

Male-Specific Territoriality and Use of Specific Calls during the Non-Breeding Season in the Polygynous Eurasian Wren *Troglodytes troglodytes*

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Male-specific territoriality and use of specific calls during the non-breeding season in the polygynous Eurasian Wren *Troglodytes troglodytes*

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Territory quality is an important factor that influences male reproductive success, especially for polygynous species, in which only males with high-quality territories that provide sufficient resources for multiple females can achieve polygyny. Because males that establish territories earlier are more likely to obtain territories of higher quality, males of polygynous species are predicted to start territorial competition before the breeding season starts. I investigated the territory formation of a polygynous species, the Eurasian Wren *Troglodytes troglodytes* during winter at their breeding site in Japan. In this population, breeding sites are typically located in mountainous areas, and wrens are thought to migrate to lowlands in winter. However, I found that many males held winter territories at their breeding site and that most maintained their territories in the subsequent breeding season. In defending winter territories, wrens used specific calls instead of songs. It is possible that, despite the cost of territorial defence during winter, it is a strategy that allows males to secure access to high-quality breeding territories, thereby increasing their reproductive success.

Key words: Eurasian Wren, polygyny, territory, non-breeding season, call

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Many birds exhibit territorial behaviour, which involves the prevention of rivals from accessing areas containing vital resources that affect fitness and survival (Hinsch & Komdeur 2017, Maher & Lott 2000). Territories are often established for reproductive purposes (Maher & Lott 2000) and territory quality may be an important factor in mate choice and reproductive success (Jennions & Petrie 1997, Maguire 2006). In many species, individuals with territories of higher quality obtain a mate earlier and raise more offspring than those with poor-quality territories (Alatalo *et al.* 1986, Korpimäki 1988, Pärt 2001, Sergio *et al.* 2009a).

Territories are especially important for males of species that regularly exhibit polygyny. In such species, males need to secure resources such as food and nesting sites within their territories sufficient for multiple females so that females can gain access to resources that exceed the costs of sharing resources with other females (Johnson *et al.* 1993). As a result,

only males with high-quality territories are accepted by multiple females (Orians 1969). Indeed, it has been shown in some species that males that monopolise high-quality territories can achieve polygyny more frequently than those that settle in poor-quality territories. For example, in the Red-winged Blackbird *Agelaius phoeniceus*, males with artificially improved territories attracted another female even after mating with the first female, whereas males with reduced-quality territories failed to attract any females (Pribil & Searcy 2001). It is presumed that males in polygynous species are under stronger selection to acquire and defend high-quality territories compared to monogamous species.

Earlier settlement on the breeding grounds enables individuals to obtain higher quality territories (Alatalo *et al.* 1984, Currie *et al.* 2000, Forstmeier 2002). This effect has been well documented, especially in long-distance migrants. For example, in a study of a polygy-

nous migrant species, the Great Reed Warbler *Acrocephalus arundinaceus*, males that arrived on the breeding grounds earlier obtained more attractive territories and thus mated with more females than latecomers (Hasselquist 1998). Conversely, in non-migratory polygynous species, only a few studies have focused on the territorial formation of males. When males of a polygynous species remain in the same area throughout the year, territorial competition among males may begin before the onset of the breeding season.

The Eurasian Wren *Troglodytes troglodytes* (hereafter ‘wrens’) is a polygynous passerine bird, widely distributed throughout the Palearctic area. In Japan, wrens typically breed in spring in mountainous areas from the subalpine to the lowland zones, whereas they are often found in lower areas in winter, suggesting that individuals migrate to avoid harsh weather in the mountains (Ueta *et al.* 2023, Ueta & Uemura 2021). Here, I report that some male wrens do not migrate, but establish territories in the mountain area in winter and use them as breeding territories in the subsequent breeding season. I also show that male wrens mainly use tic calls instead of songs to defend their winter territories.

METHODS

Study site

I conducted a survey in the Ashiu Research Forest in Kyoto, Japan (35°18'31"N, 135°43'04"E). This site is located within the transition zone between warm temperate and cool temperate forests. The altitude of this site is approximately 650–700 m and it is usually covered by 1–2 m of snow during winter. I surveyed three rivers and associated streams within the site, spanning a total of 5.5 km, because wrens typically inhabit areas along rivers or streams and hold linear territories along them.

Call recording

In a preliminary survey, I often observed wrens using specific tic calls either spontaneously or in vocal interactions with other individuals, in the same way as songs are used during the breeding season to defend territories (Figure 1). Therefore, I used the tic calls as playback to investigate winter territories.

I recorded the tic calls for playback between 9 November and 9 December 2022. I walked slowly along the rivers to search for wrens, and I started an observation once an individual was located. I continued my observation until the individual ceased calling or was

lost from sight. I used a linear PCM recorder (Portacapture X8, Tascam, Japan) and a gun microphone (MKE 600, Sennheiser, Germany) for recording. I also noted the distance between the bird and microphone and the amplitude of the call using a laser measure (GLM 40, Bosch, Germany) and a sound level meter (CHE-SD1, Sanwa Supply, Japan), respectively. After recording an individual, I moved at least 100 m further along the river to avoid recording the same individual again.

I prepared playback files from call recordings using Audacity v. 3.3.3 (Audacity Team 2023). I recorded calls both when individuals spontaneously called and when two individuals were calling in response to each other, however, I only used recordings of spontaneous calls to avoid overlapping calls. Because wrens often called continuously for longer than 1 min, I chose a 30-s calling bout from each recording and used them as a playback file. The distance between the microphone and the bird was 7 to 15 m and the mean ($\pm$ SD) amplitude was 54.2 dB $\pm$ 5.1 ($n = 15$). I filtered out sound below 4 kHz and calibrated all files to 55 dB, which is the estimated amplitude at a distance of 10 m from the caller, using measured amplitude and distance assuming a decrease in sound pressure by 6 dB per doubling of distance (Bradbury & Vehrencamp 1998). Each playback file consisted of calls recorded from a single male, and I prepared five playback files using five different males for use in the winter surveys.

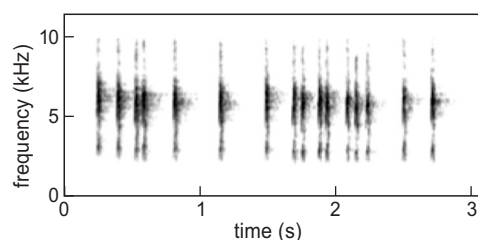


Figure 1. The spectrogram of tic calls of the Eurasian Wren.

Surveys in winter

I monitored the population of wrens to identify wintering territory holders from 9 November to 14 December 2023. Wrens at this site have been individually marked since 2022. When I found unringed birds, I captured them with mist nets and ringed them using unique colour combinations. When capturing, I took 5–20 μ l of blood by puncture of the wing vein from each individual to carry out the molecular analysis described below.

In order to determine the winter territories of wrens, I conducted line censuses with playback. For each census, I selected one playback file and repeatedly played it from a speaker (SRS-XB12, Sony, Japan) held around my waist, while walking slowly along rivers and associated streams. I conducted these censuses at least five times for each stream on different days. Thus, across all censuses, each file was used once or twice, and each individual was exposed to all five playback files. Wrens typically show territorial behaviour such as calling, searching for intruders and chasing intruders upon detecting a conspecific. Therefore, while walking, I recorded the location where wrens reacted to the playback by approaching or calling back using a GPS and identified individuals from the ring colour using binoculars. Wrens were considered to be territorial if they were recorded within 200 m of the same location in at least three censuses (the typical length of winter territory of this population was 100–200 m; see Results). This criterion for territoriality ensured that individuals were classified as territorial only if they consistently responded across multiple stimuli on multiple days. Because streams at the study site are often flanked by cliffs, wrens mostly move along streams. Therefore, the

length of the stream occupied by the focal bird was measured as the territory size of the bird. For territorial wrens, I recorded the locations at the points furthest upstream and downstream as the edges of their territory and measured the length of the stream between the two limits using QGIS (QGIS Development Team 2024).

Surveys in the breeding season

The study site was not accessible from late December until early April due to thick snow; therefore, fieldwork was not conducted during this period. I resumed monitoring of wrens on 11 April 2024. I walked along the same river where I conducted the winter surveys at least once a week to locate all breeding individuals. I determined their breeding territories by focal observation because wrens actively sing without playback. When the same individual was observed singing within 200 m of the same location at least three times, it was considered a territorial male. I observed each territorial male for 20–30 min at least once a week and recorded the locations where the male was observed during that time using a GPS. The territory length of each male was calculated using the same methods as for the winter surveys. I ended surveys on 18 July 2024 when I



Male Eurasian Wren with colour rings at the Ashiu Research Forest, Kyoto, Japan (photo Ayaka Soda, 4 April 2023).

confirmed that all individuals had completed their breeding.

Sex determination

Eurasian Wrens show little sexual dimorphism and it is difficult to determine their sex in the wild outside the breeding season. Therefore, the sex of individuals captured and ringed in winter was determined by observing their breeding behaviour during the subsequent breeding season. For four individuals that were captured in winter but were not observed in the subsequent breeding season, I applied molecular identification methods. I extracted DNA from blood samples of each individual using a DNA extraction kit (DNeasy Blood & Tissue Kit, Qiagen, The Netherlands) and amplified the CHD gene, including sex-specific introns, by PCR with sexing primers P2 and P8 (Griffiths *et al.* 1998). The thermal profile comprised an initial denaturation step of 94°C for 5 min, followed by 35 cycles of 94°C for 30 s, 53°C for 30 s and 72°C for 1 min. This was followed by a final extension step of 72°C for 5 min. I included DNA of Eurasian Wrens of known sex in the PCR run as controls, and PCR products were run through electrophoresis in 2% gels and stained with GelRed (Biotium, USA).

Statistical analysis

I used a Mann-Whitney U test to compare the territory length between winter and the breeding season. I also used a paired Wilcoxon's signed-rank test to compare the territory length between winter and the breeding season for males that maintained their territories throughout both periods. All statistical analyses were conducted using R v. 4.3.1 (R Core Team 2023).

RESULTS

In winter, 17 individuals showed typical territorial behaviour in response to the playback of tic calls (Figure 2A). Based on the observations during the breeding season or the molecular analysis (Figure S1), all 17 individuals were identified as males. Among them, 12 males were observed to maintain territoriality in the subsequent breeding season (Figure 2B). The other five males were not observed during the surveys in the breeding season and were presumed either to be dead or to have moved to other areas before the breeding season. Six other males that were not observed in winter appeared and established territories during the breeding season (Figure 2B).

The mean territory length of males in winter was significantly shorter than their breeding territories (mean: 154.8 ± 19.6 m ($\pm$ SE) and 206.1 ± 22.6 m for winter and breeding territories, respectively; $W = 72$, $P < 0.01$; Figure 3). Among the males that maintained their territories from winter to the breeding season, the difference in territory length between the two periods was not statistically significant ($W = 17$, $P = 0.09$; Figure 3), although 66.7% of the males (8/12) expanded their winter territories.

DISCUSSION

In this study, I showed that all wrens holding territories along mountain streams in winter were males. In several species, such as the American Redstart *Setophaga ruticilla*, males and females use different habitats as wintering grounds (Ornat *et al.* 1990, Wunderle 1995,

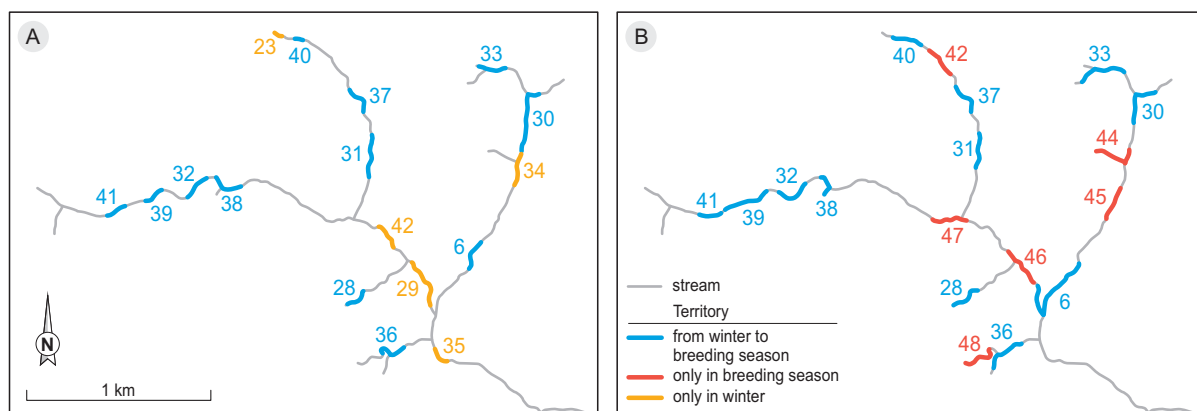


Figure 2. Results of territory mapping (A) in winter and (B) in the breeding season. Each number indicates an individual's ID. Each territory is indicated by a coloured line. In winter, 17 males established territories and 12 of them maintained their territories to the subsequent breeding season. Five males that established territories in winter were not seen in the breeding season. Six males not seen in winter established territories during the breeding season.

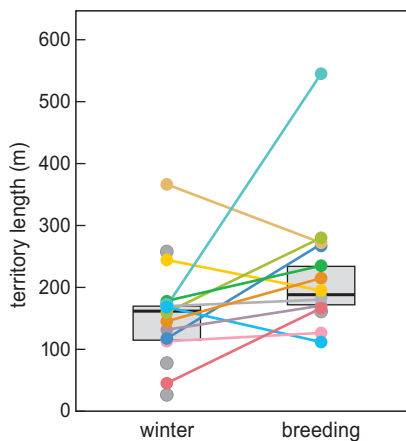


Figure 3. Comparison of territory length of males. Grey points indicate individuals that hold territories either only in winter or in the breeding season. Coloured points indicate individuals that maintained their territories from winter into the breeding season and coloured lines connect the data points for the same individuals.

Marra 2000), which may also occur in Japanese populations of the Eurasian Wren. Eurasian Wrens are often found in lowlands in winter in Japan (Ueta *et al.* 2023), but it is difficult to identify the sex from their appearance. My study suggests that the sex of these individuals may be biased towards females, which migrate to lowlands to avoid harsh weather in the mountains. Therefore, the use of mountainous areas and territoriality during winter is presumed to be a male-specific behaviour in wrens.

The use of mountainous areas as wintering habitats of insectivorous birds, including the Eurasian Wren, has received little attention because these areas are assumed to lack sufficient insects as food resources during the winter. However, in the present study, I found that male wrens defend their winter territories in such environments. One of the primary foods for these wrens is considered to be aquatic insects, which remain available along streams even during winter. In a study conducted in a temperate forest in Japan, the biomass of terrestrial invertebrates during winter was almost zero, whereas that of aquatic invertebrates increased during winter and peaked in early spring (Nakano & Murakami 2001). Therefore, holding territories along streams may allow wrens to secure enough aquatic insects to survive in the winter.

Some males failed to maintain their territories until the breeding season. This may indicate that individuals in poor condition are unable to endure the cost of staying in harsh winter weather or are unable to repel individuals in better condition from taking over their

territories (Petit *et al.* 2017, Godfrey & Bryant 2000). In contrast, some males newly gained territories during the breeding season. These individuals are supposed to be either floaters, which do not have fixed home ranges and occasionally forage in other individuals' territories in mountainous areas, or migrants that move to lowlands during winter. Floating or migrating may be an alternative winter strategy employed by younger or poorly conditioned males who cannot maintain winter territories (Hogstad 1999, Sergio *et al.* 2009b).

The winter territoriality in the wrens may enable males to secure high-quality breeding territories before the start of the breeding season. An important function of winter territories of birds is to provide food resources to territory owners (Brown & Sherry 2008, Ruiz-Sánchez *et al.* 2017), and in most species that exhibit winter territoriality, both sexes defend territories (Logan & Laura 1991, Gwinner *et al.* 1994, Cuadrado 1995, Marra 2000, Hogstad 2014, Crowther *et al.* 2018). The male-specific winter territoriality and its subsequent use of winter territories as breeding territories found in the present study may imply that winter territoriality contributes to increasing breeding success in addition to securing food. It has been reported that events or behaviours of individuals in one season can affect their performance in the subsequent season, which is called a carry-over effect (Norris *et al.* 2004, Reudink *et al.* 2009, Harrison *et al.* 2011). In White-throated Dippers *Cinclus cinclus*, some individuals form pairs and defend territories together in winter, while others are not territorial. The pairs formed in winter laid eggs significantly earlier than pairs of individuals that were not territorial in winter (Crowther *et al.* 2018). Male wrens that establish territories in winter may obtain higher-quality territories and achieve higher reproductive success than those that obtain territories after the breeding season begins. Further research will reveal the reproductive advantages of male winter territoriality.

It should be noted, however, that the present results are derived from observations from a single year. The proportion of males that choose to defend territories during winter may vary depending on weather conditions. Winter territoriality in wrens may occur primarily in years with mild winters, when the cost of survival is relatively low. Although the winter during the study year was not particularly mild, long-term observations are required to determine the generality of winter territoriality in the Eurasian Wren.

When including all individuals, winter territories were smaller than breeding territories. In contrast, when focusing only on individuals that held territories

from winter to the breeding season, there was no significant difference in territory length between the two seasons. This contrasting result suggests that individuals with relatively small winter territories are less likely to maintain them until the breeding season. However, this result should be interpreted with caution due to the small sample size, especially when comparing the territory size of individuals that remained from winter to spring. With a larger sample size, it may become evident that individuals maintaining their territories from winter to the breeding season expand their territories, potentially enhancing their ability to attract more females.

In the defence of territories, most passerine birds, including Eurasian Wrens, use songs as aggressive signals (Searcy & Beecher 2009). However, in my winter survey, wrens mainly used tic calls in territorial competitions. The production of songs results in energetic costs because it involves the coordinated movement of multiple muscles (Mencio *et al.* 2017). In winter, when food resources are limited and temperatures are low, song is especially costly as it leads to the loss of both foraging opportunities and energy for thermoregulation (Thomas *et al.* 2003, Ward & Slater 2005). Because the song of the Eurasian Wren is one of the most complex songs among Passerine birds (Kroodsma & Momose 1991), song production in winter is expected to be highly costly in this species. Therefore, tic calls could be employed in winter as a less energetically costly alternative to songs to advertise ownership of territories.

In conclusion, my results suggest that, in this non-migratory polygynous species, males start territorial competition during the non-breeding season, which may enhance their chances of mating with more females. This finding highlights the importance of considering not only behaviours in the breeding season but also those in the non-breeding season, as the latter may play a crucial role in shaping reproductive success.

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SAMENVATTING

De kwaliteit van een territorium beïnvloedt in belangrijke mate het voortplantingssucces van de bewoners van het territorium, vooral bij polygyne soorten (één mannetje met meerderde vrouwtjes). Alleen mannetjes van polygyne soorten met een hoogkwalitatief territorium zullen in staat zijn meer dan één vrouwtje aan te trekken. Hoe vroeger een mannetje zijn territorium bezet, hoe groter de kans is om een hoogkwalitatief territorium te bemachtigen. Verwacht wordt dat polygyne mannetjes al ver vóór het broedseizoen een territorium bezetten en verdedigen. Ik onderzocht in de winters van 2022 en 2023 in Japan de territoriumvorming van de polygyne Winterkoning *Troglodytes troglodytes*. Zij broeden hier vooral in bergachtige streken en men denkt dat de vogels naar lagergelegen gebieden trekken om te overwinteren. Ik ontdekte echter dat veel mannetjes 's winters een territorium in het broedgebied bezetten en dat de meeste van hen dit territorium in het broedseizoen erop behielden. Bij het verdedigen van de winterterritoria gebruikten de vogels specifieke roepjes in plaats van de zang. Het is mogelijk dat de strategie van de mannetjes in deze populatie, ondanks de kosten van het verdedigen van het winterterritorium, hen in staat stelt een hoogkwalitatief broedterritorium veilig te stellen en zo hun voortplantingssucces te vergroten.

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SUPPLEMENTARY MATERIAL

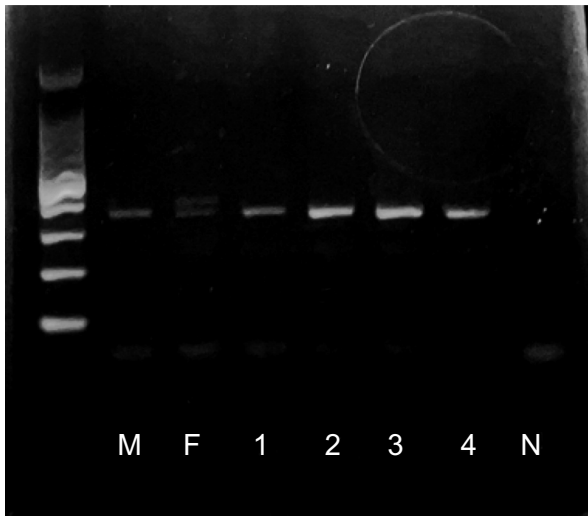


Figure S1. Results of sex determination. M: sample from a known male, F: sample from a known female, 1–4: four unidentified individuals, N: a negative control. All samples from unidentified individuals showed only one band, indicating that they were males.