journal of Mammalogy 60:467–479.

Freeman, P. W. 1981. Correspondence of food habits and morphology in insectivorous bats. Journal of Mammalogy 62:166–173.

Fry, B. 2006. Fractionation. Pp. 204–212 in Stable isotope ecology. Springer. New York.

Fuentes-Montemayor, E., D. Goulson, L. Cavin, J. M. Wallace, and K. J. Park. 2013. Fragmented woodlands in agricultural landscapes: the influence of woodland character and landscape context on bats and their insect prey. Agriculture Ecosystems and Environment 172:6–15.

Furey, N. M., and P. A. Racey. 2016. Can wing morphology inform conservation priorities for Southeast Asian cave bats? Biotropica 48:545–556.

Gardner, J. L., A. Peters, M. R. Kearney, L. Joseph, and R. Heinsohn. 2011. Declining body size: a third universal response to warming? Trends in Ecology and Evolution 26:285–291.

Ghazali, M., and I. Dzeverin. 2013. Correlations between hardness of food and craniodental traits in nine *Myotis* species (Chiroptera, Vespertilionidae). Vestnik Zoologii 47:67–76.

Goodman, R. E., G. Lebuhn, N. E. Seavy, T. Gardali, and J. D. Blusodemers. 2012. Avian body size changes and climate change: warming or increasing variability? Global Change Biology 18:63–73.

Hallmann, C. A., et al. 2017. More than 75 percent decline over 27 years in total flying insect biomass in protected areas. PLoS ONE 12:e0185809.

Handley, C. O., D. E. Wilson, and A. L. Gardner (eds.). 1991. Demography and natural history of the common fruit bat, *Artibeus jamaicensis*, on Barro Colorado Island, Panamá. Smithsonian Contributions to Zoology No. 511.

Holmes, M. W., et al. 2016. Natural history collections as windows on evolutionary processes. Molecular Ecology 25:864–881.

Høye, T. T., J. U. Hammel, T. Fuchs, and S. Toft. 2009. Climate change and sexual size dimorphism in an Arctic spider. Biology Letters 5:542–544.

Jiang, Z., S. Liu, Y. Wu, X. Jiang, and K. Zhou. 2017. China's mammal diversity (2nd ed.). Biodiversity Science 25:886–895.

Jones, G., and H. Rebelo. 2013. Responses of bats to climate change: learning from the past and predicting the future. Pp. 457–478 in Bat evolution ecology and conservation (R. A. Adams and S. C. Pederson, eds.). Springer Nature. Berlin, Germany.

Jung, K., and C. G. Threlfall. 2016. Urbanisation and its effects on bats—a global meta-analysis. Pp. 13–33 in Bats in the Anthropocene: conservation of bats in a changing world (C. C. Voigt and T. Kingston, eds.). Springer International Publishing. Berlin, Germany.

Keeling, C. D. 1979. The Suess effect: ^{13}Carbon-^{14}Carbon interrelations. Environment International 2:229–300.

Kelly, J. F. 2000. Stable isotopes of carbon and nitrogen in the study of avian and mammalian trophic ecology. Canadian Journal of Zoology 78:1–27.

Kelly, A. E., and M. L. Goulden. 2008. Rapid shifts in plant distribution with recent climate change. Proceedings of the National Academy of Sciences of the United States of America 105:11823–11826.

Khaliq, I., C. Hof, R. Prinzinger, K. Böhning-Gaese, and M. Pfenninger. 2014. Global variation in thermal tolerances and vulnerability of endotherms to climate change. Proceedings of the Royal Society B: Biological Sciences 281:20141097.

Kingsolver, J. G., H. A. Woods, L. B. Buckley, K. A. Potter, H. J. MacLean, and J. K. Higgins. 2011. Complex life cycles and the responses of insects to climate change. Integrative and Comparative Biology 51:719–732.

Kiritani, K. 2006. Predicting impacts of global warming on population dynamics and distribution of arthropods in Japan. Population Ecology 48:5–12.

Kunz, T. H. 1974. Reproduction, growth, and mortality of the vespertilionid bat, *Eptesicus fuscus*, in Kansas. Journal of Mammalogy 55:1–13.

Kunz, T. H., E. Braun de Torrez, D. Bauer, T. Lobova, and T. H. Fleming. 2011. Ecosystem services provided by bats. Annals of the New York Academy of Sciences 1223:1–38.

Lewis, S. L., and M. A. Maslin. 2015. Defining the anthropocene. Nature 519:171–180.

Li, H., et al. 2017. Using land long-term data records to map land cover changes in China over 1981–2010. IEEE Journal of Selected Topics in Applied Earth Observations and Remote Sensing 10:1372–1389.

Lin, A.-Q., et al. 2014. Phylogeography of *Hipposideros armiger* (Chiroptera: Hipposideridae) in the Oriental region: the contribution of multiple Pleistocene glacial refugia and intrinsic factors to contemporary population genetic structure. Journal of Biogeography 41:317–327.

Linton, D. M., and D. W. Macdonald. 2018. Spring weather conditions influence breeding phenology and reproductive success in sympatric bat populations. The Journal of Animal Ecology 87:1080–1090.

Lister, B. C., and A. Garcia. 2018. Climate-driven declines in arthropod abundance restructure a rainforest food web. Proceedings of the National Academy of Sciences of the United States of America 115:E10397–E10406.

Liu, J., et al. 2014a. Spatiotemporal characteristics, patterns, and causes of land-use changes in China since the late 1980s. Journal of Geographical Sciences (English version) 24:195–210.

Liu, M., and H. Tian. 2010. China's land cover and land use change from 1700 to 2005: Estimations from high-resolution satellite data and historical archives. Global Biogeochemical Cycles 24:1–18.

Liu, M., X. Xu, A. Y. Sun, K. Wang, W. Liu, and X. Zhang. 2014b. Is southwestern China experiencing more frequent precipitation extremes? Environmental Research Letters 9:064002.

Lučan, R. K., M. Weiser, and V. Hanák. 2013. Contrasting effects of climate change on the timing of reproduction and reproductive success of a temperate insectivorous bat. Journal of Zoology 290:151–159.

MacLean, S. A., and S. R. Beissinger. 2017. Species' traits as predictors of range shifts under contemporary climate change: a review and meta-analysis. Global Change Biology 23:4094–4105.

Marinello, M. M., and Bernard E. 2014. Wing morphology of Neotropical bats: a quantitative and qualitative analysis with implications for habitat use. Canadian Journal of Zoology 92:141–147.

McCain, C. M., and S. R. King. 2014. Body size and activity times mediate mammalian responses to climate change. Global Change Biology 20:1760–1769.

McGill, B. J., M. Dornelas, N. J. Gotelli, and A. E. Magurran. 2015. Fifteen forms of biodiversity trend in the Anthropocene. Trends in Ecology & Evolution 30:104–113.

McNab, B. K. 2010. Geographic and temporal correlations of mammalian size reconsidered: a resource rule. Oecologia 164:13–23.

Merilä, J., and A. P. Hendry. 2014. Climate change, adaptation, and phenotypic plasticity: the problem and the evidence. Evolutionary Applications 7:1–14.

Miles, J. E., J. S. Bale, and I. D. Hodkinson. 1997. Effects of temperature elevation on the population dynamics of the upland heather psyllid *Strophingia ericae* (Curtis) (Homoptera: Psylloidea). Global Change Biology 3:291–297.

Millien, V., S. Kathleen Lyons, L. Olson, F. A. Smith, A. B. Wilson, and Y. Yom-Tov. 2006. Ecotypic variation in the context of global climate change: revisiting the rules. Ecology Letters 9:853–869.

Newbold, T., et al. 2015. Global effects of land use on local terrestrial biodiversity. Nature 520:45–50.

Ning, J., et al. 2018. Spatiotemporal patterns and characteristics of land-use change in China during 2010–2015. Journal of Geographical Sciences 28:547–562.

Nogueira, M. R., A. L. Peracchi, and L. R. Monteiro. 2009. Morphological correlates of bite force and diet in the skull and mandible of phyllostomid bats. Functional Ecology 23:715–723.

Norberg, U. M., and J. M. Rayner. 1987. Ecological morphology and flight in bats (Mammalia; Chiroptera): wing adaptations, flight performance, foraging strategy and echolocation. Philosophical Transactions of the Royal Society B: Biological Sciences 316:335–427.

O'Connell, T. C., R. E. M. Hedges, M. A. Healey, and A. H. R. W. Simpson. 2001. Isotopic comparison of hair, nail and bone: modern analyses. Journal of Archaeological Science 28:1247–1255.

Pacifici, M., et al. 2015. Assessing species vulnerability to climate change. Nature Climate Change 5:215–225.

Park, K. J., G. Jones, and R. D. Ransome. 2000. Torpor, arousal and activity of hibernating greater horseshoe bats (*Rhinolophus ferrumequinum*). Functional Ecology 14:580–588.

Pereira, H. M., L. M. Navarro, and I. S. Martins. 2012. Global biodiversity change: the bad, the good, and the unknown. Annual Review of Environment and Resources 37:25–50.

Petry, W. K., et al. 2016. Sex-specific responses to climate change in plants alter population sex ratio and performance. Science 353:69–71.

R Development Core Team. 2017. R: a language and environment for statistical computing. R Foundation for Statistical Computing. Vienna, Austria. www.R-project.org/. Accessed June 30, 2017.

Ren, G., Y. Ding, and G. J. Tang. 2017. An overview of mainland China temperature change research. Journal of Meteorological Research 31:3–16.

Revelle, W. 2019. An introduction to the psych package: Part I: data entry and data description. http://personality-project.org/r/intro.pdf.

Rubidge, E. M., J. L. Patton, M. Lim, A. C. Burton, J. S. Brashares, and C. Moritz. 2012. Climate-induced range contraction drives genetic erosion in an alpine mammal. Nature Climate Change 2:285–288.

Ruedas, L. A., J. R. Demboski, and R. V. Sison. 1994. Morphological and ecological variation in Otopteropus cartilagonodus Knock, 1969 (Mammalia: Chiroptera: Pteropodidae) from Luzon, Philippines. Proceedings of the Biological Society of Washington 107:1–16.

Sánchez-Bayo, F., and K. A. G. Wyckhuys. 2019. Worldwide decline of the entomofauna: a review of its drivers. Biological Conservation 232:8–27.

Santana, S. E., I. R. Grosse, and E. R. Dumont. 2012. Dietary hardness, loading behavior, and the evolution of skull form in bats. Evolution 66:2587–2598.

Santana, S. E., S. Strait, and E. R. Dumont. 2011. The better to eat you with: functional correlates of tooth structure in bats. Functional Ecology 25:839–847.

Scheffers, B. R., et al. 2016. The broad footprint of climate change from genes to biomes to people. Science 354:aaf7671.

Shao, Y., J. Wu, J. Ye, and Y. Liu. 2015. Frequency analysis and its spatiotemporal characteristics of precipitation extreme events in China during 1951–2010. Theoretical and Applied Climatology 121:775–787.

Sheridan, J. A., and D. Bickford. 2011. Shrinking body size as an ecological response to climate change. Nature Climate Change 1:401–406.

Sherwin, H. A., W. I. Montgomery, and M. G. Lundy. 2013. The impact and implications of climate change for bats. Mammal Review 43:171–182.

Shi, H., and J. Chen. 2018. Characteristics of climate change and its relationship with land use/cover change in Yunnan Province, China. International Journal of Climatology 38:2520–2537.

Sikes, R. S., and the Animal Care and Use Committee of the American Society of Mammalogists. 2016. 2016 Guidelines of the American Society of Mammalogists for the use of wild mammals in research and education. Journal of Mammalogy 97:663–688.

Simmons, N. B. 2005. Order Chiroptera. Pp. 312–529 in Mammal species of the world: a taxonomic and geographic reference, v. 1 (D. E. Wilson and D. A. Reeder, eds.). Johns Hopkins University Press. Baltimore, Maryland.

Snell-Rood, E. C., and N. Wick. 2013. Anthropogenic environments exert variable selection on cranial capacity in mammals. Proceedings of the Royal Society B: Biological Sciences 280:20131384.

Song, W., and X. Deng. 2017. Land-use/land-cover change and ecosystem service provision in China. The Science of the Total Environment 576:705–719.

Stocker, T. F., et al. 2013. IPCC, 2013: climate change 2013: the physical science basis. Contribution of Working Group I to the Fifth Assessment Report of the Intergovernmental Panel on Climate Change. Cambridge University Press. Cambridge, United Kingdom.

Stoner, K. E., M. Quesada, and J. A. Lobo. 2010. Effects of forest fragmentation on the Colima long-nosed bat (Musonycteris harrisoni) foraging in tropical dry forest of Jalisco, Mexico. Biotropica 34:462–467.

Tanalgo, K. C., J. A. G. Tabora, and A. C. Hughes. 2018. Bat cave vulnerability index (BCVI): a holistic rapid assessment tool to identify priorities for effective cave conservation in the tropics. Ecological Indicators 89:852–860.

Taylor, G. K., A. C. Carruthers, T. Y. Hubel, and S. M. Walker. 2012. Wing morphing in insects, birds and bats: mechanism and function. Pp. 11–40 in Morphing aerospace vehicles and structures (J. Valasek, ed.). John Wiley and Sons, Ltd., Hoboken, New Jersey.

Teplitsky, C., and V. Millien. 2014. Climate warming and Bergmann's rule through time: is there any evidence? Evolutionary Applications 7:156–168.

Tilman, D., M. Clark, D. R. Williams, K. Kimmel, S. Polasky, and C. Packer. 2017. Future threats to biodiversity and pathways to their prevention. Nature 546:73–81.

Titeux, N., et al. 2018. Global scenarios for biodiversity need to better integrate climate and land use change. Diversity and Distributions 23:1231–1234.

Tomassini, A., P. Colangelo, P. Agnelli, G. Jones, and D. Russo. 2014. Cranial size has increased over 133 years in a common bat, *Pipistrellus kuhlii*: a response to changing climate or urbanization? Journal of Biogeography 41:944–953.

Tomotani, B. M., et al. 2018. Climate change leads to differential shifts in the timing of annual cycle stages in a migratory bird. Global Change Biology 24:823–835.

Voigt, C. C., and T. Kingston. 2016. Bats in the Anthropocene: conservation of bats in a changing world. Springer International Publishing. Berlin, Germany.

Voigt, C. C., F. Matt, R. Michener, and T. H. Kunz. 2003. Low turnover rates of carbon isotopes in tissues of two nectar-feeding bat species. The Journal of Experimental Biology 206(Pt 8):1419–1427.

Walsh, R. E., A. P. Aprígio Assis, J. L. Patton, G. Marroig, T. E. Dawson, and E. A. Lacey. 2016. Morphological and dietary responses of chipmunks to a century of climate change. Global Change Biology 22:3233–3252.

Wang, J., W. Gao, L. Wang, W. Metzner, J. Ma, and J. Feng. 2010. Seasonal variation in prey abundance influences habitat use by greater horseshoe bats (*Rhinolophus ferrumequinum*) in a temperate deciduous forest. Canadian Journal of Zoology 88:315–323.

Wang, Y., X. Chen, and F. Yan. 2015. Spatial and temporal variations of annual precipitation during 1960–2010 in China. Quaternary International 380–381:5–13.

Welbergen, J. A., S. M. Klose, N. Markus, and P. Eby. 2008. Climate change and the effects of temperature extremes on Australian flying-foxes. Proceedings of the Royal Society B: Biological Sciences 275:419–425.

Williams-Guillén, K., E. Olimpi, B. Maas, P. J. Taylor, and R. Arlettaz. 2016. Bats in the anthropogenic matrix: challenges and opportunities for the conservation of Chiroptera and their ecosystem services in agricultural landscapes. Pp. 1137–1139 in Bats in the Anthropocene: conservation of bats in a changing world (C. C. Voit and T. Kingston, eds.). Springer International Publishing. Berlin, Germany.

Wu, J. 2016. Detection and attribution of the effects of climate change on bat distributions over the last 50 years. Climatic Change 134:681–696.

Yang, Q.-S., L. Xia, Z.-J. Feng, Y. Ma, G.-Q. Quan, and Y. Wu. 2007. A guide to the measurement of mammal skull V: Insectivora and Chiroptera. Chinese Journal of Zoology 42:56–62.

Yom-Tov, Y., and E. Geffen. 2006. Geographic variation in body size: the effects of ambient temperature and precipitation. Oecologia 148:213–218.

Yom-Tov, Y., and E. Geffen. 2011. Recent spatial and temporal changes in body size of terrestrial vertebrates: probable causes and pitfalls. Biological Reviews of the Cambridge Philosophical Society 86:531–541.

Yom-Tov, Y., A. Roos, P. Mortensen, Ø. Wiig, S. Yom-Tov, and T. M. Heggberget. 2010. Recent changes in body size of the Eurasian otter *Lutra lutra* in Sweden. Ambio 39:496–503.

Yom-Tov, Y., and J. Yom-Tov. 2005. Global warming, Bergmann's rule and body size in the masked shrew *Sorex cinereus* Kerr in Alaska. Journal of Animal Ecology 74:803–808.

Zhang, L., Z. Luo, D. Mallon, C. Li, and Z. Jiang. 2016. Biodiversity conservation status in China's growing protected areas. Biological Conservation 210:89–100.

Zhang, M.-G., Z.-K. Zhou, W.-Y. Chen, J. W. Ferry Slik, C. H. Cannon, and N. Raes. 2012. Using species distribution modeling to improve conservation and land use planning of Yunnan, China. Biological Conservation 153:257–264.

Zomer, R. J., J. Xu, M. Wang, A. Trabucco, and Z. Li. 2015. Projected impact of climate change on the effectiveness of the existing protected area network for biodiversity conservation within Yunnan Province, China. Biological Conservation 184:335–345.

Submitted 19 April 2019. Accepted 30 September 2019.

Associate Editor was John Scheibe.

APPENDIX I

Specimens examined.—Detailed sampling information for two bat species included in our study of phenotypic traits. The letter "B" in the "Applied" column indicates that both the wing membrane and cranial measurements were used in the final analysis, "S" indicates that only cranial measurements were available; and "W" indicates that only wing membrane was available. The acronyms for each museum are as follows: Guangdong Institute of Applied Biology Resources (GIABR), the Kunming Institute of Zoology, the Chinese Academy of Sciences (KIZ), the National Zoological Museum of China (NZMC), the Northwest Institute of Plateau Biology (NIPB), the Shaanxi Institute of Zoology (SIZ), and the China West Normal University (CWNU).

Species	Register number	Sampling number	Sex	Sampling date	Longitude (°N)	Latitude(°E)	Source	Applied
H. armiger	0673		Male	19640918	109.451466	19.230122	GIABR	B
H. armiger	0674		Male	19640918	109.451466	19.230122	GIABR	B
H. armiger	0205		Female	19630404	109.827576	18.736005	GIABR	B
H. armiger	0294		Male	19631116	109.681835	18.908357	GIABR	B
H. armiger	0295		Male	19631116	109.681835	18.908357	GIABR	B
H. armiger	0591		Female	19640718	109.055443	19.301261	GIABR	B
H. armiger	0592		Female	19640718	109.055443	19.301261	GIABR	B
H. armiger	87		Male	19611024	112.56609	23.162299	GIABR	B
H. armiger	252		Female	19590907	114.678726	24.483399	GIABR	B
H. armiger	0560		Male	19580711	109.120674	19.334794	GIABR	B
H. armiger	0563		Male	19580711	109.120674	19.334794	GIABR	B
H. armiger	0203		Male	19630404	109.827576	18.736005	GIABR	B
H. armiger	0590		Female	19640718	109.054585	19.302881	GIABR	B
H. armiger	0675		Female	19640918	109.451466	19.230122	GIABR	B
H. armiger	0677		Male	19640918	109.451466	19.230122	GIABR	B
H. armiger	0678		Male	19640918	109.451466	19.230122	GIABR	B
H. armiger	0681		Female	19640918	109.451466	19.230122	GIABR	B
H. armiger	0682		Female	19640918	109.451466	19.230122	GIABR	B
H. armiger	55		Female	19580904	108.336182	23.099944	GIABR	B
H. armiger	56		Female	19580904	108.336182	23.099944	GIABR	B
H. armiger	253		Male	19590907	114.678726	24.483399	GIABR	B
H. armiger	187		Male	19590819	114.487152	24.378372	GIABR	B
H. armiger	188		Male	19530819	114.487152	24.378372	GIABR	W
H. armiger	0676		Female	19640918	109.451466	19.230122	GIABR	B
H. armiger	0680		Female	19640918	109.451466	19.230122	GIABR	B
H. armiger	183		Female	19581023	106.766338	22.095462	GIABR	B
H. armiger	185		Female	19581023	106.766338	22.095462	GIABR	B
H. armiger	0558		Female	19580711	109.120674	19.334794	GIABR	B
H. armiger	0559		Female	19580711	109.120674	19.334794	GIABR	B
H. armiger	0679		Male	19640918	109.451466	19.230122	GIABR	B
H. armiger	0561		Female	19580711	109.120674	19.334794	GIABR	B
H. armiger	0562		Female	19580711	109.120674	19.334794	GIABR	W
H. armiger	58		Male	19580904	108.336182	23.099944	GIABR	B
H. armiger	57		Female	19580904	108.336182	23.099944	GIABR	B
H. armiger	52		Female	19580904	108.336182	23.099944	GIABR	B
H. armiger	54		Female	19580904	108.336182	23.099944	GIABR	B
H. armiger	31		Female	19580903	108.336182	23.099944	GIABR	B
H. armiger	32		Female	19580903	108.336182	23.099944	GIABR	B
H. armiger	02899	631053	Male	19630705	104.891968	25.108606	KIZ	B
H. armiger	02895	631054	Male	19630705	104.891968	25.108606	KIZ	B
H. armiger	02901	631055	Male	19630705	104.891968	25.108606	KIZ	B
H. armiger	02896	631056	Female	19630705	104.891968	25.108606	KIZ	B
H. armiger	02906	631057	Female	19630705	104.891968	25.108606	KIZ	B
H. armiger	02898	631058	Female	19630705	104.891968	25.108606	KIZ	B
H. armiger	02903	631059	Female	19630705	104.891968	25.108606	KIZ	B
H. armiger	02907	631060	Female	19630705	104.891968	25.108606	KIZ	B
H. armiger	02897	631061	Female	19630705	104.891968	25.108606	KIZ	B
H. armiger	02900	631062	Female	19630705	104.891968	25.108606	KIZ	B
H. armiger	02904	631063	Female	19630705	104.891968	25.108606	KIZ	B
H. armiger	02902	631065	Male	19630705	104.891968	25.108606	KIZ	B
H. armiger	02908	631064	Female	19630705	104.891968	25.108606	KIZ	B
H. armiger	02905	631066	Female	19630705	104.891968	25.108606	KIZ	B
H. armiger	002881	631235	Male	19630630	104.726572	24.9182	KIZ	B
H. armiger	002890	631236	Male	19630630	104.726572	24.9182	KIZ	B
H. armiger	002888	631242	Male	19630630	104.726572	24.9182	KIZ	B
H. armiger	002889	631247	Male	19630630	104.726572	24.9182	KIZ	B
H. armiger	002887	631248	Male	19630630	104.726572	24.9182	KIZ	B
H. armiger	002893	631088	Female	19630707	104.891968	25.111715	KIZ	B
H. armiger	02894	631089	Female	19630707	104.891968	25.111715	KIZ	B
H. armiger	02884	631238	Male	19630630	104.726572	24.9182	KIZ	B

APPENDIX I Continued

Species	Register number	Sampling number	Sex	Sampling date	Longitude (°N)	Latitude(°E)	Source	Applied
H. armiger	02882	631237	Male	19630630	104.726572	24.9182	KIZ	B
H. armiger	02860	631239	Male	19630630	104.726572	24.9182	KIZ	B
H. armiger	02867	631243	Male	19630630	104.726572	24.9182	KIZ	B
H. armiger	02863	631244	Male	19630630	104.726572	24.9182	KIZ	B
H. armiger	02866	631245	Male	19630630	104.726572	24.9182	KIZ	B
H. armiger	02885	631246	Male	19630630	104.726572	24.9182	KIZ	B
H. armiger	02883	631241	Male	19630630	104.726572	24.9182	KIZ	B
H. armiger	02880	631249	Male	19630630	104.726572	24.9182	KIZ	B
H. armiger	02859	631250	Male	19630630	104.726572	24.9182	KIZ	B
H. armiger	02865	631251	Male	19630630	104.726572	24.9182	KIZ	B
H. armiger	02862	631253	Male	19630630	104.726572	24.9182	KIZ	B
H. armiger	002864	631254	Male	19630630	104.726572	24.9182	KIZ	B
H. armiger	02857	631255	Male	19630630	104.726572	24.9182	KIZ	B
H. armiger	02861	631252	Male	19630630	104.726572	24.9182	KIZ	B
H. armiger	02891	631256	Male	19630630	104.726572	24.9182	KIZ	B
H. armiger	02858	631111	Male	19630718	104.894028	25.104876	KIZ	B
H. armiger	02828	630679	Female	19631003	108.83812	27.715142	KIZ	B
H. armiger	02830	630680	Male	19631003	108.83812	27.715142	KIZ	B
H. armiger	02831	630681	Male	19631003	108.83812	27.715142	KIZ	B
H. armiger	02829	630682	Female	19631003	108.83812	27.715142	KIZ	B
H. armiger	02846	631196	Male	19630831	108.524323	25.943844	KIZ	B
H. armiger	02845	631202	Male	19630831	108.524323	25.943844	KIZ	B
H. armiger	02849	631203	Male	19630831	108.524323	25.943844	KIZ	B
H. armiger		631204	Male	19600831	108.524323	25.943844	KIZ	S
H. armiger	02850	631207	Male	19630831	108.524323	25.943844	KIZ	B
H. armiger	02854	631208	Male	19630831	108.524323	25.943844	KIZ	B
H. armiger	02852	631209	Male	19630831	108.524323	25.943844	KIZ	B
H. armiger	02851	631211	Male	19630831	108.524323	25.943844	KIZ	B
H. armiger	02847	631214	Female	19630831	108.524323	25.943844	KIZ	B
H. armiger	02853	631215	Female	19630831	108.524323	25.943844	KIZ	B
H. armiger	02848	630615	Male	19630901	108.524323	25.943844	KIZ	B
H. armiger	02834	630437	Male	19631024	106.21994	27.473552	KIZ	B
H. armiger	02840	631299	Male	19630805	105.441284	25.116067	KIZ	B
H. armiger	02832	631385	Female	19631023	106.21994	27.473552	KIZ	B
H. armiger	02839	630417	Male	19631025	106.747284	25.442655	KIZ	B
H. armiger	02842	630418	Male	19631025	106.747284	25.442655	KIZ	B
H. armiger	02844	630419	Male	19631025	106.747284	25.442655	KIZ	B
H. armiger	02841	630420	Female	19631025	106.747284	25.442655	KIZ	B
H. armiger	02843	630421	Female	19631025	106.747284	25.442655	KIZ	B
H. armiger	02838	630422	Male	19601025	106.747284	25.442655	KIZ	B
H. armiger	000826	612	Male	19600629	103.386412	29.553188	KIZ	B
H. armiger	014692	811442	Male	19641022	101.509552	24.144952	KIZ	B
H. armiger	015935	2004251	Male	20050919	100.083904	24.71405	KIZ	B
H. armiger	015936	2004252	Female	20050919	100.083904	24.71405	KIZ	B
H. armiger		57173	Male	19571103	100.622191	22.033019	KIZ	S
H. armiger	000097	75938	Male	19590728	101.382694	21.711423	KIZ	B
H. armiger	000098	75939	Male	19590728	101.382694	21.711423	KIZ	B
H. armiger	000096	75940	Male	19590725	101.382694	21.711423	KIZ	B
H. armiger	000117	75941	Male	19590728	101.382694	21.711423	KIZ	B
H. armiger	000116	75883	Male	19590618	101.382694	21.711423	KIZ	B
H. armiger	000114	75881	Male	19590618	101.382694	21.711423	KIZ	B
H. armiger	000089	75882	Male	19590618	101.382694	21.711423	KIZ	B
H. armiger	000118	75869	Male	19590620	101.382694	21.711423	KIZ	B
H. armiger	000115	75884	Male	19590618	101.382694	21.711423	KIZ	B
H. armiger	02926	640271	Male	19640731	100.580306	24.455705	KIZ	B
H. armiger		640272	Female	19640731	100.961266	24.270049	KIZ	B
H. armiger	02924	640273	Female	19640731	100.580306	24.455705	KIZ	B
H. armiger	02927	640274	Male	19640731	100.961266	24.270049	KIZ	B
H. armiger	02939	640275	Female	19640731	100.580306	24.455705	KIZ	B
H. armiger	02922	640404	Male	19641110	100.961266	24.270049	KIZ	B
H. armiger	02923	640405	Female	19641110	100.961266	24.270049	KIZ	B
H. armiger	02940	640406	Male	19641110	100.961266	24.270049	KIZ	B
H. armiger	02929	640407	Male	19641116	100.961266	24.270049	KIZ	B
H. armiger	02921	640408	Male	19641110	100.961266	24.270049	KIZ	B
H. armiger	02932	640409	Male	19641110	100.961266	24.270049	KIZ	B
H. armiger	02930	640369	Male	19640913	100.778575	24.544781	KIZ	B
H. armiger	000091	57179	Male	19571020	100.749478	24.487031	KIZ	B
H. armiger	000095	57178	Male	19571023	100.749478	24.487031	KIZ	B
H. armiger	000088	57181	Male	19571029	100.749478	24.487031	KIZ	B

APPENDIX I Continued

Species	Register number	Sampling number	Sex	Sampling date	Longitude (°N)	Latitude(°E)	Source	Applied
H. armiger	000093	57182	Female	19571115	100.749478	24.487031	KIZ	W
H. armiger	015943	206120	Female	20060404	103.382936	25.099551	KIZ	B
H. armiger	015944	206121	Male	20060404	103.382936	25.099551	KIZ	B
H. armiger	015940	206117	Female	20060404	103.382936	25.099551	KIZ	B
H. armiger	015942	206119	Female	20060404	103.382936	25.099551	KIZ	B
H. armiger	000892	610033	Female	19610623	102.609987	25.059983	KIZ	B
H. armiger	000896	610036	Male	19610615	102.609987	25.059983	KIZ	B
H. armiger	012364	205022	Female	20050520	102.464676	25.195777	KIZ	B
H. armiger	012365	205023	Male	20050520	102.464676	25.195777	KIZ	B
H. armiger	000898	610017	Male	19610809	104.702368	23.126784	KIZ	B
H. armiger	016397	206785	Female	20060402	99.703889	24.197965	KIZ	B
H. armiger	016398	206786	Female	20060402	99.703889	24.197965	KIZ	B
H. armiger	016401	206814	Female	20060502	99.703889	24.197965	KIZ	B
H. armiger	016399	206787	Female	20060402	99.703889	24.197965	KIZ	B
H. armiger	016400	206813	Female	20060502	99.703889	24.197965	KIZ	B
H. armiger	016016	206296	Male	20060602	98.801079	25.302131	KIZ	B
H. armiger	016017	206297	Male	20060602	98.801079	25.302131	KIZ	B
H. armiger	016018	206298	Male	20060602	98.801079	25.302131	KIZ	B
H. armiger	016019	206299	Male	20060602	98.801079	25.302131	KIZ	B
H. armiger	016020	206300	Male	20060602	98.801079	25.302131	KIZ	B
H. armiger		206205	Female	20060521	98.762927	24.150865	KIZ	S
H. armiger	016232	206720	Male	20070408	98.801079	25.302131	KIZ	W
H. armiger	015939	206114	Male	20060328	102.464676	25.195777	KIZ	B
H. armiger	015938	206113	Male	20060328	102.464676	25.195777	KIZ	B
H. armiger	21	3058	Male	19660712	105.583506	32.830738	SIZ	B
H. armiger	00019	03056	Female	19660712	105.583506	32.830738	SIZ	B
H. armiger	00023	03057	Male	19660712	105.583506	32.830738	SIZ	W
H. armiger	00022	03055	Female	19660712	105.583506	32.830738	SIZ	W
H. armiger	00016	03051	Male	19660712	105.583506	32.830738	SIZ	B
H. armiger	18		Male	19660712	105.583506	32.830738	SIZ	B
H. armiger		23	Male	19660712	105.543981	32.880632	SIZ	S
H. armiger		27	Male	19660712	105.543981	32.880632	SIZ	S
H. armiger		25	Male	19660712	105.543981	32.880632	SIZ	S
H. armiger		28	Male	19660712	105.543981	32.880632	SIZ	S
H. armiger		26	Male	19660712	105.543981	32.880632	SIZ	S
H. armiger		02002	Male	20020908	106.004505	31.562447	CWNU	B
H. armiger	22948	265	Male	19630910	119.223933	25.976564	NZMC	B
H. armiger	21441	91	Male	19580914	106.748013	22.120272	NZMC	B
H. armiger	21440	53	Female	19580904	108.336182	23.099944	NZMC	B
H. armiger	12761	71097	Female	19570310	108.902664	18.725763	NZMC	B
H. armiger	12749	71098	Female	19570310	108.902664	18.725763	NZMC	B
H. armiger	12750	71096	Female	19570310	108.902664	18.725763	NZMC	B
H. armiger	04973	0164	Female	19560625	103.656006	23.180764	NZMC	B
H. armiger	04953	0174	Male	19560625	103.656006	23.180764	NZMC	B
H. armiger	04950	0171	Female	19560625	103.656006	23.180764	NZMC	B
H. armiger	04951	0170	Female	19560625	103.656006	23.180764	NZMC	B
H. armiger	24107	0200	Male	19640628	99.686637	23.401386	NZMC	B
H. armiger	04967	0177	Male	19560625	103.656006	23.180764	NZMC	B
H. armiger	04966	0176	Male	19560625	103.656006	23.180764	NZMC	B
H. armiger	04959	0179	Female	19560625	103.656006	23.180764	NZMC	B
H. armiger	24106	0401	Male	19640628	99.686637	23.401386	NZMC	B
H. armiger	24104	0013	Female	19640411	99.73805	24.09987	NZMC	B
H. armiger	24105	0198	Female	19640628	99.686637	23.401386	NZMC	B
H. armiger	24101	0016	Male	19640411	99.73805	24.09987	NZMC	B
H. armiger	24100	0014	Female	19640411	99.73805	24.09987	NZMC	B
H. armiger	24108	0197	Male	19640628	99.686637	23.401386	NZMC	B
H. armiger	24102	0199	Male	19640628	99.686637	23.401386	NZMC	B
H. armiger	24103	0015	Female	19640411	99.73805	24.09987	NZMC	B
H. armiger	24015	0815	Female	19640430	98.119454	24.748195	NZMC	B
H. armiger	24014	0654	Male	19650408	97.929382	24.731864	NZMC	B
H. armiger	24016	0811	Male	19650428	98.119454	24.748195	NZMC	B
H. armiger	24019	0816	Male	19650430	98.119454	24.748195	NZMC	B
H. armiger	24017	0655	Male	19650418	97.929382	24.731864	NZMC	B
H. armiger	24012	0658	Male	19650418	97.929382	24.731864	NZMC	B
H. armiger	24013	0656	Female	19650418	97.929382	24.731864	NZMC	B
H. armiger	24018	0657	Male	19650418	97.929382	24.731864	NZMC	B
H. armiger	24020	0848	Female	19650507	98.119454	24.748195	NZMC	B
H. armiger	24011	0659	Male	19650418	97.929382	24.731864	NZMC	W
H. armiger	17516	0733	Female	19600727	101.506805	27.454665	NZMC	B

APPENDIX I Continued

Species	Register number	Sampling number	Sex	Sampling date	Longitude (°N)	Latitude(°E)	Source	Applied
H. armiger	17515	0732	Female	19600727	101.506805	27.454665	NZMC	B
H. armiger	17511	00279	Male	19600629	103.386412	29.553188	NZMC	B
H. armiger	17513	0721	Male	19600721	101.506805	27.454665	NZMC	B
H. armiger	17512	0744	Male	19600728	101.506805	27.454665	NZMC	B
H. armiger	17514	0729	Female	19600727	101.506805	27.454665	NZMC	B
H. armiger	17517	0746	Male	19600728	101.506805	27.454665	NZMC	B
H. armiger		BN-2017-01	Female	20170326	101.276253	21.921008	Resampled	B
H. armiger		BN-2017-05	Male	20170408	101.276253	21.921008	Resampled	B
H. armiger		BN-2017-06	Female	20170408	101.276253	21.921008	Resampled	B
H. armiger		BN-2017-07	Female	20170408	101.276253	21.921008	Resampled	B
H. armiger		BN-2017-08	Female	20170408	101.276253	21.921008	Resampled	B
H. armiger		BN-2017-09	Female	20170408	101.276253	21.921008	Resampled	B
H. armiger		BN-2017-10	Male	20170408	101.276253	21.921008	Resampled	B
H. armiger		BN-2017-11	Female	20170408	101.276253	21.921008	Resampled	B
H. armiger		BN-2017-12	Male	20170408	101.276253	21.921008	Resampled	B
H. armiger		BN-2017-13	Female	20170408	101.276253	21.921008	Resampled	B
H. armiger		CTD-2017-0	Male	20170519	99.212841	24.563708	Resampled	B
H. armiger		CTD-2017-0	Male	20170519	99.212841	24.563708	Resampled	B
H. armiger		EMS-2017-0	Female	20170608	103.460839	29.506348	Resampled	B
H. armiger		EMS-2017-0	Male	20170608	103.460839	29.506348	Resampled	B
H. armiger		EMS-2017-0	Male	20170608	103.460839	29.506348	Resampled	B
H. armiger		EMS-2017-0	Female	20170608	103.460839	29.506348	Resampled	B
H. armiger		EMS-2017-0	Male	20170608	103.460839	29.506348	Resampled	B
H. armiger		EMS-2017-0	Male	20170608	103.460839	29.506348	Resampled	B
H. armiger		GZ-2017-09	Male	20170416	114.796548	23.184034	Resampled	B
H. armiger		GZ-2017-10	Male	20170416	114.796548	23.184034	Resampled	B
H. armiger		GZ-2017-11	Male	20170416	114.796548	23.184034	Resampled	B
H. armiger		GZ-2017-12	Male	20170416	114.796548	23.184034	Resampled	B
H. armiger		GZ-2017-13	Female	20170416	114.796548	23.184034	Resampled	B
H. armiger		GZ-2017-14	Male	20170416	114.796548	23.184034	Resampled	B
H. armiger		GZ-2017-15	Female	20170416	114.796548	23.184034	Resampled	B
H. armiger		GZ-2017-16	Male	20170416	114.796548	23.184034	Resampled	B
H. armiger		GZ-2017-17	Male	20170416	114.796548	23.184034	Resampled	B
H. armiger		HXS-2017-0	Male	20170705	99.225007	24.600176	Resampled	B
H. armiger		HXS-2017-0	Male	20170705	99.225007	24.600176	Resampled	B
H. armiger		HXS-2017-0	Male	20170705	99.225007	24.600176	Resampled	B
H. armiger		HXS-2017-0	Male	20170705	99.225007	24.600176	Resampled	B
H. armiger		HXS-2017-0	Male	20170705	99.225007	24.600176	Resampled	B
H. armiger		HXS-2017-0	Male	20170705	99.225007	24.600176	Resampled	B
H. armiger		KM-2017–28	Male	20170502	102.293	24.483	Resampled	B
H. armiger		KM-2017–30	Male	20170502	102.293	24.483	Resampled	B
H. armiger		KM-2017–31	Male	20170502	102.293	24.483	Resampled	B
H. armiger		KM-2017–33	Female	20170502	102.293	24.483	Resampled	B
H. armiger		KM-2017–34	Female	20170502	102.293	24.483	Resampled	B
H. armiger		KM-2017–35	Female	20170502	102.293	24.483	Resampled	B
H. armiger		KM-2017–36	Male	20170502	102.293	24.483	Resampled	B
H. armiger		KM-2017–47	Male	20170503	102.293	24.483	Resampled	B
H. armiger		LX-2017-01	Male	20170710	100.707386	22.606501	Resampled	B
H. armiger		LX-2017-02	Male	20170710	100.707386	22.606501	Resampled	B
H. armiger		LX-2017-03	Male	20170710	100.707386	22.606501	Resampled	B
H. armiger		LX-2017-04	Male	20170710	100.707386	22.606501	Resampled	B
H. armiger		LX-2017-05	Female	20170710	100.707386	22.606501	Resampled	B
H. armiger		LX-2017-06	Male	20170710	100.707386	22.606501	Resampled	B
H. armiger		LX-2017-08	Female	20170710	100.707386	22.606501	Resampled	B
H. armiger		LX-2017-09	Male	20170710	100.707386	22.606501	Resampled	B
H. armiger		LX-2017-10	Male	20170710	100.707386	22.606501	Resampled	B
H. armiger		LX-2017-11	Male	20170710	100.707386	22.606501	Resampled	B
H. armiger		MB-2017-01	Male	20170515	98.82391	25.094888	Resampled	B
H. armiger		MB-2017-02	Male	20170515	98.82391	25.094888	Resampled	B
H. armiger		XM-2017-01	Female	20170513	97.582266	24.628573	Resampled	B
H. armiger		XM-2017-02	Female	20170513	97.582266	24.628573	Resampled	B
H. armiger		XMS-2017-	Male	20170821	109.660385	18.883071	Resampled	B
H. armiger		XMS-2017-	Male	20170821	109.660385	18.883071	Resampled	B
H. armiger		XMS-2017-	Male	20170821	109.660385	18.883071	Resampled	B
H. armiger		XMS-2017-	Male	20170821	109.660385	18.883071	Resampled	B
H. armiger		XMS-2017-	Male	20170821	109.660385	18.883071	Resampled	B
H. armiger		XMS-2017-	Male	20170821	109.660385	18.883071	Resampled	B
H. armiger		XMS-2017-	Male	20170821	109.660385	18.883071	Resampled	B
H. armiger		XNH-2017-0	Female	20170617	107.014999	32.857642	Resampled	B

APPENDIX I Continued

Species	Register number	Sampling number	Sex	Sampling date	Longitude (°N)	Latitude(°E)	Source	Applied
H. armiger		XNH-2017-0	Male	20170617	107.014999	32.857642	Resampled	B
H. armiger		XNH-2017-0	Female	20170617	107.014999	32.857642	Resampled	B
H. armiger		XNH-2017-0	Male	20170617	107.014999	32.857642	Resampled	B
H. armiger		XNH-2017-0	Male	20170617	107.014999	32.857642	Resampled	B
H. armiger		XNH-2017-0	Female	20170617	107.014999	32.857642	Resampled	B
H. armiger		XNH-2017-0	Female	20170617	107.014999	32.857642	Resampled	B
H. armiger		XNH-2017-0	Female	20170617	107.014999	32.857642	Resampled	B
H. armiger		XNH-2017-0	Male	20170617	107.014999	32.857642	Resampled	B
H. armiger		XNH-2017-1	Male	20170617	107.014999	32.857642	Resampled	B
H. armiger		XY-2017-05	Male	20170810	104.847087	24.922542	Resampled	B
H. armiger		XY-2017-06	Female	20170810	104.847087	24.922542	Resampled	B
H. armiger		XY-2017-08	Male	20170810	104.847087	24.922542	Resampled	B
H. armiger		XY-2017-09	Female	20170810	104.847087	24.922542	Resampled	B
H. armiger		XY-2017-11	Female	20170810	104.847087	24.922542	Resampled	B
H. armiger		XY-2017-12	Female	20170810	104.847087	24.922542	Resampled	B
H. armiger		XY-2017-13	Female	20170810	104.847087	24.922542	Resampled	B
H. armiger		XY-2017-14	Female	20170810	104.847087	24.922542	Resampled	B
H. armiger		ZWY-2017-1	Male	20170717	101.25839	21.926604	Resampled	B
H. armiger		ZWY-2017-1	Female	20170717	101.25839	21.926604	Resampled	B
H. armiger		XTBG-2017	Female	20170912	101.25839	21.926604	Resampled	B
R. leschenaultii	0337		Male	19631219	109.097414	19.123396	CIABR	B
R. leschenaultii	0338		Male	19631210	109.097414	19.123396	CIABR	B
R. leschenaultii	0344		Female	19631219	109.097414	19.123396	CIABR	B
R. leschenaultii	0693		Male	19641011	109.054585	19.302881	CIABR	B
R. leschenaultii	0575		Female	19640716	109.054585	19.302881	CIABR	B
R. leschenaultii	0576		Female	19640716	109.054585	19.302881	CIABR	B
R. leschenaultii	0341		Female	19631219	109.097414	19.123396	CIABR	B
R. leschenaultii	0342		Female	19631219	109.097414	19.123396	CIABR	B
R. leschenaultii	2022		Male	19701120	114.348621	23.661585	CIABR	B
R. leschenaultii	2023		Male	19701120	114.348621	23.661585	CIABR	B
R. leschenaultii	0430		Female	19640102	109.081321	19.118327	CIABR	B
R. leschenaultii	0431		Female	19640120	109.081321	19.118327	CIABR	B
R. leschenaultii	0343		Male	19631219	109.097414	19.123396	CIABR	B
R. leschenaultii	0345		Male	19631219	109.097414	19.123396	CIABR	B
R. leschenaultii	0339		Female	19631219	109.097414	19.123396	CIABR	B
R. leschenaultii	0340		Female	19631210	109.097414	19.123396	CIABR	B
R. leschenaultii	0348		Male	19631219	109.097414	19.123396	CIABR	W
R. leschenaultii	0350		Male	19631219	109.097414	19.123396	CIABR	W
R. leschenaultii	2018		Male	19701120	114.348621	23.661742	CIABR	W
R. leschenaultii	2019		Male	19701120	114.348621	23.661742	CIABR	W
R. leschenaultii	200		Male	19581027	107.032328	21.81772	CIABR	B
R. leschenaultii	2024		Male	19701120	114.348621	23.661742	CIABR	B
R. leschenaultii	2025		Male	19701120	114.348621	23.661742	CIABR	B
R. leschenaultii	0571		Male	19640716	109.054585	19.302881	CIABR	B
R. leschenaultii	0572		Male	19640817	109.054585	19.302881	CIABR	W
R. leschenaultii	2016		Female	19701120	114.348621	23.661742	CIABR	B
R. leschenaultii	2017		Male	19701120	114.348621	23.661742	CIABR	W
R. leschenaultii	2030		Female	19701120	114.348621	23.661742	CIABR	B
R. leschenaultii	0573		Female	19640716	109.054585	19.302881	CIABR	B
R. leschenaultii	0574		Female	19640716	109.054585	19.302881	CIABR	B
R. leschenaultii	256		Male	19581027	106.766768	22.095422	CIABR	B
R. leschenaultii	2028		Female	19701120	114.348621	23.661742	CIABR	B
R. leschenaultii	2029		Female	19701120	114.348621	23.661742	CIABR	B
R. leschenaultii	2092		Male	19700903	111.829448	23.599071	CIABR	B
R. leschenaultii	189		Male	19581029	107.032328	21.81772	CIABR	B
R. leschenaultii	190		Male	19581029	107.032328	21.81772	CIABR	B
R. leschenaultii	2020		Male	19701120	114.348621	23.661742	CIABR	B
R. leschenaultii	2021		Male	19701120	114.348621	23.661742	CIABR	B
R. leschenaultii	2093		Male	19700903	111.829448	23.599071	CIABR	B
R. leschenaultii	194		Male	19581029	107.032328	21.81772	CIABR	B
R. leschenaultii	196		Male	19581027	107.032328	21.81772	CIABR	B
R. leschenaultii	012375	2005001	Male	20050520	102.464676	25.195777	KIZ	B
R. leschenaultii	012376	205002	Male	20050520	102.464676	25.195777	KIZ	B
R. leschenaultii	012377	205003	Female	20050520	102.464676	25.195777	KIZ	B
R. leschenaultii	012378	205004	Female	20050520	102.464676	25.195777	KIZ	B
R. leschenaultii	012379	205005	Female	20050520	102.464676	25.195777	KIZ	B
R. leschenaultii	012380	2005006	Female	20050520	102.464676	25.195777	KIZ	B
R. leschenaultii	012381	205007	Female	20050520	102.464676	25.195777	KIZ	B
R. leschenaultii	012382	205008	Female	20050520	102.464676	25.195777	KIZ	B

APPENDIX I Continued

Species	Register number	Sampling number	Sex	Sampling date	Longitude (°N)	Latitude(°E)	Source	Applied
R. leschenaultii	012366	205009	Female	20050520	102.464676	25.195777	KIZ	W
R. leschenaultii	012367	205010	Female	20050520	102.464676	25.195777	KIZ	W
R. leschenaultii	012369	205012	Female	20050520	102.464676	25.195777	KIZ	W
R. leschenaultii	012370	205013	Male	20050520	102.464676	25.195777	KIZ	W
R. leschenaultii	012371	205014	Female	20050520	102.464676	25.195777	KIZ	B
R. leschenaultii	012372	205015	Female	20050520	102.464676	25.195777	KIZ	B
R. leschenaultii	012384	205062	Female	20050225	101.997972	23.597419	KIZ	B
R. leschenaultii	012385	205072	Female	20050525	101.997972	23.597419	KIZ	B
R. leschenaultii	012386	205073	Female	20050525	101.997972	23.597419	KIZ	B
R. leschenaultii	012387	205074	Female	20050525	101.997972	23.597419	KIZ	B
R. leschenaultii	012388	205075	Female	20050525	101.997972	23.597419	KIZ	B
R. leschenaultii	012389	205076	Female	20050525	101.997972	23.597419	KIZ	B
R. leschenaultii	005757	077019	Female	19701113	102.550464	24.364612	KIZ	W
R. leschenaultii	015989	206319	Male	20060608	99.081573	23.565875	KIZ	B
R. leschenaultii	016069	206656	Female	20070127	101.88858	25.971626	KIZ	B
R. leschenaultii	016070	206659	Female	20070127	101.88858	25.971626	KIZ	B
R. leschenaultii	016071	206667	Male	20070127	101.88858	25.971626	KIZ	B
R. leschenaultii	016072	206670	Male	20070127	101.88858	25.971626	KIZ	B
R. leschenaultii	016073	206671	Male	20070127	101.88858	25.971626	KIZ	B
R. leschenaultii	016074	206672	Male	20070127	101.88858	25.971626	KIZ	B
R. leschenaultii	005736	780309	Female	19700808	98.896823	26.526263	KIZ	W
R. leschenaultii	005737	780343	Female	19700811	98.896823	26.526263	KIZ	B
R. leschenaultii	005738	780344	Female	19700811	98.896823	26.526263	KIZ	B
R. leschenaultii	012204	2030001	Male	20030107	103.187027	26.089472	KIZ	B
R. leschenaultii	012205	2030002	Male	20030107	103.187027	26.089472	KIZ	B
R. leschenaultii	012206	2030003	Male	20030107	103.187027	26.089472	KIZ	B
R. leschenaultii	012207	2030004	Male	20030107	103.187027	26.089472	KIZ	B
R. leschenaultii	012210	2030007	Male	20030107	103.187027	26.089472	KIZ	B
R. leschenaultii	012209	2030006	Female	20030107	103.187027	26.089472	KIZ	B
R. leschenaultii	012208	2030005	Female	20030107	103.187027	26.089472	KIZ	B
R. leschenaultii	015629	2004327	Male	20040110	103.187027	26.089472	KIZ	B
R. leschenaultii	012181	201075	Female	20041114	98.801079	25.302131	KIZ	B
R. leschenaultii	012182	201076	Female	20041114	98.801079	25.302131	KIZ	B
R. leschenaultii		201077	Female	20041114	98.801079	25.302131	KIZ	S
R. leschenaultii		201078	Female	20041114	98.801079	25.302131	KIZ	S
R. leschenaultii		201079	Female	20041114	98.801079	25.302131	KIZ	S
R. leschenaultii		201081	Female	20041114	98.801079	25.302131	KIZ	S
R. leschenaultii		201082	Female	20041114	98.801079	25.302131	KIZ	S
R. leschenaultii		201086	Female	20041114	98.801079	25.302131	KIZ	S
R. leschenaultii		201088	Female	20041114	98.801079	25.302131	KIZ	S
R. leschenaultii		201092	Female	20041114	98.801079	25.302131	KIZ	S
R. leschenaultii		201093	Female	20041114	98.801079	25.302131	KIZ	S
R. leschenaultii	012190	201084	Female	20041114	98.801079	25.302131	KIZ	S
R. leschenaultii	015982	2004200	Female	20050913	98.886952	24.983335	KIZ	B
R. leschenaultii	015983	2004201	Male	20050913	98.886952	24.983335	KIZ	B
R. leschenaultii	015987	206310	Male	20060604	98.815155	25.160201	KIZ	B
R. leschenaultii	015988	206311	Female	20060604	98.815155	25.160201	KIZ	B
R. leschenaultii	015985	206302	Female	20060602	98.815155	25.160201	KIZ	B
R. leschenaultii	015984	206301	Female	20060602	98.815155	25.160201	KIZ	B
R. leschenaultii	015986	206303	Male	20060602	98.815155	25.160201	KIZ	B
R. leschenaultii	012122	201072	Male	20041114	98.801079	25.302131	KIZ	B
R. leschenaultii	012179	201073	Female	20041114	98.801079	25.302131	KIZ	B
R. leschenaultii	012180	201074	Female	20041114	98.801079	25.302131	KIZ	B
R. leschenaultii		201085	Female	20041114	98.801079	25.302131	KIZ	S
R. leschenaultii	012193	201087	Female	20041115	98.801079	25.302131	KIZ	B
R. leschenaultii	012202	201096	Female	20041115	98.801079	25.302131	KIZ	B
R. leschenaultii	00072	75914	Male	19590913	101.382694	21.711423	KIZ	B
R. leschenaultii	000063	75915	Male	19590913	101.382694	21.711423	KIZ	B
R. leschenaultii	000074	75916	Female	19590913	101.382694	21.711423	KIZ	B
R. leschenaultii	000076	75917	Male	19590913	101.382694	21.711423	KIZ	B
R. leschenaultii	000070	75918	Female	19590913	101.382694	21.711423	KIZ	B
R. leschenaultii	000073	75919	Female	19590913	101.382694	21.711423	KIZ	B
R. leschenaultii	000068	75920	Male	19590913	101.382694	21.711423	KIZ	B
R. leschenaultii	000067	75921	Male	19590913	101.382694	21.711423	KIZ	B
R. leschenaultii	000069	75922	Female	19590913	101.382694	21.711423	KIZ	B
R. leschenaultii	005834	84382	Male	19701231	103.057637	22.676986	KIZ	B
R. leschenaultii	005832	84383	Male	19701231	103.057637	22.676986	KIZ	B
R. leschenaultii	005833	84384	Male	19701231	103.057637	22.676986	KIZ	B
R. leschenaultii	32331	5103	Male	19700625	99.021149	25.862931	NZMC	B

APPENDIX I Continued

Species	Register number	Sampling number	Sex	Sampling date	Longitude (°N)	Latitude(°E)	Source	Applied
R. leschenaultii	32330	5104	Male	19700625	99.021149	25.862931	NZMC	B
R. leschenaultii	195	21428	Male	19581029	107.032328	21.81772	NZMC	B
R. leschenaultii	192	21429	Male	19581029	107.032328	21.81772	NZMC	B
R. leschenaultii		96026	Male	19560602	101.519809	27.018455	CWNU	W
R. leschenaultii		96027	Female	19560602	101.519809	27.018455	CWNU	W
R. leschenaultii		LT-2017-03	Male	20170701	99.253127	24.429283	Resampled	B
R. leschenaultii		LT-2017-04	Male	20170701	99.253127	24.429283	Resampled	B
R. leschenaultii		LT-2017-05	Male	20170701	99.253127	24.429283	Resampled	B
R. leschenaultii		LT-2017-06	Male	20170701	99.253127	24.429283	Resampled	B
R. leschenaultii		LT-2017-07	Female	20170701	99.253127	24.429283	Resampled	B
R. leschenaultii		LT-2017-08	Male	20170701	99.253127	24.429283	Resampled	B
R. leschenaultii		MM-2017-12	Female	20170729	99.22891	24.407752	Resampled	B
R. leschenaultii		MM-2017-15	Male	20170729	99.22891	24.407752	Resampled	B
R. leschenaultii		MM-2017-17	Female	20170729	99.22891	24.407752	Resampled	B
R. leschenaultii		MM-2017–18	Male	20170729	99.22891	24.407752	Resampled	B
R. leschenaultii		MM-2017–20	Male	20170729	99.22891	24.407752	Resampled	B
R. leschenaultii		PJG-2017-0	Female	20170726	98.841678	24.966822	Resampled	B
R. leschenaultii		XSC-2017-0	Female	20170731	98.841678	24.966822	Resampled	B
R. leschenaultii		XSC-2017-0	Female	20170731	98.841678	24.966822	Resampled	B
R. leschenaultii		XSC-2017-0	Male	20170731	98.841678	24.966822	Resampled	B
R. leschenaultii		XSC-2017-0	Male	20170731	98.841678	24.966822	Resampled	B
R. leschenaultii		XSC-2017-0	Female	20170731	98.841678	24.966822	Resampled	B
R. leschenaultii		XSC-2017-0	Female	20170731	98.841678	24.966822	Resampled	B
R. leschenaultii		XSC-2017-0	Male	20170731	98.841678	24.966822	Resampled	B
R. leschenaultii		XSC-2017-0	Female	20170731	98.841678	24.966822	Resampled	B
R. leschenaultii		XSC-2017-0	Female	20170731	98.841678	24.966822	Resampled	B
R. leschenaultii		XSC-2017-1	Female	20170731	98.841678	24.966822	Resampled	B
R. leschenaultii		XSC-2017-1	Female	20170731	98.841678	24.966822	Resampled	B
R. leschenaultii		XTBG-2017	Female	20170912	101.25839	21.926604	Resampled	B
R. leschenaultii		XTBG-2017	Female	20170916	101.25839	21.926604	Resampled	B
R. leschenaultii		XTBG-2017	Male	20170918	101.25839	21.926604	Resampled	B
R. leschenaultii		XTBG-2017	Female	20170918	101.25839	21.926604	Resampled	B
R. leschenaultii		XTBG-2017	Male	20170918	101.25839	21.926604	Resampled	B
R. leschenaultii		XTBG-2017	Male	20170918	101.25839	21.926604	Resampled	B