The Auk 120(2):497–504, 2003

EFFECT OF PAIRING STATUS ON USE OF SPACE BY TERRITORIAL WILLOW PTARMIGAN (*LAGOPUS LAGOPUS*): BACHELOR MALES CHOOSE LIFE ON THE EDGE

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ABSTRACT.—One function of territorial defense may be to facilitate mate guarding by resident males. To assess the importance of mate guarding in territoriality, we examined the spatial pattern of intrusions by male Willow Ptarmigan (*Lagopus lagopus*) on the territories of other males and we compared use of territorial space by paired and bachelor males. Because intruding males tended to remain near territorial boundaries of other males more than expected by chance, we expected paired males to avoid areas near boundaries, where the chances of the female encountering another male would be higher. We found that before females had settled onto territories, all resident males used boundary areas of their territories extensively. After females settled, however, paired males remained almost exclusively in the cores of their territories, whereas bachelor males continued to use primarily the edges of their territories. Those patterns of space use suggest that the benefits of having more exclusive access to a mate may be one of the selective forces driving territorial behavior in this species. *Received 13 February 2002, accepted 25 November 2002.*

RÉSUMÉ.—La protection du partenaire par les mâles résidents pourrait être une des fonctions de l'utilisation d'un territoire. Pour évaluer l'importance de ce phénomène sur la territorialité, nous avons examiné le patron spatial des intrusions de mâles de Lagopèdes des saules (*Lagopus lagopus*) dans le territoire d'autres mâles. Nous avons également comparé l'utilisation spatiale du territoire entre des mâles déjà en couple et des mâles célibataires. Les mâles qui tendaient à s'introduire sur les territoires voisins restaient à proximité des limites de ces derniers plus souvent qu'à la normale. Par conséquent, nous nous attendions à ce que les mâles déjà en couple évitent de se tenir à proximité des limites de territoire, où les chances pour une femelle de rencontrer un autre mâle seraient plus grandes. Nous avons trouvé que tous les mâles résidents occupaient intensivement les limites de leur territoire avant que les femelles ne s'établissent. Néanmoins, après l'établissement de ces dernières, les mâles concernés sont restés presque exclusivement dans le centre de leur territoire, alors que les mâles célibataires continuaient à utiliser principalement les limites de leur territoire. Ces patrons d'utilisation suggèrent que les bénéfices retirés d'un accès plus exclusif à un partenaire pourrait être une des forces sélectives agissant sur le comportement territorial chez cette espèce.

RESEARCHERS HAVE HYPOTHESIZED that one function of territoriality is to allow a male to guard his mate more effectively from extrapair copulations with territorial neighbors and nonterritorial individuals (Møller 1990, Currie et al. 1998). Møller (1990) found that, in birds with territories that varied in size over the breeding season, territories were largest in the period when females were fertile. That provided a larger area free from intruding males and would force an intruding male to travel further within the territory to find and mate with the resident female. However, the data in Möller's study did not test the importance of mate-guarding relative to other factors that could be causing shifts in territory size, such as changes in food availability or intruder pressure (Dunn 1992). Because those changes occur seasonally and are generally difficult to control, analyzing changes in territory size through the breeding season may not be an effective means of investigating the role that mate guarding has played in the evolution of territorial behavior.

An alternative approach to assessing importance of mate guarding as a function of territoriality is to consider a territory owner's use of space in territories that do not change size over the breeding season. If a resident male uses his territory to guard his mate, then he should use the space within his territory in a way that lessens the risk of his mate having extrapair copulations. Nonterritorial males that may attempt

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extrapair copulations tend to stay near the territorial boundaries of resident pairs (Smith 1978, Rohner 1997). Furthermore, a female near a boundary is more likely to be close to an adjacent territorial male, and neighboring males frequently sire offspring in adjacent territories (e.g. Kempenaers et al. 1997, Perreault et al. 1997, Otter et al. 1998, Stutchbury 1998, Ramsay et al. 1999). Because the risk of extrapair copulations should be higher on the perimeter of a territory, one would predict that a territorial pair would use the outer portion of their territory less than the core, assuming that the male controls the position of the pair or that the female prefers either to avoid extrapair copulations or to control when and where they occur.

Here, we examine space use patterns of male Willow Ptarmigan (*Lagopus lagopus*). We compared ways in which paired and bachelor males used their territories and the behavioral time budgets of those birds. We also examined the behavior and position of intruding males. Willow Ptarmigan are a suitable species for this study for several reasons. Ptarmigan territories typically range in size from approximately 3 to 5 ha, and ptarmigan are large, easily observed birds, making it possible to record their locations and activities during focal samples. Territories defended by ptarmigan did not change in size from the time the birds settled until after females finished laying eggs. Males settle on territories about two weeks before females so that we were able to record locations of males before and after they paired. When a female first settles on a territory and moves toward the territorial boundary, she is chased back onto the territory by her prospective mate (Hannon et al. 1998). Once paired, males usually follow females as they move around the territory until the female begins incubation (Martin 1984).

METHODS

Data for this study were collected in 1991 between 21 April and 11 May in the Chilkat Pass, in northwestern British Columbia, Canada (59°50′N, 136°30′W). The study area is subalpine tundra, and primary vegetation is shrubby willow (for a detailed description of the site, see Weeden 1960, Hannon 1983, 1984). During this study the area was covered with snow, and the height of willow twigs above the snow was only 0–0.8 m, making the birds easily visible.

Male Willow Ptarmigan returned to breeding areas in late April and established their territories. When the females arrived, they wandered about the area in groups before settling individually onto males' territories. Territorial males can be unpaired, monogamous, or polygamous, with males having up to three mates. In the year of this study, the population density was relatively low and most paired males on the study area were monogamous. Ptarmigan were captured in ground nets or with noosing poles (Hannon 1983), and were given unique combinations of colored leg bands. For this study, territories were plotted by recording locations of boundary disputes, territorial displays, songs and sightings of individual ptarmigan (Hannon 1983, 1984); we used outermost points to define the boundary, drawing minimum convex polygons. Locations were recorded from 20 April through 28 May 1991, onto scale maps relative to grid markers placed at 100 m intervals throughout the study area.

Focal individuals for this study included 12 paired, monogamous males and 7 bachelor territorial males. For each ptarmigan, there were two observation periods of 45 min, one early in the breeding season before females had settled and one after females had settled; those focal samples were taken between 0500 and 1200 hours PST. We selected samples used in this study from a larger set of data collected in a study of territorial defense (Eason and Hannon 1994); we included all males for which we had focal samples during the appropriate period. For a paired male, the first of two focal samples was the last sample taken before he acquired a mate; the second was the first sample after he paired. We selected the first sample after pairing for comparison so that we would be able to determine whether a male's behavior and use of space changed rapidly after pairing occurred. We did not observe any males on the first two days that they were paired because we did not want to interfere with pairing. Thus, all observations on paired males were on solidly pair-bonded birds (none of the pairs we observed split up after that period), and none of the males appeared to be still herding their mates away from boundaries.

We determined the median dates of the focal samples for the 12 paired males; and for bachelor males, we used the two samples that fell closest to the two median dates of the samples on paired males. For early focal samples, median date for paired males was 26 April (range = 21 April to 4 May) and for bachelor males was 1 May (range = 21 April to 3 May). For samples taken after females settled, median date was 8 May (range = 1 May to 11 May) for paired and 8 May (range = 5 May to 11 May) for bachelor males. Neither the dates of early samples (Kolmogorov-Smirnov two-sample test: D = 37.0, $n_1 = 12$, $n_2 = 7$, $P > 0.20$) nor the dates of the later samples ($D = 17.1$, $n_1 = 12$, $n_2 = 7$, $P > 0.30$) differed significantly between paired and bachelor males.

Fertile periods were not known for most of the hens of the paired males. However, of the five laying initiation dates that were known for those hens, the two earliest were 30 May. In addition, the earliest date on which any ptarmigan was known to have initiated laying on the study area that season was 25 May (range = 25 May to 21 June). Because sperm can fertilize eggs for about one week after copulation (Martin and Hannon 1988), those data suggest that our behavioral data were all collected before the hens' fertile periods. Mate-guarding behavior prior to the female's fertile period has been previously reported for a variety of species, including the Willow Ptarmigan (Martin 1984). Our postsettling observations were conducted prior to females being fertile or laying but after the initial courtship and chasing phases right after pairing.

During an observation period, we recorded activity and location of the focal bird and noted the time at which the focal individual changed location by >5 m or changed activity. If we lost sight of the focal individual, the time the bird spent out of sight was subtracted from the total time observed. Differences in total amount of time that each individual was observed were generally small, however, because the birds were rarely out of sight for >3 min.

Activities that we recorded included foraging, sitting and standing, walking, displaying to females, and defending territory. All remaining activities were lumped together as "other" activities. Territorial defense is defined here as including only the time spent in border disputes with neighbors. Giving territorial calls, which occurs in all parts of a ptarmigan's territory, is not considered territorial defense. To examine whether season, pairing status, and interaction of season and pairing status affected ptarmigan's behavior, we performed a MANOVA on the effects of those factors on the proportion of time that males spent foraging, sitting and standing, walking, displaying to females, and fighting. To achieve normality, we log-transformed those percentages before the analysis (for all log transformations, transformed percentage = log (observed percentage + 1)). As the MANOVA showed that pairing status was the only significant effect (see below), we then performed univariate ANOVA on the effects of pairing status on the ptarmigan's activity budgets, adjusting the *P*-values using a sequential Bonferroni (Sokal and Rohlf 1995) test. For data with unequal variances we used a Wilcoxon two-sample test.

In the year of this study, mean area (±SE; all means are reported ±SE) of Willow Ptarmigan territories at the site was 4.10 ± 0.23 ha ($n = 46$). For analyzing the ptarmigan's use of their territories, we divided each bird's territory into two zones: The boundary zone, which included areas within 10 m of a border, and the central core of the territory, which included all areas that were >10 m from a border. On average, the boundary zone included 20.9% (±1.22; $n = 19$) of a male's territory. We determined in which zone the focal bird was located for all the observation time during which the bird was in sight.

To determine whether the pairing status of a male affected his use of his territory, we compared percentages of time that males spent in the boundary zones of their territories before and after pairing. Bachelor and paired males differed in amount of time they spent fighting, with bachelors fighting more (see below). Because such behavior always occurred near borders, it could have biased our results toward the finding that paired males were more commonly in the cores of their territories than were bachelors; accordingly, we excluded all time spent in territorial defense from our analyses of where ptarmigan spent their time. We log-transformed percentages of time so that the transformed data were normally distributed, and we used a repeated-measures ANOVA, with season (early and late) as the repeated variable and male status as the second independent variable. *Post-hoc* tests were performed using the Dunn-Sidak procedure, and we used sequential Bonferroni tests to adjust those probabilities to compensate for performing multiple contrasts (Sokal and Rohlf 1995).

If residents of larger territories spent a higher percentage of their time in active defense than did residents of smaller territories, then the larger territories were likely energetically costlier to defend. In addition, because males would not be able to guard their mates carefully while engaged in boundary disputes, males defending larger territories with larger buffer zones might have reduced the effectiveness of those buffers if they spent more time in territorial defense. Accordingly, we tested for correlations between territory size and percentage of time spent in defense. We considered paired and bachelor males separately, and we assessed both categories of males early and late in the season.

Observations of intruding males.— After females had settled, we captured 10 bachelor territorial males and put radio collars on them. Radio collars were necessary to locate those males because of their unobtrusive behavior and tendency to leave their territories and range widely. From 21 May 1991 to 21 June 1991, we attempted to locate each radiocollared male at least every two days and record his location; we did not attempt to locate a radiocollared male more than once per day. Those males frequently left the study area and thus numbers of sightings varied among males. Of our radiocollared males, nine were bachelor males and one was a bird that had been monogamous but whose mate was killed early in the breeding season before females had finished laying first clutches. That widower and four of the bachelor males were also used as focal males for investigating use of territory as described above. The dates on which they were observed as territorial residents and the dates on which their locations were recorded as intruders did not coincide, and the widower was not recorded as an intruder until after his mate had died.

We plotted all off-territory sightings of the radiocollared males on maps of the territories on the study area, and we noted whether the sightings were within 10 m of a boundary. If those bachelor males were intruding onto the territories of paired males randomly with respect to core or boundary areas, then the expected number of intrusions into core and boundary areas would be proportional to the area of boundary zone relative to the area of core over the territories within which an individual was seen. Hence, for each male, we determined in which territories that male had been seen, calculated the proportion of the area of those territories that was in a boundary zone, and used that proportion to calculate the expected number of sightings within boundary zones for that male. We then calculated for each male the probability of obtaining the observed number of intrusions within boundary zones using a one-tailed binomial test. We combined those probabilities for all males to obtain an overall P value (Fisher's combination method; Sokal and Rohlf 1995).

In addition to recording locations of radiocollared males, we also took focal samples on 11 bachelor territorial males that were intruding on other territories. Four of those males were radiocollared. The focal samples were taken from 29 May 1991 through 3 June 1991. Each focal sample lasted 30 min, except in three cases in which the intruding male was discovered and evicted by the resident; those interrupted focal samples lasted 18.25, 21.25, and 28 min. We recorded two focal samples on nine males and one focal sample on each of two males. During all samples, the same behaviors were recorded as those described previously for the focal samples on the residents when they were on their own territories.

RESULTS

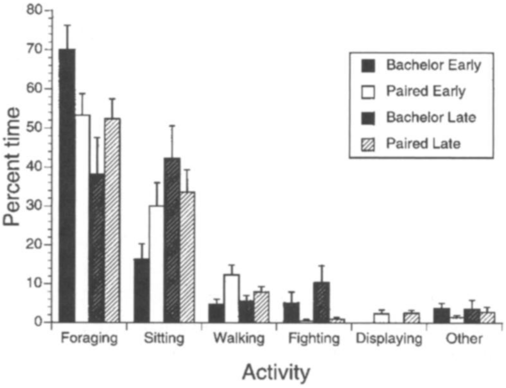

FIG. 1. Mean percent time (±SE) spent by males in various activities before (early) and after (late) females settled on territories.

Behavior of focal males.—Pairing status significantly affected ptarmigan time budgets (MANOVA, $F = 6.41$, df = 5 and 13, $P < 0.005$; Fig. 1), but season and the interaction of season and pairing status (MANOVA, season: $F = 1.61$, df = 5 and 13, $P > 0.23$; season × pairing status: $F = 1.80$, df = 5 and 13, $P > 0.18$) did not. Thus, differences in space use reported below are unlikely to be due to seasonal shifts in males' behavior. All territorial males spent >80% of their time foraging or sitting (Fig. 1), but pairing status did not significantly affect proportion of time spent foraging (ANOVA, $F = 0.30$, df = 1 and 17, $P > 0.5$) or sitting ($F = 0.45$, df = 1 and 17, $P > 0.5$). Paired males tended to spend more time walking than bachelor males ($F = 5.12$, df = 1 and 17, $P < 0.04$), but that tendency was not significant when the Bonferroni adjustment was applied, which made a P value less than 0.01 necessary to achieve the 0.05 level of significance. Bachelor males spent significantly more time fighting than did paired males (ANOVA, $F = 13.13$, df = 1 and 17, $P < 0.003$), but spent no time displaying to females during the observation periods (Wilcoxon two-sample test, $U_s = 72$, $n_1 = 12$, $n_2 = 7$, $P = 0.01$).

Use of territories and pairing status.—Males' use of their territories appeared to be strongly influenced by whether or not they were paired (Fig. 2). Pairing status, season, and interaction of pairing status and season all significantly affected the percentage of time that males spent in the boundary zones of their territories (ANOVA, pairing status: $F = 78.88$, df = 1 and 17, $P < 0.0001$; season: $F = 72.00$, df = 1 and 17, $P < 0.0001$; pairing status × season: $F = 88.84$, df = 1 and 17, $P < 0.0001$). Bachelor males used boundary zones of their territories extensively in both early and late focal periods. They were on average within 10 m

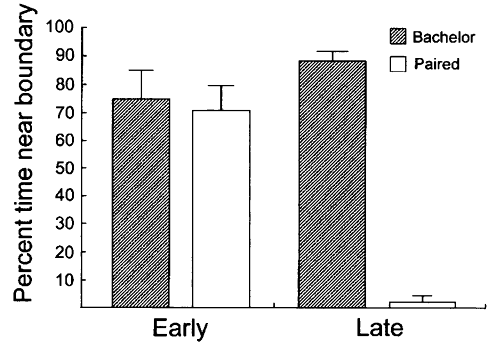

FIG. 2. Mean percent time (±SE) spent by bachelor and paired males in the boundary regions of their territories early in the breeding season before females had settled and late, after females settled.

of their territorial boundary 74.9 ± 9.4% of the time in the early focal samples and 89.4 ± 4.3% of the time in the late focal samples (Dunn-Sidak procedure: $P > 0.10$). Males that later acquired mates also used their boundary zones extensively. They spent on average 71.3 ± 8.8% of their time there, similar to bachelor males (Dunn-Sidak procedure, $P > 0.10$). In contrast, later in the breeding season, paired males reduced the time spent near boundaries to 2.4 ± 1.9% of their time (Dunn-Sidak procedure, $P < 0.0001$). Paired and bachelor males differed significantly in proportion of time they spent within 10 m of a border after the settlement of females (Dunn-Sidak procedure, $P < 0.0001$).

Although after pairing the paired males used the outer portions of their territories very little, they did still defend their entire territories. They chased intruders to their boundaries and flew to their boundaries for displays at times when they saw neighbors there, and they did visit the boundary zones even for activities other than defense. Their territories did not shrink, although their use of the outer portions of their territories decidedly declined.

Defensive costs for residents did not appear to be correlated with territory size. For bachelor males, percentage of time spent in defense was not correlated with territory size early or late in the season (Pearson correlation coefficient, early: $r = -0.001$, $n = 7$, $P > 0.99$; late: $r = -0.44$, $n = 7$, $P > 0.3$). The results were similar for males that obtained males (early: $r = -0.06$, $n = 12$, $P > 0.86$; late: $r = 0.12$, $n = 12$, $P > 0.70$).

Behavior of intruding males.—On average, radiocollared males were sighted 10.7 ± 0.82 times. The mean percentage of boundary zones in the areas over which males ranged was 19.6 ± 0.82%, and males were in those boundary zones 54.5 ± 5.14% of the times they were located. Intruding males thus remained near the boundaries of territories far more commonly than expected by chance. Looking within males, for 7 of 10 of the radiocollareded males that tendency was significant (one-tailed binomial test, $P \leq 0.025$), and the likelihood that those results were due to chance for all 10 males combined was small ($-2\Sigma \ln P_{20} = 86.48$, $P < 0.001$).

Extrapair copulations are rarely observed in studies of Willow Ptarmigan (Martin and Hannon 1988), although paternity analysis has demonstrated that they do occur (Freeland et al. 1995). The behavior of intruding males suggested that they might be attempting to obtain copulations with the mates of paired males. No intruding male was observed foraging. During the focal samples on intruding males, males were sitting on average 96.5 ± 3.3% of the time. The only other behavior recorded during those samples was walking, which occupied the remainder of the males' time (mean ± SE: 3.5 ± 3.3%). Males also flew as they were being evicted from a territory; however, that behavior was not recorded within the time-budget data because evictions were quick and males typically flew out of sight quite rapidly.

Discussion

Patterns of territorial use differed strikingly between males that acquired mates and bachelor males. All males used the portions of their territories near the boundaries extensively early in the breeding season, but after males paired they retreated to the interiors of their territories and rarely used boundary zones except for territorial defense. Bachelor males, in contrast, continued to use the boundary zones of their territories at a high rate, spending ~90% of their time there even with time spent in territorial defense excluded.

Female settlement did not affect males' time budgets, except that paired males spent time displaying to females and none of the bachelor males were observed doing so. In addition, bachelor males spent more time in territorial defense than did paired males. That may have been because of the tendency of bachelor males to remain near the territorial boundaries. At boundaries, the likelihood of sighting a neighbor would be increased and thus bachelor males may have been more likely to engage in disputes with their neighbors because of their proximity to them.

At least four alternative hypotheses could explain observed differences between paired and bachelor males in their use of space. First, bachelor males might remain on the boundaries of their territories to attract mates, whereas paired males no longer need to watch for females at territorial borders. That is unlikely to be the case. Up to 20% of males in that population can be polygynous in any particular year (Hannon and Dobush 1997). If being near the boundary is advantageous for attracting females, paired monogamous males should also spend some higher proportion of time near the boundary to see and be seen by females. That they do not suggests either that remaining on the boundary is not essential for attracting females or that the benefits of guarding their present females must be high enough to outweigh the benefits gained if another female settled. High boundary area use by all males early in the breeding season may be due to the benefits of becoming familiar with neighbors and to establishing stable, well-defined boundaries. Staying near boundaries even when not engaged in an interaction could reduce travel costs and increase the probability of immediately challenging an intruding male.

A second hypothesis that could explain the different patterns of space use observed in bachelor and paired males is related to the location of and time spent building the nest. In some species, pairs may begin to spend more time away from boundaries because they are building a nest located toward the core of the territory. In Willow Ptarmigan, nests are located closer to the centroid of the territory than if randomly chosen (Schieck and Hannon 1993); however, the nest is a simple scrape on the ground requiring little time to build. In addition, females were not laying and no nest building was observed during our focal samples.

Third, it is possible that after females settle, having two individuals on the territory makes territorial defense easier. With two individuals to chase and fight intruders, a pair might not need to guard the border so closely. In Willow Ptarmigan, however, individuals typically defend the territory against members of their own sex (Martin et al. 1990, Hannon et al. 1998).

Finally, then, the difference in use of territories by paired and bachelor males later in the breeding season is probably due to the difference in their breeding strategies. Paired males retreat to the cores of their territories with their mates, to the location where extrapair copulations are less likely. Bachelor males appear to be beginning to look for extrapair copulations. Although observations of copulations have been rare for Willow Ptarmigan, males have been seen attempting to copulate with paired females when those females are separated from their mates (Martin and Hannon 1988). When on their territories, bachelor males stay near the boundary, where they are closest to neighboring males and their mates. When intruding on other males' territories, they also tend to remain near the boundary areas more than expected based on the relative size of those areas. That may be because they are less likely to be detected there. Bachelor males appear to use the boundary zones as paths along which they move through the landscape, presumably looking for opportunities to sneak copulations on paired males' territories.

In summary, paired male Willow Ptarmigan use their territories in a way that suggests that territories play a role in mate guarding, and that the benefits of having more exclusive access to a mate may be one of the selective forces driving territorial behavior. It remains to be seen whether those benefits have played a role in determining territory size. In many species, individuals appear to defend territories larger than would be required for food resources alone (reviewed in Sherman and Eason 1998). If a male resident is defending an area sized so that the resident pair may later use the outer portion of the territory as a buffer zone separating the male and his mate from other males, then territories may generally be larger than would be predicted based on foraging considerations alone. In this study, territory size was not correlated with the percentage of time spent in active territorial defense. That suggests that defending a larger territory may not be highly energetically costly to an established resident. Furthermore, any increase in paternity certainty that results from having a large buffer zone is not compromised by the resident's having to leave his mate unguarded for more time during boundary disputes than would be the case on a smaller territory. However, larger territories may have high costs during settlement when borders are being established; in addition, patrolling may be more costly on large territories, and there may also generally be costs associated with loss of resources to undetected intruders on larger territories.

One intriguing question raised by this work is whether it is paired males or females that are primarily responsible for withdrawing to the core. Previous studies have not raised the question of whether observed changes in space use result directly from changes in male behavior or whether the males' shift is due to females' behavior. Although male Willow Ptarmigan do frequently herd females during settlement, with each male apparently attempting to keep visiting females on his territory (Hannon et al. 1998), males were not seen herding females during our observations after settlement. Rather, resident males tended to follow their mates as they moved around the territories, indicating that it may have been the females who were determining the location of the pair. If so, females may be attempting to control the occurrence of extrapair copulations and thus may be collaborating at least to some extent with males in their guarding. Alternatively, males may be subtly affecting females' movements, or males may essentially train females to avoid the boundary areas using negative reinforcement, herding them repeatedly away from boundaries just after the females settle. The question of which sex is driving the pattern of space use is one that deserves further investigation.

Acknowledgments

We thank R. Schoepf, R. Gruys, C. Schuppli and B. Sandercock for assistance in the field, and G. Cobbs and J. LaManna for statistical advice. The manuscript was improved by comments from C. R. Chandler and an anonymous reviewer. The work was supported by a NATO postdoctoral fellowship to P.E. and by a grant from the Natural Sciences and Engineering Research Council of Canada to S.H.

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