Mating Relations in the Willow Ptarmigan *Lagopus lagopus* in the Northern Limit of Its Breeding Range

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**Abstract:** Polygyny was studied in marked Willow Ptarmigans in 1989-1995 near the northern limit of their breeding range at Yaibary field station (Yamal Peninsula, northern Siberia). Of 138 males, 17 had two female partners. Bigamous males cared more after the offspring of one of their females and behaved towards this female as if they were monogamous. In all cases it was the female who started incubation first. Males did not guard the clutch of the secondary female and did not care after their offspring. Females from adjacent breeding plots showed no aggression against one another and did not defend territories. Paired males were aggressive towards settling secondary females and sometimes evicted them. Even in polygamous trios males at first attacked secondary females and did not show courtship behaviour. Females in such trios behaved peacefully. When stuffed females were exposed to the freshly mated pairs, males, unlike the females, were always aggressive, showing threats and attacks (n=12). Apparently, during the short Arctic summer females are unable to defend their territories, and polygyny is limited by the aggressive behaviour of males. The males are suggested to show behavioural polymorphism: some are aggressive towards alien females, enabling monogamy, others do not mind new females settling in their territories. Unmated females apparently seek non-aggressive males who would allow them to breed in their territories, at least solitary. No relationship was found between the quality of the male’s territory and his age and the probability of being bigamous, monogamous or unmated.

**Key words:** monogamy, polygyny, territorial behaviour, female-female aggression, male vigilance, territory quality, behavioural polymorphism, Willow Ptarmigan.

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1. Introduction

Willow Ptarmigan (*Lagopus lagopus* L.) is a typical monogamous species which forms pairs during the breeding period. However, polygynous cells consisting of one males and two (occasionally three) females were reported (Semenov-Tian-Shansky 1959, Krechmar et al. 1978, Cramp & Simmons 1980, Potapov 1985).

In the temperate areas of Canada female-female aggression was found in the Willow Ptarmigan which prevented settlement of new females in the areas already occupied by pairs (Hannon 1984, Martin et al. 1990). The authors regarded this aggression as the primary factor limiting polygyny. During our studies of Willow Ptarmigan ecology in northern Yamal (Tarasov 1997a) we often saw that females in polygynous groups behaved peacefully, they were often recorded together. Males sometimes showed aggressive behaviour against one of their females, but only during the first days after the formation of a polygynous group.

The aim of this study was to estimate the importance of monogamy and facultative polygamy in the Willow Ptarmigan in the northern border of its range, and factors which govern these mating systems.

2. Material and methods

The study was conducted in 1989-1995 at the Yaibary field station which is situated in the extreme south of the artic tundra subzone on the Yamal Peninsula, in lower part of Venuyeuyaha river (71°04' N, 72°20' E). Willow Ptarmigans were individually marked by a unique combination of metal and colour rings at the permanent 3 km² study plot. A total of 82 males and 56 females were marked. A proportion of marked individuals returned to the study plot in subsequent years which made it possible to observe identifiable birds immediately upon their arrival in spring, without a need to capture them.

To study the response of mated birds towards alien females I performed the experiments with demonstration of stuffed females in spring plumage (half moulted into summer plumage) which is typical of females during pair formation. These experiments were only possible during the first days after mating, before females started to hide. Twelve pairs were tested, along with three unmated males who were however territory owners and one female evicted by male.
3. Results

3.1. Sex ratio

Results of annual counts of males and females which lived at Yaibary field station in 1989-1995 are shown in Tab. 1. In nearly all years, both bigamous and unmated males occurred, but on average, sex ratio was close to 1:1. Of 138 males which inhabited the study plot during the observation period, 17 were mated to two females. It is noteworthy that in subsequent years, previously bigamous males were more often that by chance bigamous again (t = 2.51; p<0.05). Of seven such males who returned, four were again bigamous. Of the four males which bred at Yaibary during five seasons, one never was bigamous, the other was bigamous during four years in succession.

Unmated males comprised 10% which is a low proportion. Further south, in the Middle Yamal, this proportion was up to 30% (Ryabitsev 1988), and in Bolshezemelskaya tundra (Arctic European Russia) it could be as high as 40% in the years of high numbers (Voronin 1978, 1979). Our observations did not suggest that young males were less successful in attracting a mate than older conspecifics: of nine unmated male with known age, only two were yearlings. The share of unmated males was not proportional to the numbers of Willow Ptarmigan.

3.2. Male parental investment

Male Willow Ptarmigans are known to participate in protecting the nest against predators and in raising the young (Mikheev 1948, Dementiev & Gladkov 1952, Voronin 1978, Hannon 1984m Potapov 1985, 1987, etc). In northern Yamal males also protect the nest quite efficiently (Tarasov 1997b): sometimes they attack even Rough-legged Buzzards (Buteo lagopus), Arctic foxes, dogs. An estimate of parental investment of males in raising the young of a particular female was how far the male stayed from the nest and whether it was present near the brood afterwards. During incubation, male Willow Ptarmigans are very conspicuous against the dark tundra background due to their contrasting breeding plumage and stay 100-200 m away from the nest. As the males started to hide, this distance decreased (Figure 1A). During hatching males as a rule did not leave the nest, often they stayed only 5-10 m from it. They did not watch their territory from a high post any longer but hid between
the tussocks. However, they still fiercely defended their nests from the approaching predators.

Observations of bigamous males showed that they preferred one of the females and did not divide their parental investment between two broods. Only males were included whose both nests had been found and hatched (n = 6). During incubation, bigamous males stayed closer to one of the nests (Fig. 1B) and thus watched it closer than the other one (difference in sample sizes in the figure is due to the fact that in three cases observations were made before secondary females started incubation). Later males accompanied the brood of the primary female. In all cases it was the female which first started incubation. Towards the primary female the males behaved basically as if they were monogamous, whereas the secondary female had to incubate and raise the brood alone. In two cases secondary females with their broods joined the brood of the primary females, so that the male appeared to be together with his both females, and all members of the polygynous trio kept together. In the remaining four cases broods of primary females were recorded 11 times, always followed by the male; secondary females were encountered together with their broods eight times, always without the male. Thus, if a male is bigamous, it cares after the offspring of the primary female, whereas offspring of the secondary female in most cases received no parental care from the male.

3.3. Response of males towards alien females

Already mated males were hostile towards new females. Reaction to the stuffed dummies in all cases was similar to the response to a competitor: characteristic postures, threat calls and attacks were involved. Nine males out of 12 actually attacked stuffed females, three only threatened and imitated attacks. This aggressive behavior of males apparently should prevent the formation of polygynous groups and promote monogamy. It is worth noting that repeated presentation of dummies to the same individuals in subsequent days produced the same results. Unmated males, as expected, started to display and showed courtship behaviour, but soon lost interest to stuffed females.
3.4. Response of females towards competitors

The following response to a dummy was shown by mated females. Five females out of 12 started hiding. The remaining seven showed an interest to the dummy, and this interest was always higher than in males. These females ran towards the dummy, gave high-pitched trills, often stretched their necks and opened the tails, showing black remiges. They were quickly running around the dummy giving characteristic coarse calls, sometimes demonstrated sharp attacks, but did not actually attack. Usually at this moment the male came and hit the dummy. Sometimes he even drove off the female from the dummy. When the dummy fall down, the male stopped paying attention to it, whereas the female remained near the dummy for a long time, still running around.

In some cases the “eyebrow display” was seen, reported from the Red Grouse *Lagopus lagopus scoticus* (Watson & Jenkins 1964). This behaviour was most frequently shown by males during courtship and females in front of their mate which is interpreted as an invitation to copulate (Potapov 1985, 1987). Less frequently this display was shown by secondary females trying to settle when the resident male tried to evict them, and even by some intruder males before the male territory owner. It is noteworthy that during experiments with dummies this display was shown by females before the stuffed female.

It was only once that a female was observed attacking a dummy, under the following circumstances. In the territory of a newly formed pair another female appeared, and the male evicted the first female and paired with the intruder. When a dummy was demonstrated to the evicted female, it started to hit it immediately, without preliminary attacks and aggressive displays. This was the only case when an unmated female was tested. In some avian species territorial behaviour of females was sharply intensified when the male disappears as shown e.g. in experiments with Bramblings *Fringilla montifringilla* (Ryabitsev 1993). However, in this particular case so obvious aggression could be due to the female’s displaced behaviour caused by eviction by the male. It was not possible to make a similar experiment with mated females without influence of the male (males never leave their mates unguarded). The subsequent fate of the deserted female is not known.

In the natural situation female-female confrontations between the neighbours could only be observed in the beginning of pair formation. Females attacked each other by displaying attacks and giving threat calls. They did not actually hit one each other. Conflicts
took place in the territory of the male who was the mate of one of the females. The male stayed in the vicinity and did not participate. Sometimes conflicting females made courtship flights and gave calls. Like female-female aggression, this behaviour is very rarely observed in northern Yamal.

4. Discussion

4.1. Mechanisms supporting monogamy and facultative polygyny

Monogamy is necessary when successful raising the young needs parental investment by the male (Lack 1968). If bigamous males protect only one of their nests, it could decrease breeding success of secondary females. We detected no difference between breeding performance of monogamous and ‘solitary’ females (Tarasov 1997b), but it Canada in the years with high predator abundance only 46% of solitary females raised the young, versus 77% of mated females (Hannon 1984). In the high latitudes monogamy may be especially important, because Willow Ptarmigan chicks have poor thermoregulatory abilities (Aulie 1976) and need to be warmed by the parents. In the Arctic tundra of Yamal with its extremely cold summer a female may appear unable to warm the whole brood alone. Thus it may be assumed that they need female-female territoriality as a mechanism preventing polygyny. This female territoriality was recorded in Canada (Hannon 1983, 1984, Martin et al. 1990), but it did not prevent polygyny efficiently, as pointed by the authors.

In northern Yamal female-female territoriality is virtually non-existent, as shown by our data. Conflicts between the females were very rare. All conflicts between neighbour females, display flights and the aforementioned attack of the dummy were observed in a single season, 1993, when the progress of spring was the quickest. Blood testosterone concentration, responsible for aggressive behaviour in birds (Balthazart & Schumacher 1985, Wingfield & Ramenofsky 1985) is increased in spring in both sexes (Silverin & Wingfield 1982). It cannot be ruled out that the weather or some other factors increased testosterone level in Willow Ptarmigan females in that year.

In experiments with dummies, females showed no aggression towards it. Their response looked rather like displacement when they were running around the dummy, or like avoidance when they were hiding. They left it to their mate to evict the female intruder,
which is what actually happened. It has been suggested that mutual avoidance may be a functional equivalent of aggression (Orians 1978).

Conversely, mated males showed aggressive response towards a new female, similar to the response towards intruding male. Our observations of marked individuals during mating showed that males often evict alien females from their territory without courtship attempts. Mated males always showed a hostile response to a stuffed female. This behaviour was unexpected, because polygamy is beneficial for males, permitting them to increase the number of offspring. The urge of males to facultative polygyny is always favoured by selection, as frequently reported (Verner 1964, Verner & Willson 1966, Orians 1969, 1978, Ryabitsev 1993). Inversion of the behavioural limitation of polygyny observed in northern Yamal might be explained by the fact that during short Arctic summer and time deficit in annual cycle female prove unable to defend their territories. Under such conditions it may be favourable for the population that male aggressive behaviour takes over this function. It is noteworthy that males drove their females off the stuffed ‘intruder’. A male seems to feel uneasy when he sees two females together. This behaviour also be a result of aggression aimed at keeping monogamy which developed in the cause of evolution. However, in spite of obvious aggression of males towards new females this behaviour is not efficient enough to rule out polygyny completely. Bigamous trios were recorded nearly annually at our study plot, and we had no reasons to believe that any female did not breed because she proved unable to find mate. During the whole study period, a total of 17 bigamous males were under surveillance, and at least 12 of them had both females breeding (most of these 24 females were found incubating, the remaining ones were encountered with fledglings).

On the other hand, polygyny may be advantageous not only for males, but also for females, as a population mechanism which compensates for the shortage of males. In some years, the number of females at the study plot exceeded the number of males (Tab. 1). Furthermore, at high breeding densities some males may be in surplus. ‘Population reserve’ of breeding-ready males is well documented in Willow Ptarmigan (Mikheev 1948, Hohn 1967, Moss 1972, Воронин 1978, Bergerud et al. 1985). Surplus of females was never reported: they apparently find a chance to breed by cheating the density regulating mechanism which is the territorial behaviour of males. Facultative polygyny should be
supported by selection if it is favourable at least sometimes (Ryabitsev 1993). Therefore such polygyny preventing behavioural traits as female-female aggression may be lacking.

Last but not the least, at high latitudes, during short and cold summer, females may benefit more from paying no attention to their mates’ cheating and breeding alone than from investing time and energy in territorial defence. It is worth noting that a primary female pays no costs if a secondary female settles in the territory of her male, because bigamous males do not share their parental investment between two broods. A secondary female receives a chance to raise at least some young instead of none.

4.2. Relationship between polygyny and territory quality

It is widely assumed that territory quality plays a role in the formation of pairs or polygynous cells. The so-called threshold model of polygyny (Verner 1964, Verner & Willson 1966, Orians 1969, 1978) suggests that it is more advantageous for a female to join a mated mate in an optimal habitat and to raise her offspring alone than to be mated to a male in a suboptimal habitat. Unmated males in suboptimal habitats are sometimes mentioned in support of this view. However, if territory quality indeed matters for the females, different polygamous males would be encountered in the same patches preferred by Willow Ptarmigans in different years, and unmated males would be met in the same suboptimal patches. No such trend was found (Tarasov 1997a). Conversely, the same males tended to be bigamous during several years in succession. This suggests that females selected a male with his certain characteristics, not a territory. The decisive characteristic of a male probably was their tendency to evict (or not to evict) a secondary female.

It should be added that breeding density in the study area was low, and no acute competition for breeding areas was recorded. Territory size did not differ greatly between unmated, monogamous and bigamous males, and no relationship was found between the number of unmated and bigamous males and breeding density (Tarasov 1997a). This also suggested that polygyny was unrelated to territory quality. It is noteworthy that polygamous males of the Red Grouse had significantly larger territories than their monogamous conspecifics (Miller & Watson 1978).
4.3. Polymorphism of the males’ behaviour

Not all males were equally aggressive towards intruding females (and males). ‘Peaceful’ males who were less aggressive towards competitors and showed a weak response towards the stuffed male in breeding plumage used for capture, had a greater chance to become bigamous. Over all the study years, we failed to capture and to mark two males, in spite of numerous attempts; they both had two females. Females who failed to find a vacant male apparently settled near a mated male, choosing the one who would allow them to breed in his territory.

The aforementioned data suggest that male Willow Ptarmigans show a behavioural polymorphism in the northern limit of their distribution range. Some males are aggressive towards secondary females and thus remain monogamous. Others, even if they do not aim to become polygynous (which would increase their reproductive performance and thus would be favourable for them), at least do not prevent new females from settling in their territory. Thus polymorphic behaviour is apparently beneficial for the population: it maintains monogamy in the conditions when females cannot compete one with another directly, but does not rule out polygyny if males are in short supply. Willow Ptarmigans existing in very severe and unstable conditions in the northern limit of the species’ distribution range should benefit from the high degree of ecological plasticity, primarily from the behavioural plasticity.

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References


Table 1. Sex structure of the Willow Ptarmigan population at the Yaibary field station.

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<th>Year</th>
<th>Number of females</th>
<th>Number of males</th>
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$ r = -0.51 \ p<0.001 \ (n=66) $
Figure 1. Distance from the watching point of males to their nests during incubation. (A) monogamous males; (B) bigamous males.