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ORIGINAL PAPER

**Shizuko Hiryu · Koji Katsura · Tsuyoshi Nagato
Hideo Yamazaki · Liang-Kong Lin
Yoshiaki Watanabe · Hiroshi Riquimaroux**

Intra-individual variation in the vocalized frequency of the Taiwanese leaf-nosed bat, *Hipposideros terasensis*, influenced by conspecific colony members

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Abstract We examined the intra-individual variation in resting frequency of the constant-frequency component of the second harmonic of the pulse (F_{rest}) over 4 years in a laboratory colony of the Taiwanese leaf-nosed bat (*Hipposideros terasensis*). Patterns of change in F_{rest} were observed when individuals were added to or removed from the colony so that we investigated whether F_{rest} was affected by neighboring colony members. F_{rest} of each bat continually showed a long-term gradual change throughout the year, and all bats in the colony increased or decreased their F_{rest} in the same direction as a group non-seasonally. The greatest short-term changes were observed when new bats with a relatively low F_{rest} joined the colony and F_{rest} of new bats converged with those of the original colony members around 8 –16 days after their introduction. Conversely, a single individual showed sudden short-term decrease in F_{rest} after its isolation from other colony members. These findings strongly indicate that F_{rest} is flexible according to the presence of neighboring conspecific bats. We suggest that the audio-vocal feedback for conspecific pulses appears to be involved in the short- or long-term intra-individual variation in F_{rest} other than factors previously thought such as age or season.

S. Hiryu (✉) · K. Katsura · Y. Watanabe
Department of Electrical Engineering,
Doshisha University,
610-0321 Kyotanabe, Japan
E-mail: ZXH03766@nifty.ne.jp
E-mail: kwatanab@mail.doshisha.ac.jp
Tel.: +81-774-656300
Fax: +81-774-656300

T. Nagato · H. Yamazaki · H. Riquimaroux
Department of Knowledge Engineering and Computer Sciences,
Doshisha University, 610-0321 Kyotanabe, Japan
E-mail: hrikimar@mail.doshisha.ac.jp

L.-K. Lin
Department of Biology, Tunghai University,
407 Taichung, Taiwan
E-mail: lklin@mail.thu.edu.tw

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Introduction

Leaf-nosed bats (*Hipposideridae*) and horseshoe bats (*Rhinolophidae*), together with the mustached bat *Pteronotus parnellii* (*Mormoopidae*), all produce echolocation calls that comprise a constant-frequency (CF) component followed by a short frequency-modulated (FM) component (e.g. reviews in Pye 1972; Gustafson and Schnitzler 1979; Habersetzer et al. 1984; Jones et al. 1993). Once the bat is in flight, the echo frequency of the CF component is shifted due to Doppler effects. These bats are able to compensate for Doppler-shifted echoes by adjusting their call frequency so that the dominant second harmonic CF component (CF_2) in the Doppler-shifted echoes remains within an ‚acoustic fovea' (Doppler-shift compensation; Schnitzler 1968; Simmons 1974; Schuller et al. 1974; Gustafson and Schnitzler 1979; Habersetzer et al. 1984; Gaioni et al. 1990). In mustached bats, a physiologically specialized area is located in the primary auditory cortex referred to as the Doppler-shifted-CF (DSCF) processing area that allows the bat to detect small frequency differences in an echo CF_2 (e.g., Suga 1984; Riquimaroux et al. 1992). Ostwald (1984) demonstrated that there is a similar over-representation of CF_2 frequency in the horseshoe bats. Hence, the frequency of CF_2 component of calls is an important factor to consider when characterizing echolocation strategy in CF-FM bats.

The CF_2 frequency of calls emitted by bats at rest (F_{rest}: ‚resting frequency'), i.e. when the bat is roosting and not compensating for Doppler-shifted echoes, differs among colonies (e.g. Schuller 1980; Jones and Ransome 1993; Pearl and Fenton 1996; Guillén et al. 2000), or conspecific individuals due to physical constitution, sex, age, geography and morphometric differences (e.g. Pye 1972; Suga et al. 1987; Jones et al. 1992, 1993, 1994; Jones 1999; Guillén et al. 2000). Conversely, F_{rest} of an adult bat can show a slight but continual individual drift over several months (Suga et al. 1987; Gaioni et al. 1990), or throughout its lifetime or season (Jones and Ransome 1993). These findings suggest that F_{rest} varies within as well as between individuals over a long period of time. Although Huffman and Henson (1993a, b) demonstrated that F_{rest} changes instantaneously with an increase in the body temperature, the causes of such long-term individual shift in F_{rest} have not been well identified.

In the present study, we report the first quantitative observation of intra-individual variation in F_{rest} over a 4-year observation period in a laboratory colony of Taiwanese leaf-nosed bats, *Hipposideros terasensis*. We daily documented F_{rest}, and observed patterns of change when individuals were added to or removed from the colony. This allowed us to discuss the implications of observed changes in the context of the stability of intra-individual F_{rest}, and investigate whether F_{rest} of a new colony member is affected by that of the original colony members.

Materials and methods

Subjects

Adult Taiwanese leaf-nosed bats (*H. terasensis*) were housed in a temperature and humidity controlled facility at Doshisha University, Kyoto, Japan. The experiments comply with the "Principles of animal care", publication No. 86–23, revised 1985 of the National Institute of Health, and also with current Japanese laws for the care and use of animals. In a colony room (3 m × 2 m × 2 m), the bats were free to fly and access water and food. The characteristics of the echolocation signals of *H. terasensis* have been described previously in Riquimaroux and Watanabe (2002) and Hiryu et al. (2005). Briefly, spectrographic representation of the echolocation pulse shows a relatively long constant frequency portion (CF) followed by a short frequency modulated portion (FM; Figs. 1a, b). Pulse duration ranges between 5 and 10 ms, and the second harmonic with the greatest energy (CF_2) is approximately 70 kHz. Sex and age of the bats were not recorded.

Measurements of F_{rest} were conducted from February 2001 through December 2004. The observation period of each bat is illustrated in Fig. 2. Fifteen bats were totally used for measurement of F_{rest} over the 4-year observation period. Animals were captured in Taiwan (not from the same cave) and brought to the laboratory on four occasions (21 May, 2001; 20 July 2001; 29 October 2001; 5 September 2002), which are referred to as the *importation* events in this paper. Conversely, cases where all other colony members were suddenly removed from the colony, leaving a single bat, are referred to as the *isolation* event (24 September 2001; 11 August 2003). The two isolation events presented in this study occurred due to accidental death of all other colony members during the observation period. Therefore, the isolated bat was left alone in the colony room and no longer able to hear calls from the other colony members. Special care was given to new and original bats after the importation event, and we confirmed that there was no particular sign of distress or change in daily habit.

Recording daily changes in F_{rest}

F_{rest} was recorded from all colony members every day after the importation event for a period of several weeks, and thereafter on every alternate day. Recording was made from a bat positioned on a perch in a measurement chamber 8 m (L) × 3 m (W) × 2 m (H) to isolate from other individuals. A condenser microphone (B&K, 4939, Denmark) was set about 5 cm below the noseleaf of the bat. Echolocation pulses recorded using the microphone were amplified (B&K, 5935L, Denmark), high-pass filtered (20 kHz; NF Corporation, model 3625, Yokohama, Japan) and then digitally recorded with 16 bit conversion at a sampling rate of 384 kHz with a SONY SIR–1000W DAT recorder (Tokyo, Japan). Ten pulses were randomly selected from a set of the daily record of each bat, and the frequency of CF_2 was determined with custom software (frequency resolution was 23.4 Hz). A mean of the ten pulses was

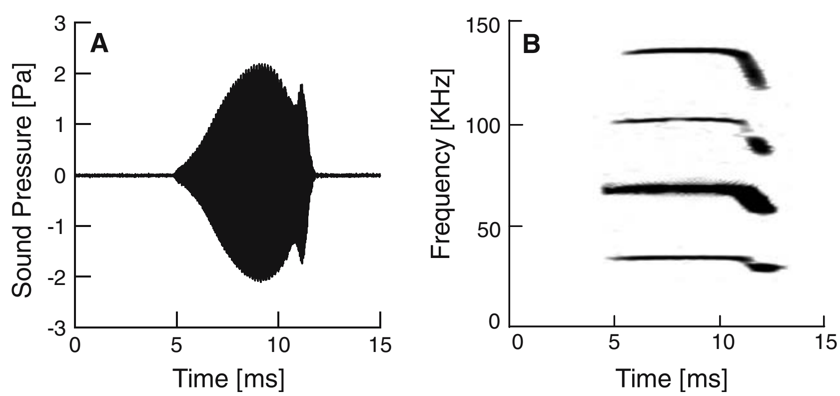

Fig. 1 Echolocation pulse of the Taiwanese leaf-nosed bat (*Hipposideros terasensis*). **a** Temporal amplitude pattern. **b** Spectrogram. There are four or more harmonics, each consisting of a long constant frequency (CF) component followed by a short frequency modulated (FM) component. The second harmonic is the most intense

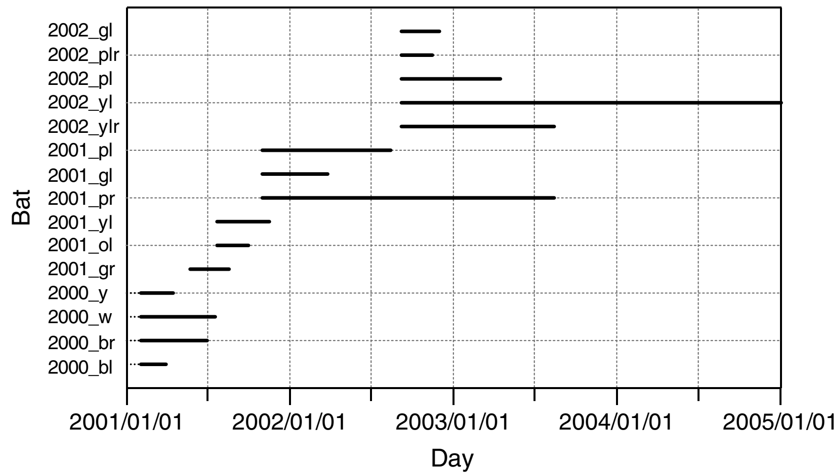

Fig. 2 Observation periods of measurement of F_{rest} for 15 bats. The capture of animals in Taiwan was undertaken four times (5/21/2001, 7/20/2001, 10/29/2001, 9/5/2002), which is referred to as the importation events in this paper. Isolation events are defined as periods when one individual was left alone in the colony room and maintained by itself without being able to hear the other bats (9/24/2001, 8/11/2003)

calculated for each bat on each day. The mean standard deviation for all 15 bats used in this study ranged from 0.121 to 0.207 kHz (Table 1). Measurements of body mass of bats started from June 2002.

Results

Figure 3a and b indicate intra-individual changes in F_{rest} for 15 bats over the 4-year observation period, and F_{rest} for two bats 2002_yl and 2001_pr are shown in Fig. 3c separately. Each bat continually showed a long-term gradual change in F_{rest} throughout the year, and all bats in the colony increased or decreased F_{rest} as a group in the same direction. The degree of the change in F_{rest}, which is the difference in frequency between the maximum and minimum F_{rest} recorded from an individual bat over the observation period, ranged from 1.47 to 4.81 kHz among the 15 bats (Table 1). The average was 3.04 kHz, which is approximately 4% of F_{rest} of *H. terasensis* which is about 70 kHz. We found that short-term dramatic changes in F_{rest} occurred following an importation or isolation event.

Short-term changes in F_{rest}

Importation event

For all four importation events, a change in F_{rest} was observed from each newly introduced bat. Intra-individual changes in F_{rest} are given in Fig. 4.

Figure 4a and b show cases where new bats with approximately 2 kHz low F_{rest} joined the colony. In the first 2–3 days after their introduction, the new bats decreased their F_{rest}, which we interpreted to be due to fatigue or stress from capture. After this initial decrease, the new bats began to increase their F_{rest}. The increase by new bat 2001_ol was 1.12 kHz in one single day (marked with arrow in Fig. 4a), and increased at a rate of 0.43 kHz/day over the subsequent 4 days based on a linear estimate of the change in F_{rest}. In another importation event (Fig. 4b),

Table 1 Changes in F_{rest} for 15 bats

Bat	Max (kHz)	Min (kHz)	Difference (kHz)	Mean of SD (kHz)	Observation period
2002_gl	70.80	67.60	3.20	0.122	09/05/02–12/02/02 (88)
2002_plr	70.83	68.31	2.52	0.151	09/05/02–11/12/02 (68)
2002_pl	70.92	67.04	3.89	0.151	09/05/02–04/11/03 (218)
2002_yl	71.23	66.42	4.81	0.161	09/05/02–12/10/04 (827)
2002_ylr	71.34	68.51	2.83	0.157	09/05/02–08/11/03 (340)
2001_pl	70.76	68.32	2.44	0.158	10/29/01–08/12/02 (287)
2001_gl	71.32	68.40	2.92	0.126	10/29/01–03/24/02 (146)
2001_pr	71.42	68.75	2.67	0.184	10/29/01–08/11/03 (651)
2001_yl	68.88	65.94	2.94	0.151	07/20/01–11/12/01 (115)
2001_ol	68.56	67.09	1.47	0.121	07/20/01–09/24/01 (66)
2001_gr	70.11	66.93	3.18	0.172	05/21/01–08/15/01 (86)
2000_y	70.45	67.08	3.37	0.179	02/01/01–05/14/01 (102)
2000_w	70.88	68.06	2.82	0.185	02/01/01–07/16/01 (165)
2000_br	70.91	67.53	3.38	0.207	02/01/01–06/18/01 (137)
2000_bl	70.69	67.53	3.16	0.186	02/01/01–03/29/01 (56)

Difference is defined as the frequency change in F_{rest} between maximum and minimum values of each bat over the observation period. Mean of SD is the mean standard deviation around the daily mean of F_{rest} for the observation period. Number shown in parentheses is the number of days over the observation period for each bat

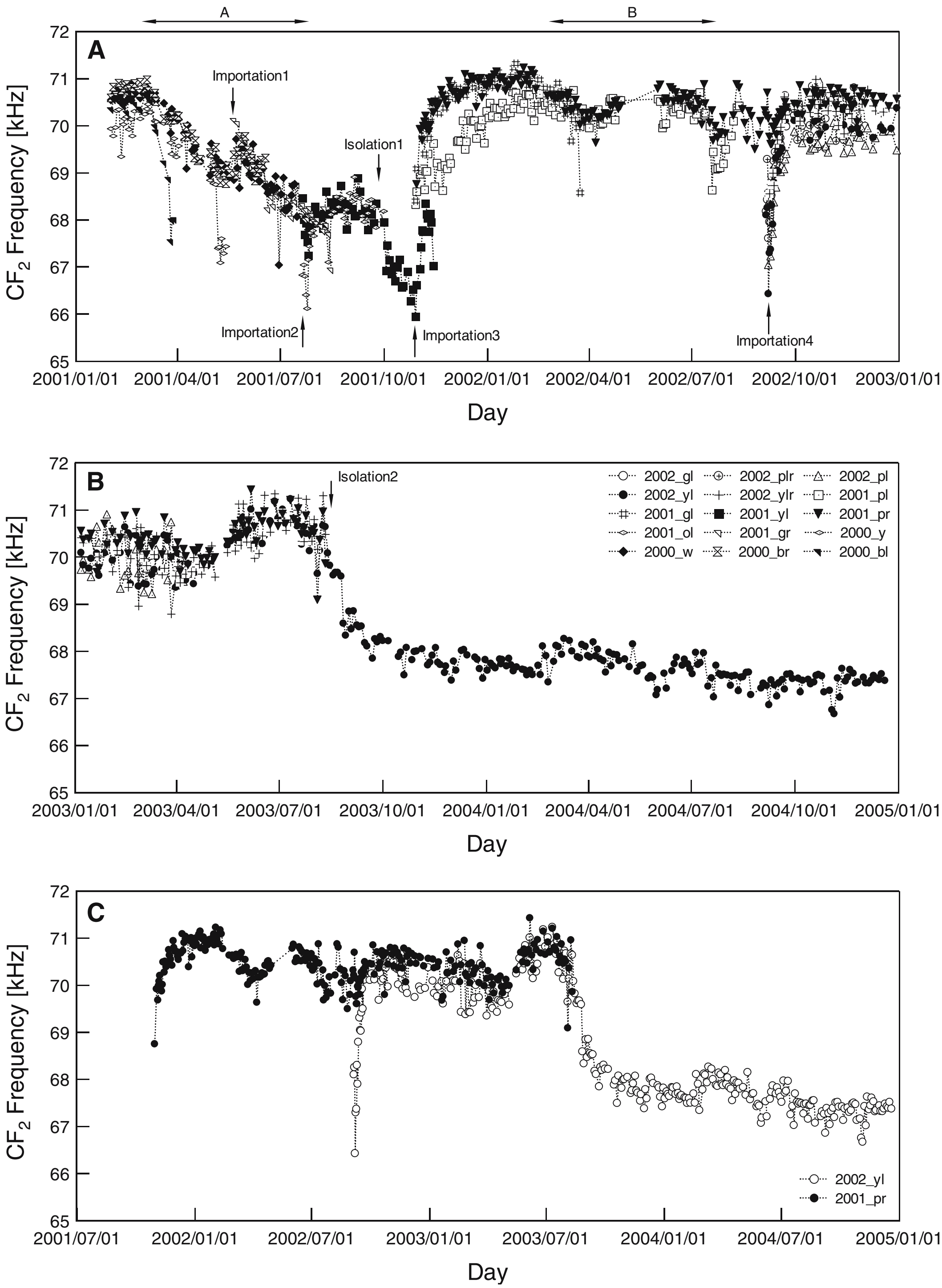

Fig. 3 Inter-individual variation in F_{rest} for 15 bats over the 4-year observation. **a** January 2001–December 2002. **b** January 2003–December 2004. **c** F_{rest} for 2002_yl and 2001_pr over 2 years. ‚Importation' indicates the time when the new bats joined into the colony; ‚Isolation' refers to an event that left a single individual by itself. See the text for description of *Arrows* at the top of Fig. 3a

all new bats continuously showed large increases in F_{rest} for 15–16 days after the initial decrease (marked with arrow), and the amount of the total increase in F_{rest} ranged from 1.72 to 3.92 kHz (mean 0.16 kHz/day among these five bats; Table 2).

Figure 4c shows that a new bat (2001_gr) that initially emitted pulses with higher F_{rest} relative to the original bats gradually decreased F_{rest} after being introduced into the colony. The total drop in F_{rest} was 1.40 kHz over 28 days until an original bat 2000_br died

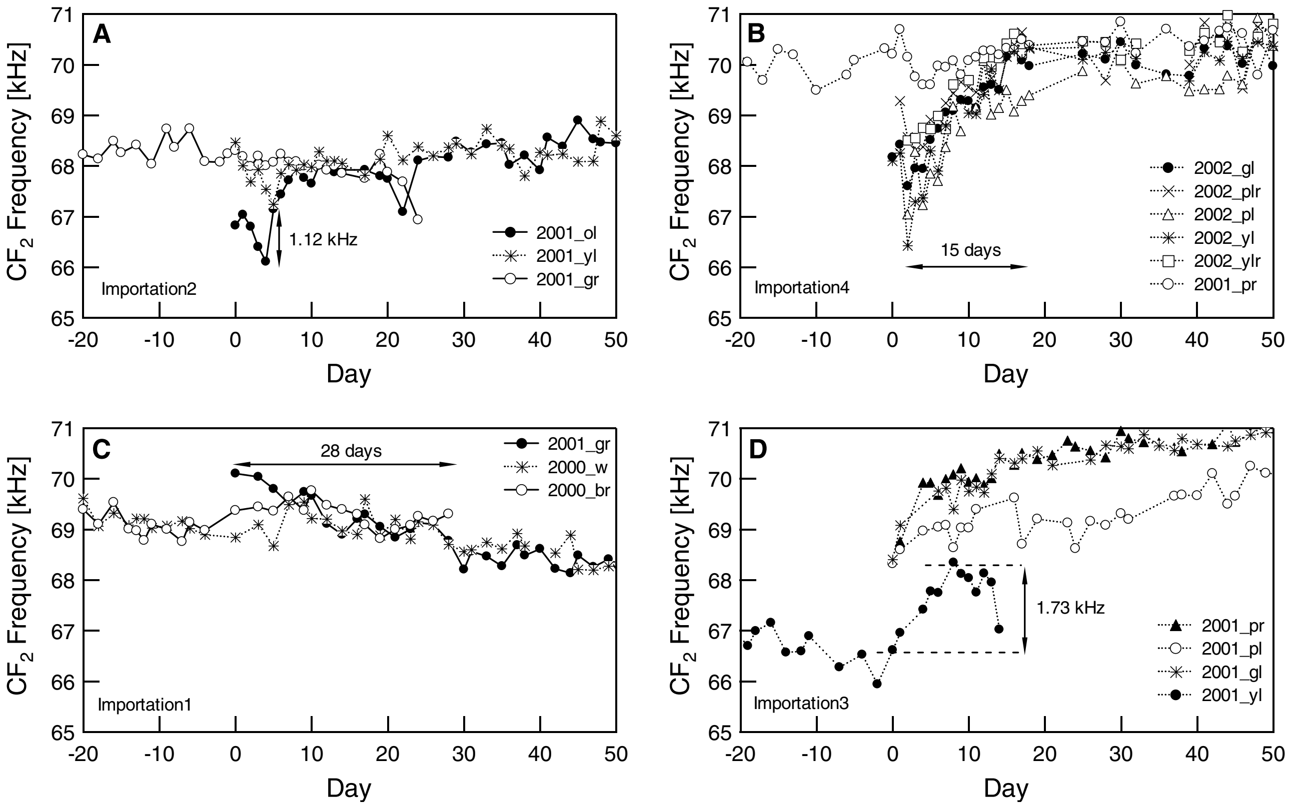

Fig. 4 Changes in F_{rest} of the new and original bats around the importation event. **a, b** New bats with relatively low F_{rest} , which increased their F_{rest}. **c** The case of a new bat with relatively high F_{rest} that decreased its F_{rest}. **d** An original bat with relatively low F_{rest} that increased its F_{rest}. See the text for description of *Arrows* in each figure

Table 2 Change in F_{rest} of the bats after the importation events

Event	Bat	Difference (kHz)	Rate of change (kHz/day)	Time to equivalency (days)
Importation2	2001_ol	1.84 (4)	0.43	8
	2001_yl	0.79 (2)	0.39	8
Importation4	2002_gl	2.37 (16)	0.15	NA
	2002_plr	2.00 (15)	0.14	9
	2002_pl	2.36 (16)	0.14	NA
	2002_yl	3.92 (16)	0.22	16
	2002_ylr	1.72 (15)	0.14	14

Number shown in parentheses is the number of days while showing continuous increase of F_{rest} by the bats after the events (described in text). Rate of change was calculated with a linear approximation for these days. Time to equivalency is the days when F_{rest} of the new bats first became equivalent with that of the original bats. There was no equivalent day observed between F_{rest} of two bats (2002_gl and 2002_pl) and original bat (2001_pr) over 30 days after their introduction
NA not available

(marked with arrow). All colony members eventually converged in F_{rest} after their introduction.

We also observed a case where the original bat (2001_yl), with approximately 2 kHz low F_{rest} compared to the new bats, increased its F_{rest} (Fig. 4d). The amount of the increase by 2001_yl was 1.73 kHz over 8 days marked with arrow (0.2 kHz/day). The subsequent decrease in F_{rest} observed after that day was due to failing health, as this bat died 14 days after the introduction. We observed in most ailing bats that F_{rest} significantly decreased shortly before they expired (Fig. 3).

These findings strongly suggest that F_{rest} is affected by the presence of neighboring conspecific bats in the bat colony. In three of the four events observed, we found that the new bats adjusted their F_{rest} to that of the old colony member(s), and in one case the opposite occurred. We estimated the day when F_{rest} of the new bats first approached the frequency of the original bats. Figure 5 represents the daily change in the frequency difference between the new and original bats for these importation events. The time point when F_{rest} of the old and new bats was no longer significantly different

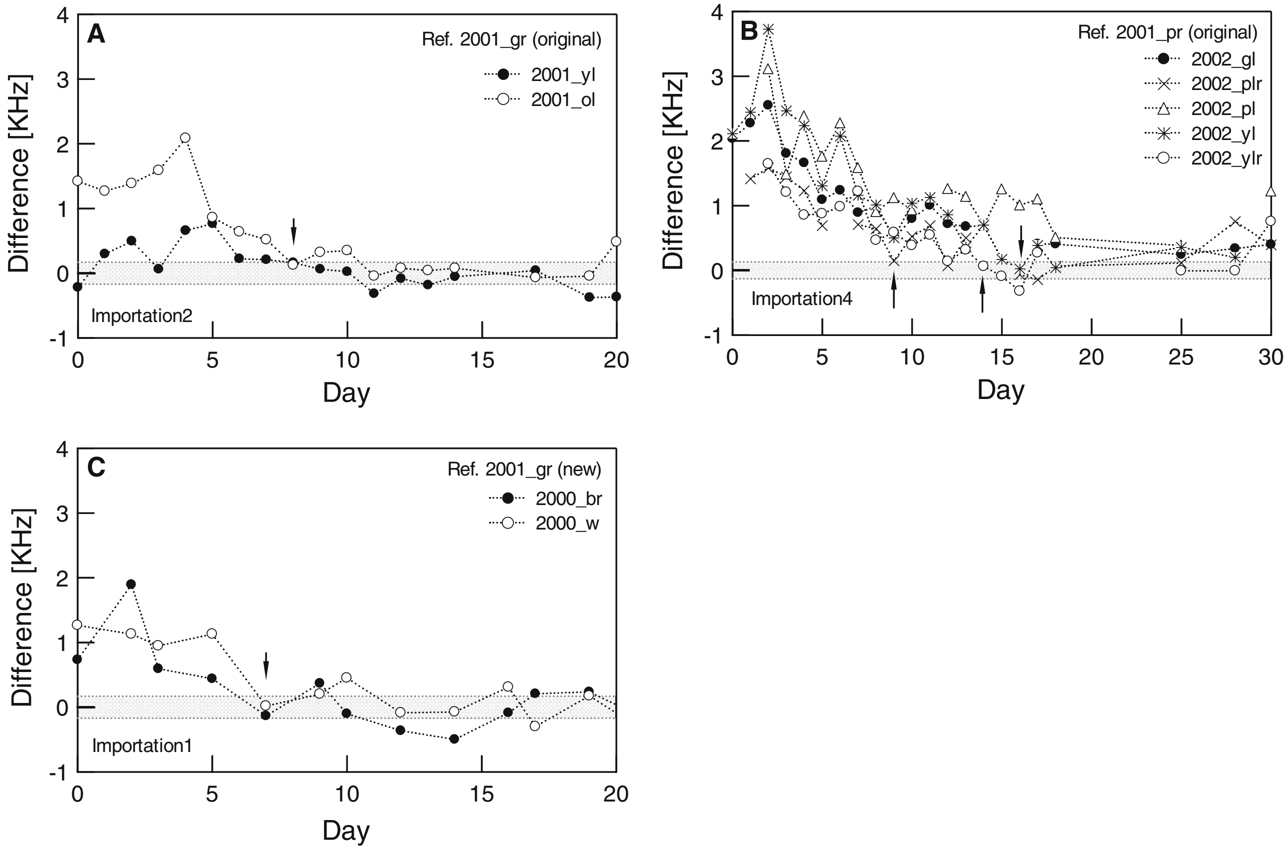

Fig. 5 Frequency differences between the new and original bats for three importation cases of (*A*) Importation2, (*B*) Importation4, and (*C*) Importation1. The *shaded bar* represents the range of mean standard deviation of F_{rest} for each reference bat. *Arrows* indicate the day when F_{rest} of the new bats first became equivalent with that of the original bats ($P > 0.05$)

($P > 0.05$, *t* test) was 8 days for both 2001_ol and 2001_yl after the importation (marked with arrow in Fig. 5a; except the period showing initial decrease on the first and third days for 2001_yl). In Fig. 5b, three bats (2002_plr, 2002_ylr and 2002_yl) among five new bats took 9, 14 and 16 days, respectively, to become equivalent with that of the original bat (2001_pr). Another two new bats (2002_gl and 2002_pl in Fig. 5b) lowered their F_{rest}, although they did not reach F_{rest} of the original bat (2001_pr) until 30 days after their introduction to the colony. In contrast, it took only 7 days for the new bats 2000_br and 2000_w to fully adjust their F_{rest} (Fig. 5c).

Isolation events

When a single bat was isolated from the other colony members and was no longer able to hear their calls, F_{rest} of the isolated bat dramatically decreased within only a few days. In case of bats 2001_yl (Fig. 6a) and 2002_yl (Fig. 6b), their F_{rest} decreased as much as 1.0 kHz within 7 days after the isolation event. In particular, 2002_yl in Fig. 6b showed a subsequent distinct decrease of approximately 1.0 kHz during 2 days on the 14th day after isolation.

Long-term changes in F_{rest}

Figure 3a and b indicate that each bat continually showed a long-term gradual change in F_{rest} throughout the period of observation, and all bats in the colony increased or decreased F_{rest} in the same direction as a group. There were repeated adjustments in F_{rest} of the same bat through its observation period. The source of these changes was not seasonal, e.g. the mean F_{rest} of the colony was observed to decrease dynamically from March 2001 to August 2001 (see arrow marked “A” at the top of Fig. 3a), while no such decrease was recorded for the same period in following years (arrow marked “B”). F_{rest} of two bats 2002_yl and 2001_pr on which F_{rest} was measured for the greatest number of days, also demonstrated no seasonal change over 2 years (Fig. 3c). In addition, changes in body mass for these two bats had no significant correlation with those of their F_{rest} ($P < 0.05$; Figs. 7a, b; calculated over all seasons for two individuals).

We continued to measure F_{rest} in 2002_yl which was housed alone for over 1 year after the isolation event in August 2002. F_{rest} of 2002_yl showed a slight gradual decrease, with a rate of 1.5 Hz/day from September 2003 to December 2004 (Fig. 3b). However, there was no

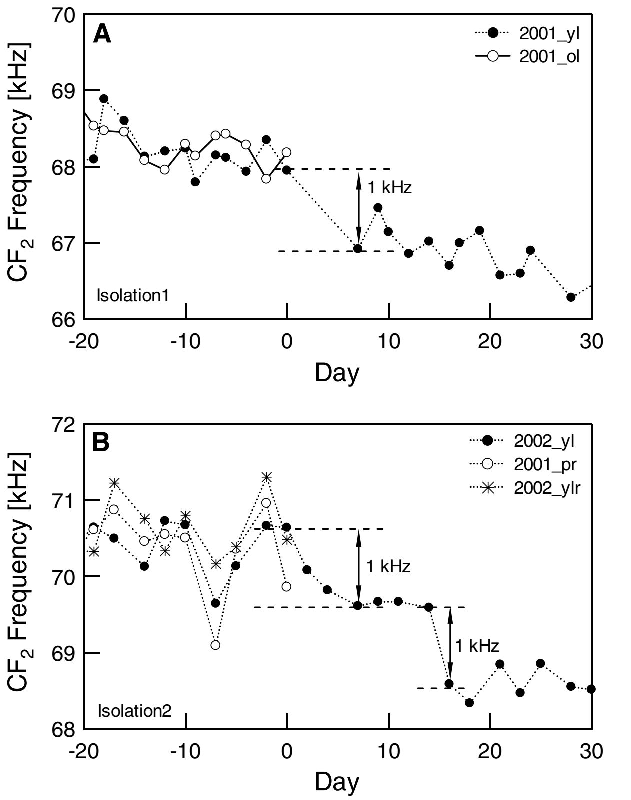

Fig. 6 Changes in F_{rest} in a single individual after the sudden disappearance of other colony members (isolation event) (*A*) Isolation1 and (*B*) Isolation2

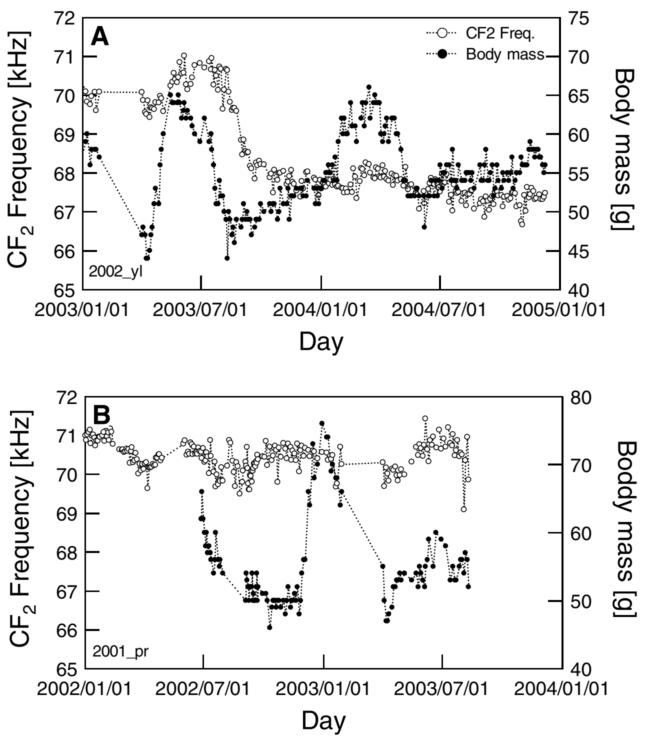

Fig. 7 Relationship between body mass and F_{rest} for **a** 2002_yl and **b** 2001_pr over seasons

other distinct long-term change in F_{rest} throughout the observed period.

Discussion

Convergence of F_{rest} among colony members

Hipposideros terasensis in a laboratory colony showed two different patterns of intra-individual shifts in F_{rest}; short-term change following an importation or isolation event, and long-term gradual change. Bats changed their F_{rest} in a short period of time after the importation to converge with that of other bats, and this pattern occurred in both new and original colony members (short-term changes, Fig. 4). Conversely, individuals suddenly decreased their F_{rest} when left alone in an enclosure after the removal of other colony members (Fig. 6; in two cases). Figure 3a and b demonstrated that each bat continually showed a long-term gradual change in F_{rest}. Although the size of the laboratory colony was so small that we could not reconstruct a true "colony", these findings imply that social interactions may have significant effects on F_{rest}.

Short- and long-term changes in F_{rest} may have different implications in the context of the stability of intra-individual F_{rest}. However, our findings strongly suggest that both short- and long-term changes in F_{rest} are controlled by the individual in response to the F_{rest} of neighboring bats. In other words, the bats appear to employ audio-vocal feedback from the F_{rest} of neighboring conspecifics, and F_{rest} is liable over a short or long term by echolocation calls of neighboring conspecific bats in a colony other than factors previously considered such as age or season (e.g. Jones et al. 1992; Jones and Ransome 1993).

The F_{rest} of bats' calls differ between social groups, which are concerned to indicate group membership (e.g. Boughman and Wilkinson 1998). Some previous data have reported that bats could modify frequency characteristics of their calls through their auditory experience (vocal learning: Esser 1994; Jones and Ransome 1993). Boughman (1998) demonstrated that bats changed their call structures to resemble other members in the same social group. We suggest that short- and long-term changes in F_{rest} may be associated with the vocal learning, caused by social interaction and/or communication within the laboratory colony members.

Our previous study demonstrated that bats kept in an experimental environment without capturing flying prey decreased their F_{rest}. However, they increased their F_{rest} once flight training began (Riquimaroux and Watanabe 2002). In the present study, all bats began to increase their F_{rest} by 1.5–2 kHz from May 2003 (Fig. 3b). Around the same time, we started another experiment on these bats which required them to fly frequently in an observation chamber. These findings suggest that increases in F_{rest} may depend upon the degree of usage of echolocation. Interestingly, we found that bats tended to match their F_{rest} to that of other bats emitting higher frequencies after an importation event (Fig. 4a, b, d). We suggest that a higher F_{rest} may facilitate echolocation. However, we cannot explain the reason of such preference of higher F_{rest} at present.

Decline in F_{rest} in isolated bats

For two isolation events, F_{rest} suddenly decreased when all bats but one were removed from the enclosure (Fig. 6a, b). This F_{rest} strongly suggests that intra-individual variation in F_{rest} is caused by isolation from other bats, and/or their echolocation calls and that a bat needs to hear the calls of conspecifics to maintain its own F_{rest}. At present, however, we cannot suggest a clear reason for the *decrease* in F_{rest} in the isolated bats.

In mustached bats, Gaioni et al (1990) have reported that isolated bats that were kept in small cages and prevented from flying showed a gradual decrease in F_{rest} over several days. F_{rest} of our two isolated bats also showed a short-term decrease within a few days after isolation, and one of them (2002_yl) showed subsequent long-term gradual decrease in F_{rest} with a rate of 1.5 Hz/day (Fig. 3b). The findings from these two cases may imply that a gradual decrease in F_{rest} of the isolated bat may have been caused by depression due to isolation or the decrease in the degree of usage of echolocation. As mentioned above, a higher F_{rest} would be expected to facilitate echolocation. However, a higher F_{rest} is not preferred by the bat which does not frequently use echolocation. This suggests that lowering F_{rest} may be related to be a part of ecological strategies by bats, such as energy conservation for echolocation due to sound production.

Adaptation of auditory system

Although frequency representation in the DSCF area in the auditory cortex of mustached bats differs among individuals depending on their F_{rest} (Suga et al. 1987), it is not well understood if the frequency representation in the DSCF area changes due to their intra-individual change in F_{rest}. Huffman and Henson (1993a) reported that F_{rest} changes instantaneously with an increase in the body temperature, or due to flight activities (i.e., F_{rest} was found to have increased after flight activity; Henson et al. 1990). They also revealed that such very short-term change in F_{rest} is accompanied by a frequency shift in the cochlear resonance as well as a tonotopic shift in the frequency response of the auditory neurons (Huffman and Henson 1993b). These findings imply that the auditory system that is individually tuned is likely to show quick adaptation for these very short-term intra-individual changes in their F_{rest}.

In the present study, the degree of the long-term change in F_{rest} recorded from an individual bat over the observation period ranged from 1.47 to 4.81 kHz among the 15 bats (Table 1). We found that short-term dynamic change in F_{rest} was as great as 0.14–0.43 kHz/day after the importation event, and 1 kHz within 7 days after the isolation event. When the echo frequency of the CF component shifts due to Doppler effects during flight, CF-FM bats compensate for these Doppler-shifts by adjusting their call frequency accordingly, thus maintaining the echo frequency at a preferred frequency (the reference frequency) that is slightly above F_{rest} (e.g., Hipposiderid bats: Gustafson and Schnitzler 1979) Unless the auditory system, which is narrowly tuned to the reference frequency, has appropriate adaptation for such large amount of change in F_{rest}, a fine-analysis of Doppler-shifted echoes is impossible. In addition, we confirmed that *H. terasensis* during flight adjust their pulse CF_2 frequency so that echo frequencies are usually slightly higher than their resting frequencies (Hiryu et al. 2005). This suggests that the reference frequency of *H. terasensis* could be changed according to the changes in their F_{rest}, although the changes in the reference frequency of *H. terasensis* were not physiologically determined over this observation period. This implies that the auditory system exhibits a flexible adaptation mechanism whereby the frequency properties change continually according to short- or long-term intra-individual change in $F_{rest.}$ Neurophysiological studies will help in elucidating the underlying causes.

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