The partitioning of temporal movement patterns of breeding red-crowned crane (Grus japonensis) induced by temperature

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Abstract: Patterns of movement through time are important components of animal behavior and key to understanding animal ecology. Due to methodological challenges, including tracing and analyzing movements and their changes, they are seldom studied to identify both seasonal patterns and their driving forces. Using seven GPS-collared red-crowned cranes (Grus japonensis, RCCs), we recorded their moving distances and concurrent climatic data to analyze the relative importance of these factors in RCC movements. Temperature was identified as the most important of these climatic variables in RCC movements. Based on temperature dependence and researcher expertise, we determined RCC temporal movement patterns as mating, brooding, wading, and growing with specific temporal periods partitioning. With the distance quantile of movement, we also identified the preferred temperature ranges in each temporal pattern. The four specific temporal partitionings of breeding movement and their preferred temperature ranges can effectively help wildlife managers devise conservation budgets and allocate resources. Our study provides a robust methodology in the partitioning of avian temporal movement patterns and further the understanding of animal behavior ecology, which is applicable to the study and conservation of other species, as well as for RCCs.

Key words: Behavioral ecology, movement, temporal pattern, wetland, Zhalong Reserve, red-crowned crane

1. Introduction

Animals move in response to both biotic and abiotic environmental variables, such as temperature, vegetation, hydrology, predation, and anthropogenic activities. Therefore, knowledge of these variables is key to understanding a species’ habitat usage and suitability, as well as its population fitness (Wong and Candolin, 2015). Even the health of individual animals can be measured by observing alterations in defined behavior sequences that indicate health-related stresses (Alados et al., 1996; Alados and Huffman, 2010). Such knowledge is essential for wildlife managers and land owners as they develop research protocols and conservation programs (Ma et al., 2013; Rehage, 2014; Ball et al., 2017).

Previous studies of animal movements focused mainly on categorizing them along with other types of behaviors (e.g., feeding, resting, traveling, diving, flying, dabbling, courtship, and vigilance) and their respective time budgets, and all of the above relied on personal observations to yield counts of those behaviors and time-budgets (Brown and Fredrickson, 1987; Charchar et al., 2017). We also observed that animals keep moving, either long or short distances, in conjunction with all types of recorded behaviors. These behaviors were also the result of movements. Investigating movement patterns during a species’ life cycle can help further understand behavioral characteristics of that species, thus providing valuable information for species protection in the long term. However, previous behavioral studies paid little attention to temporal movement patterns (patterns of movement through time) and the methods to determine them; therefore, factors contributing to movement dynamics are poorly known.

Temperature is an important ambient variable affecting all animals’ life cycles (Bale et al., 2002) and birds are...
especially sensitive to temperature, even more so than to precipitation (Pearce-Higgins et al., 2015). Notably, studies have identified temperature as some species’ dominant abiotic factor (Bale et al., 2002) because of its effects on some animals’ behaviors (Paladino, 1985; Long et al., 2012). Since a slight variation of temperature (<1 °C) can affect movement traits (Hopkins et al., 2011; Coe et al., 2015), migratory birds have advanced their spring migration time by 2.1 days per decade and 1.2 days per °C, which coincides with peak food availability (Both et al., 2009; Takuji et al., 2016). Through manipulating the velocity of animal movements and analyzing prey encounter rates (Dell et al., 2014), especially when food or space was limited, temperature was found to be a crucial component in affecting population dynamics, genetic diversity, and extinction risk (Amaresekkare and Savage, 2012; Clements et al., 2014). Given that temperature, in conjunction with movement, is important for the long-term survival of a species, the relationship of temperature and animal movement, and how temperature affects temporal patterns of movement, are essential pieces of information that have been lacking until now. These data, together with observations of other behaviors influenced by temperature during discrete periods of a species’ life history, are important for future conservation efforts.

Because of continually increasing global temperatures (Stocker et al., 2013; Santangeli et al., 2016), calculating the temperature dependence of a species’ movements and the temporal patterns of these movements fills gaps in that species’ known behavioral ecology and provides valuable information for its conservation. Birds are greatly impacted by climate change (Hedenström, 2006; Lehikoinen et al., 2010), especially large-body species with short migration distances and special dietary requirements (Takuji et al., 2016), such as the red-crowned crane (RCC) (Grus japonensis). The RCC is the crane family species with the smallest population size in the world. Merely 1800 RCCs remain alive in northeastern China, far southeastern Russia, and the Korean Peninsula (IUCN, 2012; Liying, 2012), and it was listed as a first-level protected species in China (Ma and Tang, 1998; Wang, 2011). RCCs are found in two separate populations: the continental and the island populations (Su and Zhou, 2012). The island population resides in the southeast and northeast of Hokkaido, Japan, and is nonmigratory (Masatomi et al., 2001, 2007), while the continental population is migratory, breeding in northeastern China and far southeastern Russia from March to October. From October to March they reside on the Yellow Sea coast in eastern China and the central section of the Korean Peninsula (Johnsgard, 1983; Ma et al., 2009). By using the autorecord location technology of the global positioning system (GPS), we tracked the movements influenced by temperature dynamics and other climatic variables during RCC breeding in the Zhalong Reserve, northeastern China (Figure 1), with the overall aim of (1) investigating the relationship of temperature and other climatic factors with movement, (2) identifying the temporal movement patterns of RCCs during their breeding season, and (3) determining temperature ranges that contribute to movement pattern changes in certain life periods.

2. Materials and methods

2.1. RCC movement tracing

The RCC is a precocial bird and male cranes keep moving higher than females for vigilance and foraging in breeding (Li and Zhao, 1991; Wang et al., 2011). We first obtained permits from the national authority of administration for the Zhalong Reserve to deploy collars on seven male adult RCCs, and we fitted four randomly selected RCCs with GPS collars powered by solar panels fitted on backpacks (HQXS, Changsha, China; www.hqxs.net) in 2016 and an additional three individuals in 2017. Considering the difference of arrival time for RCCs migrating back to the breeding ground in March and the available resources of climatic data, we monitored these cranes from April to October and recorded their daily and nightly movements during their breeding seasons. Using the autorecord function of GPS, we recorded the latitude and longitude of each RCC's position once each hour in 24 h a day. With the latitude and longitude of recorded positions from GPS collars, we calculated moving distances once per hour using ArcGIS 10.0. Then, based on the full records of RCCs moving each whole day, we added distances hourly to calculate the total moving distance. The total moving distance was used as a proxy to reflect moving abilities and patterns of the collared RCCs. Although the night movement of RCCs was very small and could be omitted compared to daytime movement, we still included them into distance calculations with full data collection.

2.2. Climatic data

Wind velocity, temperature, sunshine duration, relative humidity, and precipitation during the RCC breeding seasons were incorporated into our study. All the mean values of the above climatic variables for each whole day were calculated based on the monitoring data of the Qiqihaer Station of the China Meteorological Administration (Station Code 50745), located at the Zhalong Reserve Bureau.

2.3. Relationships between climatic variables and movement

In order to explore the relative strength of correlations between different climatic variables and the moving distance, we conducted a stepwise multiple regression analysis between all five climatic variables (temperature,
relative humidity, wind, solar radiation, and precipitation) and movement distance per whole day. The best fitting model was selected based on the AIC value. Each relative effect of these climate variables on movement was designated by a P-value (P = 0.05). In addition, we conducted principal component analysis (PCA) to examine the relative importance of different climatic variables in determining the moving distance by a mutual validation of our approach and results (Véran et al., 2010). Note that data were checked for normality before the analysis and log-transformed data were used when needed.

2.4. Temporal movement patterns of breeding RCCs in response to temperature

To understand the impacts of temperature on temporal movement patterns during different breeding seasons, and using the types of main behaviors of RCCs, we preliminarily categorized the RCC breeding season into four sequential breeding subseasons, mating, brooding, wading, and growing, based on previous studies of RCC breeding periods categorizing based on behavioral change with time (Li and Zhao, 1991; Li and Yang, 1999) and the experiences and expertise of the Zhalong Reserve conservation staff (Table 1). Since these breeding subseasons were developed using expertise and experience rather than hard data, the categories had to be statistically analyzed to establish correctness. Therefore, based on the moving distances and temperature data within each of the breeding subseasons, we conducted multiple comparisons in linear mixed-effects models (LMMs) with Tukey contrast corrections to test variations, two breeding subseasons at a time, for a total of six comparison pairs (Bates et al., 2014; Hothorn et al., 2015; P = 0.05). When there is a significant difference between two breeding subseasons, they are recognized as two different temporal patterns. If there was no significant difference, the two breeding subseasons were identified as the same temporal pattern and merged. Thus, we determined RCC temporal movement patterns that responded to temperature during breeding seasons. We constructed LMMs using the Lmer function and performed multiple comparisons using the multcomp package. All data analyses were conducted in R 3.5 software (R Core Team, 2015).

Figure 1. The study area of Zhalong Reserve. Inset shows its location in northeastern China.
Additionally, based on aforementioned preliminary season partitioning and the results of PCA, we conducted a multiple regression analysis including either the first or second principal component (PC1 or PC2) and the breeding subseasons as independent variables to examine the effects of breeding subseasons on the relationships between climatic variables and moving distances.

2.5. The preferred temperature range within each temporal movement pattern

Based on the temperature dependence of movement (Joern and Logan, 2006; Allenh et al., 2008), we assumed that RCCs have a preferred temperature range that would enable them to attain a higher level of movement than other temperatures. To identify the range of preferred temperatures within different temporal movement patterns, all RCC moving records per whole day in a given breeding subseason were divided into far-moving groups and short-moving groups, above and below the median values of per whole day moving distance, respectively. Then, using SPSS 18.0 for Windows (SPSS Inc., Chicago, IL, USA), we calculated the 25%, 50%, and 75% temperature quantiles within each of those 2 groups. Based on the assumptions that temperature affects movement and that extreme low and high temperatures should be ignored, we designated the 25%–75% temperature quantile ranges of the far-moving group in each temporal movement pattern as the RCC’s preferred temperature range for that pattern (Barton et al., 2009).

3. Results

3.1. The relationship between climate variables and RCC movement

During the RCC breeding seasons (April through October) in 2016 and 2017, we obtained 1256 movement data with 24 full records in a whole day from 7 GPS-collared RCCs and climatic variables, noting that they moved the least in May and the most in October (Table 1). Based on the AIC weight of each multiple regression model, wind velocity and sunshine duration were excluded at the beginning of modeling as they were weakly correlated with the moving distance. However, temperature, relative humidity, and precipitation were included in the best selected model and identified as important climatic variables affecting RCC movements (Table 2; Figure 2). Based on the P-values in regression analysis and the PCA results (Table 3; Figure 3), temperature was the most important climatic factor affecting RCC movement.

3.2. The dynamics of temporal movement patterns influenced by temperature

Significant differences in the relationship between the moving distance and temperature within each breeding subseason (mating, brooding, wading, and growing; Table 4; Figure 4) are shown in multiple pairwise comparisons. Moreover, the four sequential breeding subseasons were validated again, and RCC temporal movement patterns during the breeding seasons were also identified as follows: mating, corresponding to the period between early April and mid-May; brooding, corresponding to the period from mid-May to the end of June; wading, corresponding to the month of July; and growing, corresponding to the period from August to the onset of migration at the end of October.

3.3. The preferred temperature ranges in each temporal movement pattern

With the median values of movement distances as the benchmarks, the records of moving distances per whole day above each median value formed the far-moving RCC groups. Based on our definition of preferred temperature, the far-moving groups’ preferred temperature ranges during the mating movement pattern were from 6.15 to 12.3 °C between early April and mid-May, 16.5 to 22 °C during the brooding movement pattern from mid-May to June, 10.3 to 22 °C during the wading movement pattern in July, and 10.4 to 22 °C during the growing movement pattern from August to the end of October.

Table 1. Preliminary RCC breeding subseasons and moving distances used to establish temporal movement patterns.

<table>
<thead>
<tr>
<th>Preliminary breeding subseasons</th>
<th>Time period (month.day)</th>
<th>Behaviors</th>
<th>Mean moving distance per whole day (m), ±SD</th>
</tr>
</thead>
<tbody>
<tr>
<td>Mating</td>
<td>4.1–5.15</td>
<td>Population mixing, nesting, mating, egg laying, incubating</td>
<td>6012.7 ± 6135.3</td>
</tr>
<tr>
<td>Brooding</td>
<td>5.16–6.30</td>
<td>Brooding, rearing, feeding, swimming</td>
<td>3570.3 ± 4097.7</td>
</tr>
<tr>
<td>Wading</td>
<td>7.1–7.31</td>
<td>Feeding, wading, walking, flight attempts</td>
<td>3876.3 ± 4586.8</td>
</tr>
<tr>
<td>Growing</td>
<td>8.1–10.30</td>
<td>Feeding, flying, vigilant avoidance, migrating</td>
<td>6850.5 ± 4571.7</td>
</tr>
</tbody>
</table>

Table 2. Summary of the best selected model from stepwise regression analysis based on AIC weights.

<table>
<thead>
<tr>
<th>Variables</th>
<th>Estimate</th>
<th>SE</th>
<th>T value</th>
<th>P</th>
</tr>
</thead>
<tbody>
<tr>
<td>Intercept</td>
<td>6669.81</td>
<td>538.68</td>
<td>12.38</td>
<td>&lt;0.001</td>
</tr>
<tr>
<td>Temperature</td>
<td>−17.28</td>
<td>1.77</td>
<td>−9.76</td>
<td>&lt;0.001</td>
</tr>
<tr>
<td>Relative humidity</td>
<td>30.41</td>
<td>8.94</td>
<td>3.40</td>
<td>0.001</td>
</tr>
<tr>
<td>Precipitation</td>
<td>−9.63</td>
<td>4.23</td>
<td>−2.28</td>
<td>0.023</td>
</tr>
</tbody>
</table>
to the end of June, 24.2 to 27.4 °C during the growing movement pattern in July, and 5.1 to 19 °C during the growing movement pattern from August to the onset of migration. The mean preferred temperature during the wading pattern was much higher than those of the other patterns (Table 5).

4. Discussion
Global temperature has increased by 0.75 °C in the past 100 years as an effect mainly due to greenhouse gas emissions (Stocker et al., 2013). Furthermore, rates of future

Table 3. Loadings for the first four principle components of the climatic variables and the moving distance.

<table>
<thead>
<tr>
<th></th>
<th>PC1</th>
<th>PC2</th>
<th>PC3</th>
<th>PC4</th>
</tr>
</thead>
<tbody>
<tr>
<td>Wind speed</td>
<td>0.31</td>
<td>−0.14</td>
<td>0.75</td>
<td>−0.43</td>
</tr>
<tr>
<td>Radiation</td>
<td>0.55</td>
<td>0.25</td>
<td>−0.31</td>
<td>−0.05</td>
</tr>
<tr>
<td>Temperature</td>
<td>−0.02</td>
<td>0.73</td>
<td>−0.05</td>
<td>−0.58</td>
</tr>
<tr>
<td>Humidity</td>
<td>−0.63</td>
<td>0.19</td>
<td>−0.14</td>
<td>−0.12</td>
</tr>
<tr>
<td>Precipitation</td>
<td>−0.43</td>
<td>0.08</td>
<td>0.45</td>
<td>0.02</td>
</tr>
<tr>
<td>Distance</td>
<td>−0.12</td>
<td>−0.58</td>
<td>−0.36</td>
<td>−0.68</td>
</tr>
</tbody>
</table>

Figure 2. Partial correlations between the moving distances and temperature, relative humidity, and precipitation. Asterisk represents the partial residuals; coefficients of the selected model are given in the bottom right corner of this figure.
climate changes are projected to increase over the next century (Hole et al., 2009). Therefore, future temperature scenarios are expected to have ever broadening impacts on animals. Our study confirmed and emphasized the correlation between temperature and RCC movement by testing temperature dependence on movements not only in the entire breeding period but in sequential seasonal breeding categories. Comparing time-budgets of various behavioral types in total or in part of a life cycle, our classification of temporal movement patterns, based on distinct temporal categories, aids wildlife managers to achieve better conservation results, as they can devise conservation budgets and allocate human resources prior to each pattern change. For instance, given that

![Figure 3](image1.png)

**Figure 3.** Principal component analysis for the climatic variables and the moving distance. The first axis (PC1) explains 31.44% of total variation, and the second axis (PC2) accounts for 22.44% of total variation.

![Figure 4](image2.png)

**Figure 4.** Multiple comparisons of the moving distance among the four RCC breeding subseasons (M: mating, B: brooding, W: wading, G: growing).

<table>
<thead>
<tr>
<th>Comparison pairs</th>
<th>Estimate</th>
<th>SE</th>
<th>Z</th>
<th>P</th>
</tr>
</thead>
<tbody>
<tr>
<td>Growing–brooding</td>
<td>2756.82</td>
<td>387.31</td>
<td>7.118</td>
<td>&lt;0.001</td>
</tr>
<tr>
<td>Mating–brooding</td>
<td>1355.35</td>
<td>456.6</td>
<td>2.968</td>
<td>0.015</td>
</tr>
<tr>
<td>Wading–brooding</td>
<td>1277.42</td>
<td>484.07</td>
<td>2.639</td>
<td>0.039</td>
</tr>
<tr>
<td>Mating–growing</td>
<td>-1401.47</td>
<td>380.49</td>
<td>-3.683</td>
<td>0.001</td>
</tr>
<tr>
<td>Wading–growing</td>
<td>-1479.4</td>
<td>485.35</td>
<td>-3.048</td>
<td>0.012</td>
</tr>
<tr>
<td>Wading–mating</td>
<td>-77.93</td>
<td>569.72</td>
<td>-0.137</td>
<td>1.000</td>
</tr>
</tbody>
</table>

![Table 4](image3.png)

**Table 4.** Results of multiple comparisons of RCC breeding subseasons to establish temporal movement patterns.
temperature information is readily available during their routine monitoring program, Zhalong Reserve managers can utilize the preferred temperature range values of each temporal movement pattern to create a RCC conservation alert system keyed to avoid potential harm arising from adverse climatic incidents to improve conservation effectiveness. Our preferred temperature ranges can also be used to enhance the RCC captive breeding program currently conducted by the Zhalong Reserve.

Based on the relationship between temperature and movement in our study and in previous studies, different species have a variety of movement responses to temperature: rates increasing with temperature (Barton et al., 2009; Rall et al., 2010), decreasing with temperature (Krüger et al., 1982; Johnson et al., 2010), or remaining temperature-independent (Novich et al., 2016). Our study showed that a species may exhibit divergent relationships between temperature/climatic variables and movements during different periods of its life cycle. Seasons had significant effects on the relationships between climatic variables and movements, while the moving distance did not rely too much on humidity, precipitation, or radiation, but temperature was correlated negatively with different breeding subseasons (Figure 5). We also found that RCC maintained a high level of movement with long distance both at the beginning and at the end of the breeding season, though temperatures were the lowest during those periods. A possible explanation is that RCCs maintain a larger range at lower temperatures, thus enabling them to maximize foraging to meet the energetic demands of breeding and migration. Coincidentally, black-necked cranes (Grus nigricollis) increased their movements while foraging for food and maintaining body warmth at low temperatures during winter (Kong et al., 2008). By and large, RCC movement and temperature were significantly correlated, but during some periods temperature was not effective enough to drive RCC movements.

Table 5. The mean temperatures and selected quantiles of far-moving groups within temporal movement patterns during breeding.

<table>
<thead>
<tr>
<th>Temporal movement pattern</th>
<th>Mean temperature (°C)</th>
<th>Quantile value of temperature</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td></td>
<td>25% Quantile</td>
</tr>
<tr>
<td>Mating</td>
<td>9.15</td>
<td>6.15</td>
</tr>
<tr>
<td>Brood</td>
<td>19.31</td>
<td>16.5</td>
</tr>
<tr>
<td>Wading</td>
<td>25.55</td>
<td>24.2</td>
</tr>
<tr>
<td>Growing</td>
<td>13.7</td>
<td>5.1</td>
</tr>
</tbody>
</table>

Figure 5. Relationships between the principal components (PC1 and PC2) and the moving distance among different breeding subseasons.
We statistically validated our preliminary classification of breeding subseasons by establishing its accuracy through statistical analysis, thus making the final temporal movement patterns more scientific and powerful. Also, using telemetric monitoring techniques of GPS collars, we were able to empirically model our movement patterns on precise data and reflect behavioral characteristics with greater certainty. We noticed that the four patterns were the least temporal types, and the identification of temporal movement patterns could have been improved if we expanded the intervals of preliminary categorizing of RCC breeding subseasons. Also, despite trying our best to obtain more permits to fit cranes with GPS collars, we acknowledge that our sample size may have limited our study’s statistical precision, but not its utility. Additionally, migratory movement is closely tied to habitat variables such as landscape heterogeneity, water level, and hydrology. With that in mind, we encourage subsequent studies to continue long-term monitoring with more environmental variables and to secure more permits to fit cranes with GPS devices, which may enable increased data accumulation to improve statistical accuracy. Moreover, for the temporal movement patterns of a full life cycle, the same study of the RCC’s wintering ground should be conducted as soon as possible. Our viable approach to distinguishing temporal animal movement patterns is applicable to the study and conservation of other species, as well as for RCCs.

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