



Diel activity patterns during autumn migration to hibernation and breeding sites in a Japanese explosive breeding frog *Rana sakuraii*

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Relatively few studies have investigated diel activity patterns in amphibians; in particular, such studies focusing on autumn migration are lacking. I investigated the diel activity patterns during autumn instream migrations (to hibernation and breeding sites) of *Rana sakuraii*, an explosive breeding frog, at mountain headwaters in Japan. Successive censuses at 2-h intervals, over a period of 24 h, were conducted 15 times during 4 years (2001, 2002, 2013 and 2014). The diel activity pattern was not significantly different between the sexes. It was clearly bimodal nocturnal (almost like a crepuscular type), with the first peak appearing at 1600–2400 h and the second peak appearing at 0400–0800 h. The diel activity was highly correlated with day time, but not with water and air temperatures. However, it was controlled primarily by illumination rather than by the day time, because relatively many frogs migrated even during the day when it was very dark due to overcast or rainy weather and during the midnight time (0000–0400 h) when the environment was slightly illuminated by moonlight owing to clear weather. In contrast, the diel activity pattern during the winter breeding migration was clearly unimodal, with the peak at 1600–2400 h, probably because the ambient temperature during the second peak was too low, even though the illumination was suitable. The results presented herein demonstrate that *R. sakuraii* requires an optimum ambient illumination; consequently, its diel activity shows a bimodal nocturnal pattern.

Key words: autumn migration, bimodal nocturnal, crepuscular, diel activity, instream migration, *Rana sakuraii*

INTRODUCTION

Documents on amphibian autumn migrations are scant; only few studies have focused on such migrations in anurans (e.g. *Bufo bufo*: Heusser, 1968, Sinsch, 1988; *Rana temporaria*: Koskela & Pasanen, 1974, Verrell & Halliday, 1985, Pasanen & Sorjonen, 1994, Pasanen et al., 1994, Ludwig et al., 2013) and urodeles (*Ambystoma talpoideum*: Semlitsch, 1985; *Notophthalmus viridescens*: Hurlbert, 1969; *Triturus helveticus*: van Gelder, 1973; four *Triturus* spp.: Blab & Blab, 1981). Furthermore, to the best of our knowledge, diel activity patterns during amphibian autumn migration to hibernation or breeding sites have not been investigated. However, such studies have been less, not because few amphibians perform autumn migrations, but because the migration is likely overlooked and field research on autumn migration is very difficult compared with that during the other periods.

Of the few studies on diel activity patterns in amphibians, most have focused on the prominent activity periods when individuals can be counted easily by visual or aural observations, or captured easily using traps. For example, the diel activity patterns have been explored (1) during winter or spring breeding migrations (e.g.

Gittins, 1983; Semlitsch & Pechmann, 1985; Pechmann & Semlitsch, 1986; Miwa, 2007), (2) using calling behaviour (van Gelder & Hoedemaekers, 1971; Hatano et al., 2002; Kaefer et al., 2012), and (3) during non-breeding periods, in particular, using feeding behaviour, as in anurans (e.g. Martof, 1953; Bellis, 1962; Oplinger, 1967; FitzGerald & Bider, 1974; Hailman, 1984, Deguise & Richardson, 2009) and in urodeles (e.g. Himstedt, 1971; Jaeger et al., 1976; Parker, 1994; Bakkegard, 2002).

Studies on the diel activity patterns focus not only on the active time (e.g. diurnal or nocturnal) but also on the differences (1) between sexes (Dolmen, 1983b, 1988; Ranta et al., 1987), (2) between adults and juveniles (Martof, 1953; Ferguson, 1960; Dolmen, 1983a, b, 1988; Fasola, 1993), (3) between neotenic and terrestrial morphs of *Ambystoma tigrinum* (Rodda, 1986), and (4) between sexual and feeding behaviours (Griffiths, 1985; Martin et al., 1989). Moreover, studies on diel activity have investigated the differences in the patterns at different altitudes or latitudes within the related species (Navas, 1996), or the differences across species at the same breeding site (Jaeger & Hailman, 1981; Graves, 1999).

Moreover, factors that influence or control diel activity patterns have been discussed by several authors.

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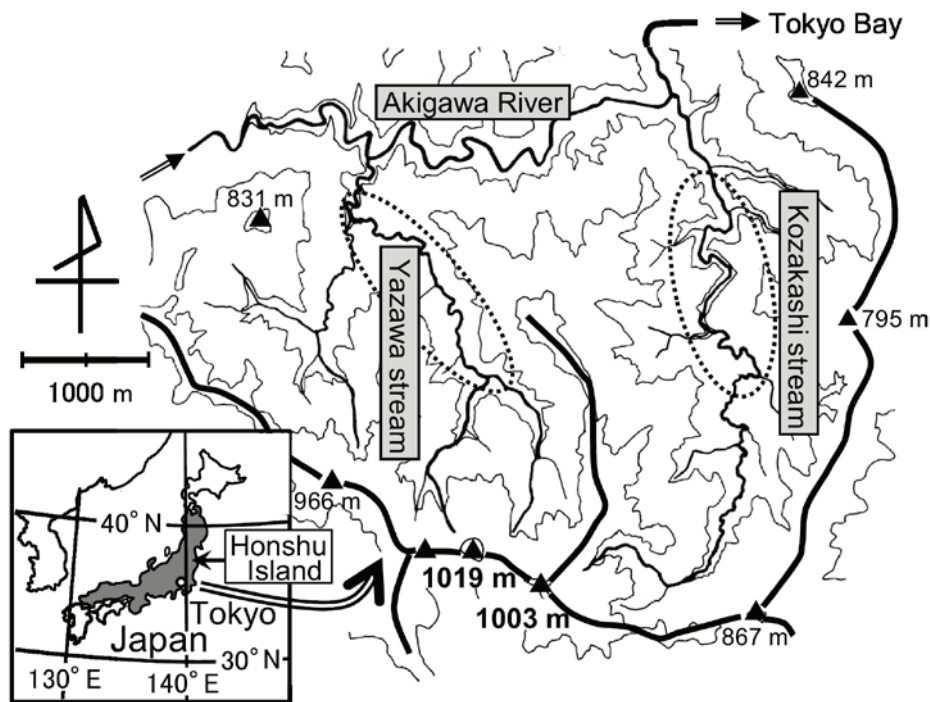


Fig. 1. Study area. Research areas along the Kozakashi and Yazawa streams are circled with broken lines. Ridge lines are shown by heavy black lines. Contour interval: 200 m.

For example, abiotic proximate factors: air or water temperatures, relative humidity, and illumination (light intensity); a biotic proximate factor: circadian rhythm; and ultimate factors: avoidance from visual predators, avoidance from desiccation, and adaptation to the diel activity patterns of the prey.

Since December 1991, I have been investigating the annual migrations of an explosive breeding frog, *Rana sakuraii*, in the Japanese mountain headwaters. I have previously reported that the diel activity of winter breeding migration was highly correlated with water temperature and was clearly unimodal, peaking at about 1600–2400 h after maximum water temperature was recorded (Miwa, 2007). Herein, I report the first study on diel activity patterns during autumn migration (to the hibernation and breeding sites) of *R. sakuraii*, focussing on the activity time and the differences between sexes as well as between autumn and winter breeding migrations. Moreover, I discuss the proximate and ultimate factors that influence the diel activity patterns during autumn.

MATERIALS AND METHODS

Study area

This field study (autumn and winter breeding migrations, etc.) began in 1991 and was conducted at the Kozakashi and Yazawa, which are two neighbouring mountain streams and tributaries of the upper basin of the Akigawa River, located about 50 km west of Tokyo, Japan, at 35°40' N and 139°9' E (Fig. 1). Both the streams are clear, narrow and rapidly flowing with rocky banks originating from the mountains at altitudes of 1,003 and 1,019 m, respectively (Fig. 1). The study was initiated at the Kozakashi stream but in 2000, the main research stream was changed to the Yazawa because forest roads were developed along the Kozakashi and some areas of this stream were disturbed owing to the abundant

inflow of soil and sand for several years. Research area along the Yazawa was upstream of the Kozakashi, and was a bit narrower and at a higher inclination than the area along the Kozakashi (Fig. 1); however, other geographical features of both the streams did not differ significantly. Research areas (about 2,500 m long) were selected along the stretches of both the streams; the areas along Kozakashi and Yazawa were at altitudes of 300–450 and 350–500 m, respectively (Fig. 1). In the study areas, riffles (shallows) were 2–4 m wide and 5–20 cm deep, rapids or small gradual cascades were 1–2 m wide and 5–20 cm deep, pools were 1–2 m wide and 0.5–2.0 m deep, and small waterfalls were 0.5–2 m wide and 0.5–5 m high. In this area, during the autumn migration period from mid-October to early December, the sunrise time ranges from 0600 to 0650 h and that of sunset from 1745 to 1655 h. Throughout the year, the minimum water temperature was usually recorded after sunrise; the mean, at about 1200 h; and the maximum, at about 1500 h (Miwa, 2002, 2007).

Study species

Rana sakuraii is one of the more abundant frogs in Japan; it inhabits cool, clear, rapidly flowing streams in the low mountain areas and is widely distributed throughout Honshu Island (the main island of Japan) except for the northern region (Miwa, 2002, 2006). This frog is the foremost migratory anuran in Japan and shows migration patterns similar to those of migratory fishes (Miwa, 2006). The annual migratory cycle of this frog can be divided into five periods: autumn migration (to the hibernation sites, the same as the breeding and spring torpor sites) from mid-October to early December; hibernation from early December to early February; winter spawning migration from early February to mid-March; a spring torpor period from mid-March to late April; and a summer active period (when frogs return to headwaters) from late April to mid-

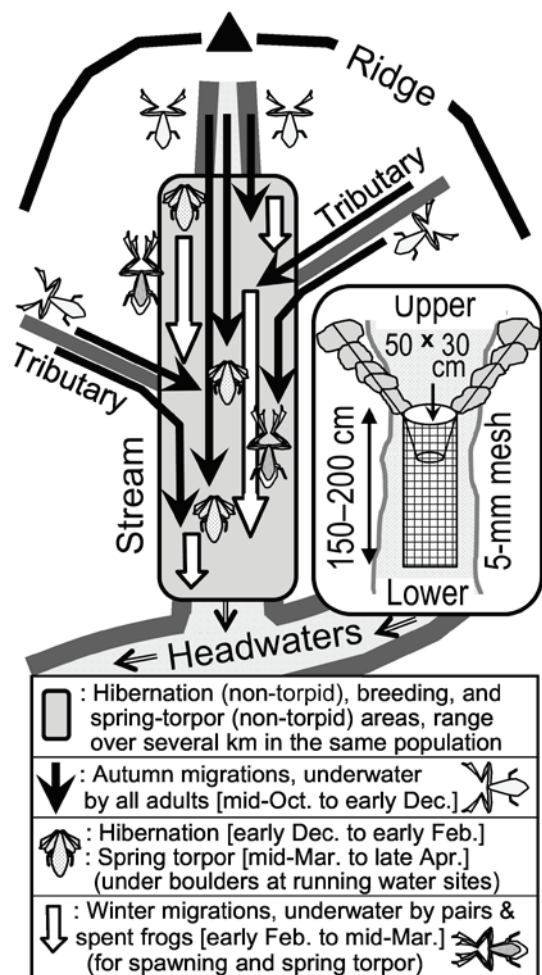


Fig. 2. Diagram of annual migrations in *Rana sakuraii* (summer migration showing the return to headwaters is not depicted) and the formation of a net-trap. The autumn and winter migration distances vary widely, ranging from several tens of metres to several kilometres (Miwa, 2002, 2006).

October (Fig. 2; Miwa, 2002, 2006). The frogs live around stream sources in summer; they migrate long distances downstream underwater in autumn and hibernate under boulders at shallow sites with running water. They swim the entire way at the bottom of the streams during both autumn and winter migrations (Miwa, 2002, 2006).

Study periods, data collection and temperature measurements

The autumn migration of *R. sakuraii* was studied from mid-October to late December for 6 years (1999, 2001, 2002,

2005, 2013, and 2014). To study the diel activity pattern, the captured frogs were censused at 2-h intervals over a period of 24 h (from 0800 h to 0800 h, the next day), 15 times (59 traps in total) during 4 years (2001, 2002, 2013, and 2014). These 15 censuses were conducted on the following dates: 23–24 (5) and 29–30 (6) November and 5–6 (5) December 2001; 8–9 (6), 11–12 (6), 12–13 (6), and 24–25 (5) November and 4–5 (5) December 2002; 7–8 (2) and 15–16 (2) November 2013; 1–2 (2), 2–3 (2), 10–11 (2), 20–21 (2), and 21–22 (2) November 2014 (the numbers in the parentheses are the number of traps).

To capture frogs migrating underwater, net traps were set at narrow points of the stream where the current was rapid (Fig. 2; Miwa, 2007). Traps were set at several points (upstream, downstream, and in small tributaries) in the same stream. The number of traps varied each year, depending on the field conditions. The frogs were retrieved from the traps at each interval and placed in buckets, their number and sex was recorded before releasing them downstream of the traps.

Both water and air temperatures were recorded every 10 min to the nearest 0.1°C using Thermo Recorder TR-52 data loggers (T and D Corporation, Japan). Water temperature was measured near the upper side of almost every trap. The sensors were placed at a depth of 20–30 cm in gaps beneath boulders, submerged in the rapidly flowing areas. Air temperature was measured at two upper-stream sites within the study area, approximately 10 cm above the ground.

Statistical analyses

I divided the 24-h period into 12 2h intervals starting from 0800–1000 h to 0600–0800 h, the next day. Moreover, I used the 0800–1600 h interval as the diurnal activity time and the 1600–0800 h interval as the nocturnal time. Thereafter the following determinations were done: (1) the difference between diurnal and nocturnal times was compared using the number of migrating individuals per hour by the nonparametric Wilcoxon Rank Sum test or chi-square test; (2) the bimodal nocturnal activity was determined by assessing the difference between the nocturnal activity times—[1600–2400 h], [0000–0400 h], and [0400–0800 h]—using the number of migrating individuals per hour and nonparametric Friedman's test with Scheffé multiple comparison procedure; (3) the difference in the diel activity patterns between the sexes was assessed using the percentage of migrating individuals during the 24-h periods employing the chi-square test or Spearman rank correlation; (4) the

Table 1. Comparisons of 15 autumn diel activity measurements between the sexes of *Rana sakuraii* during 24-h periods.

		Time of day (h)												
		08–10	10–12	12–14	14–16	16–18	18–20	20–22	22–24	00–02	02–04	04–06	06–08	Total
Total number of captures	Male	11	12	12	19	123	195	189	147	53	51	155	78	1045
	Female	7	9	8	10	55	73	72	56	21	10	64	21	406
Mean % of 15 times	Male	1.4	1.6	1.1	1.5	13.7	17.6	18.0	13.2	4.2	3.9	15.7	8.1	100
	Female	1.4	1.6	0.9	2.4	16.4	23.0	15.3	11.0	3.3	2.5	13.7	8.5	100

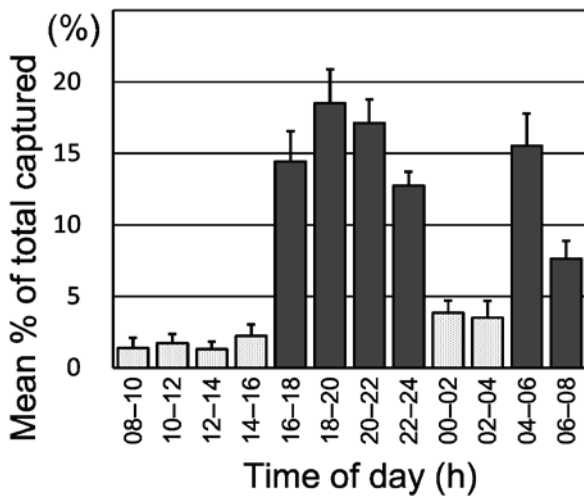


Fig. 3. Diel activity patterns during autumn migrations in *Rana sakuraii*; the mean percentage of migrating adults were measured every 2 h during fifteen 24-h periods. Bars correspond to the standard deviation.

difference in the diel activity patterns between the two streams was assessed by using the same tests as described in the previous point; and (5) correlations between diel activity and abiotic factors (air and water temperatures and day times) were assessed using the percentage of migrating individuals during the 24-h periods by using multiple regression analysis or Pearson’s correlation. Significance level was set at $P < 0.01$ for all the tests.

RESULTS

Diel activity patterns

For all six years, frogs began autumn migrations to the hibernation sites, the same as breeding sites, in mid- or late October and ended their movements in early or mid-December. They entered the stream from around the stream sources and gradually swam downstream underwater (not on the surface). I captured a total of 1,481 adult frogs (1,045 males and 406 females; Table 1) and seven juveniles (immature frogs) from 15 successive 24-h censuses by using net traps set in the streams. In addition, I captured a total of 14,003 autumn-migrating adults (9,329 males and 4,674 females) and 80 juveniles during the 6 years, including the 15 successive 24-h censuses. Diel activity patterns were clearly bimodal nocturnal (similar to a crepuscular type), with the first peak appearing at 1600–2400 h and second peak appearing at 0400–0800 h (Fig. 3). The difference between the diurnal

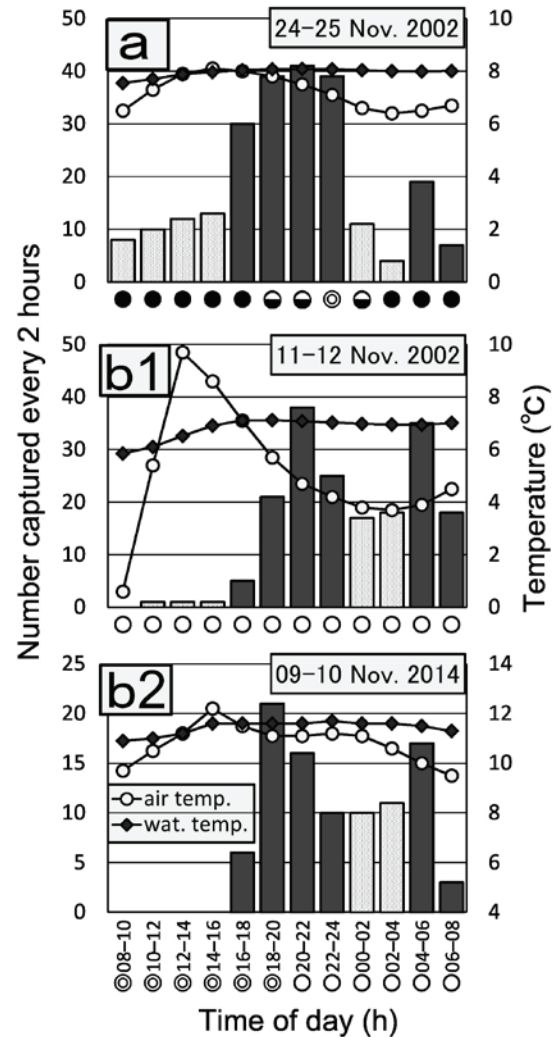


Fig. 4. Typical diel activity patterns on a dark day during the daytime (a) and during relatively illuminated mid-night time because of clear sky and moonlight (b1, b2), during autumn migrations in *Rana sakuraii*. Symbols: filled circle, rain; open circle, clear sky; open double circle, fair weather with cloudy sky; lower half filled circle, overcast sky.

and nocturnal patterns was highly significant (Wilcoxon test: $n=15$, $z=4.387$, $P < 0.001$; chi-square test: $\chi^2=153.9$, $df=14$, $P < 0.001$). Moreover, the difference between the nocturnal intervals (a: [1600–2400 h], b: [0000–0400 h], and c: [0400–0800 h]) was significant (Friedman’s test: $\chi^2=21.7$, $df=2$, $P < 0.001$; Table 2) and was clearly bimodal as determined by Scheffé multiple comparison because both the differences between the peak and bottom, i.e. a vs b and c vs b, were highly significant ($n=15$ days: $\chi^2=47.4$,

Table 2. Comparisons of autumn diel activity among bimodal nocturnal activity time—[1600–2400 h], [0000–0400 h], and [0400–0800 h]— in *Rana sakuraii*.

Test	Nocturnal activity time	Days ($n=15$)			Traps ($n=59$)		
		χ^2	df	P	χ^2	df	P
Friedman	[1600–2400], [0000–0400], [0400–0800]	21.7	2	<0.001	45.2	2	<0.001
Scheffé	[1600–2400] vs [0000–0400]	47.4	1	<0.001	86.3	1	<0.001
	[1600–2400] vs [0400–0800]	4.9	1	0.088	5.1	1	0.024
	[0000–0400] vs [0400–0800]	21.9	1	<0.001	49.5	1	<0.001

Table 3. Multiple regression analysis of the autumn diel activity against air temperature, water temperature, and time of day (category data) in *Rana sakuraii*. *n* indicates the number multiplied by 15 (24 h periods) and 12 (2 h intervals).

<i>n</i>	<i>R</i> ²	<i>P</i>	Explanatory variables and each coefficient (item or category score)					
			Air temp.	Water temp.	[0800–1600 h]	[1600–2400 h]	[0000–0400 h]	[0400–0800 h]
180	0.541	<0.001	0.052	0.000	-6.723	7.346	-4.592	3.346
			<i>P</i> =0.856	<i>P</i> =0.999	<i>P</i> <0.01	<i>P</i> <0.01	<i>P</i> <0.01	<i>P</i> <0.01

df=1, $P<0.001$; $\chi^2=21.9$; df=1, $P<0.001$, respectively). However, the difference between both the peaks, i.e. a vs c, was not very significant ($n=15$ days: $\chi^2=4.9$; df=1, $P=0.088$; $n=59$ traps: $\chi^2=5.1$, df=1, $P=0.024$; Table 2). Moreover, the diel activity patterns were not significantly different between the sexes ($\chi^2=2.164$, df=11, $P=0.998$; $r_s=0.986$), although the number of individuals was significantly different between the sexes ($t=4.142$, df=11, $P<0.001$; see also Table 1). Furthermore, the diel activity patterns were not significantly different between the two streams ($\chi^2=8.308$, df=11, $P=0.685$; $r_s=0.924$).

Factors influencing diel autumn migrations

Diel activity did not correlate with either the air or water temperatures (Pearson's correlation $r=0.125$, $t=1.73$, $P>0.05$; $r=0.098$, $t=1.36$, $P>0.05$; respectively). Moreover, although multiple regression analyses of the diel activity against air temperature, water temperature, and time of day revealed significant correlations ($R^2=0.541$, $P<0.001$; Table 3), both air and water temperatures did not reveal a significant correlation ($P=0.856$, $P=0.999$, respectively, Table 3), whereas the diel activity was highly correlated with the time of day (Table 3). However, the diel migratory movements were influenced and controlled by illumination rather than by the time of day as evidenced by the following observations: (1) relatively many frogs migrated during the daytime (0800–1600 h) when overcast or rainy weather led to very dark conditions, for example, on 24–25 November 2002 (Fig. 4a); (2) relatively many frogs migrated during the midnight time (0000–0400 h) when under clear weather conditions moonlight led to slight visibility, for example, on 11–12 November 2002 and 9–10 November 2014 (Fig. 4b1, b2).

DISCUSSION

Factors influencing and controlling diel activity

Abiotic proximate factors. Generally, seasonal activity is controlled by ambient temperatures or precipitation. For example, the factors that influence or control the amphibian breeding migrations are air temperature (Slater et al., 1985), soil temperature (Gittins et al., 1980), air temperature and daily cumulative temperature (Reading, 1998), air temperature and precipitation (Tester & Breckenridge, 1964; Hurlbert, 1969; Petranka, 1984), and water temperature and daily cumulative temperature (Beattie, 1985; Miwa, 2007).

In contrast, diel activity is generally controlled by time of day, and in effect, by the illumination (light intensity), (e.g. Bellis, 1962; Jaeger et al., 1976; Jaeger & Hailman,

1981; Hailman, 1984; Hatano et al., 2002; Kaefer et al., 2012). Moreover, as was found in the present study, Semlitsch & Pechman (1985) and Pechmann & Semlitsch (1986) reported that although the diel activity correlated with time intervals, it did not correlate with mean air temperature or rainfall. Furthermore, the fact that nocturnal movements were influenced by moonlight provides the evidence for illumination, rather than the time of day, being a primary factor. For example, Ferguson (1960) reported that, although adult toads (*Bufo fowleri*) were active from early evening to near dawn, they were absent under conditions of clear skies and full moon. Similarly, FitzGerald & Bider (1974) reported that toads (*Bufo americanus*) were less active in nights with full moon rather than in those with new moon. In the present study, although *R. sakuraii* basically showed bimodal nocturnal behaviour, many frogs migrated during the midnight time when the environment was illuminated by moonlight owing to clear weather. Moreover, Jaeger & Hailman (1973) conducted laboratory phototaxis tests with 121 anuran species and demonstrated that each anuran species has a specific adapted illumination termed the 'optimum ambient illumination' or O.A.I. (Jaeger & Hailman, 1976; Hailman & Jaeger, 1976).

Although reports on the proximate factors controlling the diel activity of amphibians are relatively few, the available data suggest that it is basically controlled by illumination, which is the primary factor instead of the time of day, and that the optimum ambient illumination differs across different anuran species. Moreover, correctly determining whether the diel activity patterns are unimodal or bimodal requires that investigations be conducted over short time intervals (at least 2-h intervals). This is because elucidation of unimodal or bimodal patterns is impossible by examining the movements at 6- or 4-h intervals, although such examinations allow the determination of diurnal or nocturnal nature of the patterns.

Ultimate factors. Generally, the following three factors—avoidance from predators (Semlitsch & Pechman, 1985; Pechmann & Semlitsch, 1986), avoidance from desiccation (Bellis, 1962; Gittins, 1983; Semlitsch & Pechman, 1985), and adaptation to the diel activity patterns of prey (Griffiths, 1985; Parker, 1994)—have been considered as the ultimate factors that control the diel activity patterns. In particular, the former two factors are usually proposed as the ultimate factors because many amphibian diel activities are nocturnal and they are basically weak under dry conditions. In the present

study, first, desiccation avoidance cannot be considered a factor that influences the autumn migrations because the entire *R. sakuraii* autumn migration occurred underwater. Second, adaptation to the diel activity patterns of the prey would also not be a factor because *R. sakuraii* do not feed under cold aquatic life periods from the time of autumn migration to the spring torpor. Based on this reasoning, I believe that the most probable ultimate factor responsible for the diel autumn migration activity of *R. sakuraii* would be the avoidance from visual predators (e.g. weasels, stoats, snakes, birds, and water shrews).

Comparisons between males and females, and adults and juveniles

Pechmann & Semlitsch (1986) reported that the diel activity pattern was not significantly different between the sexes during winter breeding migrations in four anuran species. Dolmen (1983b, 1988) reported that, although both the sexes of *Triturus vulgaris* and *Triturus cristatus* were basically nocturnal during summer, males showed diurnal activity as well. Similarly, Ranta et al. (1987) reported that females of *T. vulgaris* moved slightly more at night and in the morning, whereas males moved around midday. In the present study, no significant difference during diel autumn migrations was noted between the sexes. Although few studies have investigated sexual dimorphism in the diel activity, I think that there is no difference in the diel activity patterns between the sexes except during the breeding periods.

In contrast, relatively many studies have indicated differences in the diel activity between adults and juveniles, for example, in anurans (*B. fowleri*: Ferguson, 1960; *Rana clamitans*: Martof, 1953) and urodeles (*A. tigrinum*: Rodda, 1986; *T. cristatus* and *T. vulgaris*: Dolmen, 1983a, b, 1988; *Triturus alpestris*, *Triturus carnifex*, and *T. vulgaris*: Fasola, 1993). In all these investigated species, the adults are basically nocturnal, whereas the juveniles are diurnal. In particular, Dolmen (1983b) reported that larvae are normally diurnal, and their phase shifts from diurnal to nocturnal activity in late autumn. In the present study, immature frogs did not migrate to the breeding sites during the autumn. The percentage of juveniles to the total migrating frogs was only 0.47% (7 of 1481) and these 7 juveniles showed forced movements (caused by heavy rainfall) rather than active movements. Thus, the difference in autumn migrations between the adults and juveniles of *R. sakuraii* could not be evaluated because the juveniles did not migrate during autumn.

Comparisons between autumn and winter migrations in *R. sakuraii*

In the present study, diel activity patterns during the autumn migrations were clearly bimodal nocturnal with the first peak appearing at 1600–2400 h and the second peak appearing at 0400–0800 h. However, the pattern during the winter breeding migration was clearly unimodal, and the peak occurred at approximately 1600–2400 h (Miwa, 2007). Moreover, the diel autumn migration activity correlated with the time of day, but not with water and air temperatures, unlike the activity

during winter breeding migrations, which was highly correlated with water temperature as well as the time of day. These differences were probably related to the daily minimum water temperature during the winter time. During autumn migrations, the day difference in maximum and minimum water temperature during a day was 1.0–1.5°C and the minimum temperature was at least above 5°C, usually around 6–10°C (Fig. 4). In contrast, during the winter breeding migration period, this difference was 1.5–2.0°C; the minimum temperature was usually around 3–4°C, recorded after the sunrise at around 0800 h, and the maximum was around 5°C or more and was recorded at about 1500 h (Miwa, 2007). Frogs can hardly remain active under 5°C (Miwa, 2007). Therefore, during the winter breeding migration period, owing to very low water temperature, frogs could not migrate during the time of the second peak even though the illumination was suitable, thus, leading to a unimodal nocturnal diel activity pattern.

In conclusion, the present results demonstrate that *R. sakuraii* required an optimum ambient illumination like several other anurans, resulting in bimodal nocturnal pattern of diel activity. However, during the winter migration period, the pattern was unimodal because the ambient temperature (minimum water temperature) was too low around the sunrise time (which was the time for the second peak).

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