Activity rhythms and time budget of *Sacalia quadriocellata* in captivity

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From August 2002 through July 2004, the 24-hour time budget and activity rhythm of 15 captive, wild-caught, adult *Sacalia quadriocellata* (eight females, seven males) from Qiongzhong, Hainan Island, was observed by all-occurrence and scan sampling methods. The results showed that *S. quadriocellata* spends most of its time resting (mean 96.9%) and little time on moving (mean 3%) and feeding (mean <1%). Some differences occurred between females and males in time budget. Females spent significantly more time moving than males and less time resting. There was no difference between females and males in feeding behaviour. ANOVA indicated inter-individual variation in both females and males in all behaviours, except for “other” behaviour by males. Variation among females was greater than that in males. This discrepancy may have reflected different roles in reproduction. All behaviours had significant daily rhythms. Daily movement peaked from 0700 to 1300 and from 1900 to 0300 the next day. The feeding rhythm peaked from 0700 to 0900 and from 1900 to 0300 next day. The other behaviours showed pulse-like rhythms. Compared to movement in the field, peak times in captivity were largely coincident, although their peak and sub-peak times overlapped. This overlap probably resulted from differences in seeking food. Annually, the rhythm in moving peaked from April through September. The annual feeding rhythm peaked from April through September. Both of these rhythms had significant annual variation. Some differences in moving occurred between females and males in January, February and June. Activity was positively correlated with air temperature in the breeding room, and feeding behaviour was also positively correlated with relative humidity. Movement was not correlated with relative humidity. Cluster analysis divided the 12 months into two periods: active period (AP) and quiet period (QP).

*Key words:* all-occurrences sampling, behaviour, four-eye spotted turtle, scan sampling

INTRODUCTION

Research on the activity rhythms of freshwater turtles has concentrated on field populations (Brown & Brooks, 1993; Nieuwolt, 1996; Carter et al., 2000; Arvisais et al., 2002; Doody et al., 2002; Alison, 2003). Indoor behavioural research has been limited to studies of courtship (Auffenberg, 1966; Jackson & Davis, 1972; Hidalgo, 1982; Baker & Gillingham, 1983; Bels & Crama, 1994; Liu et al., 2008).

Wild populations of the four-eye spotted turtle, *Sacalia quadriocellata*, are being reduced rapidly because of hunting and habitat destruction (DeBruin & Artner, 1987; Lau & Shi, 2000; Gong et al., 2003). Consequently, this species is designated as endangered in the *China Red Data Book of Endangered Animals* (Zhao, 1998).

A substantial amount of research has been focused on *S. quadriocellata*. Shi et al. (2002) studied the ecology of these turtles in the field. Gong et al. (2005, 2006) studied their habitat and distributional patterns. Behavioural studies have been limited in the field because this species is uncommon, lives in small streams and is very shy. The observational limitations of such situations and the associated difficulties of working in these conditions have restricted behavioural observations in nature. Nevertheless, Liu et al. (2008, 2009) analysed courtship behaviour and constructed an ethogram of this species. Zhou (1997) studied the ecology of *S. quadriocellata* in captivity, while Wang et al. (2005b) investigated its diet in captivity, He et al. (2006) evaluated physiology under the stress of low temperatures, and Fu et al. (2006, 2007) probed seasonal changes in sexual organs. Hong et al. (2004) and Fu et al. (2004a) independently reported on the anatomy of the digestive, respiratory and urogenital systems, and Fu et al. (2004b) also explored the morphology of blood cells. Jin et al. (2000) determined the molecular weight of mitochondrial DNA in the liver of this species.

In contrast to these intense efforts, the activity rhythms and time budgets of this species have not been investigated. Hence, from August 2002 through July 2004 we examined the behaviour of captive *S. quadriocellata* using a digital surveillance system in order to present new data on wild-caught individuals in captive conditions and in their home environment, and compare these trends to previous studies on wild and captive individuals. This ap-

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approach promised to give a more complete picture of the life history of *S. quadriocellata* and provide data for their conservation.

**MATERIALS AND METHODS**

**Subjects**

Fifteen adult *S. quadriocellata* (eight females and seven males) were taken from the field near Qiongzhong, Hainan Island, China. The turtles were moved to a breeding facility at Hainan Normal University for observation. They were randomly and equally divided into three groups and each group was maintained in a pool measuring 80 cm × 60 cm. The density of turtles in each pool was about 10 per m². The pools offered structural diversity, including specific areas for hiding, feeding and sunning. The water depth was deep enough to just cover the turtles’ carapaces. All turtles were weighed and measured (Table 1). Turtles were maintained on a diet of shrimp, chopped pork, liver, heart, tomato, banana and some green vegetables. Behavioural observations began after the turtles fed normally and appeared comfortable with their new environment. During the entire observation period, all turtles appeared to be healthy and free of disease.

**Experimental methods**

The turtles were individually marked with white, oil-based paint for recognition. SUNMOON-820 vidicons (Japan) were placed in front of the glass to record the turtles’ behaviour. The cameras used a 1/3 SONY Super HAD CCD DC12V video card (minimum contrast 0.005Lux/F1, made by PAL) shot in 12.5 frames/s. The video signal was transported to and stored in a computer. A “WS” multimedia digital surveillance system (Vasion Electronic Scientific and Technical Corporation, Shenzhen, China) was used to store and replay the videos.

Observations were made from August 2002 through July 2004. Uninterrupted observations persisted for five or six days during the last ten days of every month. During the observation periods, fresh food was supplied throughout the day. At night, six flaring diodes and a 7W light covered with a yellow cloth were used for observation. The intensity of nocturnal illumination did not exceed 0.4 Lx. Air and water temperatures and air humidity were recorded daily.

Instantaneous scan sampling was used to record the frequencies of all behaviours every 4 min. All-occurrence recording captured the beginning and end of feeding, sleeping, conflict and other behaviours. Activity was defined as the combination of all behaviours except resting, and feeding, resting and other behaviour were formally defined (Liu et al., in press). Other behaviours included climbing the wall, rushing the wall and a few others that were difficult to define and had unidentified functions.

**Statistical methods**

All data were evaluated by the Kolmogorov–Smirnov test for normality. A two-tailed *t*-test was used to compare behaviours between males and females. One-way ANOVA and LSD were used to compare behaviours among different individuals. Correlation analysis was used to detect relationships between behaviours and environmental factors. Hierarchical cluster analysis (average linkage method) was used to divide the year into different phases according to behaviours. All data processing used Excel 9.0 and SPSS13.0.

**RESULTS**

The Kolmogorov–Smirnov test indicated that the distributions of all data were normal (*P* >0.05). Thus, we proceeded with analyses of the data.

**Daily time budget**

The results are presented in Table 2. Turtles spent most of their time resting and far less time moving, feeding and

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**Table 1.** Sex, size and weight of four-eye spotted turtles, *Sacalia quadriocellata*, from Hainan Island used in the investigation of behavioural rhythms.

<table>
<thead>
<tr>
<th>Turtle ID</th>
<th>Sex</th>
<th>Carapace length (cm)</th>
<th>Plastron length (cm)</th>
<th>Width (cm)</th>
<th>Height (cm)</th>
<th>Body mass (g)</th>
</tr>
</thead>
<tbody>
<tr>
<td>258</td>
<td>F</td>
<td>14.01</td>
<td>12.32</td>
<td>9.40</td>
<td>4.57</td>
<td>343.5</td>
</tr>
<tr>
<td>245</td>
<td>F</td>
<td>12.81</td>
<td>10.91</td>
<td>9.12</td>
<td>4.24</td>
<td>286.8</td>
</tr>
<tr>
<td>168</td>
<td>F</td>
<td>13.51</td>
<td>11.40</td>
<td>9.28</td>
<td>4.30</td>
<td>296.7</td>
</tr>
<tr>
<td>35</td>
<td>F</td>
<td>12.34</td>
<td>10.66</td>
<td>8.90</td>
<td>3.91</td>
<td>218.4</td>
</tr>
<tr>
<td>254</td>
<td>F</td>
<td>12.44</td>
<td>10.64</td>
<td>8.88</td>
<td>4.24</td>
<td>240.3</td>
</tr>
<tr>
<td>200</td>
<td>F</td>
<td>11.78</td>
<td>10.49</td>
<td>8.21</td>
<td>3.99</td>
<td>222.2</td>
</tr>
<tr>
<td>248</td>
<td>F</td>
<td>14.01</td>
<td>12.06</td>
<td>10.12</td>
<td>4.62</td>
<td>365.7</td>
</tr>
<tr>
<td>31</td>
<td>F</td>
<td>13.67</td>
<td>11.59</td>
<td>9.70</td>
<td>4.90</td>
<td>306.0</td>
</tr>
<tr>
<td>158</td>
<td>M</td>
<td>11.48</td>
<td>9.54</td>
<td>7.91</td>
<td>4.11</td>
<td>217.2</td>
</tr>
<tr>
<td>250</td>
<td>M</td>
<td>12.49</td>
<td>10.44</td>
<td>8.74</td>
<td>3.71</td>
<td>230.3</td>
</tr>
<tr>
<td>278</td>
<td>M</td>
<td>12.06</td>
<td>10.08</td>
<td>8.79</td>
<td>4.09</td>
<td>241.8</td>
</tr>
<tr>
<td>290</td>
<td>M</td>
<td>12.04</td>
<td>10.21</td>
<td>8.50</td>
<td>4.08</td>
<td>222.7</td>
</tr>
<tr>
<td>32</td>
<td>M</td>
<td>12.12</td>
<td>10.09</td>
<td>8.86</td>
<td>4.20</td>
<td>198.7</td>
</tr>
<tr>
<td>33</td>
<td>M</td>
<td>12.64</td>
<td>10.64</td>
<td>9.44</td>
<td>3.91</td>
<td>228.2</td>
</tr>
<tr>
<td>198</td>
<td>M</td>
<td>11.34</td>
<td>11.37</td>
<td>10.04</td>
<td>4.14</td>
<td>210.0</td>
</tr>
</tbody>
</table>
engaging in other behaviours. Female and male time budgets differed: female moving behaviour was significantly greater than male moving behaviour, and the category “other behaviours” also differed significantly between females and males. There was no significant difference in feeding behaviour between the sexes.

A one-way ANOVA confirmed variation among individual females and males in almost all behaviours (Table 2). Variation among females was greater than that among males. All types of behaviour showed highly significant differences among individual females (P<0.01). In contrast, highly significant differences emerged only in the feeding behaviour of males (P<0.01) and significant differences occurred in resting and moving behaviour of males (P<0.05). No significant difference was observed in other behaviour of males (P>0.05).

The results of the LSD analysis indicated that, in every type of behaviour, the females could be divided into at least two groups with more than one individual in each group (Table 2). Similarly, males were divided into two groups for all behaviours, except “other” behaviour. In all behaviours, one individual (No. 33) differed from all other groups for all behaviours, except “other” behaviour. In all but two groups with more than one individual in each type of behaviour, the females could be divided into at least two groups with more than one individual in each group (Table 2). Similarly, males were divided into two groups for all behaviours, except “other” behaviour. In all behaviours, one individual (No. 33) differed from all other males. The main component of “other” behaviour was escaping behaviour, which occupied a mean of 74.69% of time (±37.63 SD) in this category.

A correlation analysis was used to investigate separately the relationship between body mass and activity in all individual male and female turtles. Relative activity in males (R1 = 0.841, F1=12.101, P<0.018) was significant and much higher than that of female turtles, which was not significantly correlated with body mass (R1 = 0.283, F=0.522, P=0.497).

### Table 2. Differences in time budget for various behaviours in captive four-eye spotted turtles, Sacalia quadriocellata, from Hainan Island. *P<0.05; **P<0.01.

<table>
<thead>
<tr>
<th>Sex</th>
<th>Turtle ID</th>
<th>Resting (%)</th>
<th>Moving (%)</th>
<th>Feeding (%)</th>
<th>Other (%)</th>
<th>F value</th>
<th>t value</th>
</tr>
</thead>
<tbody>
<tr>
<td>Female</td>
<td>WL254</td>
<td>97.10±0.42</td>
<td>2.90±0.42</td>
<td>0.03±0.02</td>
<td>0.10±0.07</td>
<td>11.080**</td>
<td>–2.331*</td>
</tr>
<tr>
<td></td>
<td>WL200</td>
<td>97.69±0.50</td>
<td>2.31±0.50</td>
<td>0.44±0.15</td>
<td>0.02±0.01</td>
<td>11.078**</td>
<td>2.332*</td>
</tr>
<tr>
<td></td>
<td>WL248</td>
<td>98.66±0.31</td>
<td>1.34±0.31</td>
<td>0.05±0.03</td>
<td>0.02±0.01</td>
<td>4.319**</td>
<td>0.596</td>
</tr>
<tr>
<td></td>
<td>NM31</td>
<td>98.01±0.39</td>
<td>2.00±0.39</td>
<td>0.27±0.15</td>
<td>0.04±0.01</td>
<td></td>
<td>2.285*</td>
</tr>
<tr>
<td></td>
<td>LM35</td>
<td>96.49±0.50</td>
<td>3.51±0.50</td>
<td>0.42±0.12</td>
<td>0.02±0.01</td>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td>WL258</td>
<td>93.67±0.92</td>
<td>6.33±0.92</td>
<td>0.15±0.06</td>
<td>0.45±0.10</td>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td>WL245</td>
<td>93.97±0.67</td>
<td>6.03±0.67</td>
<td>0.55±0.11</td>
<td>0.34±0.08</td>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td>WL168</td>
<td>96.94±0.43</td>
<td>3.06±0.43</td>
<td>0.06±0.03</td>
<td>0.15±0.08</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Male</td>
<td>WL278</td>
<td>97.72±0.66</td>
<td>2.27±0.66</td>
<td>0.30±0.08</td>
<td>0.08±0.06</td>
<td>8.789**</td>
<td></td>
</tr>
<tr>
<td></td>
<td>WL290</td>
<td>97.18±0.47</td>
<td>2.82±0.47</td>
<td>0.29±0.08</td>
<td>0.08±0.03</td>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td>NM32</td>
<td>97.89±0.50</td>
<td>2.11±0.50</td>
<td>0.09±0.07</td>
<td>0.06±0.03</td>
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<td></td>
</tr>
<tr>
<td></td>
<td>LM33</td>
<td>95.51±0.81</td>
<td>4.49±0.81</td>
<td>0.55±0.16</td>
<td>0.12±0.07</td>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td>WL198</td>
<td>97.82±0.25</td>
<td>2.18±0.25</td>
<td>0.08±0.04</td>
<td>0.05±0.01</td>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td>WL158</td>
<td>97.60±0.28</td>
<td>2.40±0.28</td>
<td>0.10±0.04</td>
<td>0.07±0.03</td>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td>WL250</td>
<td>97.68±0.42</td>
<td>2.32±0.42</td>
<td>0.08±0.04</td>
<td>0.07±0.03</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Means</td>
<td>Female</td>
<td>96.57±0.26</td>
<td>3.44±0.26</td>
<td>0.25±0.04</td>
<td>0.15±0.02</td>
<td>4.589**</td>
<td>–2.331*</td>
</tr>
<tr>
<td></td>
<td>Male</td>
<td>97.35±0.21</td>
<td>2.65±0.21</td>
<td>0.21±0.04</td>
<td>0.07±0.02</td>
<td>0.9596</td>
<td>2.285*</td>
</tr>
</tbody>
</table>

### Daily rhythm

Captive male and female *S. quadriocellata* displayed very similar daily rhythms. Both of their daily activity rhythms peaked from 0700 to 1300 and 1900 to 0300 the next day (Fig. 1a). The sum of the peak time of females’ moving behaviour occupied a mean of 79.50% (±4.62 SD) of daily active time, and in males a mean of 79.57% (±4.79 SD). The difference between the sexes was not significant (two-tailed t-test: t13 = –0.029, P=0.977). Males and females displayed very similar daily rhythms in their feeding behaviour. Their daily feeding rhythm peaked from 0700 to 0900 and again between 1900 and 0300 the next day (Fig. 1b). The sum of the peak time of females’ feeding behaviour occupied a mean of 90.00% (±7.60 SD) of daily feeding time and in males a mean of 93.66% (±4.76 SD). The difference between the sexes was not significant (two-tailed t-test: t13 = –0.029, P=0.977). Other behaviour showed a pulse-like rhythm (Fig. 1c). Four peaks and four troughs occurred in the daily rhythms of both males and females. The values of the females’ peaks were significantly greater than those of males (two-tailed t-test: t13 = 2.696, P=0.018).

### Annual activity

*Sacalia quadriocellata* showed a significant annual rhythm (Fig. 2a). Differences occurred between male and female annual rhythms. The annual activity rhythm peaked from April to September in both males and females (Fig. 2a), but unlike the females, the males had troughs in February and June. Activity patterns of males and females differed significantly in both February (two-tailed t-test: t13 = 2.523, P=0.025) and June (two-tailed t-test: t13 =
Both males and females showed a significant and similar annual feeding rhythm. The annual feeding rhythm peaked from April through September (Fig. 2b). In this period, the cumulative annual feeding time averaged a mean of 81.56% ± 18.75 SD in females and a mean of 81.83% ± 17.40 SD in males. The two-tailed t-test showed that the difference was not significant (two-tailed \( t_{13} = -0.029, P = 0.977 \)). Both sexes showed three active phases in other behaviour (Fig. 2c), but compared to the females' peak in June, the males showed a trough, and the peak value of females in January was significantly greater than that in males (two-tailed t-test: \( t_{13} = 2.213, P = 0.045 \)). In other behaviour, the male and female rhythms were quite similar, the greatest difference emerging in January and June.

Monthly variation was further analysed with a one-way ANOVA. All of the four behaviours exhibited significant monthly variation (activity: \( F_{11,168} = 3.312, P = 0.0004 \); feeding: \( F_{11,168} = 4.174, P < 0.0001 \); resting: \( F_{11,168} = 3.311, P = 0.0004 \); other: \( F_{11,168} = 1.952, P = 0.036 \)). A cluster analysis incorporating all four behaviours summarized annual variation (Fig. 3). Two main groups were revealed: active period (AP; from April through September), and quiet period (QP; from October through March the following year).

**Environmental factors**

Correlation analysis was used to investigate the relationships between activity and feeding behaviours and environmental factors (Table 3). A highly significant positive correlation occurred among the behaviours and fluctuating air and water variables, except for the relationship between activity and relative humidity.

**DISCUSSION**

Endogenous activity rhythms and time budgets probably reflect adaptations to environmental conditions (Alcock, 1993). Many differences exist between field and captive environmental conditions. Consequently, some behav-
iours with high elasticity will be affected differentially. Regardless, rigid behavioural elements will be expressed in captive environments (Jiang et al., 2001).

**Daily time budget**

In captivity, female *S. quadriocellata* spent most of their time resting, as did males. This probably reflected both their physiology and the captive environment. The basal metabolic rate in turtles is very low (Zhou et al., 2001a). Thus, as a physiological constraint, the turtles probably minimized their movement and time moving. Captive *Terrapene carolina carolina* also spent 91% of their time concealed within the hide box (Casea et al., 2005). The limited space and the comparatively homogeneous environment could have also reduced the frequency and duration of some behaviours (Jiang et al., 2001). A similar phenomenon also occurs in captive *Leiolepis reevesii* (Wang et al., 2005a).

Differences in the activity, resting and other behaviours between males and females may reflect their different reproductive roles. In general, reproductive investment between males and females differ substantially, with females having a far greater investment than males (Emlen & Oring, 1977). Turtles are no exception. In wild animals, foraging often occupies greater than 50% of the time budget in most species (Segal, 1989; Croke, 1997; ILAR, 1998). The greater levels of female activity, including searching for food, probably reflects their increased energy requirements. Relative reproductive efforts are also reflected in the larger body size of female *S. quadriocellata* (Shi et al., 2002). Nevertheless, the expectation of differential feeding behaviour was not strongly

<table>
<thead>
<tr>
<th>Case</th>
<th>0</th>
<th>5</th>
<th>10</th>
<th>15</th>
<th>20</th>
<th>25</th>
</tr>
</thead>
<tbody>
<tr>
<td>Label Num</td>
<td>+-----------------+-----------------+-----------------+-----------------+-----------------+-----------------+-----------------</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
</tbody>
</table>

![Cluster analysis of annual activity rhythms of captive four-eye spotted turtles, Sacalia quadriocellata, from Hainan Island. The numbers on the y-axis represent 12 months, while the x-axis shows the value of average linkage distance between groups.](image)

**Table 3.** Correlations between behaviours and environmental factors in captive four-eye spotted turtles, *Sacalia quadriocellata*, from Hainan Island.

<table>
<thead>
<tr>
<th>Activity and relative humidity</th>
<th>Activity and relative humidity</th>
<th>Activity and relative humidity</th>
<th>Feeding and relative humidity</th>
<th>Feeding and relative humidity</th>
<th>Feeding and relative humidity</th>
</tr>
</thead>
<tbody>
<tr>
<td>$R$</td>
<td>0.412</td>
<td>0.419</td>
<td>0.009</td>
<td>0.454</td>
<td>0.470</td>
</tr>
<tr>
<td>$df$</td>
<td>49</td>
<td>49</td>
<td>49</td>
<td>49</td>
<td>49</td>
</tr>
<tr>
<td>$F$</td>
<td>9.820</td>
<td>10.204</td>
<td>0.004</td>
<td>12.462</td>
<td>13.617</td>
</tr>
<tr>
<td>$P$</td>
<td>0.003</td>
<td>0.002</td>
<td>0.950</td>
<td>0.001</td>
<td>0.001</td>
</tr>
</tbody>
</table>
supported by our analyses; they were not statistically significant. Fiennes (1966) pointed out that captive feeding consists of infrequent meals of highly processed food and this requires little time and effort. Hence, highly processed and similar foods probably lead to similar feeding time budgets. This shift in relative feeding efforts has been shown to be common in many other kinds of captive animals (Chang et al., 2001; Teng et al., 2003; Wang et al., 2005a), but further study is required to elucidate the behavioural mechanisms of sexual separation in turtles.

The LSD analysis indicated that the degree of heterogeneity in females was much greater than that in males (Table 2). Female and male individual hourly activity rates were very similar (Fig. 4). Thus, differences in individual activity patterns were due to relative intensity at different hours of the day. This may have been caused by inter-individual variation and/or different responses to the captive environment.

Could individual variation be due to differences in body weight? Relative activity in males was much higher than in females. It is possible that individual turtles who were better acclimated to captivity would be healthier and, consequently, heavier and more active. However, there was no correlation between female body weight and activity, suggesting that this scenario was not true. Thus, the activity behaviour of females was not affected by factors related to their body weight.

An explanation for the greater extent of variation in females remains elusive. Females had more complex reproductive structures than males, a generalization that is also true for S. quadriocellata. Thus, more complicated regulation mechanisms probably evolved in females. Zhou et al. (2001b) reported that stress could disturb behaviour and hormonal secretions in individual turtles. Such disruption can affect a female’s natural regulation mechanisms and behaviours (Gregory et al., 1996; Mahmoud et al., 1989; Ruby et al., 1994). Perhaps differences in water quality, temperature, illumination and crowding between field and captivity could cause stress, and because regulation in females is very complex, the effects caused by stress are likely to be equally complicated. Taken together, these factors may have led to greater heterogeneity in female behaviour. If this is true, then the kinds of stress that act on regulation need further study. Conversely, it is possible that the sample size was too small to detect behavioural regulation.

Daily rhythm

Animal activities change with time, season, environment, illumination, temperature and food resources, forming...
rhythms (Alcock, 1993). Like many species of turtles, *S. quadriocellata* has two activity peaks in its daily rhythm, one in the morning and the other in the afternoon. Plummer (2003) points out that these two peaks in *T. ornata* coincide with optimum temperature for body movement.

Behaviours and rhythms of *S. quadriocellata* in the field (Shi et al., 2002) were very similar to those observed in captivity. However, some differences also occurred, particularly in movement. In the field, *S. quadriocellata* moved most frequently at night from 1800 to 0600 the next day, although some movement occurred in the daytime from 0600 to 1200 (Shi et al., 2002). In nature, movement was related to suitable temperatures, lower disturbance and relative abundance of food. In contrast to natural conditions, activity in captivity peaked in the daytime, and at night there was a sub-peak. Interestingly, the peak times were largely coincident between the field and captivity. In nature, feeding behaviour is concentrated from 1700 to 0300 (Shi et al., 2002) and the activity peak is correlated with feeding. In captivity, food was abundant. Thus, the time required for finding food vanished. Daytime activities in the field associated with basking and searching for more suitable habitat persisted in captivity. Consequently, diurnal activity in captivity corresponded to that in the field, but nocturnal activity in captivity was substantially reduced. Thus, the daily activity rhythm of captive *S. quadriocellata* was a distortion of the endogenous, natural rhythm. Gattermann et al. (2008) found that female *Mesocricetus auratus* shifted from diurnal to nocturnal activity patterns when maintained in captivity. This shift in activity was caused by the removal of predators. Similarly, the absence of predators may have caused the different rhythms between field and captive *S. quadriocellata*. However, our data could not address this possibility.

Escape was the most frequent component of “other” behaviour (mean 74.69%) and may have been expressed only in captivity. Similar observations have been made in *Lepidochelys olivacea* (Gu et al., 2006), *T. c. carolina* (Casea et al., 2005) and *Caretta caretta* (Zhu, 2002), among others. The rhythm of other behaviour had nearly the same shape as escape behaviour (Fig. 5). Escape behaviour may have reflected constraints imposed on the turtles by the size of the holding pools, and the unnatural environment. Arena & Warwick (1995) indicated that non-avian reptiles had strong innate drives and were not subject to parental and social education. Non-avian reptiles may be less tolerant and less adaptable to an unnatural, captive environment. This would have led to the occurrence of abnormal behaviour (e.g. rushing wall). Evidence for this explanation came from the pulse-shaped rhythm. Ceaseless movement would have led to fatigue and not a pulse-shaped rhythm involving a repeated cycle of escape→fatigue→rest.

Escape behaviour was more common in females than in males. This could have occurred for two reasons. First, given their larger body sizes and the necessity of greater energy sources for reproduction, escape behaviour could have reflected an increased search for food resources. Given that food was limitless, this appears unlikely. Second, and more likely, escape behaviour could have resulted from the search for a place to lay eggs.

**Annual activity**

The annual activity rhythm and feeding behaviour of captive *S. quadriocellata* were very similar to those described by Zhou (1997). Differences existed between females and males in their moving behaviour in January, February and June. Zhou (1997) reported that, in captivity, *S. quadriocellata* always laid eggs in spring from the last ten days of May to the middle ten days of June. In comparison, Shi et al. (2002) discovered that wild *S. quadriocellata* laid eggs in winter from January to February.

Differences in the activity patterns of males and females may have reflected different sexual roles. In both of the egg-laying periods, activity peaks in males occurred one or two months earlier than those of females seeking sites to lay eggs. Brown & Brooks (1993) found a similar phenomenon in wild *Chelydra serpentina*. They attributed this to male mate-searching, followed later by females moving to find nesting sites. Thus, different reproductive strategies might have been responsible for sexual differences in annual activity in captive *S. quadriocellata*.

The cluster analysis divided the activity rhythms into two periods: AP and QP. These periods of activity corresponded with the very dry and rainy seasons in Hainan Island. Many behavioural differences were observed between dry season and rainy season. Greater activity in the rainy season than in the dry season has been documented in many chelonians (Plummer, 2003; Alison, 2003; Meshaka & Blind, 2001; Lue & Chen, 1999). These patterns were repeated in captive *S. quadriocellata*, probably for two reasons: the endogenous rhythms that formed under the particular natural climate, and tempera-
ture. These two factors probably worked together synergistically.

Figure 6 summarizes the annual activity rhythms of the active and quiet periods. The shapes of the curves are quite similar, and the beginning and end points of all peaks are the same. The similarities may be caused by the nearly constant photoperiod in the tropics.

Environmental factors

Being an ectotherm, the activity of S. quadriocellata was highly correlated with temperature. In captivity, no relationship was observed between activity and relative humidity, although the latter was highly significantly correlated with feeding (Table 3). Shi et al. (2002) discovered that S. quadriocellata were more active after rain. They interpreted this to reflect an increased abundance of food items (e.g. insects and worms) for this species. Following rains, wild S. quadriocellata always displayed feeding behaviour.

The time budget and activity rhythm of captive S. quadriocellata reflected endogenous factors and their restricted environment. Captive S. quadriocellata expressed behaviours not reported from wild turtles. Nevertheless, much work remains to be done for the successful captive reproduction and protection of S. quadriocellata.

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