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ARTICLE

Impacts on Bats by a Supertyphoon vs. Ordinary Typhoons along a Habitat Urbanization Gradient

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ABSTRACT

Two major human-caused threats to ecosystems are habitat modification and the increasing frequency and intensity of extreme weather events. To study the combined effect of these threats, the authors used acoustic monitoring of bats along a habitat modification gradient on the island of Okinawa, Japan. During the observation period, the island experienced numerous typhoons and one supertyphoon. Native bat species remained active even at high wind speeds (up to 30 m/s in some cases). Milder typhoons had no observable effect on bat populations, with activity levels fully recovering within a few hours or days. The super typhoon also did not seem to affect bats in fully or partially forested habitats but caused their local disappearance at the urban site, which they have not re-colonized three years after the event. Notably, bats that disappeared at the urban site were species roosting in well-protected places such as caves and concrete structures. In all cases, the biomass of small flying insects and the acoustic activity of insects recovered within days after extreme weather events. Thus, the striking difference between habitats in supertyphoon effects on bats cannot be explained by the super typhoon directly killing bats, destroying their roosting sites, or decreasing the abundance of their prey. The results underscore the importance of preserving natural habitats in areas particularly affected by changing climate and show that the survival of species and ecosystems during the numerous episodes of climate change in the Earth's history does not necessarily mean their ability to survive the accelerating climate change of our time.

Keywords: Acoustic monitoring; Chiroptera; Climate change; Extreme weather events; Hurricanes; OKEON; Okinawa; Urbanization gradient

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1. Introduction

Human impacts on global ecosystems are multiple and complex, but two factors are now becoming particularly prominent: Accelerating climate change and direct habitat alteration. Do the effects of these two processes simply add up, or is there a magnification of the impact when they act in combination? To find out, we looked at the combined effects of extreme weather events, which are increasing in frequency and intensity due to climate change [1-4], and of urbanization of landscape (the most radical form of habitat alteration) on the populations of insectivorous bats in an island ecosystem.

Bats are one of the groups of mammals most exposed to tropical cyclones [5] and represent an ideal bioindicator group for studies of their effects on populations [6,7]. One of the reasons for using bats as bioindicators is that their foraging activity can be recorded with automatic ultrasound detectors, providing information about long-term trends in their abundance.

We used acoustic monitoring by automatic ultrasound recordings. This method has to be used with caution for studies of short-term or minor population changes because the results are greatly affected by weather and other short-term environmental factors, as well as by pseudoreplication (a bat performing multiple passes over the microphone or repeatedly vocalizing from perch located in its vicinity can considerably skew the data) and by recorder placement [8]. It is, however, highly reliable for studies of major long-term population trends, particularly local extinctions [9-12].

Despite the limitations of the small number of sites, our experimental design allowed us to monitor the status of study taxa along the gradients of both factors, and to test a few hypotheses using strong inference. (1) If bats are equally sensitive to extreme weather events in all habitats, they can be predicted to respond to those events similarly at all study sites. If not, there should be observable differences between the study sites. (2) If the native bat species' adaptations to such events are fully sufficient to survive even the most extreme of them, there should be no difference in population effects between typhoons of different intensities; if not, supertyphoons should have a greater impact than milder typhoons.

The results of the study have serious implications for bat conservation at a time when both the rates of habitat modification and the intensity of extreme weather events are increasing exponentially.

2. Methods

2.1 Study area

At 1200 km^2, Okinawa is the largest island in the Ryukyu (Nansei) island arc, stretching between Taiwan and the main islands of Japan. Okinawa has a subtropical maritime climate, with an average temperature of 22.3 °C and annual rainfall of 2083 mm [13]. There is no pronounced dry season, and temperature changes are sufficiently mild to allow bat foraging activity in all months. The southern part of the island is densely populated and almost completely built over; the central part is approximately 60% forested; the northern part is mostly covered by primary and secondary evergreen broadleaf forests [13]. The island has been inhabited by humans for at least 32,000 years, and urbanization in the south started at least a thousand years ago [14].

Okinawa is located in the part of the world most affected by tropical cyclones, called typhoons in the northwestern Pacific region. The island experiences direct hits almost annually, sometimes more than 10 times a year, and often in rapid succession. Super typhoons (typhoons with sustained wind speeds of more than 67 m/s [3]) are much less frequent, impacting the island a few times per decade. According to the data provided by Japan Meteorological Agency, during the study period (1 Mar 2018-31 Oct 2020) Okinawa experienced 12 typhoons, one of which (Trami) had super typhoon-strength winds when passing the island, with a radar-recorded sustained wind speed of 72 m/s and surface sustained wind speed of 56 m/s (**Table 1** notes that maximum wind speeds recorded by Doppler radars at higher altitudes are much higher than wind speeds recorded by ground-based weather stations).

Table 1. Typhoons on the island of Okinawa during the study period.

Number	Name	Date	Status at landfall	Max. sustained surface wind speed at Okinawa, km/h
201806	Gaemi	16 Jun 2018	typhoon	72
201807	Prapiroon	2 Jul 2018	typhoon	125
201810	Anpil	21 Jul 2018	typhoon	63
201814	Yagi	11 Aug 2018	typhoon	76
201818	Rumbia	15 Aug 2018	typhoon	80
201824	Trami	30 Sep 2018	super typhoon	201
201825	Kong-Rey	4 Oct 2018	typhoon	106
201917	Tapah	21 Sep 2019	typhoon	144
201927	Fung-Wong	23 Oct 2019	typhoon	102
202008	Bavi	24 Aug 2020	typhoon	90
202009	Maysak	01 Oct 2020	typhoon	166
202010	Hayshen	06 Oct 2020	typhoon	162

2.2 Study sites

Our long-term study sites (**Table 2**, **Figure 1**) were selected among pre-established OKEON monitoring sites to form a gradient from (1) an old secondary or primary forest with a closed canopy and no human-made structures, through (2) a younger secondary forest with clearings and a few buildings nearby and (3) woodland/settlement edge with highly fragmented tree cover and numerous buildings nearby, to (4) an agricultural field with isolated trees, surrounded by the urban landscape. We also conducted short-term sampling using various methods (see below) at numerous locations throughout the island.

2.3 Study species

Seven species of echolocating bats have been recorded in Okinawa. All of them have easily distinguishable vocalizations [15,16]. Their natural history on Okinawa has been poorly studied, even though most of them are endemic to the Ryukyus and of conservation concern [17].

Yambaru myotis (*Myotis yanbarensis*), birdlike noctule (*Nyctalus aviator*), and an unknown species tentatively identified as Chinese pipistrelle (*Hypsugo pulveratus*) [15], were recorded in our long-term study sites only twice, six times, and once, respectively (each species at just one site), and were excluded from the analysis due to this paucity of data.

The remaining four species, all very small insectivores breeding in late spring-early summer (outside the typhoon season), are:

(1) Okinawan horseshoe bat (*Rhinolophus pumilus*, **Figure 2A**). Mostly a forest species that forage below the canopy, often from a perch, and roosts predominantly in caves and cave-like man-made structures [18], although it would also roost in hollow trees (VD pers. obs.). This species is highly sedentary, so much so that bats in the southern and northern parts of Okinawa differ in echolocation frequencies [19], suggesting a lack of gene flow. Among our study sites (**Table 2**), OIST site had bats with the "southern" echolocation frequency, while Hentona and Manabi-no-Mori sites had bats with the "northern" frequency.

(2) Ryukyu bentwing (*Miniopterus fuscus*, **Figure 2B**). A fast flyer that forages above and below the canopy and also in open areas ([20]; also our data). It is an intra-island migrant, with most of the Okinawa population spend late winter and early spring in a roost inside a road bridge in the north of the island and the rest of the year in a cave in the far south of it [21]. Unless this species forages exceptionally far from roosts, there must be other, possibly smaller, unknown roosts on the island, because we recorded it throughout the year at all our sites (with clear peaks in early spring and virtually no records in summer at Manabi-no-Mori, see Results).

Table 2. Ultrasound recorders on the island of Okinawa, Japan, that were used for systematic data collection.

Site	Dates of operation	Coordinates	Elevation, m	Habitat	Operation schedule
Manabi-no-Mori	11 Jun 2018-30 Oct 2020	26°43'19" N 128°15'32" E	146	old secondary subtropical rainforest*dominated by itaji (*Castanopsis sieboldii*), with trees mostly 10-20 m tall, on a north-facing ravine slope above small stream, with primary forest immediately uphill (**Figure 1E**)	2 weeks on, 2 weeks off; continuous after 1 July 2019
OIST	1 May 2018-31 Oct 2019	26°27'34" N 127°50'9" E	132	dense secondary forest*dominated by Taiwanese cherry (*Prunus campanulata*), with trees mostly 4-6 m tall, on a north-facing hillslope, near small clearings and a few houses (**Figure 1D**)	continuous
Hentona	11 Jun 2018-22 Feb 2020	26°42'11" N 128°07'53" E	12	degraded coastal woodland*dominated by introduced Australian pine tree (*Casuarina equisetifolia*), with trees 3-4 m tall, on a south-facing slope above a built-over area (**Figure 1C**)	2 weeks on, 2 weeks off; continuous after 1 July 2019
Ginowan	5 May 2018-7 Jun 2019; 1-30 Nov 2021	26°16'52" N 127°44'39" E	4	taro field with isolated trees surrounded by densely built-over urban area (**Figure 1B**)	2 weeks on, 2 weeks off

* Habitat classification according to Saito (2011).

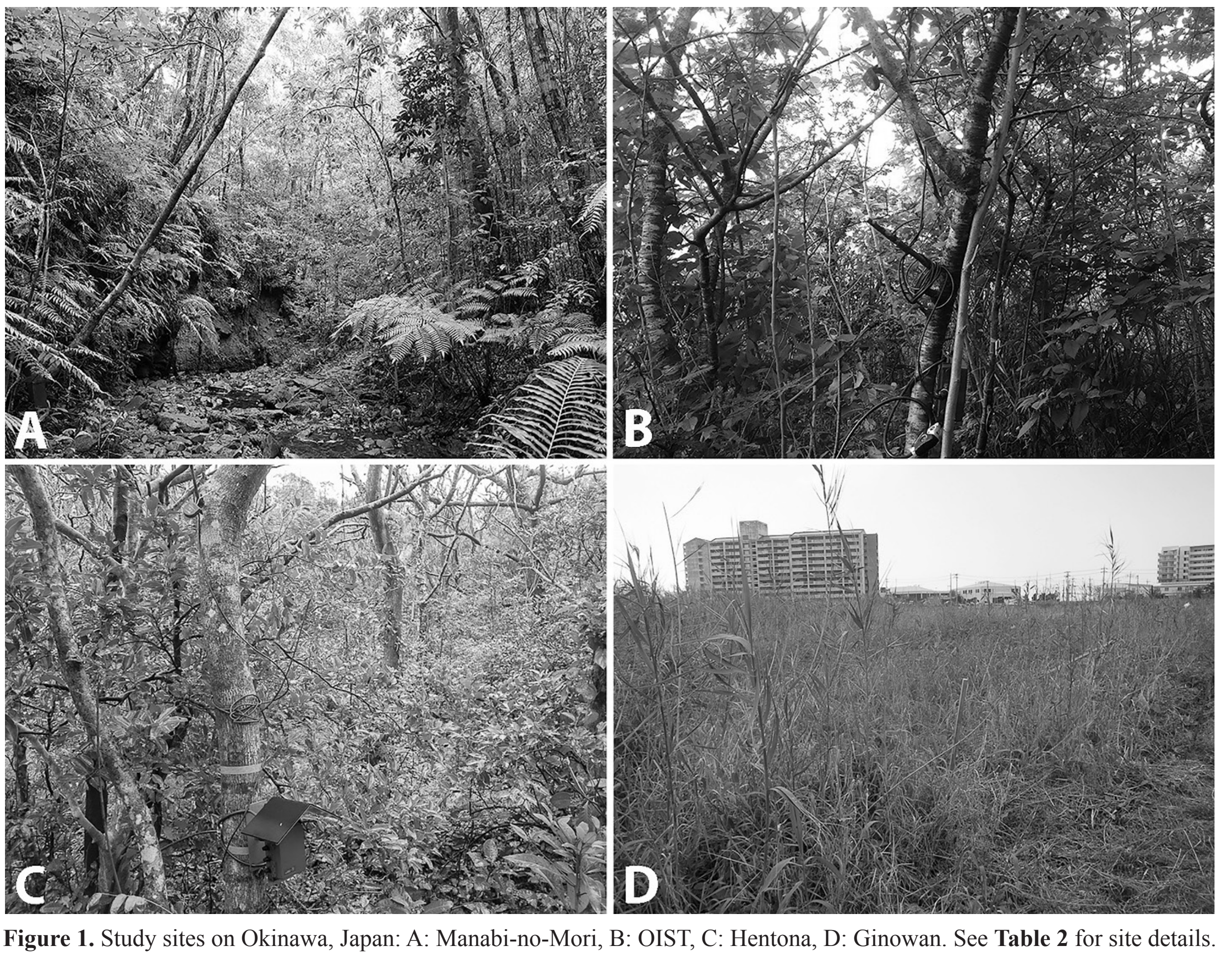

Figure 1. Study sites on Okinawa, Japan: A: Manabi-no-Mori, B: OIST, C: Hentona, D: Ginowan. See **Table 2** for site details.

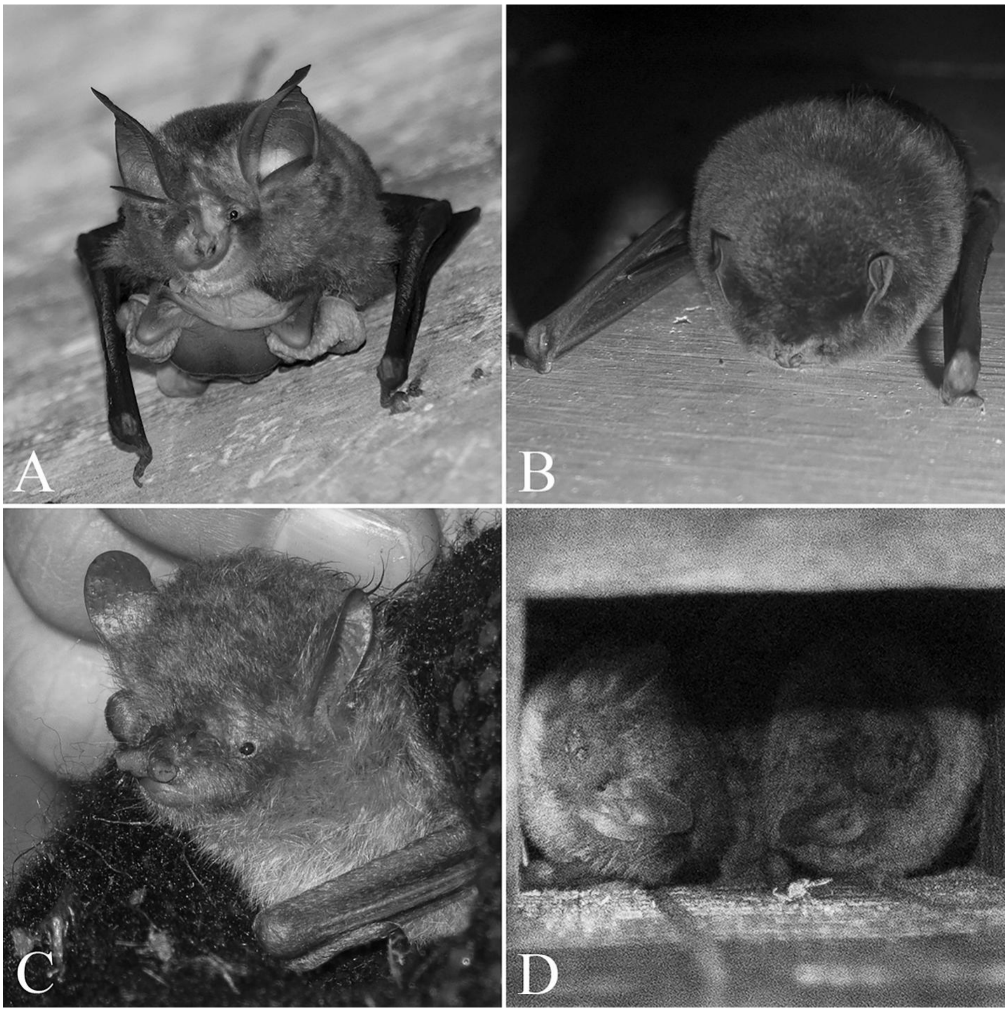

Figure 2. Bat species regularly detected by automatic recorders: A: Okinawan horseshoe bat (*Rhinolophus pumilus*, female with newborn), B: Ryukyu bentwing (*Miniopterus fuscus*), C: Ryukyu tube-nosed bat (*Murina ryukyuana*), D: Japanese pipistrelle (*Pipistrellus abramus*).

(3) Ryukyu tube-nosed bat (*Murina ryukyuana*, **Figure 2C**). A slow flyer that forages below the canopy, sometimes in dense thickets, and roosts in clumps of dry leaves and other vegetation shelters, usually in the undergrowth [22,23]. It occurs only in continuous forests of northern Okinawa and was recorded only at one of our sites, the relatively pristine Manabi-no-Mori site (**Figure 1A**). Its echolocation calls have very low intensity and can only be recorded at extremely close range, so most of our recordings were of social calls.

(4) Japanese pipistrelle (*Pipistrellus abramus*, **Figure 2D**) is the "house bat" in most of the Far East, occurring mostly in urban and agricultural landscapes, roosting in human-made structures, such as concrete buildings and bridges, and foraging over open areas [24,25]. Possibly a recent colonizer on Okinawa, it was localized and declining Okinawa and occurred only in two urban areas at the beginning of our study (H. Tamura, unpublished data, 2018). It was recorded only at one of our sites, the urban Ginowan site (**Figure 1D**).

2.4 Collecting bat data

The OKEON Churamori Project (https://okeon.unit.oist.jp/) is conducting ecoacoustic monitoring on Okinawa to study population trends of local fauna [26]. The main focus of the project is insect and bird research. As part of this project, four SM4BAT-FS automatic recorders with SMM-U2 ultrasound microphones (Wildlife Acoustics, USA) were installed at four study sites (**Table 2**) to study bat behavior and activity dynamics. The recorder at Ginowan site was installed on a pole 1.5 m above ground in an open field; the other recorders were installed on trees 2-3 m above ground, at the edges of less cluttered forest patches that could be used as bat flyways, with microphones facing those patches and pointing upwards at approximately 45°. The units operated from sunset to sunrise, with 12 dB gain, 256 kHz sample rate, 1.5 ms minimal duration, 20 kHz minimum trigger frequency, 12 dB trigger level, and 3 s trigger window. Kaleidoscope software (by Wildlife Acoustics, USA) was used to produce and analyze sonograms. The recordings were collected every two weeks, screened manually (as most of them contained only insect calls) and identified to species. Due to technical malfunctions, site access issues and other practicalities, the recorders did not always operate on the same dates (**Table 2**).

We also conducted non-systematic observations using EcoMeter Touch 2 portable bat detector (also by Wildlife Acoustics) and Quantum Lite XQ23V thermal imager (by Pulsar, Lithuania). Such observations were conducted in June 2019 and June 2020 at 12 locations within a 5-km radius of the Ginowan site and at a known location of a Japanese pipistrelle population in southern Okinawa. The results of these observations are presented below for context but were not included in the analysis.

2.5 Collecting insect and weather data

Concurrently with ultrasound recordings, we recorded weather data and flying insects at our sites. Flying insects were caught with malaise traps SLAM-Large BT1005 (manufactured by MegaView Science Co., Ltd., Taiwan), with three traps at each site that were checked every two weeks. Each trap was covered with protective netting to exclude insects larger than 1 cm (to protect rare species). Sometimes the traps didn't work during the first collection period after a typhoon because of wind damage.

Our automatic recorders also recorded very large numbers (sometimes hundreds per night) of calls from nocturnal insects, presumably mostly Orthoptera, despite the fact that only ultrasound frequencies (20 kHz and higher) were sampled.

2.6 Data analysis

We used the Mann-Whitney test for comparing the activity of each bat species and insect numbers before and after each typhoon at each site, and Wilcoxon matched-pairs test for comparing these variables as before and after averages for all typhoons and sites. One case where bats disappeared completely was excluded from the latter test (see below).

3. Results

3.1 Bat behavior during typhoons

Bats of all species did not show decreased activity during the approach of typhoons, ceased vocalizing only when maximum wind speeds exceeded 20 m/s (with a few records even during maximum wind speeds of 30 m/s), and resumed normal activity immediately after a typhoon's passage (**Figure 3**). This was true for recorders installed in protected as well as open locations, and for all species—not just the fast-flying, long-winged Ryukyu bentwing but even for the short-winged Ryukyu tube-nosed bat which has slow, bat-like flight (VD pers. obs.).

Interestingly, the only record of an Okinawan horseshoe bat ever obtained at the Ginowan site was made at 01:33 on 28 September 2018, less than 48 hours before the arrival of super typhoon Trami, hinting at the possibility of some unusual movement at that time, perhaps to avoid unsafe habitats (a pre-typhoon behavior documented in other animals [27]).

3.2 Effects of typhoons on bat populations

At three of the four study sites, there was no observable effect of typhoons on any bat species we monitored (**Figure 4**): Bat activity recovered to pre-typhoon levels within hours of the typhoon's passage and was not affected in the long term, either ($P > 0.5$ in all tests).

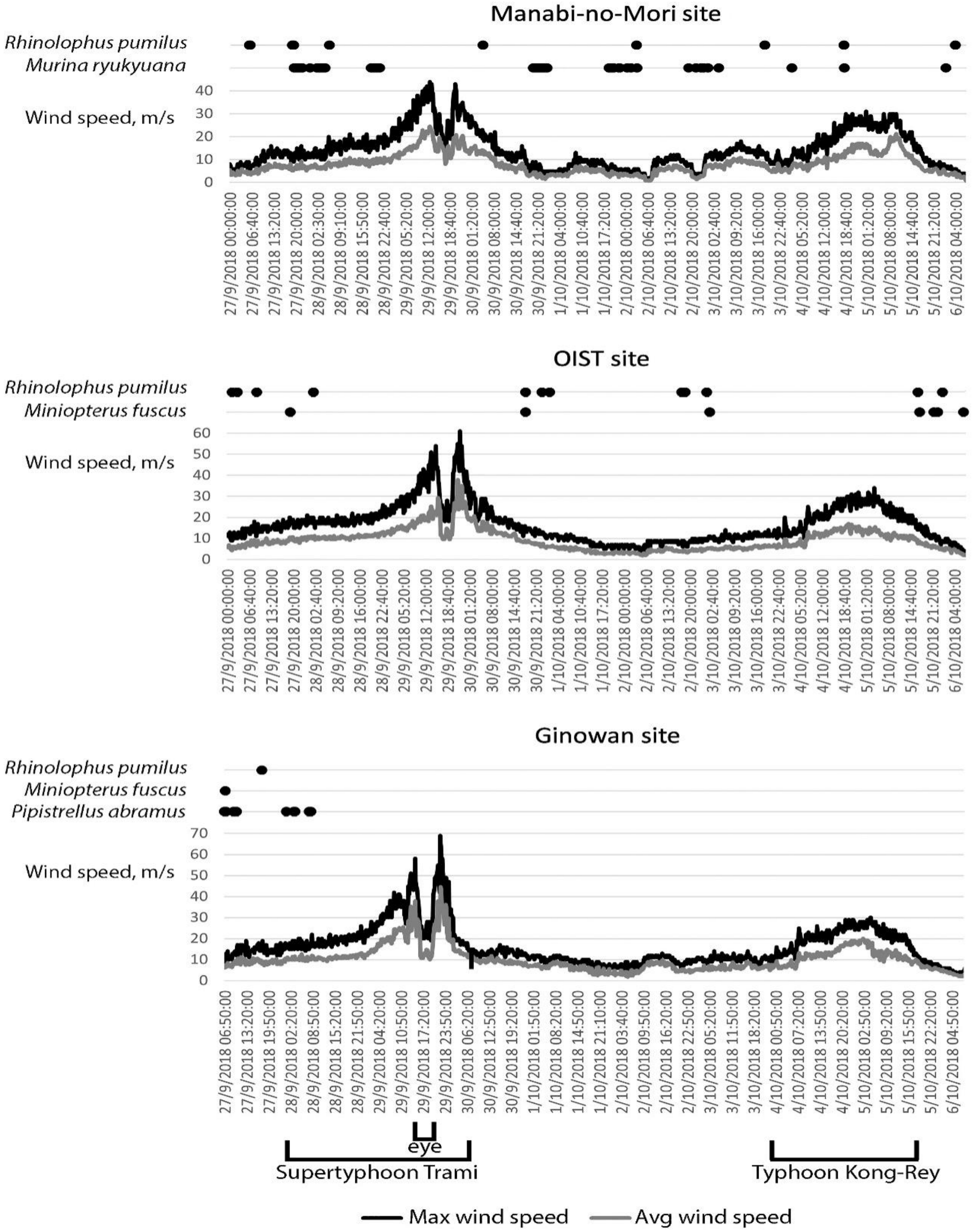

Figure 3. Acoustic detections of bats by automatic recorders at 3 long-term study sites in Okinawa, Japan during the passage of super typhoon Trami and typhoon Kong-Rey on 27 September-6 October 2018, and wind speeds during that period.

At the urban Ginowan site, however, the first five typhoons of 2018 did not have any observable effect (P > 0.5 in all tests), but after the passage of super typhoon Trami, none of the two species previously recorded regularly at that site (~4 times per night for *M. fuscus* and ~1/2 times per night for *P. abramus*) were recorded again. They appear to be locally extinct at the site and were not recorded during a follow-up survey in November 2021. Their disappearance happened on the day of Trami's passage (**Figures 3 and 4**), and this clearly was not a coincidence ($P < 0.003$). Japanese pipistrelles still survive in low numbers in southern Okinawa, where we recorded them with a hand-held detector on 25 June 2019 (at 26°10'20" N, 127°39'22" E). As for Ryukyu bent wings, it is unknown if they died out in Ginowan or migrated elsewhere on the island; on 27 June 2019, this species was recorded by a hand-held bat detector at a forest edge just 3 km from the Ginowan site (26°15'56" N 127°46'54" E).

3.3 Effects of typhoons on insects

Surprisingly, there was no observable effect of typhoons on flying insects' biomass (P > 0.3 in all tests). Even super typhoon Trami followed by typhoon Kong-Rey didn't seem to have any effect, except for the few hours immediately after the event (**Figure 5A**). In the long term, the monthly average biomass of flying insects at Ginowan site, where bats disappeared during typhoon Trami and were never recorded again, increased by about 1/3 between November 2018 and November 2021.

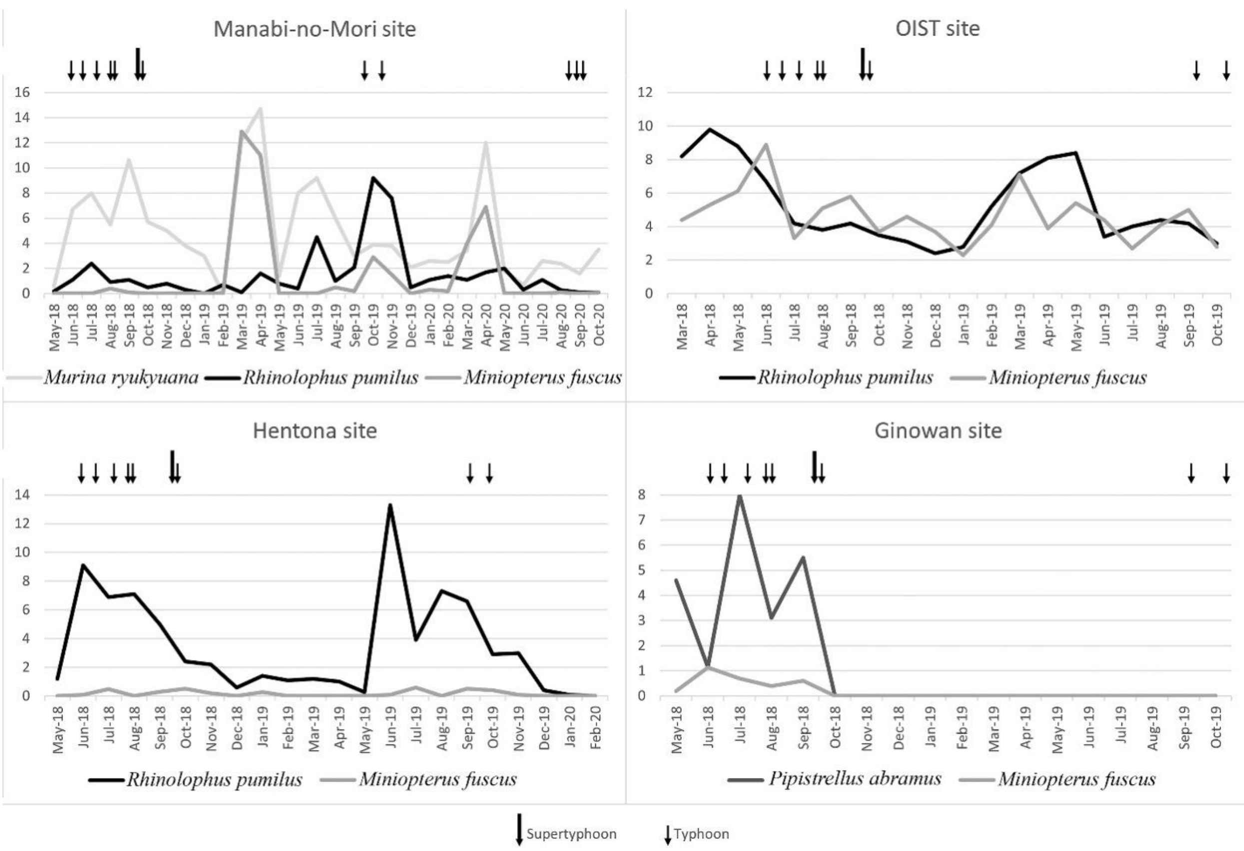

Figure 4. Monthly averages of the number of bat recordings per night, obtained by automatic recorders at 4 long-term study sites in Okinawa, Japan. Times of typhoon and supertyphoon hits on the island are marked on top of each chart.

Ultrasound recorders did not record any lasting effect of typhoons on the number of insect calls. Some insects were called even during the passage of the eye wall of Trami, when the wind speeds reached 70 m/s. Call numbers returned to pre-typhoon levels within a few days after each typhoon's passage (**Figure 5B**). In the long term, the average nightly number of insect calls at the Ginowan site, where bats disappeared during typhoon Trami and were never recorded again, increased approximately five-fold between November 2018 and November 2022.

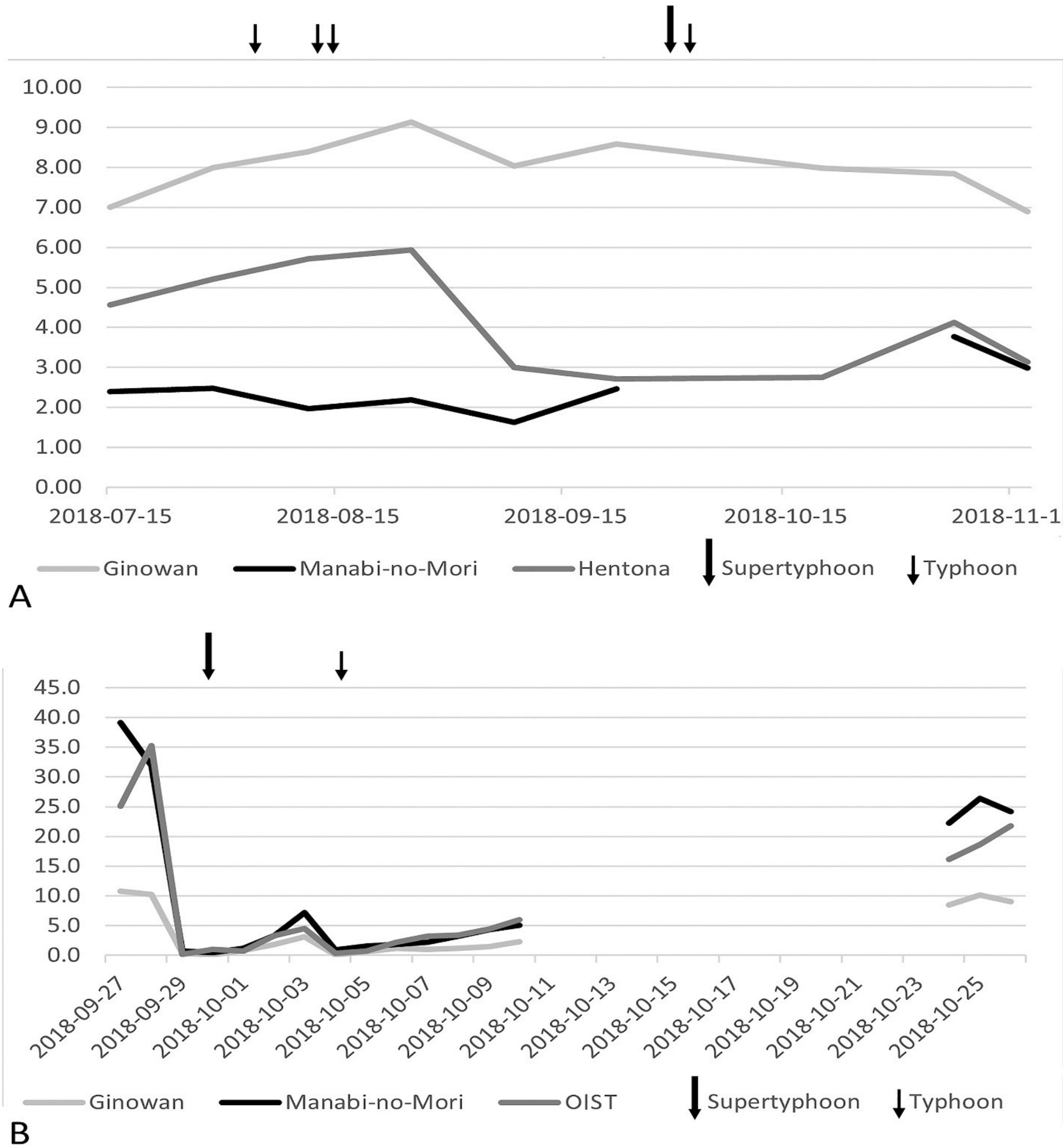

Figure 5. Effects of super typhoon Trami (30 September 2018) and typhoon Kong-Rey (5 October 2018) on insect populations at two long-term study sites in Okinawa, Japan: A: biomass of flying insects smaller than 1 cm, collected by malaise traps in July-October 2018; B: nightly averages of the numbers of acoustic recordings of insects (at or above 20 kHz) per hour on 27 September-27 October 2018 (the recorders did not work on October 11-23).

4. Discussion

Extreme weather events are a major evolutionary force exerting strong selection pressure [28]. Due to the high frequency of typhoons in Okinawa, native bat species can be expected to be well adapted to them behaviorally and physiologically [29]. Indeed, at non-urban sites our results are consistent with high survival of each species throughout all typhoons without observable negative effects, even when super typhoon Trami was followed by typhoon Kong-Rey within just five days (**Table 1**, **Figure 4**), resulting in massive damage to the island's vegetation, particularly in semi-open coastal areas such as our Hentona site. Studies of the effects of hurricanes on bats in the West Indies [30-32] and Mexico [7] have also shown that small insectivorous species (to which group all focal species of our study belong) are relatively little affected; those studies were conducted entirely in forested habitats except for the latter one.

But at the urban Ginowan site, super typhoon Trami resulted in the local disappearance of both bat species previously observed. Why did this happen?

Direct killing of bats or destruction of their roosting sites by the super typhoon cannot explain the observed pattern. At the Manabi-no-Mori site, the Ryukyu tube-nosed bat, which roosts in vegetation rather than in sheltered caves or concrete structures, did not seem to be affected at all (**Figure 3**). On the other hand, both species at Ginowan disappeared, even though they roost in concrete structures and other well-protected locations.

Of these two species, the Japanese pipistrelle, a bat of mostly urban habitats throughout much of its range, might be a relatively recent colonizer in Okinawa (judging by its roosting only in man-made structures in cities and by lack of morphological differences from conspecifics elsewhere), thus lacking adaptations to super typhoons. Its populations on Okinawa and adjacent islands were already highly localized and declining ([33]; also H. Tamura, unpublished data, 2018), and such populations are known to sometimes go extinct after very strong tropical cyclones [34,35]. However, the other of these two species, the Ryukyu bentwing, is endemic (thus native) to the Ryukyu Islands, and for that species, we observed no decline at our other sites. Yanbaru myotis, an extremely rare and local Ryukyu endemic (not included in our analysis because it was detected at long-term study sites only twice, at Manabu-no-Mori), continued to be regularly detected by targeted searches in its core habitat area following super typhoon Trami [23,36]. Apparently, the reasons for the disappearance of bats at the Ginowan site must be site-specific rather than species-specific.

Another possible explanation is the destruction of bats' prey species by the super typhoon. But there was no lasting effect on flying insect biomass as measured by malaise traps (**Figure 5A**) or on the calling activity of nocturnal insects (**Figure 5B**), the latter presumably small Orthoptera that are eaten by both Japanese pipistrelle and Ryukyu bent wing [24,37]. A dip in insect biomass that lasted for only a few days would be extremely unlikely to have a negative effect on bats. Okinawan bats can survive for a few days without food and can enter torpor if needed even at high ambient temperatures: Thermal imaging showed that some bats in small caves and bridge colonies remain active during winter nights when the air temperature drops almost to freezing and there are no flying insects, while other bats are in torpor on summer nights (VD pers. obs.). There is a possibility that some insects critically important for bats at the Ginowan site were disproportionally affected by the super typhoon, but their decline was recorded by neither the malaise traps nor the acoustic recorders. Indeed, there was a noticeable absence of some taxa such as large butterflies in the first few weeks after the passage of Trami, Kong-Rey and some other typhoons (VD pers. obs.), so it is possible that larger moths were also missing. This, however, is still an unlikely reason for the disappearance of bats at the Ginowan site because (1) both bat species recorded there were dietary generalists [20,24,25,37], and (2) there were alternative foraging/roosting areas available within a short distance, including the OIST site just 20 km away where bats didn't seem to have been negatively affected. Bats can easily shift to new foraging areas after hurricanes [38]. Also, note that the

Ginowan site had more small flying insects than other sites both before and after the typhoons.

It is also unclear why the Ginowan site was not recolonized by bats three years after their disappearance. Japanese pipistrelle was already a rare and declining species on the island, and its remaining population after the super typhoon is more than 10 km away (see above). But Ryukyu bentwing is still common in forested parts of the island, occurs just 3 km from the Ginowan site, and could recolonize easily. Habitat change is unlikely to have played a role: Many taro fields in the area were abandoned and became overgrown during that time, but the numbers of flying and ultrasonically active insects increased (approximately by 1/3 and five-fold, respectively) rather than decreased.

Whatever the mechanism, our results allowed testing the predictions made above, showing that (1) there is a major difference in bats' susceptibility to extreme weather events between more- and less-modified habitats, and (2) that in the more modified habitats, native species' adaptations become insufficient for surviving such events.

Similar results along modification gradients were obtained by Sil-Berra et al. [7] who used a different methodology (mist netting) to sample bat activity in Jalisco, Mexico, before and after Hurricane Patricia (category IV, equal to a super typhoon). That study was more short-term and covered only one extreme weather event, while our study covered 12. Sil-Berra et al. mist netted bats twice before and twice after a hurricane at each site, while we used continuous acoustic monitoring. Sil-Berra et al. observed a population decrease in nectarivorous bats, but an increase in insectivorous bats, both particularly pronounced in disturbed habitats. Other studies of the effects of hurricanes on bats, all conducted in the West Indies (except for a few studies of *Pteropus* flying foxes on Pacific Ocean islands), did not look at differences between habitats (see [7] for bibliography).

5. Conclusions

We have found that particularly intense extreme weather events can have severe effects on bats, affecting even species well adapted to them, when these events happen in profoundly altered habitats.

Our results also show that such effects can be difficult to understand and, consequentially, to predict. This (1) shows that combined effects of extreme weather events and habitat alteration might be worse than the effects of each of these factors by themselves; (2) underscores the importance of preserving natural habitats in areas particularly affected by the changing climate; and (3) shows that the survival of species and ecosystems during the numerous episodes of climate change in the Earth's history does not necessarily mean their ability to survive the accelerating climate change of our time.

Author Contributions

Vladimir Dinets designed the study, processed the recordings, and wrote the first draft of the manuscript. Nicholas R. Friedman helped design the study, operated the equipment, and provided technical expertise. Masako Ogasawara and Masashi Yoshimura oversaw the work of field crews servicing the equipment and collecting data, and processing the insect samples. Evan P. Economo led the study and OKEON project in general. All authors participated in the fieldwork and in editing the manuscript.

Conflict of Interest

The authors declare that there is no conflict of interest.

Data Availability Statement

All raw data are stored at OIST and can be provided upon request.

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References

[1] Webster, P.J., Holland, G.J., Curry, J.A., et al., 2005. Changes in tropical cyclone number, duration, and intensity in a warming environment. Science. 309(5742), 1844-1846. DOI: https://doi.org/10.1126/science.1116448

[2] Hoyos, C.D., Agudelo, P.A., Webster, P.J., et al., 2006. Deconvolution of the factors contributing to the increase in global hurricane intensity. Science. 312(5770), 94-97. DOI: https://doi.org/10.1126/science.1123560

[3] Tsuboki, K., Yoshioka, M.K., Shinoda, T., et al., 2015. Future increase of super typhoon intensity associated with climate change. Geophysical Research Letters. 42(2), 646-652. DOI: https://doi.org/10.1002/2014GL061793

[4] Li, L., Chakraborty, P., 2020. Slower decay of landfalling hurricanes in a warming world. Nature. 587(7833), 230-234. DOI: https://doi.org/10.1038/s41586-020-2867-7

[5] Ameca y Juárez, E.I., Mace, G.M., Cowlishaw, G., et al., 2013. Assessing exposure to extreme climatic events for terrestrial mammals. Conservation Letters. 6(3), 145-153. DOI: https://doi.org/10.1111/j.1755-263X.2012.00306.x

[6] Russo, D., Salinas-Ramos, V.B., Cistrone, L., et al., 2021. Do we need to use bats as bioindicators? Biology. 10(8), 693.

[7] Sil-Berra, L.M., Sánchez-Hernández, C., de Lourdes Romero-Almaraz, M.L., et al., 2021. Vulnerability to natural disturbance in communities of Neotropical bats: Short-term impact of Hurricane Patricia on the Mexican Pacific Coast. Forest Ecology and Management. 479, 118596. DOI: https://doi.org/10.1016/j.foreco.2020.118596

[8] Adams, A.M., 2013. Assessing and analyzing bat activity with acoustic monitoring: Challenges and interpretations [Ph.D. thesis]. London, ON: The University of Western Ontario. p. 195. Available from: https://ir.lib.uwo.ca/cgi/viewcontent.cgi?article=2679&context=etd

[9] Murray, K.L., Britzke, E.R., Hadley, B.M., et al., 1999. Surveying bat communities: A comparison between mist nets and the Anabat II bat detector system. Acta Chiropterologica. 1, 105-112.

[10] O'Farrell, M.J., Gannon, W.L., 1999. A comparison of acoustic versus capture techniques for the inventory of bats. Journal of Mammalogy. 80(1), 24-30. DOI: https://doi.org/10.2307/1383204

[11] Furey, N.M., Mackie, I.J., Racey, P.A., 2010. The role of ultrasonic bat detectors in improving inventory and monitoring surveys in Vietnamese karst bat assemblages. Current Zoology. 55(5), 327-341. DOI: https://doi.org/10.1093/czoolo/55.5.327

[12] Whitby, M.D., Carter, T.C., Britzke, E.R., et al., 2014. Evaluation of mobile acoustic techniques for bat population monitoring. Acta Chiropterologica. 16(1), 223-230. DOI: https://doi.org/10.3161/150811014X683417

[13] Walker, R., 2014. Okinawa and the Ryukyu Islands. Tuttle Publishing: Claredon, VT. pp. 1-636.

[14] Toshiaki, A., 2001. History of Ryukyu. Toyo Kikaku: Naha, Japan. pp. 1-480.

[15] Dinets, V., Friedman, N.R., Yoshimura, M., et al., 2020. Acoustic detection of an unknown bat species in Okinawa. Mammal Study. 45(4), 353-356.

DOI: https://doi.org/10.3106/ms2019-0077

[16] Preble, J.H., Vincenot, C.E., Hill, D.A., et al., 2021. Capturing endangered endemic Okinawan bats with acoustic lures. Journal for Nature Conservation. 64, 126074.
DOI: https://doi.org/10.1016/j.jnc.2021.126074

[17] Preble, J.H., Ohte, N., Vincenot, C.E., 2021. In the shadow of the rising sun: A systematic review of Japanese bat research and conservation. Mammal Review. 51(1), 109-126.
DOI: https://doi.org/10.1111/mam.12226

[18] Sano, A., Armstrong, K.N., 2015. *Rhinolophus pumilus* Andersen, 1905. The wild mammals of Japan (2nd ed.). Shoukadoh: Tokyo, Japan. pp. 63-64.

[19] Yoshino, H., Matsumura, S., Kinjo, K., et al., 2006. Geographical variation in echolocation call and body size of the Okinawan least horseshoe bat, *Rhinolophus pumilus* (Mammalia: Rhinolophidae), on Okinawa-jima Island, Ryukyu Archipelago, Japan. Zoological Science. 23(8), 661-667.
DOI: https://doi.org/10.2108/zsj.23.661

[20] Sano, A., 2015. *Miniopterus fuscus* Bonhote, 1902. The wild mammals of Japan (2nd ed.). Shoukadoh: Tokyo, Japan. pp. 128-129.

[21] Tamura, H., 2002. Movement pattern and life history of the bent-winged bat *Miniopterus fuscus* on Okinawa-jima Island [Master's thesis]. Naha, Japan: University of the Ryukyus. p. 160.

[22] Kawai, K.K., 2015. *Murina ryukyuana* Maeda & Matsumura, 1998. The wild mammals of Japan (2nd ed.). Shoukadoh: Tokyo, Japan. pp. 120-121.

[23] Preble, J.H., Vincenot, C.E., Saito, K., et al., 2021. Roosting ecology of endangered plant-roosting bats on Okinawa Island: Implications for bat-friendly forestry practices. Ecology and Evolution. 11(20), 13961-13971.
DOI: https://doi.org/10.1002/ece3.8101

[24] Lee, Y.F., Lee, L.L., 2005. Food habits of Japanese pipistrelles *Pipistrellus abramus* (Chiroptera: Vespertilionidae) in northern Taiwan. Zoological Studies. 44(1), 95-101.

[25] Kawai, K.K., 2015. *Pipistrellus abramus* (Temminck, 1840). The wild mammals of Japan (2nd ed.). Shoukadoh: Tokyo, Japan. pp. 82-84.

[26] Ross, S., Friedman, N.R., Dudley, K., et al., 2018. Listening to ecosystems: Data-rich acoustic monitoring through landscape-scale sensor networks. Ecological Research. 33, 135-147.
DOI: https://doi.org/10.1007/s11284-017-1509-5

[27] Weimerskirch, H., Prudor, A., 2019. Cyclone avoidance behaviour by foraging seabirds. Scientific Reports. 9(1), 1-9.
DOI: https://doi.org/10.1038/s41598-019-41481-x

[28] Donihue, C.M., Herrel, A., Fabre, A.C., et al., 2018. Hurricane-induced selection on the morphology of an island lizard. Nature. 560(7716), 88-91.
DOI: https://doi.org/10.1038/s41586-018-0352-3

[29] McNab, B.K., 2010. Physiological adaptation of bats and birds to island life. Island bats: Evolution, ecology and conservation. University of Chicago Press: Chicago, IL. pp. 153-175.

[30] Jones, K.E., Barlow, K.E., Vaughan, N., et al., 2001. Short-term impacts of extreme environmental disturbance on the bats of Puerto Rico. Animal Conservation Forum. 4(1), 59-66.
DOI: https://doi.org/10.1017/S1367943001001068

[31] Fleming, T.H., Murray, K.L., 2009. Population and genetic consequences of hurricanes for three species of West Indian phyllostomid bats. Biotropica. 41(2), 250-256.
DOI: https://doi.org/10.1111/j.1744-7429.2008.00466.x

[32] Gannon, M.R., Willig, M.R., 2009. Island in the storm: Disturbance ecology of plant-visiting bats on the hurricane-prone island of Puerto Rico. Island bats: Evolution, ecology, and conservation. University of Chicago Press: Chicago, IL. pp. 281-301.

[33] Asari, Y., Kimoto, Y., 2018. Bat species found during capturing and acoustic surveys in Amami-Oshima Island, Japan. Fauna Ryukyuana, 47, 1-6. Available from: http://hdl.handle.net/20.500.12000/46811

[34] Pratt, H.D., 1994. Avifaunal change in the Ha-

waiian Islands, 1893-1993. Studies in Avian Biology. 15, 103-118.

[35] Boesman, P., Collar, N.J., 2020. Further vocal evidence for treating the Bahama Nuthatch *Sitta* (*pusilla*) *insularis* as a species. Bulletin of the British Ornithologists' Club. 140(4), 393-403. DOI: https://doi.org/10.25226/bboc.v140i4.2020.a4

[36] Preble, J.H., 2022. Conservation ecology of Okinawa's endangered plant-roosting bats, *Murina ryukyuana* and *Myotis yanbarensis* [Ph.D. thesis]. Kyoto, Japan: Kyoto University. p. 212.

[37] Fukui, D., Okazaki, K., Maeda, K., 2009. Diet of three sympatric insectivorous bat species on Ishigaki Island, Japan. Endangered Species Research. 8(1-2), 117-128.

[38] Nagel, J., 2019. Using bioacoustics to measure the effects of hurricanes on bats in St. Thomas, U.S. Virgin Islands [Master's thesis]. St. Thomas, US Virgin Islands: University of the Virgin Islands. p. 120.