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Capercaillie *Tetrao urogallus* lek formation in young forest

Jørund Rolstad, Erlend Rolstad & Per Wegge

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Capercaillie *Tetrao urogallus* leks have repeatedly been reported to be located in old forest. However, two conditions may have biased this widely held view. First, leks are known to be continuously used over several decades, and therefore might have been established when forest stands were younger. Second, stand-replacement logging (clearcutting) was not widely applied until the 1950s, leaving even-aged regenerating stands too young for leks to have been established in the latter part of the 20th century. Here we report eight cases of lek formation in young plantations from south-central Norway. Stand age ranged within 26-46 years when display activity started. At six of the sites, we confirmed that females were regularly feeding on pine trees in winter prior to lek establishment, and at four of these sites displaying males were observed courting the females in late winter. These findings support the hotspot model of lek formation put forward by Gjerde et al. (2000), and it offers promising options for managing capercaillie leks in commercially utilised forests.

Key words: capercaillie, forest management, hotspots, lek formation, Tetrao urogallus

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The capercaillie *Tetrao urogallus* is a boreal forest grouse distributed throughout the northwestern and central Palaearctic region. During the mating season, males gather at traditional display grounds where females mate with one or a few high-ranking males (Hjorth 1970). Within display grounds, males establish display territories spaced 50-150 m apart (Rolstad 1989), and during daytime, when males are off the lek, they live solitarily in separate home ranges that extend radially ca 1 km out from the lek centre (Wegge & Larsen 1987). Within forested landscapes display grounds typically are spaced ca 2 km apart (Wegge & Rolstad 1986, Beshkarev et al. 1995, Storch 1997, Pakkala et al. 2003).

Several scholars of grouse ecology have pinpointed the capercaillie's preference for older successional stages (Seiskari 1962, Zeimentz 1974, Müller 1978, Swenson & Angelstam 1993). In particular this preference applies to lekking grounds, which repeatedly have been reported to be located in old forest (Klaus et al. 1968, Roth & Nievergelt

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1975, Hjorth 1982, Rolstad & Wegge 1987c), but also, to a certain degree, to daytime ranges (Wegge & Rolstad 1986, Rolstad & Wegge 1987c, Finne et al. 2000). This has subsequently led to a general notion that clearcutting of lekking grounds is detrimental to the species (e.g. Gamlin 1988). Experimental cuttings have shown that certain low-intensity loggings, i.e. single-tree and small group selection cuttings, are acceptable ways of harvesting timber without disrupting the traditional use of the lek (Valkeajärvi & Ijäs 1987, Valkeajärvi et al. 2005, Rolstad & Wegge 1989a). Nevertheless, because leks and their matching daytime ranges cover large areas, maintenance of both in commercially utilised landscapes has become a challenge in current forest management.

A careful look at the literature on capercaillie leks reveals a few cases of leks being reported in younger forests than usually referred to. Rolstad & Wegge (1987c) found one out of 24 leks in a 60-year-old pine plantation at Varaldskogen in Norway. They also reported a radio-marked male mating females in a ca 40-year-old pine plantation after the old lek had been clearcut (Rolstad & Wegge 1989a, Lek 1 in our study). Most noticeably, in a survey of 100 leks in Sweden, Winqvist (1983) reported eight leks to be situated in middle-aged thinned pine plantations, although age of stands was not recorded. Concordantly, Valkeajärvi & Ijäs (1986) reported three of five surveyed leks in central Finland mainly to be situated in younger and middle-aged plantations 45-60 years old. Because the latter two studies were published in local Swedish and Finnish journals, these findings have not been widely recognised. Recently, compelling evidence of many leks being confined to forest tracts with a high proportion of low-volume (36-100 m^3 ha^{-1}), thinned stands comes from a satellite image based study of 42 leks in eastern Finland (Miettinen et al. 2005).

Boreal forests have been exposed to natural large-scale, stand-replacing disturbances, such as wildfires, windthrows and insect outbreaks (Zackrisson 1977, Niklasson & Granström 2000). It could therefore be argued that capercaillie, as a species, ought to be familiar with such disturbances, be it natural or man-made. In this paper, we document eight cases of male capercaillie initiating new leks in young forest. We discuss our findings in the light of current hypotheses of lek formation, and assess the implications for forest management.

Methods

Study areas

We surveyed and monitored leks at Varaldskogen (60°08'N, 12°30'E) and, about 100 km to the west, at Nordmarka (60°08'N, 10°45'E), in south-central Norway. Varaldskogen is characterised by a moderate continental climate, with a yearly mean precipitation of 600 mm and snow covering the ground from December to April. Scots pine *Pinus sylvestris* is most prevalent, but locally Norway spruce *Picea abies* forms pure stands on better soils. Capercaillie were monitored within a 50-km^2 area on the border with Sweden. A detailed description of the Varaldskogen study area has been published elsewhere (e.g. Rolstad et al. 1988). Nordmarka is more humid, with almost twice as much precipitation, and snow covering the ground from November to May. Most of the Nordmarka plateau is dominated by Norway spruce, but our study was confined to a 50-km^2 eastern section with more pine forest. Both study areas have been subjected to extensive commercial forestry, which has been conducted since the 1950s using stand-replacement logging, i.e. mostly clearcutting. In both areas, old forest ($>$ 100 years) remnants from the pre-1950 selective cuttings comprised about 15% of the productive forested land, the rest being composed of even-aged plantations ($<$ 60 years). This history of commercial forestry has resulted in a landscape mosaic of forest stands varying in size from one to 50 ha. Because new clearcuts often are placed next to older ones, clearcut areas and young plantations often cover several km^2. At present, the largest block of continuous old forest covers 300 ha. Due to new environmental regulations, recent clearcuts are made smaller, typically 2-10 ha. At Varaldskogen, the spring density of capercaillie males has been rather stable during the last 15 years, averaging 0.6 male per km^2 (P. Wegge, unpubl. data). At Nordmarka, male density was higher, approximately one male per km^2, and slightly increasing according to lek censuses (E. Rolstad, unpubl. data).

Fieldwork

Surveying and monitoring of leks at Varaldskogen were part of a long-term and still ongoing population study, which started in 1979. Details regarding demography, capture methods and telemetry equipment have been published elsewhere (e.g. Wegge & Larsen 1987, Rolstad et al. 1988). Each year potential lek habitat was surveyed in late win-

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ter and early spring by foot, cross-country skiing or with a snowmobile. Signs of display tracks were subsequently resurveyed to check for permanent activity. Known leks and radio-marked birds were monitored regularly, usually on a daily basis during the peak mating season in late April and early May. In particular, we paid attention to areas where females were feeding in winter, because we found that younger males often visited these areas (Gjerde at al. 2000). Fieldwork at Nordmarka was initiated in 1995. In general, it followed the same procedures as in Varaldskogen, although less extensively, and it did not involve telemetry.

At all leks, display activity was concentrated within well-defined areas of 1-2 ha, situated within fairly homogeneous forest stands. Structural measures were taken within 2-6 0.03-ha circular plots (10 m radius), centred at display sites of the attending males, and averaged for the whole stand. Stand volume (m^3 0.1 ha^{-1}) was calculated from basal area (m^2 0.1 ha^{-1}), measured with a relascope, and tree height (m), using stand volume functions (Næsset & Tveite 1999). Composition of tree species (pine, spruce and deciduous) was assessed on a 10-grade scale. Age of trees was recorded by counting yearly bud scars or branch rosettes, which were easily recognised because trees were so young. Composition of the forest landscape surrounding each lek was obtained from forest management databases and 1:10,000 forest planning maps.

Results

At Varaldskogen, three new leks were initiated in young plantations (26, 37 and 42 years old; Table 1). Seven older leks were situated in old forest within the 50 km^2 study area. At Nordmarka, five new leks were initiated in young plantations (36, 39, 40, 45 and 46 years old; Fig. 1, see Table 1), whereas three older leks were confined to old forest stands within the 50 km^2 area. Because Nordmarka was less intensively surveyed, we cannot exclude the possibility that other leks might have been present in young forest.

Lek phenology

Lek 1 (Hockasuo) was initiated in 1987 by a 3-year-old radio-marked male after parts of his former lek area situated 1.8 km north of Lek 1 had been clear-cut the previous winter. Prior to lek initiation, the 37-year-old pine plantation had been thinned to

Table 1. Number of lek attending capercaillie, forest stand characteristics within lek areas, and percent of forest stand age classes within daytime ranges of the surrounding landscapes, of the eight leks situated in young plantations at Varaldskogen and Nordmarka, south-central Norway. If not otherwise stated data refer to the year of lek initiation.

Lek	Number of birds attending the lek[1]		Stand age (years)		Volume (m^3 0.1 ha^{-1})		Tree density (0.1 ha^{-1})		Tree height (m)	Tree species (tenths)			Within daytime areas[2] % of forest stand age classes (years)		
	Displaying males	Females	When initiated	In 2006	Before thinning	After thinning	Before thinning	After thinning		Pine	Spruce	Deciduous	Plantations[3] 0-25	Plantations[3] 26-70	Old natural forest[4] > 70
Varaldskogen:															
1. Hockasuo	3	6	37 (1987)	56	14	10	160	80	12	9	1	0	45	50	5
2. Siggasuo	3	8	26 (2003)	29	5	-	113	-	7	8	1	1	27	38	35
3. Lebiko	1	6	43 (2006)	43	15	6	160	60	12	9	1	0	13	79	8
Nordmarka:															
4. Djupdalen	8	15	39 (1996)	49	10	8	200	100	12	9	1	0	14	44	42
5. Anderstjern	2	5	36 (1999)	43	8	-	120	-	7	3	6	1	21	63	16
6. Måsjøen	3	6	40 (2001)	45	8	-	120	-	10	5	4	1	24	57	19
7. Bikkjemyra	3	6	46 (2002)	50	20	14	150	80	11	5	4	1	33	51	16
8. Skillingen	6	20	45 (2005)	46	13	7	125	70	12	7	2	1	20	63	17

[1] Minimum numbers observed during the year of maximum attendance.
[2] Within 1 km radius of the lek centre at the time of lek initiation.
[3] Formerly clearcut stands.
[4] Formerly selectively cut and naturally rejuvenated stands.

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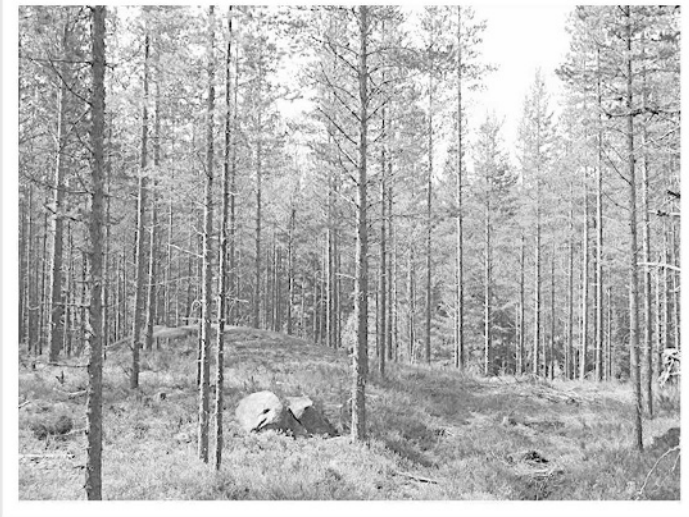


Figure 1. Central part of Lek 4, Djupdalen at Nordmarka, where most matings have taken place during the last five years. The picture was taken in summer 2005 when the pine plantation was 48 years old (see Table 1 for details on stand characteristics).

half of the pre-thinning density (see Table 1). At that time several females used the area regularly for late-winter feeding. In 1987, the 3-year-old male started to display within this winter feeding area, where he later copulated with several females. The next two years two new males arrived, and 5-6 females visited the lek. During the 1990s, 2-3 males attended the lek regularly with at least twice as many visiting females. During this decade, females continued feeding in the area in winter. In recent years (2000-2006) display activity has declined (1-2 males) and fewer females (3-5) have visited the lek. In the same period, few signs of females feeding in late winter have been found.

Lek 2 (Siggasuo) was initiated in 2003 by a presumably 3-year-old male who 'stole' the females from two older males that were displaying in a neighbouring old forest stand. Early in the mating season, 6-10 females visited the two older radio-marked males. After the two old males got involved in serious fights, the 3-year-old male withdrew and started to display 150-200 m away in a 26-year-old pine plantation, being followed by the females, which he later mated. The next three years (2004-2006), three males (including one of the two older radio-marked males) and 6-8 females attended this new site, leaving the original old forest lek site devoid of birds. Prior to lek initiation, the young pine plantation had been utilised for winter feeding, but mostly by males. However, at the time the 3-year-old male started displaying in the area, winter feeding activity had ceased for the season. During the last three years the stand has been heavily used by males, but more sporadically by females, for winter feeding.

Lek 3 (Lebiko) was initiated in 2006 by a displaying male of unknown age, accompanied by three 1-year-old males. He copulated with a minimum of six females. Several females had frequently used the area for feeding in winter since 2000. In 2003 the stand was heavily thinned because of a fungal outbreak, reducing tree density by 63% (see Table 1). Although winter tracks of male capercaillie were observed in the neighbourhood of this lek prior to 2006, we could not substantiate that females actually were courted.

Lek 4 (Djupdalen; see Fig. 1) was initiated in 1996 by a male of unknown age who was courting females that were still feeding in winter in a 36-year-old pine plantation. He finally succeeded in copulating with several females the same spring. During the following years, the number of displaying males increased steadily, levelling off at 6-8 males in recent years. Initially the forest stand was very dense (see Table 1), which apparently hampered the display activity of the males. However, when the stand was thinned in 2000, males seem to have been attracted to the newly created gaps and openings in the stand. In recent years the lek has been visited by $>$ 15 females, and females still use the stand for feeding in late winter and early spring.

Lek 5 (Anderstjern; Fig. 2) started out with two males of unknown age displaying in 1999. Until now, only 1-2 males have attended the lek, but it

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Figure 2. Central part of Lek 5, Anderstjern at Nordmarka, showing 42-year-old mixed pine and spruce forest in summer 2005 (see Table 1 for details on stand characteristics).

has been visited by > 5 females each year. We were not aware of females feeding in the area prior to lek initiation, thus, what attracted the males to the site in the first place is unknown.

Lek 6 (Måsjøen) was initiated by a male of unknown age in 2001. Although we could not positively confirm that females attracted him, several female feeding sites were observed in the vicinity during late winter. In 2005 and 2006, the lek was attended by three males and > 6 females, and the area was still used by females for feeding in winter.

Lek 7 (Bikkjemyra; Fig. 3) was established in 2002 by a male of unknown age that was courting females feeding in winter. He succeeded in copulating with several females the following spring. In spring 2005 and 2006, the lek was attended by three males and > 6 females. The stand was heavily thinned in winter 2003/04, which appeared to benefit display activity, because males used the newly created openings in the stand. Both females and males have utilised this forest stand for feeding in winter in recent years.

Lek 8 (Skillingen) was initiated in 2005 by two males of unknown age, one of which copulated with several females. In 2006 as many as six males and > 20 females attended the lek during the peak mating season. The forest stand had been regularly utilised by > 5 females for feeding in winter since 1998, and they were still feeding there in 2006. During 2000-2003, 1-2 males courted females in late winter and early spring. In 2001 the forest stand was heavily thinned.

Stand age, forest structure and landscape composition

Age of stands ranged within 26-46 years, and tree heights within 7-12 m (see Table 1). Tree species composition varied from almost pure pine stands

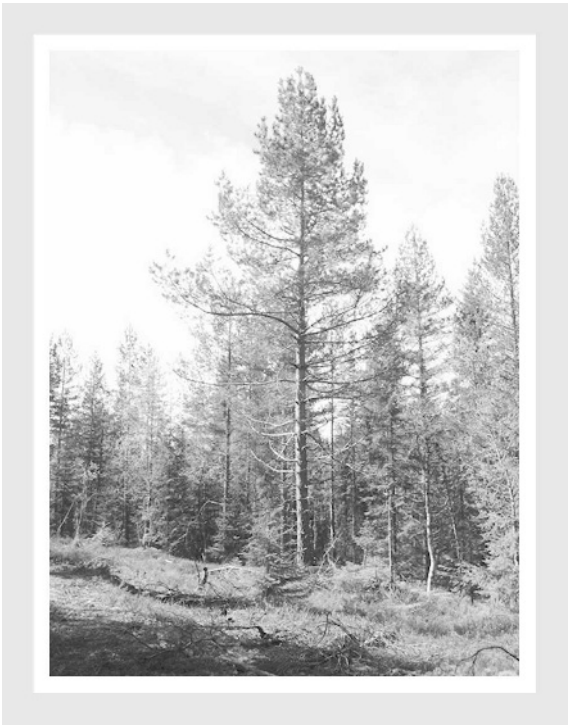


Figure 3. A 49-year-old pine tree rich in branches at Lek 7, Bikkjemyra at Nordmarka, in summer 2005. Such branch-rich trees were frequently used as roosting trees during the display season (see Table 1 for details on stand characteristics).

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(Leks 1-4) to a mixture of pine, spruce and deciduous trees (mainly birch *Betula pubescens*; Leks 5-8). All leks contained some trees with large branches that supported roosting males (see Fig. 3), although barely so at Lek 2, where males were observed falling off branches several times. At two leks (Leks 4 and 7), thorough thinning of the stands appeared to stimulate display activity. At Lek 4 thinning of the forest also may have made room for new males.

Leks 5, 6, 7 and 8 at Nordmarka were all confined to a forested landscape heavily influenced by clearcutting during 1960-1980. They were situated in extensive areas of young plantations, 50-100 ha in size, and with $< 15\%$ of older stands (> 70 years old) in the landscape matrix. Leks 1 and 3 at Varaldskogen were situated in a similar landscape. Lek 2 at Varaldskogen and lek 4 at Nordmarka, were different. They were both confined to rather small pine plantations, four and 10 ha in size, respectively, which were adjacent to extensive forests 70-120 years old (naturally regenerated and formerly selectively logged).

Discussion

Lek habitat and forest management

Why have capercaillie leks been so rarely reported in younger forests? Two conditions may have biased reports of forest stand age. First, the capercaillie is long-lived (in captivity: 18 years (del Hoyo et al. 1992); in the wild: eight years (P. Wegge, unpubl. data)) and attends traditional lekking grounds that may be used for several decades (Rolstad & Wegge 1989b). Therefore, known leks might have been established when forest stands were younger. Considerably stronger bias may hamper surveys where leks have been pointed out by old hunters, bird-watchers or foresters (Rolstad & Wegge 1989b). Finally, young forests might simply not have been surveyed, because they were assumed unsuitable as lek habitat.

Second, in Fennoscandia clearcutting was not widely practised by the forest industry until the 1950s, at which time it replaced traditional selective cutting methods. This means that it was not until late in the 20th century that the new plantations had reached the ages of 30-50 years. In the 1970s to 1990s most plantations presumably were too young for capercaillie leks to establish.

In a review paper, Rolstad & Wegge (1987a) concluded that the capercaillie seems relatively tolerant to micro-habitat characteristics at the forest stand scale, but that both sexes may be more influenced by habitat relationships at the landscape scale. During daytime, males live solitarily off the lek up to 1 km from the lek centre (Wegge & Larsen 1987, Wegge et al. 2003). Thus, during the mating season the population of lekking males utilises a forested area of 3-5 km^2. Males appear to prefer old forest around the lek, and it has been shown that daytime ranges increase in size with decreasing amounts of old forest (Wegge & Rolstad 1986). Although these findings date back to a time when young forest may have been too young, as discussed above, it is worth noting that the largest of our young forest leks (i.e. Lek 4), in terms of attending males, and second in terms of number of years attended, was surrounded by extensive old forest habitat (see Table 1). On the other hand, the very reason for finding three presumably neighbouring leks in young forest at Nordmarka (Leks 5, 6 and 7) may have been because all were situated in a larger tract of plantations that had been clearcut and rejuvenated in the 1960s-1970s. This might have eradicated traditional leks and thereby increased the probability of younger birds to recruit into younger stands.

Our recordings from Varaldskogen and Nordmarka fully agree with the findings of Winqvist (1983) from Sweden. Although stand age was not recorded in his study, several photos indicate even-aged stands 35-50 years old. The reason for finding leks in younger stands as early as 1983 presumably was that the stand-replacing harvesting method was applied earlier in Sweden (1930s) than in Norway (1950s). Conforming results also come from eastern Finland (Miettinen et al. 2005), showing that a large proportion of 42 recorded leks were situated in forested landscapes with a high proportion of low-volume, thinned stands. Using satellite images, the authors assessed stand volumes to be in the range of 36-100 m^3 per ha, corresponding well with our data ranging within 50-140 m^3 per ha after thinning.

How does this translate into forest management? Up to now, the general recommendation has been to leave capercaillie leks alone, or apply harvesting methods of the selective cutting type, which leave behind forest stands that mimic old forest, i.e. multi-layered stands with > 400 trees per ha. Experimental cuttings have shown that such light to moderate selective cuttings are accepted by the

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birds, thereby preserving lekking grounds at the traditional sites (Ijäs & Valkeajärvi 1982, Valkeajärvi & Ijäs 1987, Rolstad & Wegge 1989a), and even increasing display activity and number of attending males (Rolstad 1989). The fact that males are able to initiate leks in stands as young as 35-40 years (Lek 2 which was established in a 26-year-old stand might be considered an outlier), opens up new opportunities for large-scale forest planning. In a landscape perspective, areas of younger forests can be surveyed for signs of females feeding in winter and for tracks in the snow of courting males. When lekking activity has been confirmed, stands can be thinned to a tree density of $< 1{,}000$ trees per ha, which subsequently will promote display activity by males.

Lek formation

Capercaillie males initiating leks in younger stands is in line with the hotspot model of lek formation, which says that males should settle at sites with high female encounter rates (e.g. Gibson 1996, Gjerde et al. 2000). At four of the leks (Leks 1, 4, 7 and 8) we confirmed that males actually were courting females at their winter feeding sites, which implies that this was the proximate reason for the males to come to these sites and start displaying. Although conclusive data were not recorded at Leks 3 and 6, hotspot settlement behaviour may also have been at work there. However, for leks to become permanently established at new sites, females must choose to mate with the new males instead of seeking old mates at traditional leks. Females apparently chose to copulate with new males at all eight leks.

Whereas hotspot settlement of males at female winter feeding sites was involved in the establishment of four (possibly six) of the leks, our field observations suggest another male-initiated process to have caused Lek 2 to become established in young forest. The 3-year-old male that initiated lekking behaviour in this plantation had a daytime range (*sensu* Wegge et al. 2005) that extended in this direction from the former abandoned lek in the old forest 200 m away. Rather than him actively seeking females, the females apparently followed him, as he successively withdrew from the old lek area into the young plantation. This male-initiated behaviour, i.e. trying to draw females into his section of the lekking ground, subsequently into his daytime area, and finally mating females there, may be more prevalent than previously believed, and may in certain cases result in relocation or establishment of new leks according to the hotshot model of lek formation (Beehler & Foster 1988, Höglund & Alatalo 1995).

According to the hotspot model of lek formation (Gjerde & Wegge 1989, Gjerde et al. 2000), in a longer time perspective, females are predicted to abandon their original late winter/early spring feeding areas and relocate to new areas between leks. We do not have data to support this view. At Leks 1, 4, 6 and 7, females were still observed feeding within the general area of the lek during consecutive winters following lek establishment, but at Lek 4 they seemed to relocate well in advance (4-5 weeks) of the peak mating season. However, most of the leks have been monitored for a short time period only, and we do not have telemetric data to document female movements.

In the French Pyrenees, Ménoni (1997) reported that capercaillie leks were established near brood habitats where hens defend nesting territories in spring. This settlement of males at female hotspots was possible because female brood rearing habitats were spatially concentrated, in heathlands and subalpine meadows adjacent to, and just above, the timberline. In our study areas, female nesting ranges were scattered throughout the landscape, making this kind of hotspot settlement of males unfeasible (Wegge & Rolstad 1986).

A caveat

Our results confirm former notes on capercaillie males establishing new leks in young forest stands. If we exclude Lek 2, which was unusual both in terms of lek formation and stand age (10 years younger than the second youngest), we recorded seven leks in stands 36-46 years of age. Although this is encouraging when it comes to forest management, a caveat should be filed in closing. Most of the leks found in young forest so far have been rather small in terms of number of attending birds, and mostly younger birds of both sexes may have been present. This might well be what we should expect because of their short history of usage. In commercial forestry, rotation intervals usually range from 70 to 100 years. Although this may not be very different from the return intervals reported for natural forest fires (e.g. Zackrisson 1977, Niklasson & Granström 2000), logging disturbance occurs in a much more systematic and regular pat-

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tern than natural disturbances. Clearcutting of traditional leks, combined with short rotation cycles, may therefore prevent the development and persistence of large capercaillie leks, which in turn, may influence females' choice of mates, and finally fitness components of evolutionary significance. We do not yet know the outcome of such a change in the sociobiological setting. Until we know more about the long-term effects of an increase in lek turnover and shifts in location, we advocate a cautious and conservative approach to be followed when managing forests for capercaillie leks. Most importantly, other seasonal requirements, e.g. brood habitat (Wegge at al. 2007), may be more decisive for capercaillie numbers in managed forests.

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