Intraspecific Comparison of Ecology and Mating System of the Great Reed Warbler *Acrocephalus arundinaceus*: Why Different Results from Different Populations?

Yasuo Ezaki¹ & Eiichiro Urano²

¹Institute of Natural and Environmental Sciences, Himeji Institute of Technology (and Museum of Nature and Human Activities, Hyogo), Yayoi-ga-oka 6, Sanda, Hyogo 669-13 Japan
²Applied Ornithology Laboratory, National Agriculture Research Center, Kannondai, Tsukuba, Ibaraki 305 Japan

In the last 20 years intensive studies on the ecology and mating system of the Great Reed Warbler *Acrocephalus arundinaceus* have been conducted at five different localities in Japan and Europe. Although all the populations showed similar territorial polygyny, the studies showed partly different results and conclusions concerning the evolution of polygyny in this species. Here, we compare ecology and behaviour of the warblers from different populations based on published information, focusing on aspects of territorial polygyny inherent in the polygyny-threshold-model. Breeding results in one of the European populations were unique in that secondary females were far less successful than monogamous females compared to almost equivalent success in other four populations. Although causes of offspring mortality were not the same between populations, the European populations commonly showed higher rates of chick starvation in secondary nests than in monogamous nests, but this was not the case for the Japanese populations. Benefits which compensate for these costs of polygyny were found in three of the five populations. Despite variations in breeding results, all studies showed the existence of a potential cost of polygyny: reduced paternal care in secondary nests leading to a realized cost depending on climatic and ecological conditions. Evidences of female choice based on behavioural observations were available at some populations. In one of the populations the benefit of polygyny was linked to variance in territory quality caused by habitat heterogeneity and habitat partitioning pattern between males. But information on these aspects of ecology has not been collected enough for the other populations. Features of territory differed greatly between populations and it suggests the possibility that different mechanisms work to cause polygyny in different populations. Despite these regional differences, however, the polygyny-threshold-model is generally applicable to this species.

Key Words: Breeding results, Cost of polygyny, Female choice, Habitat, Territory

In wide-ranging species different populations often live in greatly different environmental conditions. Thus different populations of a species can exhibit different breeding strategy and social systems because of adaptive responses to local environment (Lott 1991).

The Great Reed Warbler *Acrocephalus arundinaceus* is a wide ranging species
breeding in the Palaearctic Region from the Far East to Europe (Cramp 1992). It has a social system of territorial polygyny both at the eastern and the western end of its breeding range (Haneda & Teranishi 1968, Saitou 1976a, Dyrcz 1977) and some regional differences in ecology are known. For example, post-nuptial moult occurs in the breeding area in the eastern populations but on the way to the wintering ground in the western populations (Ezaki 1984, Cramp 1992).

In the last 20 years intensive studies on colour-banded birds have been conducted on two Japanese and three European populations in Poland, Germany and Sweden. Although all the populations were similar in showing polygynous mating systems, there were some differences in their ecology and behaviour. The most marked difference is related to adaptiveness of polygyny for females. Catchpole et al. (1985) studying the German population, presented data indicating polygyny to be maladaptive for secondary females conforming to the female-deception-hypothesis of Alatalo et al. (1981, 1982), whereas Ezaki (1990) studying one of the Japanese populations found adaptiveness of polygyny for both primary and secondary females, supporting the polygyny-threshold-model of Verner (1964) and Orians (1969).

In this paper, we compare the ecology and behaviour of the Great Reed Warbler between the five different populations based mainly on published information. We elucidate similarities and differences between the populations and suggest that the polygyny-threshold-model is applicable to this species despite intra-specific variations in some aspects of its ecology and behaviour.

**PRINCIPLES OF TERRITORIAL POLYGyny**

Orians (1969) proposed an elegant working hypothesis, now called the polygyny-threshold-model (PTM), that explained the evolution of polygyny from the viewpoint of females. The mating system explained by the PTM is territorial polygyny: males establish territories before females arrive at the breeding ground; pairs are formed by female settlement in male territories where they nest and rear offspring; and females arriving later may settle in territories where the male has already mated with a female that arrived earlier.

Orians (1969) assumed a situation where females arriving later could choose between territories of mated and unmated males. In addition to this, he assumed the existence of costs to females associated with polygyny, which include competition between females and division of paternal care between nests. He then speculated under what situations females would choose already-mated males. The keypoint is the difference of territory quality occupied by different males as well as quality of males per se. If quality of territories occupied by mated males are superior to that of unmated males, late arriving females would gain benefits compensating for or exceeding the costs of choosing already-mated males. In this circumstance polygyny is adaptive for females. Evidently the PTM is constructed on the evolutionary view that polygyny is adaptive for females, which can be regarded as the basic assumption of the model. On this basis, logic of the PTM starts from two assumptions, female choice and cost of polygyny, and leads to the conclusion of benefit of polygyny and variance in territory quality. The ultimate cause of the variance in territory quality and hence of polygyny lies in the heterogeneity of the breeding habitat. The relationships between habitat; territory;
female choice; cost; benefit and adaptiveness can be shown schematically (Fig. 1). We subsequently focus on these six points when comparing different populations of the Great Reed Warbler.

**POPULATIONS COMPARED AND POLYGyny**

The populations compared are Lake Biwa (LB) and Kahokugata (KH) in Japan, Milicz (ML) in Poland, Franken (FR) in Germany and Lake Kvismaren (LK) in Sweden (Table 1). The five study sites are either located at the western end (Europe) or eastern end (Japan) of the breeding range, separated east-west from each other for more than 7,000km. The European populations belong to subspecies *arundinaceus* and the Japanese populations to *orientalis*. The northernmost

<table>
<thead>
<tr>
<th>Population (abbreviation)</th>
<th>Location</th>
<th>Subspecies</th>
</tr>
</thead>
<tbody>
<tr>
<td>Franken, Germany (FR)</td>
<td>49° 40’N, 10° 51’E</td>
<td><em>arundinaceus</em></td>
</tr>
<tr>
<td>Kahokugata, Japan (KH)</td>
<td>36° 40’N, 136° 42’E</td>
<td><em>orientalis</em></td>
</tr>
<tr>
<td>Lake Biwa, Japan (LB)</td>
<td>35° 05’N, 135° 56’E</td>
<td><em>orientalis</em></td>
</tr>
<tr>
<td>Lake Kvismaren, Sweden (LK)</td>
<td>59° 10’N, 15° 25’E</td>
<td><em>arundinaceus</em></td>
</tr>
<tr>
<td>Milicz, Poland (ML)</td>
<td>51° 34’N, 17° 19’E</td>
<td><em>arundinaceus</em></td>
</tr>
</tbody>
</table>
population is at 59° 10'N and the southernmost at 35° 05'N.

Basic breeding biology is common to the five populations (Dyrcz 1977, 1981, Ezaki 1981, 1990, Catchpole et al. 1985, Urano 1985, 1990a, c, Bensch 1993). They are summer visitors and breed in Phragmites reed marsh, usually in the submerged zone. Males arrive at the breeding ground earlier than females and establish all-purpose territories. Pairs are formed by female settlement in male territories, and some males attract more than one mate. Nest building and incubation of eggs are performed by females, whilst male parental care is restricted to feeding offspring. These common features in the five populations conform to the basic situation assumed for the PTM.

The rate of polygyny (percent of polygynous males) varied between populations from slightly more than 10% to almost 50% (Catchpole et al. 1985, Urano 1985, Dyrcz 1986, Ezaki 1990, Bensch 1993). These differences, however, do not seem attributable to intrinsic differences between the populations, since annual variation of rate of polygyny in a population ranged between 20 and 57% (Urano 1990b) almost overlapping the range of variation between populations.

**COST, BENEFIT AND ADAPTIVENESS**

Three of the six factors affecting territorial polygyny, cost, benefit and adaptiveness can be assessed from breeding results. When females choose either already-mated males or unmated males during the same period, the average success of the former (secondary females) should not be lower than the latter (usually monogamous females), if polygyny is adaptive for females. The costs and benefits of polygyny can be detected as differences in offspring mortality between the two types of females.

The success of females of different mating status in the five populations are given in Fig. 2. FR is different from other populations in that secondary females were far less successful than monogamous females. As a result the PTM was rejected only for FR (Catchpole et al. 1985) whilst for other populations it was supported (Ezaki 1990, Bensch 1993) or at least not rejected (Dyrcz 1986, Urano 1985).

In the FR populations the causes of offspring mortality were not investigated. The authors described in the text "Breeding success was so low in secondary females that no one of these females was able to fledge more than three young from the usual clutch of five eggs". Starvation was speculated as the most likely cause of deaths in the nest (Catchpole et al. 1985). In the KH population, success and mortality factors were analyzed in a life table. Survival rate of eggs on day 9 of nestling development were similar between secondary and monogamous nests. As the clutch size was not different between the two female categories, they produced almost the same number of fledglings. The principal mortality factor was nest predation both for secondary and monogamous nests (Urano 1985). At LB, clutch size and the number of fledglings per nest were almost the same between secondary and monogamous females that paired and bred during the same period. However, principal mortality factors were not same between the two female groups. In the monogamous nest predation was by far the most important mortality factor. In secondary nests, predation risk was low but the proportion of unhatched eggs was significantly greater. At LK, breeding results were compared
Fig. 2. Relative success of primary to monogamous and secondary to monogamous females at the five populations calculated from data in Catchpole et al. (1985), Urano (1990b), Dyrcz (1986), Ezaki (1990), Bensch & Hasselquist (1991b). In order to reduce the effect of year-to-year variation at KH, LK and ML relative success was calculated for each year and then averaged to give a mean value for each population. Data from FR are from one season and for LB data of all the study years were pooled because sample sizes in each year were small. For LK, total nest losses are excluded from the calculation since these values were not available for each mating category in the published articles.

Breeding results observed at the five populations are summarized in Table 2. As described earlier, secondary females raised significantly fewer fledglings than monogamous females only in the FR population. The principal mortality factor in monogamous nests was nest predation in all populations except FR for which a detailed analysis of mortality factors was not conducted. Mortality factors at
Table 2. Comparison of success and egg/chick mortality as a result of predation (PR), starvation (ST) and failure to hatch (FH) between monogamous (M) and secondary (S) females in different populations.

<table>
<thead>
<tr>
<th>Population</th>
<th>Relative success</th>
<th>Mortality factors in the nest of</th>
<th>Detection of costs from breeding results</th>
<th>Compensation of costs</th>
</tr>
</thead>
<tbody>
<tr>
<td>FR</td>
<td>M&gt;S</td>
<td>—</td>
<td>Yes</td>
<td>No</td>
</tr>
<tr>
<td>KH</td>
<td>M=S</td>
<td>PR</td>
<td>No</td>
<td>—</td>
</tr>
<tr>
<td>LB</td>
<td>M=S</td>
<td>PR</td>
<td>Yes</td>
<td>Yes**</td>
</tr>
<tr>
<td>LK</td>
<td>M=S</td>
<td>PR</td>
<td>Yes</td>
<td>Yes**</td>
</tr>
<tr>
<td>ML</td>
<td>M=S</td>
<td>PR</td>
<td>Yes</td>
<td>Yes**</td>
</tr>
</tbody>
</table>

*smaller characters indicate minor factors

**clutch size larger in S than M nests

Table 3. The benefits of polygyny for secondary females in different populations and the authors' view on the causal factor of the benefit.

<table>
<thead>
<tr>
<th>Population</th>
<th>Benefits revealed in breeding results</th>
<th>Causal factors</th>
<th>References</th>
</tr>
</thead>
<tbody>
<tr>
<td>FR</td>
<td>No</td>
<td>dense vegetation</td>
<td>CATCHPOLE et al. 1985</td>
</tr>
<tr>
<td>KH</td>
<td>No</td>
<td>dense vegetation</td>
<td>URANO 1985</td>
</tr>
<tr>
<td>LB</td>
<td>reduced predation</td>
<td>better food condition</td>
<td>EZAKI 1990</td>
</tr>
<tr>
<td>LK</td>
<td>larger clutch</td>
<td>collective defense</td>
<td>BENSCHE 1993</td>
</tr>
<tr>
<td>ML</td>
<td>reduced predation</td>
<td>collective defense</td>
<td>DYRCZ 1977</td>
</tr>
</tbody>
</table>

Secondary nests were different between populations. At KH, predation was the main cause of mortality in secondary nests as well as in monogamous nests and hence no cost of polygyny was detected from breeding results. In the other four populations principal mortality factors were different between female categories, and so costs of polygyny were detected. It is notable that starvation was the common cause of mortality in the three European populations and hence detected as the cost of polygyny, whereas not in the two Japanese populations. Compensation for costs of polygyny by benefits was detected in the three populations. At LB and ML, the patterns of compensation were similar in that predation pressure was low in secondary nests compared with monogamous nests. Compensation at LK was achieved by an increase in clutch size in secondary nests in comparison with monogamous nests.

The benefits of polygyny to females mating with already-mated males are given in Table 3. At FR and KH the authors were not required to assume benefits since secondary females were less successful than monogamous females in the former and no differences were recognized in success and egg/chick mortality factors in the latter, respectively. The benefit of reduced predation pressure in secondary nests was linked to a higher nest cover due to denser vegetation of the polygynous territories at LB and to collective nest defense by multiple families in the polygynous territories at ML. At LK it was suggested that the benefit of a larger clutch size in secondary nests was related to better food supplies in the polygynous territories.
POTENTIAL COST AND ITS REDUCTION

All the studies showed that secondary females are at a disadvantage because they received reduced paternal help in clutch provisioning (Catchpole et al. 1985, Dyrcz 1986, Ezaki 1990, Urano 1990c, Bensch 1993). This issue was intensively studied at KH and ML. At ML, the proportion of food delivered by males was significantly lower to secondary nests than to monogamous and primary nests. Owing to this reduced male help, individual chicks in secondary nests received less food from their parents than those in other nests (Dyrcz 1986). At KH provisioning by males was analyzed for three different nestling stages (early, middle and late). As at ML, the proportion of food delivered by males was significantly lower to secondary nests than to monogamous nests during early and middle nestling stages. In contrast with ML, however, the total food that individual chicks received from parents was not different between female categories (Urano 1990c). This suggests that the reduction of paternal help at secondary nests was compensated for by more frequent food delivery by females at KH but not at ML. Compensation by females for a complete absence of male help after mate desertion was reported at LB (Ezaki 1988). Reduced paternal care at secondary nests observed in all the populations can be regarded as a 'potential cost' of polygyny. This potential cost was realized as an increase in starvation of chicks in the three European populations but not in the two Japanese populations. The difference may lie in the extent to which the female can increase her provisioning effort and so reduce the potential cost of polygyny.

The more effective reduction of potential cost of polygyny (compensation for reduced paternal care) in Japanese populations is attributable to climatic differences (Urano 1990c). In the warmer climate at Japan, the female is able to reduce the time spent for brooding the chicks, especially in early nestling stages, and so may concentrate her efforts in food delivery. In cooler Europe, however, females are unable to increase provisioning effort because more time is required for brooding.

A longer time interval between nesting cycles of primary and secondary females in the same territory can also reduce the cost of polygyny (Urano 1990c) because the polygynous male is able to divide his provisioning effort more effectively between his multiple broods and so reduces the labour of his mates. The interval between nesting cycles were greater in the two Japanese populations compared with two of the European populations (Fig. 3). However, the benefit of longer time intervals is unclear in Japan because secondary females can compensate for reduced paternal care by themselves in the generally warmer climate, although the effect of increased paternal care could appear during a prolonged cold spell (Urano 1985).

The longer time interval of nesting cycles in Japan compared with Europe is contradictory to a possible reproductive strategy of females. In Europe where the summer climate is cooler than in Japan (Urano 1990c), more male help in provisioning nestlings is required for successful breeding. Hence in Europe females paired with already-mated males should increase the nesting time interval between themselves and the primary females in order to gain more help from the male, but the reverse is the case. The reduced time interval in Europe may be a product of other ecological constraints. Fig. 4 shows the temporal settling patterns of females.
Fig. 3. Frequency distribution of time intervals of first egg dates of females nesting in the same territory at four populations in Japan (KH, LB) and Europe (ML, LK). Data are from Dyrcz (1977), Ezaki (1990), Urano (1990a) and Bensch & Hasselquist (1992). At LK, the territories containing nests of radio-tracked females are excluded. Two graphs are presented because there were large differences in sample sizes between the studies.

at LK compared with those at LB. Despite variation between years, the data indicate the possibility that the pairing season in Europe is shorter and more synchronous than in Japan. A short and synchronous pairing season could constrain the time interval between nesting cycles within a territory. The settling pattern of females in the other Japanese population (KH) is similar to that at LB (Urano 1985) but information on the other European populations is not available from published articles.

Since the reduced help to secondary nest is determined by the hatching order (relative age of nestlings) but not by the pairing order (original mating status) (Bensch 1993), another way in which secondary females can reduce the cost of polygyny is through the exchange of status with the primary female (Temrin & Jakobsson 1988, Urano 1990c). If the nest of the primary female is destroyed before hatching, secondary females have the chance of becoming the first female to
hatch eggs in a territory. Thus on average, the cost of polygyny for secondary females will be reduced by heavy predation pressure and other factors causing total nest loss (Urano 1990c, Bensch & Hasselquist 1991b). At LK, the nests in primary position during the egg-laying period faced a three times higher risk of total nest loss compared with nests in monogamous and secondary position, and it was suggested that this nest loss was caused not by predation but by competitive nest destruction by secondary females in the same territory (Bensch 1993). This effect would be weak in Japanese populations where nesting cycles are staggered to a greater degree because during the egg-laying of primary females, secondary females are less likely to exist in the same territory (Ézaki 1990, Urano 1990a).

**FEMALE CHOICE**

The existence of female choice at pairing can be assessed by recording the instances of unmated males in a population. It was reported that unmated males existed on the same day or during the same period when polygyny was established.
at the FR, KH, LB and LK populations (Catchpole et al. 1985, Urano 1985, Ezaki 1990, Bensch & Hasselquist 1992). Furthermore, at ML unmated males sang for a long periods (Dyrcz 1986). These facts suggest that females in all the populations had actual chances of choosing between mated and unmated males on the day they mated with the former.

Female choice can be studied by examining the pattern of settlement of females in territories where males have different mating statuses (Ezaki 1990). For example, at LB males were divided into two categories: early arrivals and later arrivals. Early arrivals (early males) usually became polygynous whereas later arrivals (late males) tended to remain monogamous or solitary. Early males attracted first mates earlier than late males mainly because at that time most of the late males had not yet settled. When early males attracted their second mates, however, late males had already established territories and competition could occur for later-arriving females. Such competition was observed on 18 occasions (Ezaki 1990) and half of the females settled in the territories of already-mated early male and the other half in the territories of the unmated late male. This apparently equivalent choice must be modified, since many of the matings with unmated late males (6/9) occurred when all the early males were not singing long songs and so were not attracting additional females due to the nesting stage of their first mates (pre-laying and post-hatching). It follows that real mate competition for females actually occurred between already-mated early males and unmated late males on 12 occasions and in 75% (9/12) of them the females settled in the territories of the former. This indicates that the attractiveness for females of already-mated males was at least equivalent to that of unmated males.

Strong behavioural evidence of female choice was also presented by Bensch & Hasselquist (1992). By tracking females attached with radio-transmitters they found that settling females visited from 3 to 11 male territories, including both mated and unmated individuals, and thereafter mated with one of the males which was not necessarily the last they visited. This indicated that females selected mates from a variety of options which included both mated and unmated males. Besides such active mate choice, Bensch & Hasselquist (1992) also suggested that settling females had the opportunity to hear the call of primary females that had already started nesting in the territory. Consequently it seems that the chances of female deception were minimal, which was also suggested by behavioural data obtained at other populations (Ezaki 1981, Urano 1990a).

**FEMALE CHOICE FACTORS AND TERRITORY QUALITY**

The cues determining female choice can be assessed from characteristic features of the polygynous males and territories (Table 4). Common features pointed out by the authors in different populations are that polygynous males were those that arrived at the breeding ground early in the season and occupied relatively large territories with higher quality (tall, thick and dense) vegetation. Food availability and male song repertoire size were also pointed out as important in some populations. From an evolutionary point of view the cues determining female choice should be linked to the benefits obtained when choosing already-mated males, since this link is essential for the behaviour of female choice to be favoured in the population. In the three populations where a benefit of polygyny was detected from
Table 4. Possible cues determining female choice in different populations. Blanks indicate no information.

<table>
<thead>
<tr>
<th>Population</th>
<th>Characteristic features of polygynous males</th>
<th>territories</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>settling time</td>
<td>size</td>
</tr>
<tr>
<td>FR</td>
<td>large-repertoire</td>
<td>large</td>
</tr>
<tr>
<td>KH</td>
<td>early</td>
<td>large</td>
</tr>
<tr>
<td>LB</td>
<td>early</td>
<td>large</td>
</tr>
<tr>
<td>LK</td>
<td>early</td>
<td>large</td>
</tr>
<tr>
<td>ML</td>
<td>early</td>
<td>large</td>
</tr>
</tbody>
</table>

Table 5. Features of male territories in different populations. At ML territory size was large in extensive reed beds and small in narrow belts of reeds. For FR and ML territory sizes are given separately for polygynous (P), monogamous (M) and unmated (U) males.

<table>
<thead>
<tr>
<th>Population</th>
<th>Average size or size range (m²)</th>
<th>Average area of emergent vegetation (m²)</th>
<th>References</th>
</tr>
</thead>
<tbody>
<tr>
<td>FR</td>
<td>5240(P), 3360(M), 3540(U)</td>
<td>654(P), 465(M), 175(U)</td>
<td>CATCHPOLE et al. 1985</td>
</tr>
<tr>
<td>KII</td>
<td>c.a. 685</td>
<td>c.a. 685</td>
<td>calculated from URANO 1990b</td>
</tr>
<tr>
<td>LB</td>
<td>c.a. 700</td>
<td>c.a. 700</td>
<td>EZAKI 1990</td>
</tr>
<tr>
<td>LK</td>
<td>c.a. 2000-20000</td>
<td>not described</td>
<td>BENSCH &amp; HASSELQUIST 1992</td>
</tr>
<tr>
<td>ML, large</td>
<td>1640(P), 1239(M)</td>
<td>1640(P), 1239(M)</td>
<td>DYRCZ 1986</td>
</tr>
<tr>
<td>ML, small</td>
<td>436(P), 320(M)</td>
<td>436(P), 320(M)</td>
<td>DYRCZ 1986</td>
</tr>
</tbody>
</table>
breeding results, only Ezaki (1990) succeeded in showing this link. At LB he emphasized this link by relating the benefit of reduced predation rate in secondary nests to dense vegetation which is one of the characteristic features of polygynous male territories. Variance in vegetation density between territories was suggested to be a principal female choice factor (Ezaki 1990). At ML Dyrcz (1977, 1986) emphasized the connection between food supply (territory near foraging ground) and polygyny. But this factor was not linked to the benefit of reduced predation detected in the breeding results at ML.

It is also useful to compare territory features between the different populations (Table 5). The difference in average territory size between FR and the two Japanese populations was approximately seven-fold. Although not specifically stated, territory sizes at LK were similar to those observed at FR, but information on ML indicates that the territories at the European populations are not always large compared with those in Japan. At ML two types of breeding habitats were distinguished; narrow belts of reeds along dikes of ponds and extensive reed beds. In the former small territories of similar size to those seen in the Japanese populations were formed, although in the latter larger territories which were comparable to the other European populations were formed. The coexistence of different sized territories in different habitats concurs with the comparative work by Saitou (1976b) on territory and mating system of a Japanese population of Great Reed Warblers between two different breeding habitats. In this study warblers formed small contiguous territories in the suitable and preferred *Phragmites* reed marsh and large isolated territories in the less-suitable and less-preferred *Lottoboeia* reed marsh. This suggests the possibility that habitat quality could be different between the two types of breeding habitats observed at ML, but no information is available on this point. Despite differences in territory sizes, areas of emergent vegetation in a given territory was not much different between FR and the two Japanese populations. In the Japanese populations, as described below for LB, small territories are formed when males partition a single habitat patch between them, and so the area of emergent vegetation in a territory coincides to territory size. The large difference between territory size and emergent vegetation area at FR indicates that large bodies of open water are included in a territory. This suggests that a territory contains several habitat patches, each of which is small compared with those in Japan. Such examples of territories containing more than one habitat patches can also be found at LK. It is possible that differences in habitat distribution patterns and population densities affect the territory size and the habitat composition within a territory.

Differences in territory features between the populations suggest that the variance in territory quality that works at female choice could be different between populations. At LB the variance in territory quality, as described below, was formed on the basis of habitat heterogeneity within a single habitat patch. This variance did not occur between territories at FR (and probably also at LK) where a territory covers more than one habitat patch. A different level of habitat heterogeneity will work as the cause of variance in territory quality for larger territories.
HABITAT HETEROGENEITY

The relation between habitat heterogeneity and variance in territory quality was studied at LB (EZAKI 1990). The reed marsh was divided into two zones of different vegetation density, which provided different degrees of cover for nests in the two zones. This habitat heterogeneity caused variance in territory quality that influenced female choice, because the benefit of polygyny (reduced predation pressure) accrued from the monopolization of the high-density zone by early-arriving (polygynous) males. This study also clearly showed that variance in territory quality was a product not only of habitat heterogeneity but also of the habitat partitioning pattern between males due to their territorial behaviour (EZAKI 1990, 1994). At LB early arriving males occupied large territories that were later reduced in size with the arrival of additional males due to partial encroachment. Early arriving males continued to occupy the dense vegetation area throughout the breeding season by ceding only the part of his territory with lower vegetation density. The attraction of secondary females occurred during or after this territory reduction process, which means that territory defence played an important role in producing variance in territory quality and hence in establishing polygyny in this population. Thus for LB heterogeneous vegetation density and the resulting variance in territory quality was concluded to be the ultimate cause of polygyny.

Another candidate of habitat heterogeneity as the ultimate cause of polygyny is related to food supply. DYRCZ (1977, 1986) postulated that short distances between territories and foraging grounds outside reed marshes were a characteristic feature of polygynous territories and suggested food supply to be the ultimate cause of polygyny at ML. At FR CATCHPOLE et al. (1985) noted that the long edge (water-reed interface) of polygynous territories may be a good foraging site for resident birds (ORIANS 1980). These studies suggest food supply to be the ultimate cause of polygyny, although this has still to be shown definitively in a warbler population. It was studied at LB (EZAKI 1992) where parent warblers on average collected 55% of food for the nestlings at the communal foraging grounds outside the reed marsh. Although the degree of dependency on the communal foraging ground was related to the distance between the territory and the foraging ground as well as mating status of the parents, the rich food there was available to all the parents and starvation of chicks was rare irrespective of the distance between the territory and the foraging ground. Hence at least in this study food supply was not considered important in causing polygyny.

CONCLUSION

In reviewing the studies on five Great Reed Warbler populations we have found that the breeding results were different between populations. As a consequence, different views were presented on the costs, benefits and adaptiveness of polygyny for different populations. We also knew that sufficient information on the ecological factors has not been collected to assess the importance of habitat heterogeneity and territory quality as the ultimate factors that favour polygyny. Although these factors were recognized as important in establishing polygyny at LB, the differences between populations, not only in breeding results but also in
features of territory, suggest the possibility that different mechanisms work to cause polygyny in different populations. We do not, however, propose to abandon any general explanations of polygyny for the Great Reed Warbler. In this review we knew that some cost of polygyny existed at least potentially in all the populations and that strong behavioural evidence of female choice (and of minimal possibility of female deception) was obtained at LK where males hold large territories (and hence female deception, if ever, is most likely to occur). It follows that the two assumptions of the PTM were generally supported for the species.

Reduced paternal care is a potential cost of polygyny, but it was not realized in all populations and it is thought that climatic and ecological conditions may influence this. From an evolutionary viewpoint, the behaviour of females choosing already-mated males suggests there must be some 'potential benefit' attending polygyny. From information on the five populations, higher vegetation density and better food supply at a territory are possible potential benefits for a female in a polygynous situation. As with the potential cost, the potential benefit may or may not be realized as a result of climatic and ecological conditions such as predation pressure and general food availability. Demographic factors can affect the realization of the cost and benefit also. The different breeding results between populations are explicable as different combinations of different realization patterns of the costs and benefits (see Table 2). Therefore the PTM is generally applicable to polygyny of the Great Reed Warbler despite the differences found between populations.

It was recognized in the 1960's that animals do not always live in the environment in which their behaviour has evolved (Lack 1965). Nowadays, the breeding habitat of the Great Reed Warbler and its surrounding area are under a strong human pressure (Urano et al. 1993). We therefore cannot reject the possibility that the realization patterns of the costs and benefits are strongly influenced by artificial alterations of the environment at each site. It does not mean, however, that empirical studies at different localities under strong human pressure do not contribute to the elucidation of the evolution of the mating system. On the contrary, the very different results obtained from different populations under different environments (natural and artificial) have advanced our understanding of the general rules influencing the ecology and the mating system of this species. Further and comparable intensive studies of different populations are now required to refine our current knowledge.

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特集「オオヨシキリの生態と配偶システム」

オオヨシキリの生態と配偶システムの個体群間比較：
個体群によって結果が異なるのはなぜか？
(Intraspecific comparison of ecology and mating system of the Great Reed Warbler Acrocephalus arundinaceus: Why different results from different populations? 44 : 107-122.)

江崎 保男1・浦野 栄一郎2

分布域の広い生物種は、地域によって異なる環境に適応してきた結果、個体群によって異なる生態や社会システムを示すことがある。旧北区に広く分布するオオヨシキリは、ヨーロッパの個体群も日本の個体群もなわばり型一夫多妻制の社会をもつことが知られているが、個体群によって生態や社会行動に違いのあることもわかった。この論文では、個体識別に基づいて詳しく研究されてきたオオヨシキリの5個体群について、個体群間の類似点と相違点を明らかにし、なぜ個体群によって結果が異なるのかを論じる。

なわばり型一夫多妻制の進化を雌にとっての適応性という観点から説明する作業仮説として「一夫多妻のいきいきモデル（PTM）」（VERNER 1964, ORIANS 1969）が、知られている。このモデルは、「雌は一夫多妻で繁殖するとコストがかからないにかもかわらず、未婚雄でなく既婚雄を選んで一夫多妻になるのはなぜか？」を説明するもので、「既婚雄が未婚雄よりはるかによいわばりをもっていれば、その既婚雄をつがうことで、一夫多妻繁殖のコストを補償するないしは上回る利益が得られるから」というのが、その答えである。そして、生態場所の不均質性によって、雌のなわばり間でその質に大きな差があることが、一夫多妻の究極的な原因と考えられている。本論文では、このモデルの論理を表す6つのキーワード（下線；Fig. 1）に焦点を当てて、オオヨシキリの個体群間比較を行う。

対象とするのは、日本の琵琶湖（LB）と北海道（KH）、ポーランドのMilicz（ML）、ドイツのFranken（FR）およびスウェーデンのKvismaren湖（LK）の各個体群である（Table 1）。ヨーロッパの個体群は亜種 arundinaceus に、日本の個体群は orientalis に属する。基本的な繁殖生態で各個群で違いはなく、いずれも、雄が雌よりも先に渡来してなわばりをもつ。雌が雌のなわばりに定着の形でつながりが成立する、一部の雄が一夫多妻となる、といった点で、PTM で前提となる基本条件を満たしている。各個体群の一夫多妻雄の割合は10%以上から50%近くまでの幅があったが、1個体群の年変異も大きかったので、一夫多妻雄の割合の違いが、個体群間の何らかの差異に基づいているわけではない。

6つのキーワードのうち、繁殖のコスト、利益および適応性については、繁殖結果から評価できる。
まず、PTM が当てはまるのであれば、既婚雄を選んだ雌の平均繁殖成功が同じ時期に未婚雄を選んだ雌と比べて低くなることはないだろう（雌にとっての適応性）。また、異なるタイプの雄を選んだ雌の間で繁殖や雌の死亡原因を比べることで、一夫多妻繁殖のコストと利益を検討できる場合がある。

FR では一夫一妻雌に比べて一夫多妻第二雌の成功度が極端に低く（Fig. 2）、PTM が否定されたが、LB と BK では PTM が支持され、ML、KH でも否定はされなかった。卵・雌の死亡要因は、一夫一妻雌では各個体群とも捕食したが、第二雌果については個体群によって異なり、ヨーロッパの 3 個体群では雌の進食が多く、日本では、LB で非卵生、KH で捕食が多かった（Table 2）。LB と ML では第二雌の巢に対する捕食圧が低く、また BK では第二雌の一卵卵数が多いため、結果的に、既婚雌を選んだ第二雌と未婚雌を選んだ雌の繁殖成功に差はなかった。これらの利益は、LB ではなわばり内の植生が密なことによって、ML では複数家族での集団防衛によって、LK ではおそらくなわばり内の御条件の良さによって得られたものと考えられている（Table 3）。

第二雌の雌に対する雄による給食が少ないことは、各個体群に共通する一夫多妻繁殖の（潜在的）コストである。ヨーロッパの個体群では、このために第二雌の雌が多く進食したが、日本の個体群では進食は少なかった。日本で第二雌の雌も十分に給食され、進食が少なかったのは、繁殖期の気候がより温暖なため、雌が抱卵時間を減らして卵運びに集中でき、雄による給食不足を耐える方法であったろう。また、日本ではヨーロッパに比べ、雌同士の繁殖サイクルのずれが大きいため（Fig. 3）、雄が両雌の雌に給食することも可能となる。これはにくに寒かったり雨が続くような場合では意味をもつだろう。ヨーロッパでは、日本と比べて雌の定着（つがい形成）期間がより短く、同調なこと（Fig. 4）が、雌同士の繁殖サイクルを大きく保とうとする場合の要因になっている可能性がある。一夫多妻雌がどちらの雌の雌に給食するかは、つがい形成順ではなく、孵化順によって決まる。捕食圧が高い地域では、第一雌の雌が繁殖失敗すると第二雌の雌が実質的には第二果として雌の給食を受けられるが、第二雌にとってのコストは平均的には小さくなるだろう。

いずれの個体群でも、雌は既婚雄・未婚雄が共存する状況下で既婚雄を選ぶ機会があったと考えられる。LB ではそのような状況12例中9例で、既婚雄が雌を得ていた。LK で電波発信機をつけた雌を追跡した結果、雌は実際に既婚雄・未婚雄両方の複数のなわばりを訪問し、それらの雌の中から配偶者を選んでいることが示された。

一夫多妻雌の特徴として複数の個体群に共通するのは、より早く繁殖地に定着し、比較的大きく、より質の高いなわばりをもっている点である（Table 4）。LB では一夫多妻雌のなわばりとヨシの密度が高いことと、第二雌の巢で捕食される確率が高いこととの関わりが強調される。わけわめで差のないヨシの密度が雌における選択の重要な要素であると示唆された。ML では一夫多妻雌のなわばりの雌条件のよさが考慮されたが、捕食される確率が下がることは結びつかない。個体群間ではなわばり面積に差があり、ヨーロッパ（FR、LK）の方が日本（LB、KH）よりもずっと大きいが（Table 5）、ML では日本と同じレベルの狭いなわばりと他のヨーロッパ並に広いなわばりの両タイプがみられる。またなわばり面積は大きく違っても、ヨシが生えている部分の面積は日本と FR とあまり違わない。これらの事実は、日本ではヨシのパッチを複数の雌がなわばりとして分割しあっているが、ヨーロッパでは一つのなわばりが、複数の小さなパッチとその間の水面から成っていることを示したものであろう。個体群間でなわばりの特徴に違いがみられる背景には、生息場所（ヨシのパッチ）の分布パターンの違いとオオヨシキリの生息密度の違いがありそうだ。

雌による配偶者選択の際に働くなわばりの質の変異に関して、LB では、生息場所であるヨシの密度の不均質性とその結果生じたなわばりの質の変異が、一夫多妻の究極的原則であると結論づけられ、ML と FR では、なわばりによる雌条件の変異が強調されている。

比較した個体群間で、繁殖の結果だけでなくなわばりの特徴上にも違いがみられたことは、個体群により異なる仕組みによって一夫多妻が生じている可能性を示唆する。とはいえ、オオヨシキリの一夫
多妻制に関する一般的な説明を放棄する必要はないだろう。実際に雄の読死に結びつくかどうかは別にして、すべての個体群で、雄は一夫多妻第二種の個体群にあり絶滅しないこと（一夫多妻繁殖のコスト）と、雌が雄を選んでいるという行動上の有力な証拠が、なわちが広い（したがって雄が既婚であることを雌に対してこまかすようにと考えられる）LK の個体群から得られたことから、オオヨシキリでは PTM の論理の出発点となる「雌にコストがかかるのに既婚雄を選ぶ」という前提が当てはまる。進化的観点からは、コストがかかるにもかかわらず雌が既婚雄を選ぶふるいには、これを補償する何かの（潜在的）利益があるはずと考えられる。（潜在的）利益が、コストと同様に、生態的、気候的、個体群の統計学的要因によって、繁殖結果に影響したりしなかったりするだろう。個体群によって異なる結果は、各個体群をとりまくそれらの要因によって、コストと利益が繁殖結果に現れるかどうかの組み合わせの違いとして説明できる（Table 2 参照）。したがって、オオヨシキリの一夫多妻制には PTM が一般的に適用できる。今日、オオヨシキリの繁殖場所と周辺の環境は人間活動の影響下にある。また、繁殖活動の変化を含む、各調査地での環境の自然的変化が強く影響している可能性は否定できない。とはいえ、異なった（自然・人为）環境にある個々の個体群から得られる、異なった結果は、本種の生態と配偶システムに関する一般則を解明するのに役立ってきた。生態学的に比較可能な、各地の詳細な研究が今後とも必要である。

ヨーロッパとアジアの異なる個体群における
オオヨシキリの繁殖生態

（Breeding biology and ecology of different European and Asiatic populations of the Great Reed Warbler Acrocephalus arundinaceus. 44:123-142）

DYRCZ, A.
Department of Avian Ecology, Wroclaw University, Sienkiewicza 21,
50-335 Wroclaw, Poland

本論文では文献および未発表データに基づいて、オオヨシキリの個体群を比較することを目的とし、とくに基亜種 A. a. arundinaceus と東アジア亜種亜種 A. a. orientalis との違いに注意を払う。異なる地域（Figs. 1 & 2）の個体群（基亜種13、東アジア亜種6）での研究を比較の対象とする。

大部分（17）の個体群において、本種はさまざまな種類のヨシ原に生息し、ほとんどの場合、ヨシの茎に営巣する。2個体群は例外的で、チェコのNamestské 養魚池では抽水植物帯に優占するガマに営巣し、極東アジアのChanka湖では湖岸沿いに広大なヨシ原があるにもかかわらず、大部分の経緯は林縁のやぶや低木に造られた（Table 1）。Chanka湖では比較的多くの果が乾燥した土地に造られたが、このようなことはヨーロッパではきわめてまれであり、日本でもまれである。

一般的な亜種 orientalis の個体群では基亜種に比べ繁殖密度がはるかに高い（Table 2）。理由の一部は亜種 orientalis の生息場所の方が人間による変化をより強く受けているためと考えられる。日本のヨシ原ではオオヨシキリが繁殖鳥の優占種だが、ヨーロッパではこれからは、ヨーロッパヨシキリ、オオジュリン、オオペリなどの方が数が多い。ヨーロッパではオオヨシキリと競合する可能性があるヨーロッパヨシキリが日本に生息しないことは、日本でオオヨシキリが非常に高密度な理由の1つかもしれません。