Communication

# Network Analysis Using Markov Chain Applied to Wildlife Habitat Selection 

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#### Abstract

In the present study, behavioral states for habitat selection are examined using a discretetime Markov chain (DTMC) combined with a network model with wildlife movement data. Four male boars (Sus scrofa Linnaeus) at the Bukhansan National Park in South Korea were continuously tracked with an interval of approximately 2 h to 313 days from June 2018 to May 2019. The time-series movement positions were matched with covariates of environmental factors (leaf types and water) in field conditions. Stationary probabilities were used to quantify the habitat selection preference of wild boars, including maximum probability (0.714) with the "broadleaf without water habitat" where in-degree centrality was at its maximum (0.54), but out-degree centrality was low and even (0.17) for all states. Betweenness was the maximum for the "needleleaf without water habitat", suggesting its role as a bridging habitat between other habitats. Out-closeness scores presented the highest values in the "broadleaf without water habitat" ( 0.26 ). Similarly, the first hitting time to the habitat was shortest at the "broadleaf without water habitat" (3.64-5.16 h) and slightly longer than one day in other examined habitats, including "broadleaf with water," "needleleaf without water," and "no-leaf without water". The network model using the Markov chain provided information on both local movement behavior and general resource-use patterns of wild boars in field conditions.


Keywords: wildlife; transition probability; movement; habitat; centrality

## 1. Introduction

The analysis of wildlife movement behavior is essential for understanding host population invasion and extinction. Movement behaviors reflect the internal capacity of animals (e.g., locomotion [1] and memory [2]) and adaptive responses to external environmental conditions, such as resource availability [3] and landscape structure [4]. Consequently, movement enables animal dispersal into suitable habitats, increasing their local survival and allowing them to achieve optimal fitness under variable environmental constraints [5].

In wildlife ecology, animal movement has been examined using various computational approaches [6-9], with either data-based or mechanistic models. In mammals, data-based models have been applied mainly to habitat selection/suitability and species distribution using empirical (e.g., [10,11]), statistical [12-17], and machine learning approaches [18-21].

Mechanistic models deductively address the regularity of life events according to physi$\mathrm{cal} /$ mathematical rules. Behavioral state-space models have been proposed to determine the inner intentions of animals and their connection to observable events (i.e., movement data) [22-24]. Furthermore, a switching diffusion model was applied to indicate changes in behavioral states during animal movements based on physical dispersal processes [17,25]. In addition, individual-based models (IBM) have been used as useful platforms for accommodating mechanistic rules of life events [5,26-28].

Network models have unique properties that express complex life events and can be applied to either data-driven or mechanistic models due to their flexibility [29-33]. Networks depict various ecological events, including the spatial and temporal behavior of species [30,34,35], and have been applied to numerous mammal studies, representing associations between individuals [36], human-wildlife interactions [37], habitat suitability [38], defining corridors [20,39], and epizootic transmission [40,41]. Centrality, an outcome of network analysis, effectively provides comprehensive information regarding the importance of specific nodes within the network [42]. Jacoby et al. (2012) effectively analyzed the movement and spatial dynamics of sharks based on centrality and betweenness to determine their local and global network properties [43].

In network models, input variables are conventionally represented as object existence/preference; for instance, the spatial co-occurrence of organisms presenting either animal-animal or animal-human associations [36,37], habitat preference for species distribution [44], or ecological distances for determining connectivity between regions [38]. In this study, we use transitional probabilities to quantify the relationships between habitats for network analysis. Considering effectivity of randomness in modelling behavioral selection [44-46], Markov chains have been used in numerous studies, including capturerecapture sampling [47], home range [48], choice behavior [49], disease spread [50,51], movement [52], health status [53], life-event prediction [54], and sampling methodology [55]. In mammals, Markov chains have been applied to many species, including mice [47], squirrels [56], cattle [57], and lions [58].

Transition probabilities are inherent features of Markov chains, and an animal's local movement behavior would be realistically presented, since it reflects the probabilistic selection of one local habitat to other habitats based on specific environmental cues in a time series under field conditions. This approach could be compared to previous studies with networks applied to ecology, in which weights were mainly obtained by position-oriented data, for instance, animal habitat preference [59] or ecological distances between individuals (e.g., corridor analysis) [60]. In these cases, time-series data for habitat selection are not required as the input for the network models. In contrast, constant time-interval data together with transition probabilities for animal movements have been more suitable in revealing specific behavioral characteristics of habitat selection under field conditions [22-24].

The present study hypothesizes that transition probabilities, according to a Markov chain based on time-series data, would realistically represent wildlife resource-use patterns under field conditions. Additionally, the habitat conditions (environmental factors) defined as states in the Markov chain could also be used as nodes in the network model concurrently. Therefore, the time-series movement data could be effectively transformed in networks, presenting the overall movement patterns in wildlife resource-use for habitat selection. We selected the field data of wild boar (Sus scrofa Linnaeus) movements as an example, and the time-series movement data indicated transitions between environmental resources (leaf types and water). Subsequently, a transition probability matrix and stationary probabilities were obtained from input data using a Markov chain. Then, the transition probabilities were inputted into the network model, and centrality was obtained to characterize habitat selection behavior during animal movements under field conditions.

## 2. Materials and Methods

### 2.1. Movement Data

The continuous movement of wild boars was observed individually in the Bukhansan National Park, located north of the Han River in the southern peninsula of Korea ( $37^{\circ} 35^{\prime} 39^{\prime \prime}$ $\mathrm{N} \sim 37^{\circ} 44^{\prime} 09^{\prime \prime} \mathrm{N}, \& 126^{\circ} 56^{\prime} 08^{\prime \prime} \mathrm{E} \sim 127^{\circ} 02^{\prime} 41^{\prime \prime} \mathrm{E}$ ) area (ca. $79.9 \mathrm{~km}{ }^{2}$ ) (Figure 1). The park contains 692 floral and 1802 faunal species and cultural heritage artifacts, such as Buddhist temples. The region has an average temperature of $12.2{ }^{\circ} \mathrm{C}\left(8.6-33.2^{\circ} \mathrm{C}\right)$ and annual precipitation of $1212.33 \mathrm{~mm}(1000-1500 \mathrm{~mm})$ [61].


Figure 1. Survey area and movement locations of wild boar individuals based on telemetry data during the survey period in Republic of Korea (ROK). (Inset in the top left subfigure presenting ROK (Republic of Korea (mainland)), and the area with black color in bottom left subfigure indicating the Bukhansan mountain for the survey).

Individuals were selected to monitor different representative life-history stages in different periods (Appendix A Table A1) Movement coordinates of wild boar individuals were continuously tracked at approximately two-hour intervals at the Bukhansan Mountain (Mt.) area in Seoul, Korea, from June 2018 to May 2019, using a GPS collar (Globalstar track, Lotek Inc. ${ }^{\circledR}$, Toronto, ON, Canada) (Appendix A). If the weight of the transmitter exceeds $5 \%$ of the body weight, it could affect the animal's behavior [62]. Therefore, in the present study, GPS collars weighing less than $2 \%$ of the body weight were selected to minimize the transmitter effect. Upon permission from the Korea National Park Service (KNSP) Authority following the Animal Protection Act (Law No. 16544) and Laboratory Animal Act (Law No. 15944), the boars were tracked under the guidance of the Korea National Park Research Institute (KNPRI) (\#794; 20170406). Detailed survey methods followed guidelines prescribed by Sikes et al. (2016) [63].

Due to field conditions and difficulty in data transmission, reliable data sources from either Collar or Web (https: / /www.atsidaq.net, last accessed on 19 December 2019) were applied for analysis (Appendix A). Movement tracks were separated according to life stages and individuals to minimize data heterogeneity. The life history of wild boars is presented seasonally as fertility, perinatal, brooding, and mating [64,65]. We followed these seasonal grouping criteria but were only able to analyze the males. Wild boar seasonal behavior is mainly determined by the reproductive cycle; hence, these terms are appropriate to indicate distinct seasons. Considering activities in Korean conditions, the months for each life stage were assigned as February-April, May-July, August-October, and November-January, corresponding to fertility, perinatal, brooding, and mating, respectively. Data including
identification (Id), observed month, life stage, and the number of examined coordinates are shown in Appendix A.

For all individual movements, time-series data were obtained with a mean interval of 1.999 h and a standard deviation of 0.015 h during the observation period. We considered 2 h as the time unit for the discrete-time Markov chain (DTMC). However, due to field conditions and the collar tracking range, approximately $8 \%$ of the total observed points were missed and not used as the input data for the analysis. After pre-treating the data, 2970 of 3223 points in the time series were obtained for analysis (Appendix A). The initial data for four individuals, $\# 67, \# 05, \# 68$, and \#06, were analyzed for modeling, since they had a sufficient number of recorded points ( $>171$ ).

### 2.2. Habitat States

The open-source geoprocessing platform QGIS 3.12 [66] was used to collect the habitat information from the Ministry of Environment, Republic of Korea [67]. A point sampling tool [68] was applied to raster maps to record the relative habitat information of the observed movement points in $30 \times 30 \mathrm{~m}$ patches. The forest occupied $89.6 \%$ of the total survey area and comprised $54.8 \%$ broad-leaved, $13.0 \%$ needle-leaved (coniferous), $21.8 \%$ mixed-leaved forests, and 10\% other areas (Appendix B Figure A1a). "Water" denoted the presence of water within the spatial unit of $30 \times 30 \mathrm{~m}^{2}$. "No water" denoted the absence of water in this spatial area. The area was mostly "no water" occupying $95.2 \%$ of the total area (Appendix B Figure A1b).

The local environments, such as forests, leaves, and water, are the necessary basic natural resources (i.e., shelter, food, and water) of wild animals [69]. Accordingly, we categorized the local habitats according to the forest, leaf type, and water. This study divided the leaf type into "broadleaf" and "needleleaf". Broad-leaved forests provide the majority of natural foods (e.g., acorns) for wild boars [70,71]. Mixed-leaved forests, consisting of broad and needle leaves, were merged with the broadleaf group in this study. Additional habitats were defined according to the water as stated above. Resource availability determined wild boar individual habitat selection behavior in this study (Table 1). In total, six different habitats were defined based on behavior: broad and mixed leaf with water (U1; presented collectively as broadleaf), broadleaf without water (U2), needleleaf with water (U3), needleleaf without water (U4), no forest with water (U5), and no forest without water (U6).

Table 1. Behavioral states defined according to the different resources available at different habitats.

|  | Forest |  |  |
| :---: | :---: | :---: | :---: |
|  | Broadleaf | Needleleaf | No Forest |
| Water | U1 | U3 |  |
| No water | U2 | U4 | U6 |

Under natural conditions, the highest proportion of individuals in the survey area was observed in the U2 habitat (0.67) under natural conditions, followed by U4 (0.12) and U6 (0.11) (Appendix B Figure A1c). Overall, the proportions were matched between the data for field visits by wild boars and were statistically the same according to the Kolmogorov-Smirnov test ( $p=0.8096$ ) (Appendix B Figure A1c).

### 2.3. DTMC and Centrality

We opted to use a DTMC [72] to analyze the regularity in habitat transitions of wild boar movements based on field data. Assuming that the next state depends only on the current state as memoryless characteristics [73], the DTMC was applied to the movement data to reveal habitat selection patterns residing in the probabilistic transitions between
different behavioral states. The DTMC provides stable transition probabilities in the discrete chain sequence of random variables $X_{1}, X_{2}, \ldots, X n$ (with $n \geq 0$ ) [73,74].

$$
P\left(X_{n+1}=j \mid X_{n}=i, X_{2}=i_{n-1}, \ldots, X_{0}=i\right)=P\left(X_{n+1}=j \mid X_{n}=i\right)
$$

where $X_{n}=i$ is the state $i$ at time $n$. The behavioral state is expressed in Table 1, as stated above.
$P$ is defined as the transition probability matrix (TPM) between states; stationary state probabilities $(\pi)$ are obtained by satisfying the following conditions (see [73,74] for more explanation):

$$
\pi P=\pi
$$

where $\sum_{i} \pi_{i}=1$, and $\pi_{i}$ is the stationary probability of each state, $i$.
Regardless of the initial conditions, the stationary state probabilities can be estimated, given the sufficient data [73,74], and the stationary state probabilities were obtained using a MATLAB R2020a platform [75]. Statistical significance of the differences between TPMs was examined according to two-sample Kolmogorov-Smirnov (KS) tests [76].

To determine how quickly the state is visited, the first hitting time was calculated. The mean first hitting time $H$ on state $i$ from state $k$ is defined as:

$$
H_{k}(i)=\inf \left\{n \geq 0: X_{n}=i \mid X_{0}=k\right\}
$$

Centrality measurements obtained from the network model can be used to express the importance of states (nodes) in habitat selection. Among the numerous centralities [32,77], degree, closeness, and betweenness were measured in this study. Equations are presented in Appendix C.

- Degree centrality represents connectedness with other nodes and is calculated based on the number of connecting edges and weights for each node.
- Betweenness centrality measures how many times each node appears on the shortest path between two nodes of the network.
- Closeness centrality addresses the closeness of the target node to other nodes and is calculated as the sum of the lengths of the shortest paths between the nodes and all other nodes in the network.
The centralities were estimated using the Centrality of Graph and Network Algorithm toolbox in MATLAB R2020a [78]. Network diagrams were drawn according to the optimized choice of the network layout, considering the minimization of crossing links, total area, and number of bends, as well as the maximization of angles between the links and symmetry display [78].


## 3. Results

### 3.1. The Transition Probability Matrix (TPM)

Table 2 presents the TPMs for wild boar movements between habitats with different resources at different life stages observed in four individuals. The probabilities of remaining in the same habitat (diagonals) were high overall, ranging from 0.71 to 0.86 with a maximum for U2. In addition to U2, although some variability existed, wild boar individuals visited the habitats of U1, U4, and U6 with relatively high probabilities. Brooding and mating stages had high probabilities of transition from U1 to U2 with 0.63-0.79 and 0.76-0.74 (solid rectangles, Table 2), respectively. However, perinatal and fertile stages had relatively low levels with $0.51-0.55$ and 0.43 (dashed rectangles, Table 2), respectively, although the probability for the fertile stage was based on only one observation. The transition from U6 to U2 had a high probability $(0.80-0.83)$ during the mating stage, whereas the probabilities were low at other stages in the range of $0.31-0.55$ (Table 2). Due to the extremely small number of observations, no significant patterns could be discerned for U3 and U5.

Table 2. TPMs (in percent) of visiting habitats with different resources (forest, leaf type, and water) by wild boar individuals in different life stages: (a) \#67M_Fer., (b) \#67M_Peri., (c) \#67M_Brood., (d) \#67M_Mati., (e) \#05M_Peri., (f) \#06M_Brood., (g) \#68M_Brood., and (h) \#68M_Mati. (Fer.: Fertility; Peri.: Perinatal; Brood.: Brooding; and Mati.: Mating; Symbol, "-", within the table indicating no-observation; Colorbar assisting visualization of probability levels).


Solid rectangles are transition probabilities from U1 to U2 (see Table 1) in brooding and mating, and dashed for perinatal and fertile stages; * time.

We examined the statistical differences between the TPMs shown in Table 2 with the two-sample Kolmogorov-Smirnov (KS) test for different observations [76] (Table 3). To match the matrix element between each observation, we added zero probabilities to the transition matrix for the habitats for which the data were missing, as often observed in the cases of U3 and U5 (Table 2). The $p$-values corresponding to the differences between observations are listed in Table 3, with the null hypothesis that the TPMs are from the same population. The overall $p$-values were substantially high, supporting the lack of statistical differences between TPMs based on a significance level of 0.05 . The minimum $p$-value was observed between \#67_Peri. and \#67_Fer. with 0.055 (Table 3), indicating that these two TPMs tended to be more heterogeneous than the other states. Each TPM component (local probabilities according to habitats between observations) would not necessarily be the same, although the TPM matrices are statistically the same overall.

Table 3. Kolmogorov-Smirnov $p$-values in examining differences between TPMs of different observations.

| ID_Sex_Lifes <br> Stage * | \#67M_Fer. | \#67M_Peri. | \#05M_Peri. | \#67M_Brood. | \#06M_Brood. | \#68M_Brood. | \#67M_Mati. | \#68M-Mati. |
| :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: |
| \#67M_Fer. | 1.000 | 0.055 | 0.180 | 0.971 | 0.999 | 0.999 | 0.999 |  |
| \#67M_Peri. |  | 1.000 | 1.000 | 0.460 | 0.180 | 0.180 | 0.297 |  |
| \#05M_Peri. |  |  | 1.000 | 0.658 | 0.102 | 0.297 | 0.297 |  |
| \#67M_Brood. |  |  | 1.000 | 0.658 | 0.971 | 0.999 |  |  |
| \#06M_Brood. |  |  |  | 1.000 | 0.999 | 0.851 | 0.297 |  |
| \#68M_Brood. |  |  |  | 1.000 | 0.999 |  |  |  |
| \#67M_Mati. |  |  |  |  | 1.000 |  |  |  |
| \#68M_Mati. |  |  |  |  | 0.999 |  |  |  |

Significant at $p<0.05 ;$ * Fer.: Fertility; Peri.: Perinatal; Brood.: Brooding; Mati.: Mating.

Considering the probabilities were not symmetric between incoming and outgoing probabilities, overall bidirectional transitions were observed for each habitat in Figure 2 in violin-type maps by summarizing TPMs (Table 2) for each habitat. Figure 2a shows the profiles of incoming probabilities from the source state (previous time) to the receiving state (current time). The thickness of each horizontal violin indicates the degree of incoming incidence according to the transition probabilities observed in Table 2. For example, U2 had an overall high incidence of entering probabilities from other states, including maximum incidences of probabilities of $0.7-0.8$, indicating the high probability that wild boars came to U2. For other habitats, the probabilities were generally $<0.1$, suggesting a low probability that wild boars entered from other states.


Figure 2. Profiles of the transition probabilities (a) incoming to and (b) outgoing from the current habitat (Table 1).

The profiles of outgoing probabilities could also reveal how wild boars would emerge from the current habitat to the future habitat (Figure 2b). Overall, the outgoing probabilities were low, indicating that wild boars moved to other habitats with lower probabilities. The outgoing probabilities for U2 were considerably lower than the entering probabilities, as shown in Figure 2a. U6 had relatively fat tails, indicating that wild boars moved to diverse habitats from the no-leaf and no-water habitats.

### 3.2. Stationary State Transition Probabilities and Network Compositions

Table 4 provides the stationary probabilities for different states according to the DTMC for each observation. For example, in individual \#67M, U2 showed the highest range with the maximum probability at the mating stage ( 0.784 ) and minimum probability at the brooding stage ( 0.624 ). For other individuals, the probabilities at U 2 were also high in both
the brooding ( $0.800-0.814$ ) and mating ( 0.800 ) stages. State U1 showed lower probabilities (0.027-0.087) for \#67M across life stages, but was relatively higher for other individuals (0.097-0.151) (Table 4). According to the statistical test between stationary probabilities and land-cover distributions in field conditions, all observations were the same, with high $p$-values ranging from 0.838 to 0.955 , except for the brooding stage (last column in Table 4). Overall commonness was observed across observations, including maximum probability at U2.

Table 4. Stationary probabilities for the habitat transitions of wild boar individuals across different life stages in different individuals according to DTMC. (Colorbar assisting visualization of probability levels).

| Habitats/ Individual ** | U1 | U2 | U3 | U4 | U5 | U6 | $\Sigma$ | $p$-Values * |  |
| :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: |
| \#67M_Fer. | 0.069 | 0.717 | 0.000 | 0.118 | 0.000 | 0.096 | 1.000 | 0.928 | 0.814 |
| \#67M_Peri. | 0.087 | 0.676 | 0.002 | 0.150 | 0.005 | 0.080 | 1.000 | 0.914 |  |
| \#05M_Peri. | 0.151 | 0.496 | 0.003 | 0.284 | 0.005 | 0.061 | 1.000 | 0.838 | 0.000 |
| \#67M_Brood. | 0.027 | 0.624 | 0.004 | 0.106 | 0.000 | 0.239 | 1.000 | 0.925 |  |
| \#06M_Brood. | 0.097 | 0.814 | 0.000 | 0.000 | 0.007 | 0.082 | 1.000 | 0.465 |  |
| \#68M_Brood. | 0.112 | 0.800 | 0.000 | 0.006 | 0.006 | 0.076 | 1.000 | 0.495 |  |
| \#67M_Mati. | 0.077 | 0.784 | 0.000 | 0.102 | 0.001 | 0.036 | 1.000 | 0.851 |  |
| \#68M_Mati. | 0.132 | 0.800 | 0.000 | 0.000 | 0.026 | 0.042 | 1.000 | 0.955 |  |
| Mean | 0.094 | 0.714 | 0.001 | 0.096 | 0.006 | 0.089 |  |  |  |
| (SD) | (0.037) | (0.089) | (0.002) | (0.058) | (0.04) | (0.090) |  |  |  |

* Significant at $p<0.05$ between stationary probabilities and land-cover distributions in field conditions according to the Kolmogorov-Smirnov test; ** Fer.: Fertility; Peri.: Perinatal; Brood.: Brooding; and Mati.: Mating.

Table 5 presents the average transition probabilities for all observations for four individuals ( $n=2970$ points). As expected, the probabilities of remaining in the same habitats (i.e., diagonal) were the highest at U2 (0.80), followed by U4 (0.55), and U6 (0.44). U 1 , the habitat with all resources (broadleaf with water), had a probability of 0.24 for remaining in the same habitat. However, the transition probability to U2 was high (0.61, dashed rectangle, Table 5).

Table 5. Average TPMs between habitat states in wild boar movements (Colorbars assisting visualization of probability levels).

|  | U1 | U2 | U3 | U4 | U5 | U6 | $\Sigma$ | $n$ |  |
| :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: |
| U1 | 0.24 | 0.61) | 0.00 | 0.06 | 0.01 | 0.08 | 1.00 | 254 | 0.80 |
| U2 | 0.08 | 0.80 | 0.00 | 0.06 | 0.00 | 0.06 | 1.00 | 2069 | ${ }^{0.00}$ |
| U3 | 0.00 | 0.50 | 0.00 | 0.50 | 0.00 | 0.00 | 1.00 | 4 |  |
| U4 | 0.04 | 0.37 | 0.00 | 0.55 | 0.00 | 0.04 | 1.00 | 347 |  |
| U5 | 0.14 | 0.50 | 0.07 | 0.07 | 0.14 | 0.07 | 1.00 | 14 |  |
| U6 | 0.05 | 0.45 | 0.00 | 0.04 | 0.02 | 0.44 | 1.00 | 282 |  |
| Average | 0.09 | 0.54 | 0.01 | 0.22 | 0.03 | 0.12 | 1.00 | \2970 |  |

Figure 3 presents the network diagram based on all observations for the four individuals. According to the flows between nodes in the figure, U1, U2, U4, and U6 are strongly connected. U2 was located at the center of the network based on the transition matrix property (for determining the positions of nodes and edges, see Materials and Methods). Peripheral state U5 was related to U2 and U6, while U3 was associated with U2 and U4. State U5 was more closely associated with the states other than U3, suggesting more involvement of the "no-leaf but with water habitat" in the network than the "needleleaf with water habitat" (Figure 3). However, there were limited observations in these habitats (Table 5).


Figure 3. Network of visiting states in the movements of wild boar individuals in different habitats. The red dots indicate nodes (i.e., habitats; Table 1) in the network while arrows represent edges connecting the nodes, showing the direction of transition (i.e., wild boar movement) between nodes in network. The size of shaded circles presents the intensity of centrality.

### 3.3. Hitting Time and Centrality

Table 6 shows the first hitting time from each state to arrive at every other state based on the DTMC. As expected, the habitat with the most frequent visits, U2 (broadleaf without water), had the shortest hitting time from all other states, including itself, ranging from 1.82 to 2.58 units ( $3.64-5.16 \mathrm{~h}$ with 2 h matching one-time unit; see Materials and Methods), followed by U4 (needleleaf no water) ranging from 9.61 to 17.75 units (19.22-35.50 h). U1 (broadleaf with water) also had a short time with 12.91-15.27 units (25.82-30.54 h). The first hitting time to U6 (no forest without water) took a relatively long time, ranging from 16.02 to 17.94 units ( $32.04-35.88 \mathrm{~h}$ ) (Table 6). Furthermore, according to the hitting time, it took approximately 4 h to reach U 2 , while the other states required slightly more than one day, except for U3 and U5. The time periods of U3 and U5 were exceptionally long, with 3980.37-4338.89 units and 346.37-359.12 units, respectively. This was understandable, considering that the visiting points to the habitats with water (either coniferous leaf or no forest) were extremely limited (Table 2) and would be difficult to visit again under field conditions.

Table 7 shows the centrality measurements, indicating the importance of the nodes in the network of visiting states (Equation (A1), Appendix C). Because the flows between states are bidirectional, both incoming and outgoing centralities can be extracted differently from the network. As expected, higher scores of in-degree centrality (connections to other states regarding incoming probabilities) were presented with U2 (0.54), followed by U4 ( 0.21 ) and U6 (0.12). In contrast, the out-degree centrality, presenting outgoing connections to other states, was low and equal between all states with 0.17 (Table 7), indicating the outgoing links would be low with limited visits to other states, though U2 had high incoming connections from various states (Figure 2).

Table 6. First hitting time from each of starting to arriving habitat (Symbols in the top row explained in Table 1).

| $\boldsymbol{t}$ |  | $\boldsymbol{t}+\mathbf{1}$ | U1 | U2 | U3 | U4 | U5 |  |
| :--- | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: |
|  |  |  | 0.00 | 1.82 |  | 17.24 | 353.12 | 16.02 |
|  | U1 |  | 13.74 | 0.00 | 4338.09 | 17.22 | 357.71 |  |
|  | U2 |  | 15.27 | 2.29 | 0.00 | 3.61 | 359.12 | 17.94 |
|  | U3 |  | 14.80 | 2.58 | 4338.89 | 0.00 | 358.52 | 17.29 |
|  | U4 |  | 12.91 | 2.04 | 3980.37 | 16.39 | 0.00 | 16.47 |
|  | U5 |  | 14.35 | 2.20 | 4326.75 | 17.75 | 346.37 | 0.00 |

Table 7. Centrality measurements in the network of habitats visited by wild boar individuals. (Symbols in the top row explained in Table 1).

|  | U1 | U2 | U3 | U4 | U5 | U6 |
| :---: | :---: | :---: | :---: | :---: | :---: | :---: |
| In-degree | 0.09 | 0.54 | 0.01 | 0.21 | 0.03 | 0.12 |
| Out-degree | 0.17 | 0.17 | 0.17 | 0.17 | 0.17 | 0.17 |
| Betweenness | 0.18 | 0.00 | 0.00 | 0.41 | 0.29 | 0.12 |
| In-closeness | 0.16 | 0.06 | 0.25 | 0.18 | 0.18 | 0.16 |
| Out-closeness | 0.17 | 0.26 | 0.04 | 0.18 | 0.15 | 0.19 |

Betweenness was the highest in U4 (0.41), suggesting its role as a bridging habitat, through which wild boars would pass when visiting final habitats (Equation (A2), Appendix C). In contrast, U2 and U3 had zero betweenness values, suggesting that U2, the habitat with the highest visits, did not serve as a bridging habitat; U2 itself would mostly be the endpoint due to higher incoming probabilities (Figure 2, Tables 2 and 5).

The closeness centrality, which indicates how close a state is to other states, had the lowest value (0.06) for in-closeness, but the highest value (0.26) for out-closeness at U2, demonstrating the contrasting role of U2 regarding bidirectional closeness (Equation (A3), Appendix C). U3 had the maximum value of in-closeness and minimum value of out-closeness (Table 7), but the results for U3 were based on a small number of samples (Table 5).

Centrality measurements were superimposed on the network diagram to provide a comprehensive view of the visiting patterns of wild boars according to habitat state changes (Figure 3). U4 and U5 serve as bridge states (dotted circles with pale green shade), whereas U2 serves as a sink state with high levels of in-degree centrality (solid circle with blue shade). U2 also had the maximum value of out-closeness (solid circle with pink shade), whereas in-closeness was highest with U3 (dotted circle with pink shade). Centrality measurements provide an overview of habitat selection patterns regarding the visits by wild boars during movement.

## 4. Discussion

Although U2 was identified as a major habitat for wild boar movements (Appendix B), the incoming and outgoing probabilities were contrasting. U2 had the maximum incoming probabilities, but was low for outgoing probabilities (Figure 2 and Table 5). Similarly, U2 had the maximum in-degree centrality (0.54), but minimum out-degree centrality (0.17) (Table 7). Consequently, U2 served as a strong receiving state from all other states, but was a weak source state for other states; U2 had many inflows but a limited outflow, especially to U3 and U5 (Table 2 and Figure 3).

Betweenness quantifies the role of habitats in forming a bridge between other habitats. U4 played a vital role in betweenness in the network of habitat selection (Figure 3 and Table 7). Maximum betweenness was observed with U4, rather than U2, which had the maximum stationary probability (Table 4), suggesting U4's role as a bridging habitat [70]. It is conceivable that wild boars would pass by U4 to reach the target habitats in this study. In contrast, U2 had zero values of betweenness, suggesting that U2 would be directly linked
to other habitats, since it would mostly be the endpoint, allowing no other bridging habitats between the two endpoints as stated above (Table 7, and Figures 2 and 3).

U4 (needleleaf without water) had a high value of betweenness due to either its geographic location or wild boar behavioral characteristics in choosing habitats. According to Appendix B Figure A1c, the occupancy of U4 was low (around 0.12), similar to U1 and U6, but was substantially lower than U2 (0.67). This indicated that U4 was generally not distributed widely in the survey area and was not interspersed between other habitats (such as U2) to serve as a bridge in field conditions.

Although the proportion of time spent in U4 (needle-leaf without water) and U6 (no forest without water) by wild boars was similar, at approximately $11 \%$ under natural conditions (Appendix B Figure A1c), the betweenness was substantially different between them, showing 0.41 for U4 and 0.16 for U6 (Table 7). U4 also had high value of in-degree centrality $(0.24)$ than that of $\mathrm{U} 1(0.09)$ or U6 ( 0.19 ). These findings suggest that wild boars may pass more frequently through U4 (coniferous leaves without water) than habitats with either U1 (broadleaf with water) or U6 (no leaf no water) under field conditions; however, the spatial proportions were similar between U1, U4, and U6. Additionally, the stationary probabilities at U4 were in relatively high ranges at the perinatal stage with $0.15-0.28$ (Table 4), possibly indicating a higher chance of passing through U 4 at the perinatal stage. The results stated above indicate that high betweenness in U4 is more related to behavior. However, we could not find any specific behavioral cues that could explain visiting U4 before reaching end habitats. More research is warranted regarding habitat selection by wild boars in both field observations and modeling studies to confirm whether the high betweenness in U4 was due to either behavioral differences or random effects in field conditions.

The closeness centrality, which indicates the degree of linking, either towards (incloseness) or outwards (out-closeness), presented contrasting results with U2 (Table 7). U2 had several incoming connections (i.e., high values in the numerator in Equation (A3) in Appendix C); however, the degree of connections was also high (i.e., high values in the denominator in Equation 1), contributing to a decreased in-closeness value of 0.06. The reverse situation occurred for the outgoing closeness of U2. With lower outgoing probabilities for the denominator, the out-closeness resulted in a high out-closeness value of 0.26 (Table 7). The maximum in-degree (0.54) and minimum in-closeness (0.06) and betweenness ( 0.00 ) indicated that U 2 is a governing state that was not expendable in the habitat network in this study. In contrast, U 4 had an expendable role as a bridging state in the habitat transition network as stated above. Together with stationary probabilities and centrality measurements, the complexity residing in the habitat network was objectively revealed, providing a comprehensive view of the behavior states of wild boars in selecting habitats with different resources, as demonstrated in this study.

The combinational model of the Markov chain linked to networks provides an extra dimension of information, compared to conventional methods of habitat selection, including Jacobs Index [79] and Bailey intervals [13]. Although these indices provide information on the selection of habitats (or food), the proposed model effectively delivers transitional information between states and overall patterns of habitat selection during wild boar movements based on TPMs obtained from time series input data.

In the present study, a relatively small number of wild boars was used for modeling. In the future, more movement data with different individuals (sex and age), seasons and weather (e.g., thermoregulation [80]) would be needed to confirm the usefulness of the model. Additional analyses considering the distances to water resources warrant future studies. In this study, the proportion of habitats with water was low for field distribution and wild boar visits (Figure 3, Table 2, Table 4, and Table 5). We defined the habitat with water only when the water was within the spatial unit ( $30 \mathrm{~m} \times 30 \mathrm{~m}$ ). However, wild boar individuals may readily move to nearby habitats at distances greater than 30 m to drink water. There are some threshold distances that mammals will typically travel to obtain water; as reported in other species, 100 m is the required distance for providing water
for wildlife care [81]. Beyond this distance, animals may experience water stress. Further studies are required to define the range of spatial habitats for water sources.

## 5. Conclusions

The network model using a Markov chain effectively quantified the visiting patterns of wild boars in field conditions (Tables 4 and 5). Based on the time-series data, the transition probabilities of habitat changes in the local movement of wild boars were provided to the network, offering a comprehensive view on resource-use patterns with centrality measurements during animal movement (Figure 3).

U2 (broadleaf without water) was demonstrated to be a governing state that was not expendable in the habitat network, considering the maximum in-degree ( 0.54 ) as well as minimum in-closeness (0.06) and betweenness (0.00). The betweenness index indicated that U4 (needleleaf without water) served as a bridging habitat between different habitats. U 2 had the shortest hitting time, ranging from 3.14-5.16 h , while other states had relatively long periods, ranging from $25.82-35.88 \mathrm{~h}$, except U3 (needleleaf with water) and U5 (no leaf with water), which could be explained by the absence of food and water. Along with stationary probabilities, centrality measurements, and hitting times, the habitat network complexity was addressed, providing a comprehensive and objective view of the behavior of wild boars in habitat selection.

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## Appendix A

Table A1. Individual identification (Id), life stages, observed months, and the number of recorded points for wild boar movements based on telemetry data during the survey period.

| Id_Sex_Life Stage * | Observed Months | Recorded Points | Sources |
| :---: | :---: | :---: | :---: |
| \#67M_Fer. | Feb, Mar | 407 | Collar |
| \#67M_Peri. | May, Jun, Jul | 439 | Collar |
| \#05M_Peri. | May, Jun | 378 | Web |

Table A1. Cont.

| Id_Sex_Life Stage * | Observed Months | Recorded Points | Sources |
| :---: | :---: | :---: | :---: |
| \#67M_Brood. | Aug, Sep, Oct | 529 | Collar |
| \#06M_Brood. | Sep, Oct | 135 | Web |
| \#68M_Brood. | Oct | 171 | Collar |
| \#67M_Mati. | Nov, Dec, Jan | 675 | Collar |
| \#68M_Mati. | Nov | 236 | Collar |
|  |  | $\sum 2970$ |  |

* Fer.: Fertility, Peri.: Perinatal, Brood.: Brooding, and Mati.: Mating.


## Appendix B



Figure A1. Proportion of landcovers in the Bukhansan National Park, Korea, with (a) leaf types, (b) water, and (c) proportion of different habitats according to field and movement data.

## Appendix C

Degree centrality [32,78]:

$$
\begin{equation*}
\mathrm{C}_{\mathrm{D}}(u)=\frac{k_{u}}{N-1} \tag{A1}
\end{equation*}
$$

where $C_{D}(u)$ is the centrality score at node $u, k_{u}$ is the number of connecting edges of node $u$, and $N$ is the number of nodes in the network [32]. Since transition probabilities are directional in the probabilities of visiting habitats in our study, we obtained the incoming (in-degree) and outgoing (out-degree) of the directed Markov chain graph.

Betweenness centrality [32,78]:

$$
\begin{equation*}
c(u)=\sum_{s, v \neq u} \frac{n_{s t}(u)}{N_{s t}} \tag{A2}
\end{equation*}
$$

where $n_{s t}(u)$ is the number of shortest paths from $s$ to $v$ that pass through node $u$, and $N_{s t}$ is the total number of shortest paths from $s$ to $v$. In the present study, the transition probabilities were considered as the length of the edge to determine the shortest paths between nodes $s$ and $v$.

Closeness centrality [32,78]:

$$
\begin{equation*}
c(u)=\left(\frac{A_{u}}{N-1}\right)^{2} / C_{u} \tag{A3}
\end{equation*}
$$

where $A_{u}$ is the number of reachable nodes from node $u, N$ is the number of nodes in the graph, and $C_{u}$ is the sum of the weighted distances from node $u$ to all reachable nodes. The in-closeness centrality is based on the distances from all other nodes to node $u$, whereas the distances from node $u$ to all other nodes present the out-closeness centrality for a directed graph.

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